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ANNUAL VARIATION IN NUMBERS OF BREEDING CALIFORNIA GULLS AT MONO LAKE, CALIFORNIA: THE IMPORTANCE OF NATAL PHILOPATRY AND LOCAL AND REGIONAL CONDITIONS

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Abstract. The California Gull (*Larus californicus*) breeding colony at Mono Lake, California, is the second largest in the world, but its size can fluctuate annually by >45%. We examined six groups of factors that potentially could affect the numbers of pairs nesting each year, including availability of nesting habitat, numbers of potential breeding gulls, environmental conditions along the Pacific coast in the preceding winter, spring conditions at the lake, food availability at the lake, and prior breeding experience. Four variables explained >80% of the variation in the numbers of breeding gulls at Mono Lake between 1987 and 2003: the potential number of four-year-old gulls returning to the lake to breed for the first time, winter coastal conditions associated with the Pacific Decadal Oscillation, density of endemic brine shrimp (*Artemia monica*) close to the time of egg-laying, and mean temperature in the month before egg-laying. Of the four factors the latter two, which reflect local conditions near the time of egg-laying, had the most profound direct effect on the numbers of breeding gulls. Yearly variation in the snow pack and spring runoff affects brine shrimp numbers through changes in limnological conditions, thus regional climate patterns may indirectly influence gull numbers.

Key words: *breeding numbers, California Gull, constraints, Larus californicus, Pacific Decadal Oscillation, philopatry, prey.*

Variación Anual en el Número de Gaviotas *Larus californicus* que Nidifican en el Lago Mono, California: La Importancia de la Filopatría Natal y de las Condiciones Locales y Regionales

Resumen. La colonia reproductiva de la gaviota *Larus californicus* que se encuentra en el Lago Mono, California, es la segunda más grande del mundo, pero su tamaño puede fluctuar anualmente en más del 45%. Examinamos seis grupos de factores que podrían potencialmente afectar el número de parejas que nidifican cada año, incluyendo la disponibilidad de hábitat de cría, el número de gaviotas potencialmente reproductivas, las condiciones ambientales predominantes en la costa Pacífica durante el invierno previo, las condiciones de la primavera en el lago, la disponibilidad local de alimento y la experiencia reproductiva previa. Cuatro variables explicaron más del 80% de la variación en el número de gaviotas que criaron entre 1987 y 2003: el número potencial de individuos de cuatro años de edad que regresaron al lago a reproducirse por primera vez, las condiciones asociadas con la oscilación del Pacífico, la densidad del camarón endémico *Artemia monica* cerca del momento de puesta de los huevos y la temperatura media del mes anterior a la puesta. Los últimos dos factores, los cuales reflejan las condiciones locales predominantes poco antes de la puesta, tuvieron el efecto directo más profundo sobre los números de individuos nidificantes. La variación anual en la cantidad de nieve acumulada y la escorrentía de la primavera afectan la abundancia de *A. monica* a través de cambios en las condiciones limnológicas, por lo que los patrones climáticos regionales podrían influenciar indirectamente el número de gaviotas.

INTRODUCTION

The numbers of nesting birds at a given colony often exhibit large-scale fluctuations from year to year (Croxall and Rothery 1991, Oro et al. 2004). Understanding the combination of influences from intrinsic features of the population's size and demographic history and the impacts of local and regional environmental conditions is fundamental to understanding the evolutionary ecology of these species and the management of their populations. Colonial seabirds are generally long-lived, and they often have large colony sizes, minimal losses from predation, and relatively well-known food resources. These factors together make it possible to investigate the impacts of colony history and environment on the breeding decisions of large numbers of birds.

The California Gull (*Larus californicus*) is a long-lived species, individuals of which typically do not begin to breed until four years of age (Winkler 1996). As with other species of larids (Fairweather and Coulson 1995, Gonzalez-Solis et al. 1999), California Gulls probably maintain long-term pair bonds, show considerable nest-site fidelity, and, once reproductively mature, may skip breeding in some years (Pugesek and Wood 1992, Pugesek et al. 1995). If sufficient nesting habitat remains free of ground predators, variation in numbers of breeding gulls can reflect the action of at least four different processes: emigration and immigration of breeding gulls, individual decisions on whether or not to breed in a given year, variation in the number of young birds that join the breeding population for the first time, and variation in over-winter survival of adults and subadults. By correlating changes in population size with ecological conditions and historical population variables, researchers have shown that sizes of breeding populations of gulls and other colonial seabirds are strongly affected by food supply (Aebischer and Wanless 1992, Phillips et al. 1996, Suryan and Irons 2001), climate change (both through variations in the food supply [Aebischer et al. 1990, Weimerskirch et al. 2003], and other causes [Barbraud and Weimerskirch 2001, Gjerdrum et al. 2003, Jenouvrier et al. 2005]), and recruitment of young breeding gulls (Wooller et al. 1992, Frederiksen et al. 2004).

The nesting colony of California Gulls at Mono Lake, California, is the second-largest breeding aggregation of this species in the world (Winkler 1996), and has been continuously and systematically monitored over the last 21 years (Shuford and Ryan 2000; PRBO, unpubl. data; J. R. Jehl Jr., pers. comm.). During this time, the colony has ranged from approximately 35 000 to 65 000 nesting birds. The relative ecological simplicity and isolation of this high desert lake facilitate understanding the causes of these fluctuations. The annual mixing regime of the lake has varied widely in parallel with rates of freshwater inflow, and has undergone two periods of chemical stratification (meromixis; 1983–1988 and 1995–2003) during which plankton productivity was depressed (Jellison and Melack 1993a, 2001). Fluctuations in lake level and chemistry have been caused primarily by diversions of tributary streams between 1941 and 1992 and substantial climatic variation. Extensive ecological studies and long-term monitoring of Mono Lake's key invertebrates and limnology, from 1982 to the present (Jellison and Melack 1993b, Herbst 1999), are key to understanding the causes of fluctuations in the numbers of nesting California Gulls.

In this paper, we evaluate the effects of several factors, ranging from weather to prior reproductive success, that might have affected the numbers of breeding individuals in the gull population. We used multivariate regression and mixed statistical models to interpret the causes of changes in colony size, to provide information on the influence of various factors on gull population fluctuations in general, and to aid in the evaluation and management of population fluctuations at the Mono Lake colony in particular.

