

**2023 Annual Report**

**Mono Lake Limnological Monitoring**

**Robert Jellison, Caroline Vignardi, and John M. Melack**

Earth Research Institute

University of California

Santa Barbara, CA 93106

Submitted to:

Los Angeles Department of Water and Power

30 April 2024



# CHAPTER 1

## INTRODUCTION

### Overview

Saline lakes are widely recognized as productive aquatic habitats, that harbor distinctive assemblages of species, and often support large populations of resident or migratory birds. Saline lakes throughout the world are threatened by decreasing size and increasing salinity due to climate changes and diversions of freshwater inflows for irrigation and other human uses. At Mono Lake, California, diversions of freshwater streams out of the basin beginning in 1941 has led to a decline in surface elevation and an approximate doubling of the lake's salinity. In 1994, the State Water Resources Control Board (SWRCB) of California issued a decision to amend Los Angeles' water rights (Decision 1631) by restricting water diversions until the surface elevation of the lake reached 1,948 m (6392 ft).

Long-term monitoring of the plankton and their physical, chemical, and biological environment is essential to understanding the effects of changing lake levels and salinities and has been mandated by the SWRCB. Measurements of the vertical distribution of temperature, dissolved oxygen, conductivity, and nutrients are requisite for interpreting how variations in these variables affect the plankton populations. The limnological monitoring program at Mono Lake includes the collection and interpretation of limnological data.

This report fulfills the requirements for limnological monitoring of Mono Lake set forth in State Water Resources Control Board Order Nos. 98-05 and 98-07. The limnological monitoring program consists of four components: meteorological, physical and chemical, phytoplankton, and brine shrimp populations. Meteorological data are collected with sensors on Paoha Island, while the other three components are assessed during monthly surveys (except when the lake is inaccessible in winter). The methodology employed is detailed in Chapter 2, results and discussion of the data obtained during 2023 are presented in Chapter 3, methodological comparisons with monitoring conducted from 2012 to 2022 by LADWP are provided in Chapter 4, and long-term integrative trends and variation are presented in Chapter 5.

## Background

Limnological and related environmental conditions in Mono Lake are reviewed in Melack et al. (2017) and summarized here.

Mono Lake (38°N, 119°W) lies in a hydrologically closed basin on the western edge of the North American Great Basin below the eastern slope of the Sierra Nevada. Most precipitation falls as snow on the western side of the basin and during snowmelt flows into the lake. Groundwater enters the lake via springs and seepage. Annual evaporation from the lake is estimated to be equivalent to about 1 m of water. Daily air temperatures range from around -11°C in winter to a maximum of around 24°C in summer.

Mono Lake is hypersaline, and, as the lake level declined from 1940 to 1980, the lake's salinity increased from 48 g kg<sup>-1</sup> to 87 g kg<sup>-1</sup>. During the period from 1991 through 2023 mean salinity at 2 m ranged from 69 to 91 g kg<sup>-1</sup>. Sodium is the major cation and carbonate, chloride, and sulphate are the major anions. The high salinity and particular chemical composition result in distinct physical properties of the lake water, e.g., density increases as a monotonic function of temperature decrease to below 0°C.

Vertical stratification and mixing alternate between periods with stratification continuing for several years (meromictic conditions) and periods when the lake mixes thoroughly during winter (monomictic conditions). The quantity of freshwater introduced during snowmelt from the Sierra Nevada and the proportion diverted to the City of Los Angeles determine the occurrence and persistence of these two states. Concentrations of soluble reactive phosphorus are high, and inorganic nitrogen can limit algal growth. Two major sources of recycled ammonium are brine shrimp excretion and vertical mixing of ammonium-rich deep water. Mixing in winter is, therefore, a key factor in controlling nutrient supply to the upper water column.

Few species of phytoplankton occur in the lake, and the unicellular green alga, *Picocystis* sp. accounts for most of the algal biomass, as indicated by chlorophyll concentrations. Cyanobacteria and bacillarophytes also occur. Strong redox gradients associated with vertical stratification result in stratified microbial communities, aerobic and anaerobic methane oxidation, and dissimilatory sulphate reduction.

The phytoplankton usually have large seasonal variations in abundance with maxima in early spring, low values from late spring to late summer as a result of grazing by *Artemia monica*, and increased abundances in autumn and winter as *Artemia* grazing declines. The brine shrimp (*Artemia monica*) is the dominant and often sole species of zooplankton in the pelagic waters. *Artemia* hatch in late winter and spring from cysts; a second, summer generation is produced ovoviviparously. In autumn, the *Artemia* population declines, because of predation by migratory grebes, decreasing water temperature and senescence. In near-shore habitats, the alkali fly (*Ephydra hians*) is abundant seasonally.

The brine shrimp and alkali fly larvae provide food for large numbers of birds including a breeding colony of the California gull (*Larus Californicus*) and migratory eared grebes (*Podiceps nigricollis*), Wilson's phalaropes (*Phalaropus tricolor*) and red-necked phalaropes (*Phalaropus lobatus*). No fish occur in the lake. The grebes depend on the abundant *Artemia* during autumn when they molt and increase their body weight before continuing their southward migration late in the year.

## **CHAPTER 5**

## SEASONAL, ANNUAL, AND LONG-TERM TRENDS

### Introduction

Seasonal and long-term variation in the ecology of lakes is caused by a wide range of anthropogenic and climatic variables acting over various time scales. At Mono Lake, the diversion of streams out of the basin is the largest anthropogenic impact (Patten 1987, CSWRCB 1994). Climatic differences among years have led to large changes in snowmelt runoff, alterations in stratification and associated ecological effects.