METHODS

STUDY SITE

Mono Lake, a terminal lake high in dissolved chlorides, carbonates, and sulfates, lies at an altitude of approximately 1945 m at the foot of the Sierra Nevada and at the edge of the Great Basin desert in eastern California. The surrounding habitat includes high sagebrush desert, riparian woodland, piñon-juniper woodland, alkaline and freshwater marshes, and, at higher altitudes, montane forest, meadows, and

freshwater lakes, all of which are frequented by foraging California Gulls.

California Gulls have nested at Mono Lake since at least 1863 and probably much longer (Jehl et al. 1984, Winkler and Shuford 1988). At various times the gulls have nested on the lake's two largest islands, Negit (103 ha) and Paoha (810 ha), and on two groups of smaller islands (individually ranging from <0.3–5.3 ha), collectively referred to as the Negit and Paoha Islets (for maps see Jehl et al. 1984). During the study period 1983–2003, 70–85% of all nests were on the Negit Islets (including $\leq 12\%$ on Negit Island in some years). The number of nests and reproductive success on these islets were measured by WDS and colleagues. All remaining nests were located on the Paoha Islets, where comparable data were collected by J. R. Jehl Jr. from 1983–2001, and by WDS's colleagues in 2002 and 2003 (1983–2000 nest count data from both sources summarized in Shuford and Ryan 2000; 2001 data from J. R. Jehl Jr., pers. comm.). Except where specifically noted, all researchers used similar methods for data collection (Jehl 1994, Shuford and Ryan 2000).

NUMBER OF BREEDING GULLS AND PRODUCTIVITY

We assumed that one pair of breeding gulls attended each nest. Thus, we estimated the number of nesting adults by counting all active nests just after the peak in nest initiation, typically late May. At this time the number of active nests exhibits a short-lived plateau before beginning to decline from losses to intraspecific predation and abandonment (PRBO, unpubl. data). This method likely underestimated the actual number of breeding gulls because some pairs might have lost nests before the count and either did not attempt renesting or had not done so by the time of the count. Also, a small fraction of the population might have initiated nesting after the count.

We estimated the number of chicks that successfully fledged from the lake each year on the basis of average fledging success from nests in six to eight 200 m² fenced plots on the Negit Islets. Fledging success in each plot was calculated from the counts of nests within each plot in May, the banding of chicks in early July, and recovery of banded chicks that died on the island of banding (in each plot, average nest

productivity = [number of chicks banded – number found dead]/number of nests). The size of the lake-wide fledging cohort was estimated by the product of the total number of nests (including the Paoha Islets) and average fledging success per nest (= mean across all fenced plots). Although estimating colony-wide nesting success from the success of nests within wire enclosures is typical in studies of colonial seabirds (Nisbet and Drury 1972, Rimmer and Deblinger 1992, Shealer and Haverland 2000), in years of extremely poor productivity at Mono Lake, nests in some enclosures may fare considerably better than those outside plots, leading to an overestimate of total fledging success (Jehl 2001). Even if our lake-wide estimates were inaccurate as a result, these errors would most likely contribute only to unexplained variance and would not introduce bias into our modeling results or their interpretation. However, we refit the best final models excluding the potentially suspect years (1996–1999; Jehl 2001), and also after adjusting the lake-wide estimates of fledging cohorts by Jehl's recorded bias for the Paoha Islets (25%, 28%, and 28% of expected numbers in 1997, 1998, and 1999, respectively; Jehl 2001). In neither case were our results significantly affected.

PREDICTORS OF NESTING

We evaluated a wide range of factors that could potentially have influenced the number of breeding gulls each year at the Mono Lake colony (Table 1). We chose factors for analysis based on general biological considerations, natural history of gulls (Winkler 1996), and previous studies at Mono Lake (Winkler 1983, Winkler and Shuford 1988). Predictors can be grouped into three broad categories: constraints on the maximum number of nests (available nesting habitat, number of potential breeding gulls), factors that influence the likelihood of nesting by potential breeding gulls (the overwintering environment, weather conditions near time of egg-laying, food availability near egg-laying), and breeding experience of an individual (previous reproductive success). Approximately half the factors we examined could not be measured directly, so we used indirect measures that could reasonably be expected to correlate with the factor of interest. While this strategy requires particular caution when inter-

TABLE 1. Possible factors influencing the number of breeding gulls and included in analyses. See methods for details of how each factor was measured or estimated. We use subscripts to identify different aggregates of data and to indicate relative time periods ('t' refers to the year being modeled).

Predictor	Potential effect
Constraints	
Individual islet area habitat _{Negit_islets}	Area available on the nesting islands could limit the number of nesting pairs. Analyses of the number of breeding gulls on each of five Negit Islets used an estimate of the area of each islet. Lake-wide analyses used the area of all of the Negit Islets in aggregate.
Aggregate islet area habitat _{islet}	
Potential breeding gulls breeders _{t-1} cohort _{t-4} cohort _{t-3}	The number of potential breeding gulls, both new and returning, should influence colony size. Adults that bred the previous year, and survived over winter, form one pool of potential breeding gulls. Two additional pools of potential breeding gulls are represented by cohorts of fledglings that have reached breeding age, one estimated by the number of young fledged four years previously, the other by the number fledged three years previously.
Conditions	
Over-winter conditions MEI _{fall} PDO _{fall} PDO _{winter}	Environmental conditions during the fall and winter might affect the likelihood that individuals choose to breed by influencing the probability of return to the Mono Basin, body condition, or other cues used in breeding decisions. Three broad measures correlated with oceanic conditions along the Pacific Coast during the previous winter were examined: the multivariate El Niño-Southern Oscillation Index (MEI; October–December average), the Pacific Decadal Oscillation Index (PDO; October–December average), and the PDO Index averaged for October–March.
Weather conditions temp _{March} temp _{April} wind _{March} wind _{April}	Temperature and wind conditions from adult arrival at the colony until egg-laying could affect the availability of food resources and the energy budget of potential breeding gulls (e.g., cold temperatures may lead to poor condition), thus influencing the likelihood of breeding. We examined the effects of average temperature and wind speed in both March and April (gulls first arrive in the Mono Basin in March).
Food availability shrimp _{May} shrimp _{May(late)}	The type and availability of food resources prior to egg-laying, and the energy required to exploit them, could affect nesting decisions directly, or indirectly by predicting resource availability later in the breeding season. We evaluated the effect of average brine shrimp density in Mono Lake during the first half and second half of May (adult shrimp are unavailable before May and egg-laying is completed by late May–early April).
Experience	
Reproductive success RS _{t-1} RS _{t-1,t-2}	Breeding experience may affect the likelihood of breeding again the following year. For example, a positive effect of experience would be expected if successful reproduction increased the likelihood of mate fidelity, indicated a good breeding site, or both, while a negative effect of experience would be expected if successful reproduction had long-term negative effects on body condition. We examined two measures that might influence the average likelihood of breeding: average nest productivity in the previous year, and the combined average of the previous two years.

preting the results of analyses, for example because nonsignificance may not relate to the relationship being tested but rather to a poorly chosen metric, it seems justified by the resulting increase in the breadth of analysis. Below we detail each of the independent variables included in analyses.