Water diversions by the Los Angeles Department of Water and Power beginning in 1941, led to a 14 m drop in surface elevation and an increase in salinity from 48 g kg<sup>-1</sup> in 1940 to 87 g kg<sup>-1</sup> in 1980 (Blevins 1984). Based on laboratory studies (Dana & Lenz 1986; Dana et al. 1993, 1995), this salinity increase influenced several life-history aspects of *Artemia*, a primary food source for large migrating and nesting bird populations. The decreased volume of the lake at the lower surface elevations resulted in another significant source of variation, recurring multiyear episodes of persistent chemical stratification (meromixis). At decreased lake volumes, above average years of snowmelt runoff during which freshwater flows into the upper layer of the lake can initiate multiyear periods of meromixis. The increased vertical density stratification reduces vertical mixing of ammonium and phytoplankton growth during summer and prevents the winter period of holomixis in which nutrients accumulated in deep anoxic waters are returned to the upper waters. These effects are well-documented (Jellison & Melack 1988, Jellison et al. 1993, Melack & Jellison 1998, Melack et al. 2017). However, the overall effects on the seasonal *Artemia* population are difficult to discern due to considerable differences in characteristics of different meromictic events and multiplicity of factors affecting the seasonal development of the *Artemia*. The increased variability due to recurring episodes of meromixis increases the difficulty of discerning and attributing causes to long-term trends in *Artemia* population dynamics.

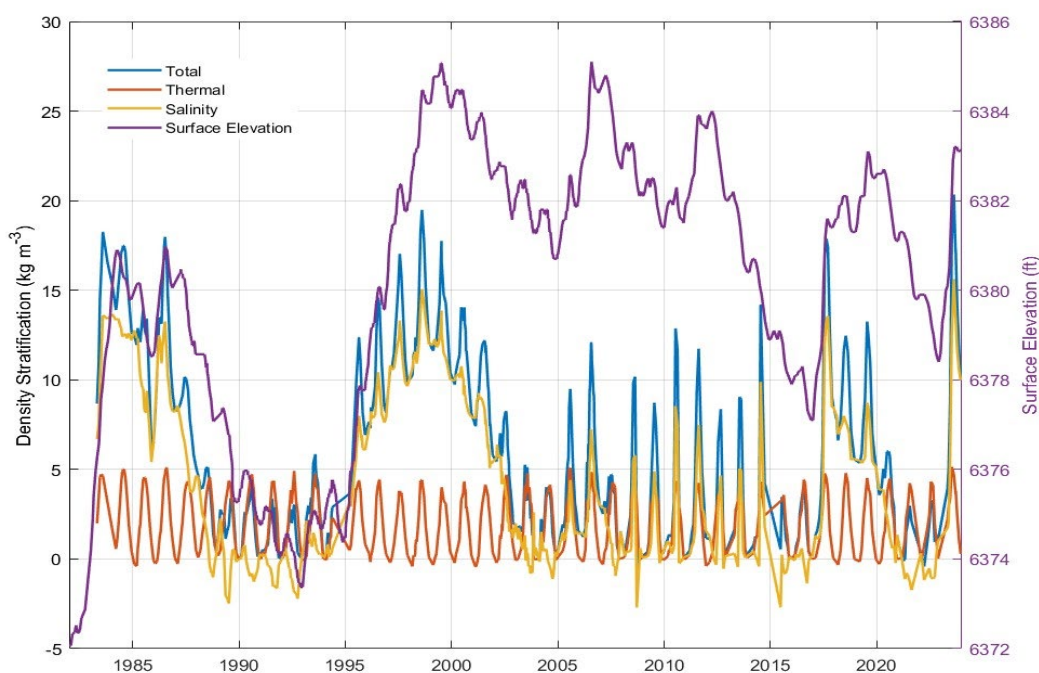
### Density Stratification and Meromictic Episodes

Most large temperate lakes undergo a regular seasonal regime of thermal stratification when upper (epilimnion) waters warm during spring and summer and then cool through autumn and winter. In Mono Lake, the high salinity and particular chemical composition result in distinct physical properties of the lake water. In contrast to freshwater, the density of the Mono Lake water increases as a monotonic function of temperature decrease, even below 4°C. Thus, an

extended period of holomixis can occur through winter until waters begin to warm in late February.

Density stratification between 2 and 32 m due to thermal stratification is quite regular and varies from  $-0.4$  to  $5.1 \text{ kg m}^{-3}$  (Fig. 57). Overlain on the seasonal pattern of thermal stratification is that due to salinity stratification. Salinity stratification varies from year to year depending on existing salinity stratification and on the variation in timing and volume of seasonal freshwater inflows. Density stratification due to salinity has varied from  $-2.7$  to  $15.6 \text{ kg m}^{-3}$  from 1983 to 2023. Often density stratification was sufficient to prevent the winter period of holomixis.

Fig. 1. Density stratification between 2 and 32 m at Station 6, 1983–2023.



High snowmelt runoff in 2023 resulted in a 4.5 ft rise in surface elevation and initiated the 6<sup>th</sup> episode of meromixis (Fig. 58). While the end of an episode is defined by holomixis, the beginning is not well defined because Mono Lake has a summer period of stratification due to warming of the upper water column. Here we define the beginning of a meromictic episode to be the date when the rise in surface elevation that resulted in meromixis began (Table 22). The end of an episode was calculated as the mean of the two sampling dates bracketing holomixis as indicated by temperature, conductivity, dissolved oxygen and ammonium profiles. The amount

of freshwater inflow required to initiate an episode of meromixis depends on a variety of factors including the lake volume, salinity, the timing of the inflows relative to seasonal thermal stratification, and other climatic factors (e.g., precipitation, evaporation, wind speeds). Recent history would suggest at the current lake levels that an annual surface elevation rise of ~2 ft will likely initiate an episode of meromixis (Fig. 59, Table 22). In 2011, a surface elevation rise of 2.4 ft from the 1 December 2010 elevation prevented winter holomixis and initiated a 2-yr period of meromixis. Somewhat lower elevation rises in 1993 (1.7 ft) and 2005 (1.9 ft) did not initiate meromixis. Since water diversions began in 1941, the only year where the annual surface elevation change exceeded 2 ft prior to 1983 was in 1969 when surface elevation rose 2.5 ft. Whether this initiated a short period of meromixis is unknown. As the lake's salinity was lower, the density gradient formed from inflowing freshwater would have been less and a larger rise may have been required to prevent winter holomixis.

Table 1. Meromictic episodes

Meromictic Episode	Begin Date	Beginning Elevation (ft)	End Date	Ending Elevation (ft)	Initial Year Rise (ft)	Duration (years)
1	1982-06-02	6372.3	1988-11-22	6377.1	8.6	6.5
2	1994-11-21	6374.4	2003-11-30	6381.3	3.5	9.0
3	2005-12-01	6381.9	2007-11-18	6382.8	3.2	2.0
4	2010-12-01	6381.5	2012-12-02	6382.0	2.4	2.0
5	2017-01-01	6377.1	2020-12-02	6381.1	4.5	3.9
6	2022-12-01	6378.4			4.8	

Fig. 2. Surface elevation and meromictic episodes at Mono Lake. Straight lines indicate the duration of each episode (see text).

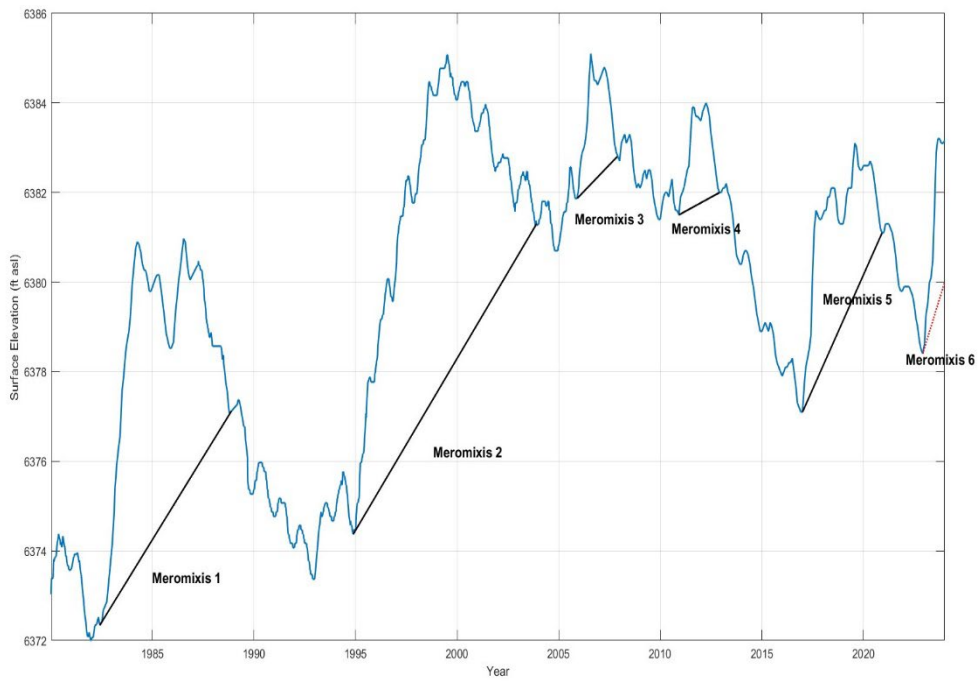


Fig. 3. Yearly change in surface elevation (ft).