Habitat availability. The total island area available for nesting has varied with changing lake levels. We estimated island areas at the 1 July lake elevation for each of the Negit Islets

(habitat_{islet}) from nonlinear area:elevation curves unique to each island (S. Stine, California State University East Bay, unpubl. data). Area estimates were not available for the Paoha Islets because these islets were subject to considerable erosion by wave action and islet areas did not reliably correlate with changes in lake level over time. Aggregate measures of available nesting habitat (habitat_{Negit_islets}) excluded the large islands of Paoha and Negit because there has been no confirmed gull

nesting on Paoha since the early 1900s (Winkler and Shuford 1988), and Negit Island was only sparsely occupied during this study. Inclusion of either of these two large islands would unduly influence the measure of habitat availability and swamp potential effects of area changes on the smaller islets where the majority of gulls nest. For example, Negit Island accounted for <9% of nests in all but three years, but was 20 times larger in size than the next-largest islet, which annually held approximately 50% of all nests established lake-wide.

Number of potential breeding gulls. The pool of potential breeding gulls should influence the actual number of birds breeding each year, unless available nesting habitat is completely saturated. Potential breeding gulls in year t include those that bred previously at Mono Lake and survived to year t , whether or not they actually return to the Mono Basin. This component is estimated by the number of breeding gulls at Mono Lake in year $t-1$ (breeders $_{t-1}$), because California Gulls show strong site fidelity (Winkler 1996) and surviving breeding gulls are expected to return in future years. The magnitude of variation in survival probability across years and age classes, and in the proportion of potential breeding gulls that opt out of breeding any given year, is currently unknown, but such variation will contribute primarily to unexplained variance in statistical models and should not introduce any systematic bias.

Most California Gulls breed for the first time at four years of age or older, although some males may breed at three years of age (Johnston 1956). The number of offspring fledged from the Mono Lake colony and subsequently recruited as breeding gulls in year ' t ', which includes individuals that actually nest in year t as well as those that delay for one or more years, should be correlated with our estimate of fledgling numbers in year $t-4$ (cohort $_{t-4}$) and $t-3$ (cohort $_{t-3}$ = early-starting males). The proportion of these fledging cohorts actually recruited is currently unknown, but again, annual variation in survival and recruitment probability should be unbiased and will contribute only to unexplained model variance.

The remaining gulls potentially breeding at Mono Lake are immigrants from other colonies (both former breeding gulls and new young adults). Strong site fidelity to the colony in

which these gulls bred for the first time leads us to expect these numbers to be relatively small compared to the overall size of the Mono Lake colony, and would contribute only to unexplained variance in our analyses.

Over-wintering environment. Many California Gulls spend the winter along the Pacific coast, mostly in California (Winkler 1996), although the specific winter distribution of gulls nesting at Mono Lake is unknown. Coastal feeding conditions over winter might influence the propensity of potentially breeding gulls to initiate nesting in the spring. To try and assess this factor we examined two different indices of climatic patterns in the Pacific Ocean that have been shown to affect marine and terrestrial productivity on the western coast of North America.

The multivariate El Niño-Southern Oscillation (ENSO) index is an integrated measure of the strength of the Walker Cell circulation over the western Pacific and associated climatic variables (Wolter and Timlin 1993, 1998). A second large-scale climate phenomenon, called the Pacific Decadal Oscillation (PDO), is linked to the ENSO cycle but has a stronger fingerprint in the northern Pacific and western North America (Hare and Mantua 2000). The ENSO and PDO cycles are both associated with changes in the California Current, sea surface temperatures, and the strength of upwelling along the California coast, which affect the population sizes of many marine organisms (Ainley et al. 1995, Tanasichuk 1999, Hare and Mantua 2000, Botsford 2001). 'Warm' phases of the PDO (anomalously warm sea surface temperatures in the north Pacific) are associated with depressed productivity off the west coast of the continental United States, whereas 'cool' phases show increased productivity (Mantua 2001).

We used the mean of these indices for the period October–December of year $t-1$ (MEI $_{fall}$, PDO $_{fall}$; National Oceanic and Atmospheric Administration 2004, University of Washington Joint Institute for the Study of the Atmosphere and Oceans 2004, Mantua et al. 1997). We also examined the mean PDO index for the entire winter period (October–March; PDO $_{winter}$), because interannual anomalies in sea surface conditions are typically strongest during this six-month period (Mantua 2001). We examined these indices in models as both continuous and dichotomous ('cool' vs. 'warm') variables.

Weather before egg-laying. Environmental conditions in the weeks immediately preceding egg-laying can modify the availability of food resources and the energy costs of potentially breeding gulls. Our expectation was that relatively cold and windy conditions would tend to depress the likelihood of breeding. California Gulls breeding at Mono Lake may be particularly dependent on stored energy reserves for egg production, because many individuals initiate breeding at a time when prey availability in the Mono Lake ecosystem is minimal to nonexistent (Winkler 1985; see 'Food availability' below). Daily maximum wind speed and minimum and maximum temperature were recorded at Cain Ranch, approximately 16 km from the nesting islands (data courtesy of Los Angeles Department of Water and Power). Because California Gulls arrive at Mono Lake sometime in March and begin egg-laying in late April, we used average March and April wind speed ($\text{wind}_{\text{March}}$, $\text{wind}_{\text{April}}$) and temperature ($\text{temp}_{\text{March}}$, $\text{temp}_{\text{April}}$) in analyses. Rainfall and snowmelt were not explicitly modeled because they are incorporated in our measure of habitat availability through their effect on lake level, and in our measure of food availability.