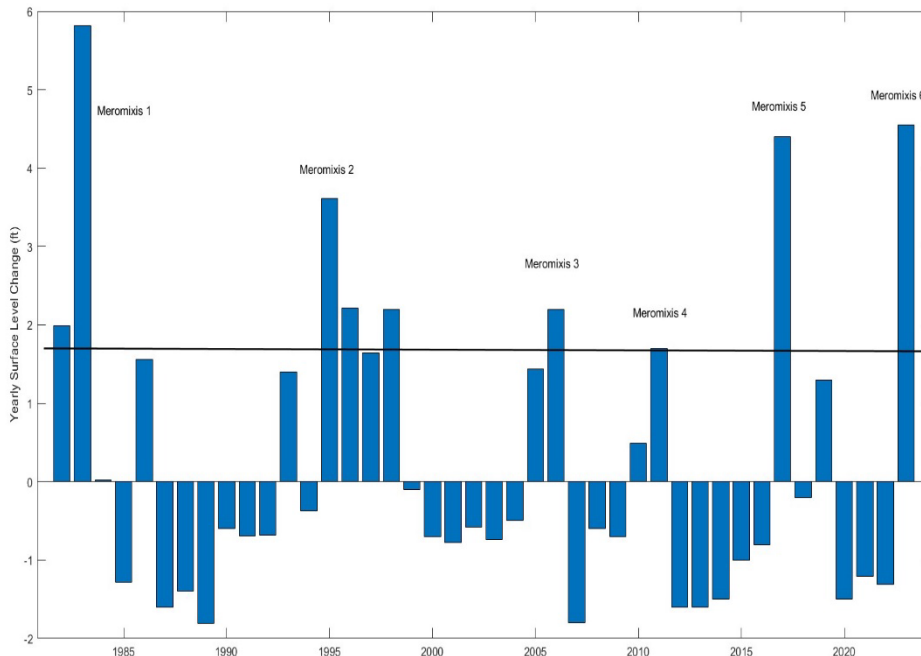
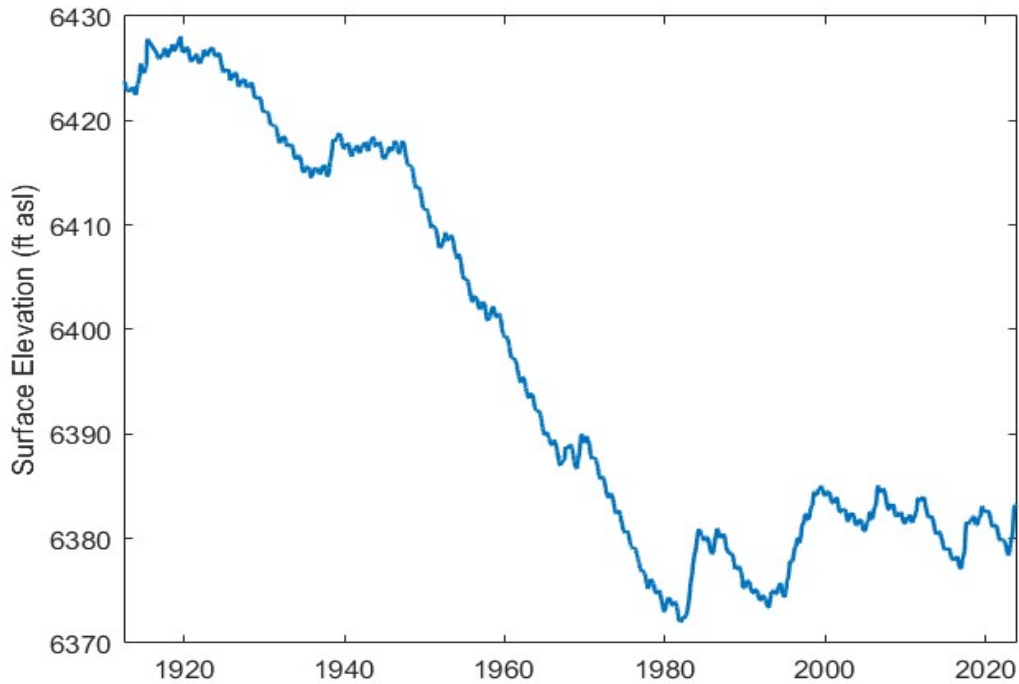


Fig. 4. Historic (1912–present) surface elevations of Mono Lake (ft asl).



### Long-term Trends in *Artemia*

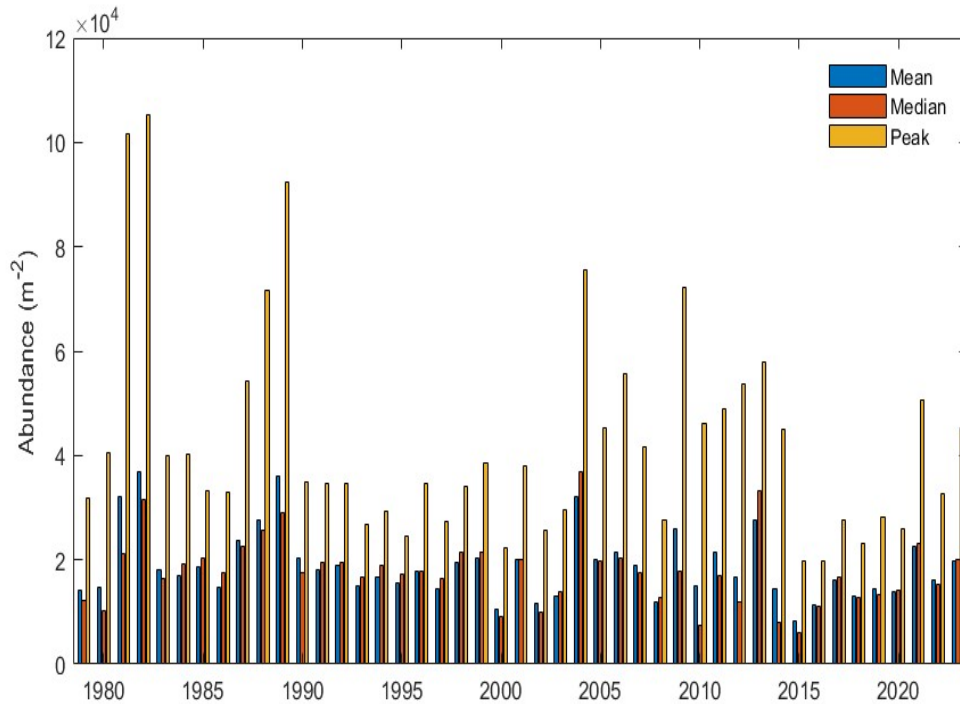
#### *Artemia* Mean Annual Abundance, 1979–2023

The seasonal (1 May–30 November) mean daily abundance of the adult *Artemia* has varied 4-fold from 8,100 to 36,900 m<sup>-2</sup> with an overall mean of 19,000 (Table 23, Fig. 61) over the past 45 years. The peak abundance has varied over 5-fold from 19,700 to 105,200 m<sup>-2</sup> with an overall mean of 43,500.

Table 2. Mean annual adult *Artemia* abundance (1 May –30 November) and centroid of distribution, 1979–2023. The centroid of *Artemia* distribution is the average of time weighted by adult abundance.