Food availability. The type and availability of food resources immediately prior to egg-laying could influence the decision to breed through effects on females' abilities to obtain sufficient energy for egg production, or as indicators of feeding conditions later in the season. California Gulls are extremely opportunistic foragers (Winkler 1996), and collectively gulls that breed at Mono Lake range throughout the Mono Lake Basin, north and south of the basin, and (as temperatures rise) high into the Sierra Nevada in search of food. However, many individuals forage extensively on the lake's surface and along its shores. The chemistry of Mono Lake restricts the diversity of potential prey within the lake itself, but two species, an endemic brine shrimp (*Artemia monica*) and the alkali fly (*Ephydra hians*), can reach extremely high densities during the gull breeding season (Melack and Jellison 1998; D. Herbst, pers. comm.). Adult brine shrimp and alkali fly larvae, pupae, and adults predominate in the diet fed to nestling gulls (Winkler 1983, 1996; DWW and PHW, unpubl. data). For these analyses, we had quantitative data only for brine shrimp.

Jellison and colleagues sampled the brine shrimp population twice per month (1982–1992) or monthly (1993–2003) at 12–20 pelagic stations distributed throughout the lake. Basic sampling methods are detailed in Melack and Jellison (1998). Shrimp were classified as adults (including instars ≥ 12), juveniles (instars 8–11), or nauplii (instars 1–7) according to Heath's (1924) classification.

We calculated the lake-wide mean abundance of shrimp by averaging station replicates and then stations. As sampling frequency and dates varied among years, semimonthly lake-wide estimates were derived by averaging daily values linearly interpolated between sampling dates. Adult shrimp rarely appear in the water column before May, and gulls have not been observed feeding on them until mid-May (PHW, pers. obs.), so we used mean adult shrimp densities during the first half of May ($\text{shrimp}_{\text{May}}$) and the second half of May ($\text{shrimp}_{\text{May}(\text{late})}$) as indices of food availability.

Past reproductive success. Breeding experience at a particular location may influence the likelihood of repeat breeding at that site. Prior breeding may have prolonged effects on body condition (Reid 1987, Golet et al. 1998, Alonso-Alvarez et al. 2004, Barbraud and Weimerskirch 2005), or on dispersal probability and mate fidelity (Bried and Jouventin 1999, Dubois and Cézilly 2002, Bried et al. 2003). Although the effects of breeding experience, if they exist, are expressed by changing individual decisions, generally 'good' and 'bad' years for nest productivity should also affect the average likelihood of nesting. We tried to capture any influence of past breeding experience on the mean likelihood of nesting in year t by using our estimate of average fledging success in year $t-1$ (RS_{t-1}) and an average of the two preceding years ($\text{RS}_{t-1,t-2}$).

STATISTICAL ANALYSES

Our primary objective was to find the set of factors that best explained variation in the numbers of nesting California Gulls in the entire Mono Lake colony. Our approach was to build multivariate linear models that initially included variables representing each of the above factors, and then sequentially delete the least predictive factors to arrive at a reduced model that could be used to investigate further how each influenced the number of breeding

gulls. However, even our 21-year dataset provided a critically small sample size for the purpose of evaluating 14 predictors of interest together with their possible interactions (Tabachnick and Fidell 1983). To avoid overfitting problems with the lake-wide data, we first developed an 'islet-subset' model in which the dependent variable was the yearly nest count on each of the five largest Negit islets (Twain, Little Tahiti, Little Norway, Steamboat, and Java), plus the Paoha Islets considered as a single unit. Each of these units was occupied in all years of the study (giving a maximum $n = 126$), and together they accounted for an average of 92% of all nests each year. Using mixed model regression and a term for repeated measures, we could examine the largest number of variables together in one model, while statistically controlling for the correlation among counts from the same islet across years. Our model-building strategy was to begin with a model that included all main effects plus the most biologically relevant interactions. Where alternate variables within the same class of predictors were highly correlated (e.g., $\text{shrimp}_{\text{May}}$ and $\text{shrimp}_{\text{May}(\text{late})}$), only one was in the initial model, and alternates were tested after a reduced model was determined. In addition, breeders_{t-1} and RS_{t-1} were highly correlated, so only breeders_{t-1} was included in the initial model. Terms were deleted from the model sequentially, those with the highest P -values first, until all remaining variables were significant at $P \leq 0.15$. This lenient cutoff ensured that all potentially important effects were considered. The resulting model identified a smaller set of potential predictors that we examined in more detail on the islet-subset data, and then used to model the annual lake-wide counts of breeding gulls. All correlated alternate predictors were examined for better fit in the final model. Limited degrees of freedom (maximum $n = 21$) restricted the lake-wide models to only three or four variables, so we fit main effects from the islet-subset model first, then replaced any non-significant main effects with alternate main effects and interaction terms. We constructed alternate models such that all terms in the final islet-subset model were examined for the lake-wide data. Interaction terms in multivariate models can be particularly difficult to interpret. We explored the effect of such terms by creating discrete categories for one of the predictors in the

interaction. After adjusting the dependent variable to reflect the influence of all terms in the model except the interaction term, we then examined correlations between the dependent variable and the continuous variable in the interaction, at each level of the new discrete variable. All analyses were run using SAS statistical software (SAS Institute 2003). Predictors were considered significant at $P \leq 0.05$. Unless otherwise noted, reported values are means \pm SE.

RESULTS

NUMBERS OF BREEDING GULLS

Estimates of the numbers of nesting gulls at Mono Lake fluctuated dramatically over the study period, and large changes often occurred between consecutive years (Fig. 1a). Factors that contributed the most to observed variation were availability of food resources, the number of potential breeding gulls, and climatic conditions.