Year	Mean (m <sup>-2</sup> )	Median (m <sup>-2</sup> )	Peak (m <sup>-2</sup> )	Centroid (day of year)
1979	14,100	12,300	31,700	216
1980	14,600	10,200	40,400	236
1981	32,000	21,100	101,700	238
1982	37,000	31,700	105,200	260
1983	18,100	16,500	39,900	230
1984	17,000	19,300	40,200	203
1985	18,500	20,300	33,100	220
1986	14,700	17,400	33,000	192
1987	23,800	22,700	54,300	232
1988	27,600	25,800	71,600	206
1989	36,100	29,100	92,500	256
1990	20,200	17,600	34,900	230
1991	18,100	19,500	34,600	227
1992	18,900	19,500	34,600	220
1993	15,000	16,700	26,900	215
1994	16,600	18,800	29,400	213
1995	15,600	17,200	24,400	203
1996	17,700	17,900	34,600	215
1997	14,400	16,400	27,300	203
1998	19,400	21,400	34,000	227
1999	20,200	21,500	38,400	225
2000	10,600	9,100	22,400	210
2001	20,000	20,000	38,000	209
2002	11,600	10,000	25,500	199
2003	13,100	13,800	29,500	203
2004	32,200	36,900	75,500	174
2005	20,000	19,800	45,400	192
2006	21,500	20,300	55,700	185
2007	18,800	17,500	41,800	186
2008	12,000	12,700	27,600	189
2009	26,000	17,900	72,100	179
2010	14,900	7,400	46,200	191
2011	21,300	16,900	48,900	193
2012	16,700	12,000	53,800	178
2013	27,700	33,300	57,800	195
2014	14,300	8,100	45,000	194
2015	8,200	6,200	19,900	183
2016	11,400	11,000	19,700	221
2017	16,200	16,600	27,700	223
2018	12,900	12,800	23,200	215
2019	14,400	13,400	28,200	220
2020	13,800	14,300	25,900	208
2021	22,600	23,100	50,700	198
2022	16,200	15,400	32,700	222
2023	19,800	20,000	45,300	219
Mean	18,800	17,800	42,700	210
Min	8,200	6,200	19,700	174
Max	37,000	36,900	105,200	260

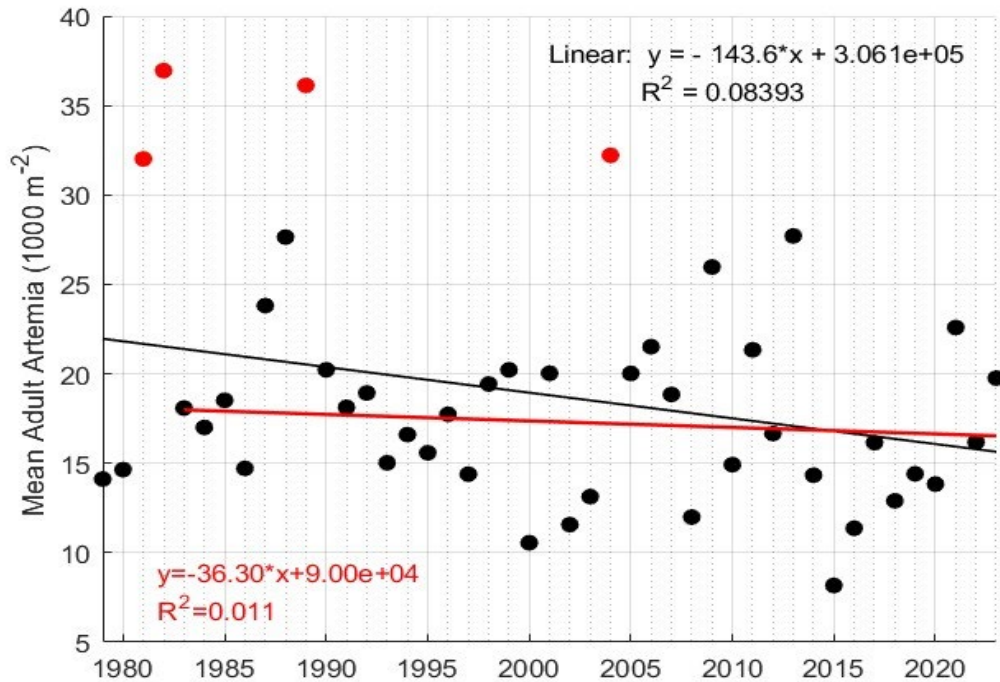
Fig. 5. Summary statistics of the seasonal (1 May through 30 November) lakewide abundance of adult *Artemia*, 1979–2023. Values are based on interpolated daily abundances.



A linear regression of the mean annual abundance on year explains a small proportion (~8%) of the overall variation and is only marginally significant ( $p$ -value = 0.053). The slope of -143.6 would suggest a 29% decline of ~6,300 mean annual abundance from 1979 to 2023. However, given the low  $r^2$ , the 95% confidence bounds of the slope range are -289 to 2.3. In fact, much of negative slope of the regression is driven by 4 years of exceptionally high abundance (1981, 1982, 1988, 2004). During the period 1979–81, Lenz (1982, 1984) documented a progressive increase in the ratio of peak summer to spring abundances of adult brine shrimp. The smaller spring generations resulted in greater food availability and higher ovoviviparous production by the first generations, leading to larger second generations. The small spring generation of *Artemia* in 1982 also led to the exceptionally large 2<sup>nd</sup> generation (Melack et al. 2017). The two extended periods of meromixis that broke down in 1988 and 2003 resulted in a large pulse of ammonium accumulated in the monimolimnion into the euphotic zone, higher phytoplankton densities and increased ovoviviparous reproduction and survival resulting in large 2<sup>nd</sup> generations in 1989 and 2004 (Melack et al. 2017). If these four years are

removed as outliers, then the regression explains a trivial amount of the overall variation ( $r^2=0.011$ ) and is not statistically significant ( $p\text{-value}=0.51$ ).

Fig. 6. Long-term trend in mean seasonal adult *Artemia* abundance, 1979–2023. Regressions with and without the four outlier years (see explanation in text).



*Artemia* abundance has a strong seasonal component. Seasonal-trend decomposition using locally estimated scatterplot smoothing (STL) is widely used to estimate trend and seasonal components in environmental time series. Here, we use STL to decompose *Artemia* population data collected over the 41-years period from 1983 to 2023 into trend, seasonal, and noise (unexplained) components to help interpret the long-term monitoring data. The time-series decomposition of adult *Artemia* has significant annual variation in the annual trend ( Fig. 63, top panel). Four of the five prominent peaks in the trend panel occur during the year after the breakdown of meromictic events in 1989, 2004, 2013, and 2020 suggesting increased nutrient availability from the upward flux of nutrients accumulated in the deep monimolimnion, subsequent increase in algal abundance, and possibly cyst hatching from recently oxygenated sediments as likely causes. Additional noise or unexplained variation mostly coincides with the peaks in trend suggesting these years are unusual and cannot be explained as part of a larger trend or seasonal variation. The magnitude of the seasonal component appears to vary slightly

over a longer ~20-yr period. The 3<sup>rd</sup> peak in 2009 is the exception in that it occurs two years after the breakdown of a 2-yr episode initiated in 2005. Regression of the 41-yr trend component yields a 27% decline from ~12,800 to 9,300 m<sup>-2</sup> in the trend line of adult *Artemia*. Note the seasonal and noise components must be added to the trend line to obtain the observed data, and the line estimates the annual mean trend not abundance during the 1 May–30 November period. As with the analysis of mean annual abundance, removing the two unusual years (1989 and 2004) of high abundance following the breakdown of an extended period of meromixis results in a smaller estimate of decline (~20%) that explains a trivial portion of the overall variation ( $r^2=0.004$ ) and is not statistically significant (p-value= 0.15). While a long-term decline in abundance cannot be shown to be statistically significant, the role of episodes of meromixis on the observed variability in the *Artemia* population is clear.

Fig. 7. STL decomposition of adult *Artemia* abundance, 1983–2023, into trend (top panel), seasonal variation (2<sup>nd</sup> panel), “noise” or residual (3<sup>rd</sup> panel), and the observed data (bottom panel).

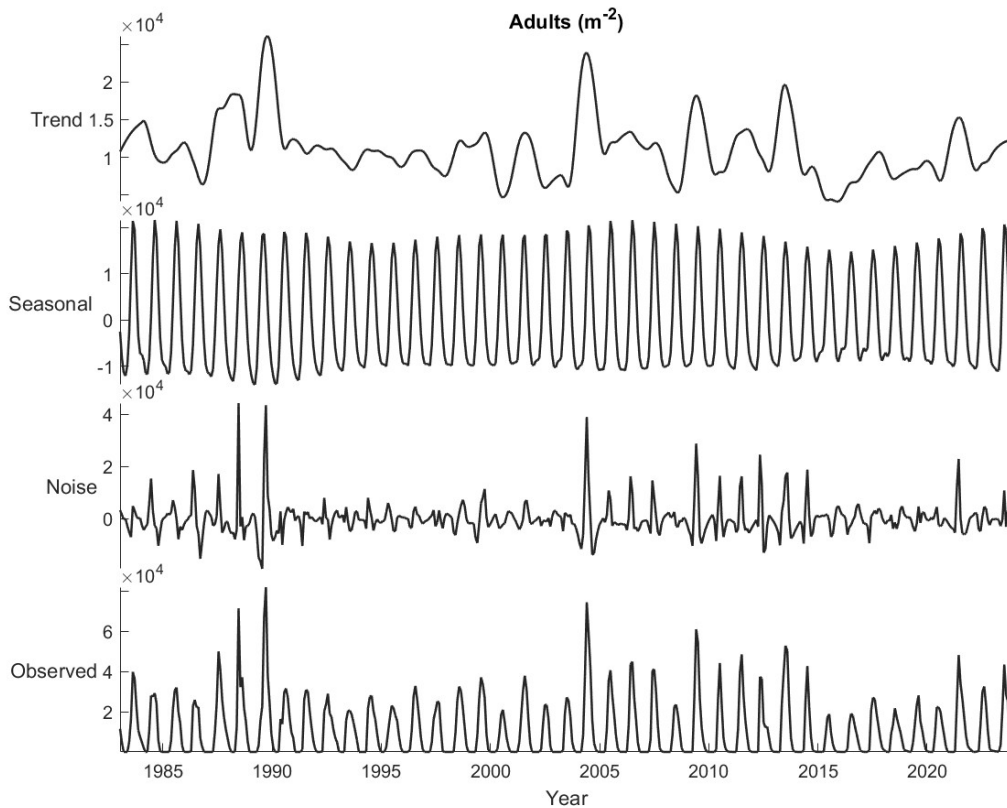
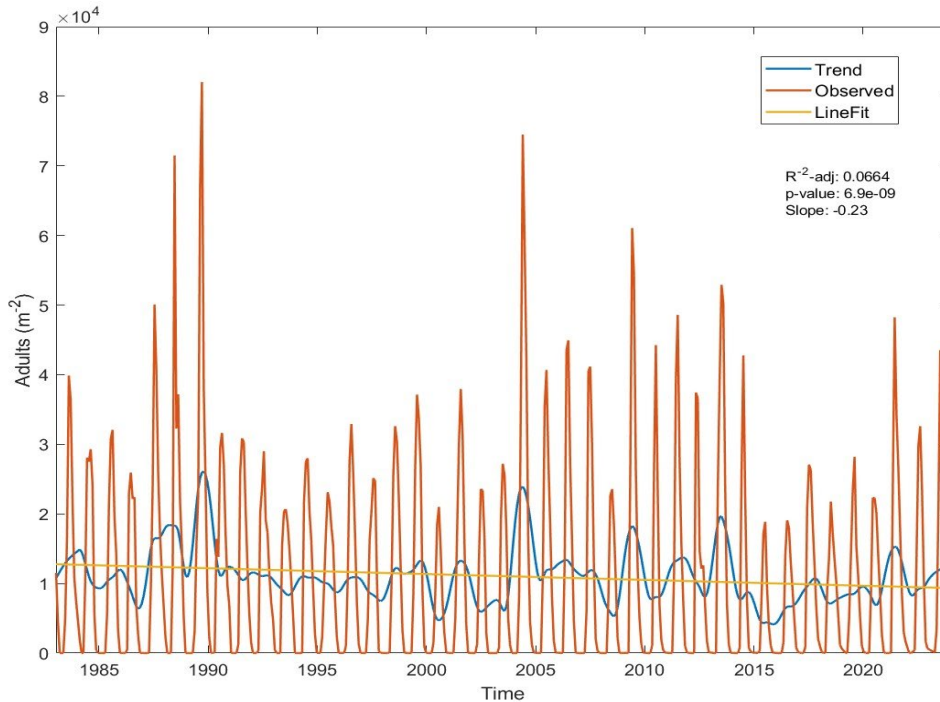