PREDICTORS OF NESTING

Initially we investigated how all variables (Table 1), and potentially relevant interactions, correlated with variation in the numbers of breeding gulls on a subset of islets. The number of gulls breeding annually on each islet was correlated with the number of breeding gulls the previous year, islet size, phase of the Pacific Decadal Oscillation (PDO) over winter, densities of brine shrimp, and interactions between the number of potential first-time breeding gulls and both temperature and islet size (Table 2). When the model was reexamined substituting correlated main effects (e.g., MEI_{fall} replacing PDO_{fall}), and evaluating additional possible interaction terms (e.g., $\text{cohort}_{t-4} * \text{PDO}_{\text{fall}}$), no alternatives improved the overall model and only $\text{shrimp}_{\text{May}(\text{late})}$ (replacing $\text{shrimp}_{\text{May}}$) was significant ($P < 0.01$). Our average measures of previous reproductive success (RS_{t-1} , RS_{t-2}) proved difficult to evaluate because of highly significant correlation with breeders_{t-1} (a correlation that suggests successful reproductive decisions by many individuals). However, models replacing breeders_{t-1} with RS_{t-1} explained significantly less variation in numbers of breeding gulls.

The final islet-subset model indicated that regional as well as local factors at Mono Lake

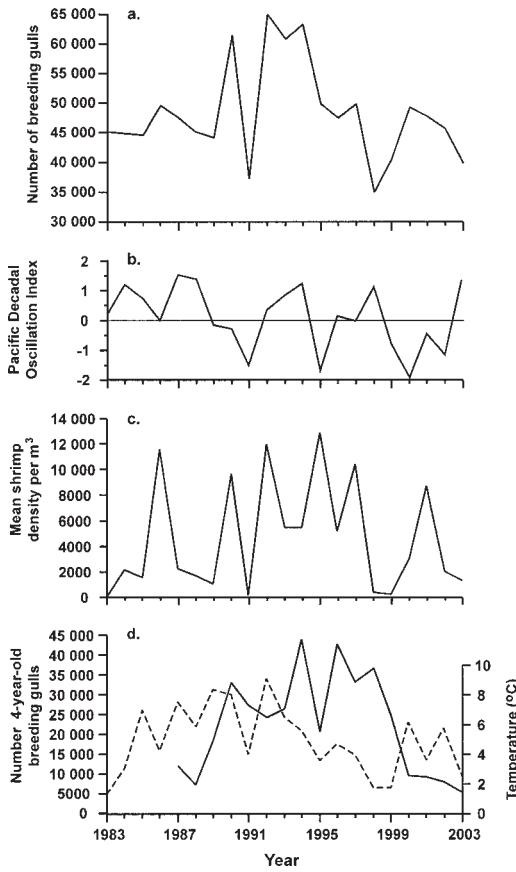


FIGURE 1. Numbers of breeding gulls at Mono Lake and significant predictor variables in analysis models, 1983–2003. (a) Observed number of breeding gulls, estimated from nest counts in late May of each year, (b) average Pacific Decadal Oscillation index from October–December in the previous year. Index values greater than zero indicate ‘warm’ phases of the oscillation; negative values indicate ‘cool’ phases, (c) average density of brine shrimp, 1–15 May, and (d) number of potential four-year-old breeding gulls (solid line; estimated from nesting success in year $t-4$), and average temperature in April (dashed line).

affected the likelihood of gulls breeding. The Pacific Decadal Oscillation (PDO_{fall}) effect (Fig. 1b), and its interaction with $breeders_{t-1}$, suggests that climatic conditions, or climate-caused biological conditions, in winter habitats affected by this ocean cycle influenced the likelihood that potential breeding gulls initiated nesting. The density of brine shrimp early in the egg-laying period ($shrimp_{May}$) had a particularly strong effect (Fig. 1c), while the likelihood of nesting by potential first-time breeding gulls ($cohort_{t-4}$) was influenced by early-season

TABLE 2. The correlation between the number of gulls breeding annually on each of five Negit Islets occupied in every year of the study ($n = 85$), and 15 variables that might influence the likelihood of breeding. Mixed regression models were used, with ‘islet’ and ‘year’ treated as random effects, and islet name included as a repeated measure to account for the correlation between counts on the same islet across years (the best correlation structure was autoregressive [$^*AR(1)$]; SAS Institute 2003)). All 15 variables were included in the initial model, but seven variables were sequentially deleted from the model in the listed order, and the model run again (lowest P -value achieved in any model shown). Eight variables were significant and remained in the final model. These are ordered with main effects followed by interaction terms (denoted by ‘*’). Coefficients and significance values are from this final model of eight variables. The Paoha Islet unit could not be included in this analysis because islet area remained a significant predictor and we lacked yearly estimates of area for this unit.

	Coefficient	P -value
Predictors removed		
$temp_{April}$	–	0.99
$cohort_{t-4} * PDO_{fall}$	–	0.86
$wind_{March}$	–	0.77
$cohort_{t-4} * shrimp_{May}$	–	0.68
$temp_{March}$	–	0.69
$cohort_{t-4}$	–	0.41
$wind_{April}$	–	0.30
Significant predictors remaining		
$breeders_{t-1}$	0.055	0.02
$habitat_{islet}$	2026.000	< 0.01
PDO_{fall}	–2990.000	< 0.01
$shrimp_{May}$	0.107	< 0.01
$cohort_{t-4} * temp_{April}$	–0.004	0.09
$habitat_{islet} * cohort_{t-4}$	0.014	< 0.01
$habitat_{islet} * breeders_{t-1}$	–0.024	< 0.01
$breeders_{t-1} * PDO_{fall}$	0.059	< 0.01

temperatures (Fig. 1d). The habitat effect ($habitat_{islet}$) indicated that more nests were initiated on a given islet as the available habitat increased, as would be expected. However, significant interactions of opposite sign between both $breeders_{t-1}$ and $cohort_{t-4}$ and $habitat_{islet}$ suggest complex effects, possibly relating to islet-specific differences in how topography limits potential nest density and competition.

The islet-subset model in Table 2 is based on data from only part of the nesting colony, and our primary interest was to explain variation in the total number of nesting gulls at Mono Lake. Therefore, we applied the islet-subset model to lake-wide data in a series of steps. In the first step, including only the four main effects from

the islet-subset model, both $breeders_{t-1}$ and PDO_{fall} were nonsignificant. In the second step we replaced these two predictors with a main effect for potential first-time breeding gulls ($cohort_{t-4}$) and an interaction between $cohort_{t-4}$ and $temp_{April}$. At this step, $habitat_{Negit_islets}$ became nonsignificant, partly due to a significant correlation between $habitat_{Negit_islets}$ and $temp_{April}$ ($r = 0.51, P = 0.02$), which may be spurious. However, when compared to $habitat_{Negit_islets}$, $temp_{April}$ explained considerably more variation in breeding numbers and was a robust predictor in all models. The resulting lake-wide model (Table 3a) required only two factors and an interaction to explain approximately 81% of the variation in numbers of nesting gulls among years (Fig. 2).