Fig. 8. Long-term trend of adult *Artemia* with seasonal component removed.

Beginning in 2000, the biomass of *Artemia* was determined by weighing of samples after enumeration and determination of reproductive characteristics. These data provide a second measure of food availability to migrating and nesting bird populations at the lake. Seasonal trend decomposition of the biomass data reveals prominent peaks following the breakdown of meromixis in 2004, 2013, and 2021. The trend line regression explains a very small portion of the observed variation ( $r^2=0.001$ ) and is not statistically significant ( $p\text{-value}=0.59$ ).

Fig. 9. STL decomposition of *Artemia* biomass, 2000–2023, into trend (top panel), seasonal variation (2<sup>nd</sup> panel), “noise” or residual (3<sup>rd</sup> panel), and the observed data (bottom panel).

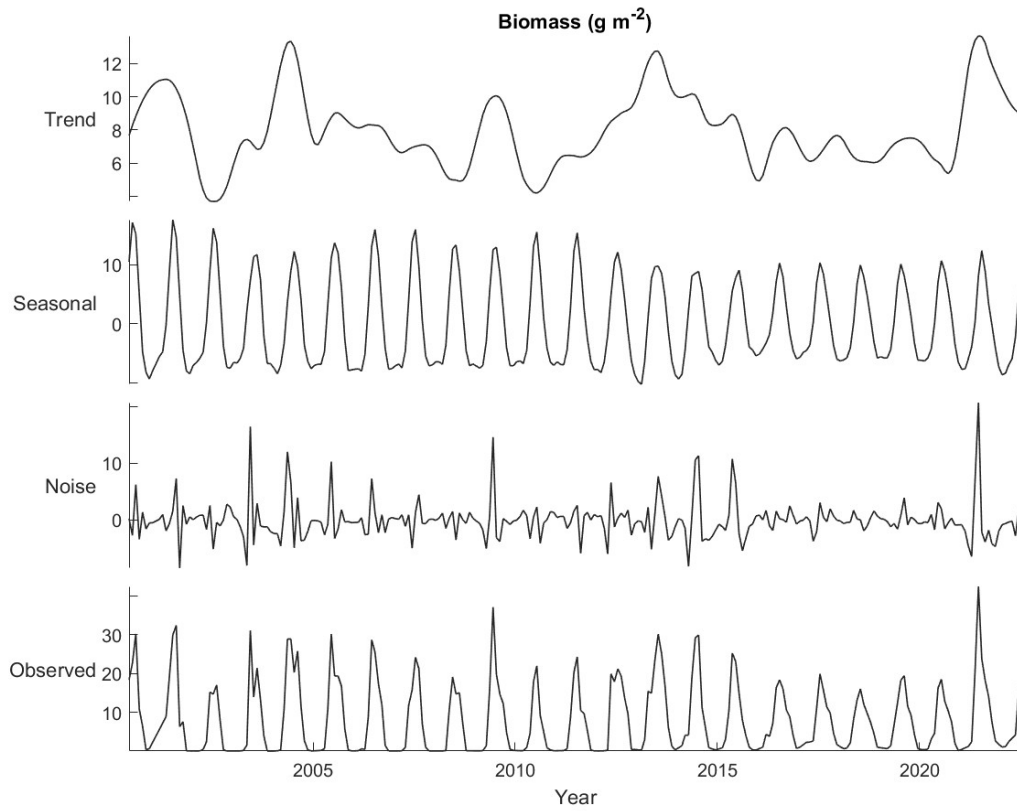
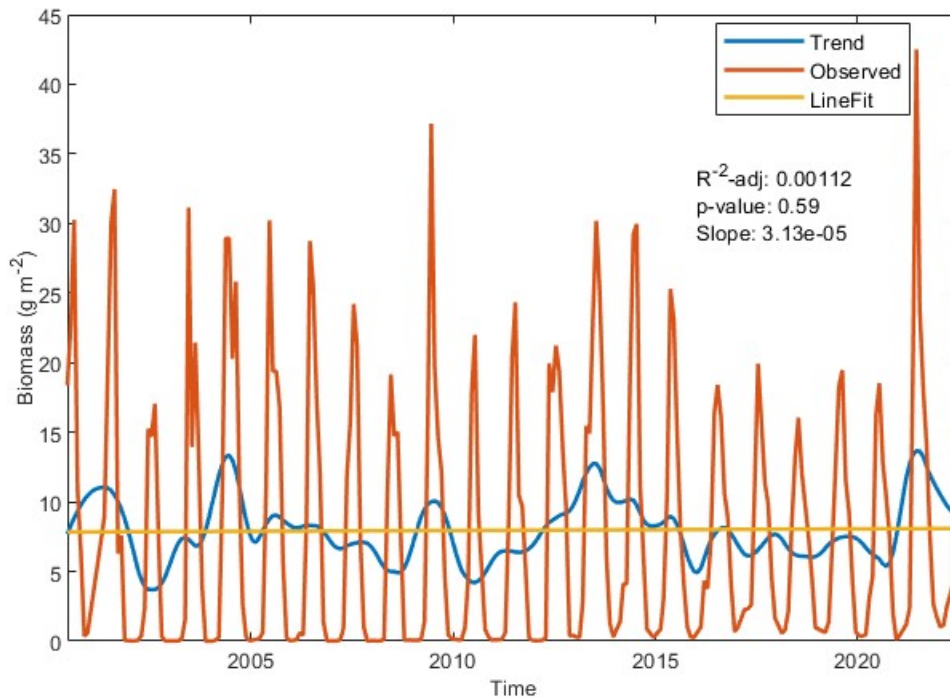