The lake-wide model (Table 3a) is consistent with the results from models of breeding gulls on each of five Negit Islets (Table 2). However, the islet-subset model included the regional effect of the Pacific Decadal Oscillation (PDO_{fall}). Because the lake-wide dataset is so limited in sample size, the failure of a PDO_{fall} main effect in the first step may have been an artifact of model construction; in the islet-subset model, the interaction of $PDO_{fall} * breeders_{t-1}$ as well as the main effect of PDO_{fall} was necessary for either term to remain statistically significant. When we replaced the interaction effect of $cohort_{t-4} * temp_{April}$ in the lake-wide model (Table 3a) with a PDO_{fall} main effect and $PDO_{fall} * breeders_{t-1}$ interaction, the resulting model was significant and explained as much

variation as the original model (Table 3b, Fig. 2). The apparent PDO_{fall} main effect (and its interaction with potential breeding gulls) remained strong whether the interaction term included all potential breeding gulls (i.e., $breeders_{t-1} + cohort_{t-4}$), only the older breeding gulls ($breeders_{t-1}$), or only potential first-time breeding gulls ($cohort_{t-4}$). The local environment terms, $shrimp_{May}$ and $temp_{April}$, were the strongest predictors in the models, together explaining about 70% of variation in breeding gull numbers (Fig. 2). The additional predictors added approximately 10% to the total variance explained.

EXAMINATION OF STATISTICAL INTERACTIONS

We more closely examined the interaction between $temp_{April}$ and $cohort_{t-4}$ (Table 2, 3a) by creating a categorical variable for temperature. We assigned each year to either a ‘cold’ or ‘warm’ spring category on the basis of whether $temp_{April}$ was above or below the median ($4.7^{\circ}C$) for all years in the study. The partial correlation between the number of breeding gulls (adjusted for $shrimp_{May}$ and $cohort_{t-4}$ main effects) and the size of the four-year-old cohort was considerably stronger in warm than in cold springs (Fig. 3). Two alternative hypotheses might explain the observed interaction. The ‘favorable conditions’ hypothesis suggests that under generally advantageous conditions (warm spring temperatures and high food abundance) a higher proportion of the

TABLE 3. Two general linear models showing the variables that significantly correlated with the lake-wide number of breeding gulls at Mono Lake. Models were derived from the islet-subset model (Table 2), and each explains >80% of total variation in the number of breeding gulls. Sample sizes: model a, $n = 17$ years (1987–2003; the lag variable $cohort_{t-4}$ reduced the sample of years by four), model b, $n = 19$ years (1984–2003; the lag variable $breeders_{t-1}$ reduced the sample of years by one).

Predictor	Coefficient	Standardized coefficient	F-value	P-value
Model a $R^2 = 0.81$				
intercept	40 455.00	0.000		
$shrimp_{May}$	0.82	0.396	8.5	0.01
$cohort_{t-4}$	-2.07	-0.435	19.0	< 0.01
$cohort_{t-4} * temp_{April}$	0.55	0.887	21.7	< 0.01
Model b $R^2 = 0.82$				
intercept	33 998.00	0.000		
$shrimp_{May}$	1.28	0.669	33.6	< 0.01
$temp_{April}$	1597.00	0.418	13.4	< 0.01
PDO_{fall}	-13 944.00	-1.822	7.6	0.02
$breeders_{t-1} * PDO_{fall}$	0.30	2.039	9.3	< 0.01

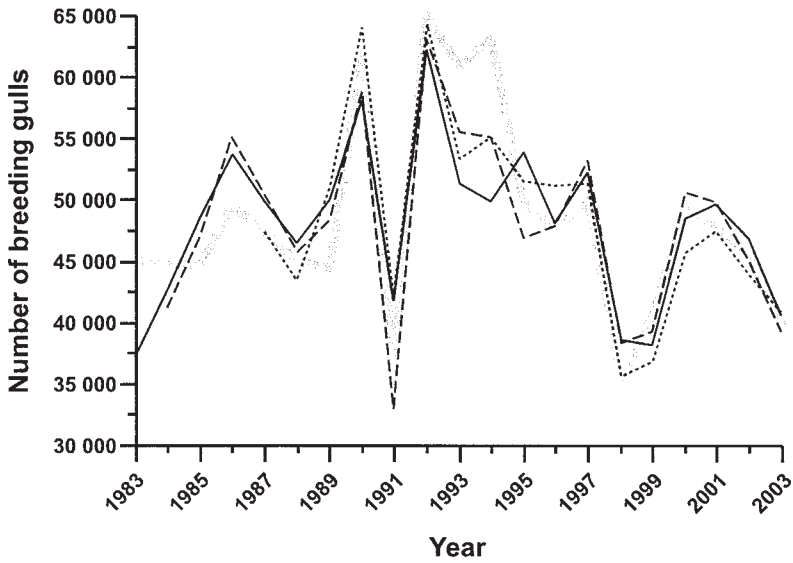


FIGURE 2. The numbers of breeding gulls at Mono Lake, 1983–2003: observed (heavy gray line), and predicted by three general linear models using the lake-wide data. Model 1: $\text{shrimp}_{\text{May}} + \text{temp}_{\text{April}}$ (solid line), brine shrimp abundance in early May and mean April temperature, factors that together explain 70% of the variation in breeding numbers. Model 2: (model 1) + $\text{cohort}_{t-4} + \text{cohort}_{t-4} * \text{temp}_{\text{April}}$ interaction (dotted line; Table 3a), the number of potential four-year-old breeding gulls and its interaction with April temperature, added to model 1. Model 3: (model 1) + $\text{PDO}_{\text{fall}} + \text{breeders}_{t-1} * \text{PDO}_{\text{fall}}$ interaction (dashed line; Table 3b), the average Pacific Decadal Oscillation index October–December, and its interaction with the number of potential adult breeding gulls, added to model 1. Plots of model predictions begin in years after 1983 for models that include lag variables (cohort_{t-4} , breeders_{t-1}) based on data from previous years.

potential first-time breeding gulls are able to initiate a nesting attempt. An alternative ‘predation’ hypothesis suggests that a constant proportion of potential first-time breeding gulls initiate nests each year, but when food availability is low and energy demands high (e.g., cold spring temperatures), more birds turn to egg predation to supplement or replace other foraging strategies. Thus, more nests might be lost to predation before the census in late May. To test these hypotheses, we conducted an analysis in which we examined the effect of ‘large’ and ‘small’ (above and below the median of 24 179 gulls, respectively) values of cohort_{t-4} on breeding numbers in cold years ($\text{temp}_{\text{April}} < 4.7^\circ\text{C}$). The number of breeding gulls was slightly, but not significantly, larger in cold years when cohort_{t-4} was large. Thus, the ‘predation’ hypothesis was not supported.

The islet-subset model (Table 2) and the alternative lake-wide model (Table 3b) include an interaction between breeders_{t-1} and PDO_{fall} , as well as a PDO_{fall} main effect. Overall, birds were less likely to initiate nests following

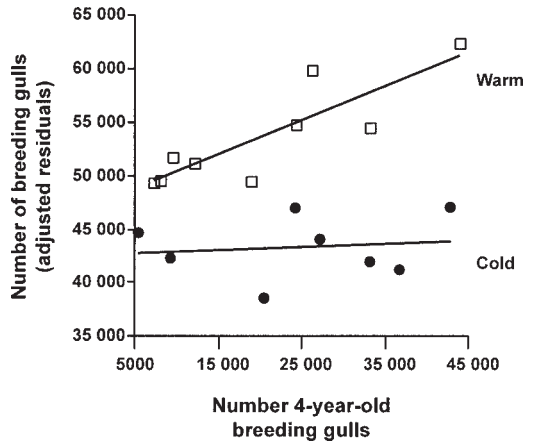


FIGURE 3. The influence of April temperatures on the relationship between the numbers of potential four-year-old breeding gulls (as estimated from nesting success in year $t-4$), and total number of breeding gulls. ‘Adjusted residuals’ are residuals from a model including only $\text{shrimp}_{\text{May}}$ and cohort_{t-4} main effects (Table 3a), recentered on the mean number of breeding gulls. Unfilled boxes show April temperatures $> 4.7^\circ\text{C}$ (median April temperature across years), filled circles show April temperatures $< 4.7^\circ\text{C}$.

a winter when the Pacific Decadal Oscillation index was positive (warm phase) rather than negative, as indicated by the negative coefficient of the PDO_{fall} effect. However, the interaction coefficient is positive, and partial residual plots show a positive relationship between $breeders_{t-1}$ and the number of breeding pairs following winters with 'warm' ocean conditions, and a slightly negative relationship after 'cool' winters. The positive correlation in warm years is strongly influenced by the number of breeding gulls on the largest islet (Twain) in 1993 and 1994, years with unusually high estimates of potential breeding gulls coinciding with a 'warm' PDO phase (Fig. 4).

DISCUSSION

The number of California Gulls initiating breeding at the Mono Lake colony fluctuated widely during this 21-year study, often dramatically from one year to the next. We examined more than 14 factors that might have affected breeding decisions at Mono Lake and showed that decisions were largely based on two local environmental parameters, density of endemic brine shrimp close to the time of egg-laying, and mean temperature in the month before egg-laying (or unknown correlated parameters). In addition, we found some suggestion that broad regional effects associated with the Pacific Decadal Oscillation (PDO) may also have played a role.

The size of the population of potential breeding gulls at a colony (surviving former breeding gulls, young birds reaching breeding age, and immigrants) sets an upper bound to the number of pairs that may actually breed. Although our estimates of potential returning and new breeding gulls ($breeders_{t-1}$ and $cohort_{t-4}$, respectively) were crude, each of the best models explaining observed variation in the numbers of breeding gulls included one or both of these estimates. In the islet-subset analyses, adding information about the number of pairs initiating nests the previous season ($breeders_{t-1}$) and its interactions resulted in an increase from 16% to 48% in the amount of variation explained by the model. Improvement in the lake-wide models was less marked (increases of $\approx 10\%$), although it was difficult to critically evaluate alternative models because of limited sample size. From the perspective of this paper, the most interesting effects of

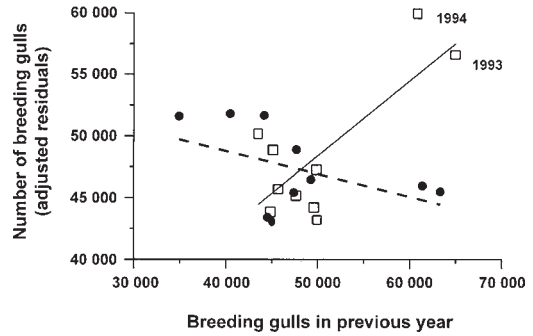


FIGURE 4. The influence of the Pacific Decadal Oscillation on the relationship between the number of potential breeding adult gulls (estimated from the number breeding in year $t-1$) and total number of breeding gulls. Unfilled boxes show years during 'cool' phases of the PDO cycle, filled circles show years during 'warm' phases of the cycle. Two years with strong statistical influence are indicated. 'Adjusted residuals' are residuals from a model including $shrimp_{May}$, $temp_{April}$, and PDO_{fall} main effects (Table 3b), recentered on the mean number of breeding gulls.

potential breeding gulls were exerted through their interaction with climatic variables.

Weather conditions and the availability of food were by far the most important predictors of breeding gull numbers at Mono Lake. Although breeding decisions were likely influenced by regional as well as local conditions, it was at the local scale that we found the strongest effects. Together, early spring temperatures and densities of endemic brine shrimp accounted for most of the variation in the lake-wide numbers of breeding gulls. The critical role of food supply on the numbers of gulls in breeding colonies has been shown in many other studies (Croxall and Rothery 1991, Chapdelaine and Rail 1997, Coulson and Coulson 1998, Raven and Coulson 2001, Suryan and Irons 2001, Oro et al. 2004). Adult brine shrimp generally do not appear in Mono Lake until May, and gulls generally do not begin feeding on these shrimp until mid-May (PHW and DWW, unpubl. data). However, the first gull eggs are laid in late April before the shrimp become available, and $\geq 75\%$ of breeding gulls have completed laying by mid-May (Winkler 1983; WDS, unpubl. data). It is unclear what the gulls eat before shrimp become readily available. Alkali flies are in low supply in early spring (D. Herbst, pers. comm.), and other foods in the Mono Basin are

very scarce. Gull stomachs soon after clutch completion at Mono Lake are generally empty, in contrast to those collected at the same stage at Great Salt Lake (Winkler 1985), suggesting that females at Mono Lake produce clutches of eggs predominantly from stored energy reserves. All available evidence is consistent with Winkler's (1985) conclusion that foraging conditions are extremely limited for gulls at Mono Lake before the emergence of brine shrimp. So what mechanisms might explain the strong correlation between breeding decisions by significant numbers of gulls and the density of brine shrimp at a time of year when they do not appear to be a food source? It is possible that gulls may be responding to other prey scattered around the Mono Basin whose availability is correlated with that of brine shrimp. Alternatively, gulls could be seeing shrimp in the water before they are large or abundant enough to serve as profitable prey and yet are a reliable cue to future conditions. The breeding decisions of later nesting pairs, including four-year-old gulls breeding for the first time, may be made late enough to be influenced directly by early May shrimp densities.

Warm temperatures in April, when gulls are arriving in the Mono Basin, establishing pair bonds, and defending nesting sites, might influence future availability of all types of potential prey, both within and around the lake. Temperature also affects energy budgets and thus may influence breeding decisions. Similar effects of early spring conditions may also explain the interaction of spring temperatures ($\text{temp}_{\text{April}}$) with the cohort of four-year-olds (cohort_{t-4}) deciding whether or not to breed for the first time. It may be that in warmer springs more food is available at the time that later-nesting birds (more likely to be younger birds; Pugsek 1983) begin nesting, causing more young birds to commit to breeding in those years. This could explain why the 'favorable conditions' hypothesis better explains the $\text{temp}_{\text{April}} * \text{cohort}_{t-4}$ interaction than does the 'predation' hypothesis.

At the regional scale, we have shown that nesting decisions may be affected by ocean or coastal conditions over the winter period, related to fluctuations in the PDO. Major changes in marine ecosystems and weather along the west coast of North America have been correlated with changes between warm

and cool phases in the PDO (Latif and Barnett 1994, Hare et al. 1999). Although these phase changes occur on time scales of 20–30 years, recent studies have shown that at least some fisheries show a response to shorter-period fluctuations in the index (Hare and Mantua 2000, Chavez et al. 2003). On the west coast of the contiguous United States, enhanced marine productivity, cooler and wetter winters with increased snow pack, and later vernal warming are associated with 'cool' phases of the PDO, whereas the opposite conditions characterize 'warm' phases. Several studies have suggested that periodic shifts in ocean conditions along the Pacific coast of North America cause significant changes in seabird productivity or survival (Wilson 1991, Massey et al. 1992, Wilson et al. 2000, Gaston and Smith 2001). While these shifts have most often been attributed to El Niño-Southern Oscillation (ENSO) events, they may be more directly affected by the PDO (Mantua 2001).

Thus it is not surprising that variation in winter conditions experienced by most breeding gulls at Mono Lake would be linked more closely to variation in the PDO. We found that more nests were initiated when the average PDO index was negative in the preceding fall and early winter. This is consistent with better feeding conditions along the coast over winter, possibly resulting in better average body condition for potential breeding gulls. Interpretation of the interaction between breeders_{t-1} and PDO_{fall} is not clear, though the strong statistical influence of a single large islet (Twain) suggests important islet-specific effects. Although we have no reason to suspect that data from this islet are outliers, Twain is the largest islet occupied by gulls (accounting for 50%–60% of all nests annually), and is unusual among the islets used for nesting in having extensive areas of shallowly sloping beaches of sand and small gravel. Changes in the amount of nesting habitat, caused by changes in lake level, had a significant effect on the numbers of breeding gulls only in the islet-subset models, but again the data from Twain had strong statistical influence. We suspect the significant interaction between breeders_{t-1} and PDO_{fall} arose through islet-specific differences in both the amount of habitat available as water levels changed, and the degree of competition for such habitat.

Although our support for a regional effect on breeding numbers is relatively weak, it appears that PDO and ENSO connections with regional climate patterns had a strong indirect effect on the gull colony at Mono Lake, with the greatest perturbations to aquatic productivity during the study period resulting ultimately from extremely high snow packs in the Sierra Nevada. The voluminous spring inflows that result from these events can reach a threshold that triggers meromictic conditions in Mono Lake. Such an event can have a lasting effect on prey availability because it can take several years for meromixis to break down. After the onset of meromixis, algal production is depressed and brine shrimp numbers, apparently one of the proximate cues used by gulls in nesting decisions, are reduced for several years (Jellison and Melack 1993a, 1993b). We explored the possibility of such indirect effects by measuring the correlations between the PDO and levels of brine shrimp and temperatures in spring, both of which are very low. However, because the effects of meromixis can be long lasting, they decouple the effects of annual variation in the PDO on spring conditions at the lake and make detecting such indirect effects very difficult.

The data presented here support an interpretation that local environmental conditions are the most important proximate factor affecting the number of gulls breeding annually at Mono Lake. Individual breeding decisions appear to be made on the basis of local conditions prior to egg-laying. In the absence of a mechanism for birds to obtain information from afar about conditions at the lake, our analyses suggest that most or all of the potential breeding population returns to the Mono Basin each year, at least long enough for individuals to assess local ecological conditions and make decisions about whether or not to initiate nesting. The apparent influence of over-winter conditions linked to the PDO may act through adjustments to nesting likelihood once birds have returned to the basin.

Regardless, the results of this study indicate that most of the variation in the size of the breeding population at Mono Lake can be explained by variation in the Mono Lake environment itself. This justifies continued efforts to monitor and safeguard the Mono Basin environment for its large populations of

breeding and migratory birds. Our analyses suggest that numbers of brine shrimp are one of the most important predictors of the numbers of breeding gulls in the Mono Lake ecosystem. Shrimp availability almost certainly plays a key role in nesting success and thus also affects the numbers of young breeding gulls returning to the lake in future years. Future management of Mono Lake for large gull populations should thus strive to preserve both predator-free nesting islands and a large and sustained population of brine shrimp.

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