Fig. 10. Long-term trend of *Artemia* biomass with seasonal component removed.

#### *Temporal Distribution of Artemia Abundance*

The temporal distribution of *Artemia* abundance may have significant effects on nesting gulls and migrating grebes. Small 1<sup>st</sup> generations have been shown to affect gull breeding and success (Wrege et al. 2006). A small 2<sup>nd</sup> generation leads to an early decline in autumn population and significantly impacts migrating grebe populations (Jehl 2007, Boyd et al. 2021). There have been large differences in the size of the 1<sup>st</sup> (May-June) and 2<sup>nd</sup> (August) generations of *Artemia* from 1979–2023 (Fig. 67). Adult abundance exceeded 40,000 m<sup>-2</sup> during May–June in eleven of the 42 years, while autumn abundance approached 100,000 m<sup>-2</sup> in 1982 and 1989. These two years along with 1983 had very low abundance of adults in May–June. Changes in the relative size of the two generations causes shifts in the overall temporal distribution. The centroid of the abundance distribution shifted from day 173 (23 June) to 260 (16 September) from 1982 to 2004 (Fig. 68). From 1979 to 2005 there was a general shift in the abundance centroid to earlier in the year. A linear regression explained 33% of the variation (p-value = 0.002) and indicated a shift from day 235 to 199, over a month earlier in the year. From 2006–2015, it remained early (mean, 187) before increasing to nearly a month later (mean, 215) during 2016–2023. These temporal shifts in prey distribution may not impact avian populations if food

is not limiting or alternative prey are available (e.g., alkali flies, Herbst 1990, Elphick & Rubega 1995). However, abundance ranged from ~6–34,000 m<sup>-2</sup> on 1 June (a period critical for gulls) and from ~2,000–25,000 m<sup>-2</sup> on 1 October (a period critical for grebes). The years in which *Artemia* abundance was at the lower end of these range would certainly impact gulls and grebes.

Fig. 11. Adult *Artemia* abundance, 1982–2023. Red lines shows years when May–June abundance exceeded 40,000 m<sup>-2</sup>. Blue lines indicate years of exceptionally high autumn abundance.

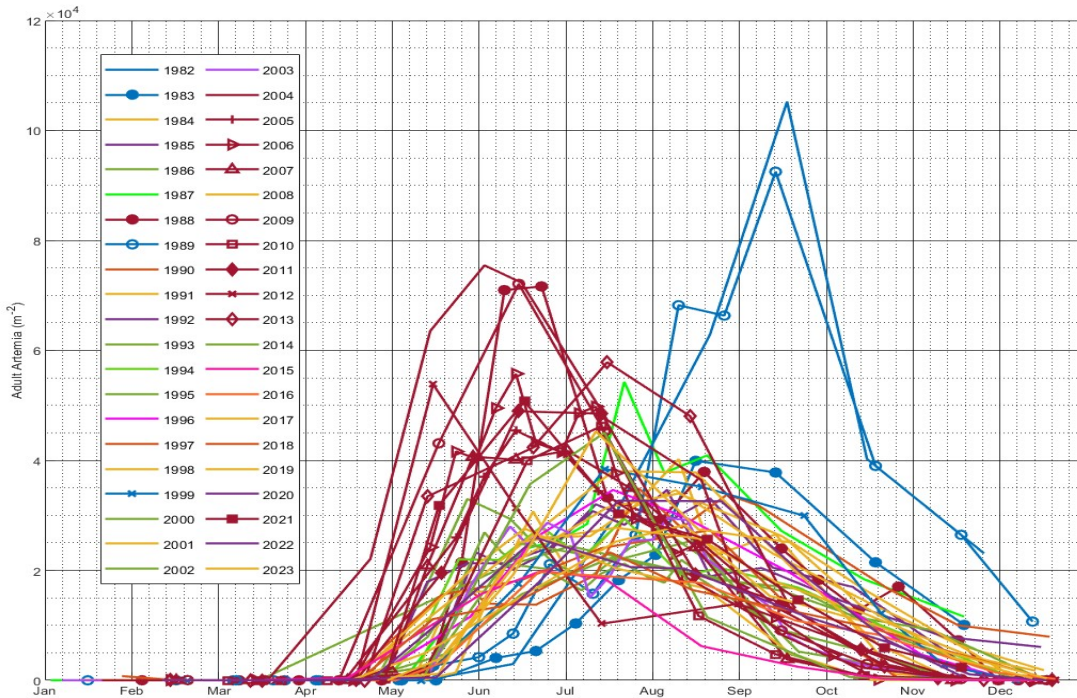
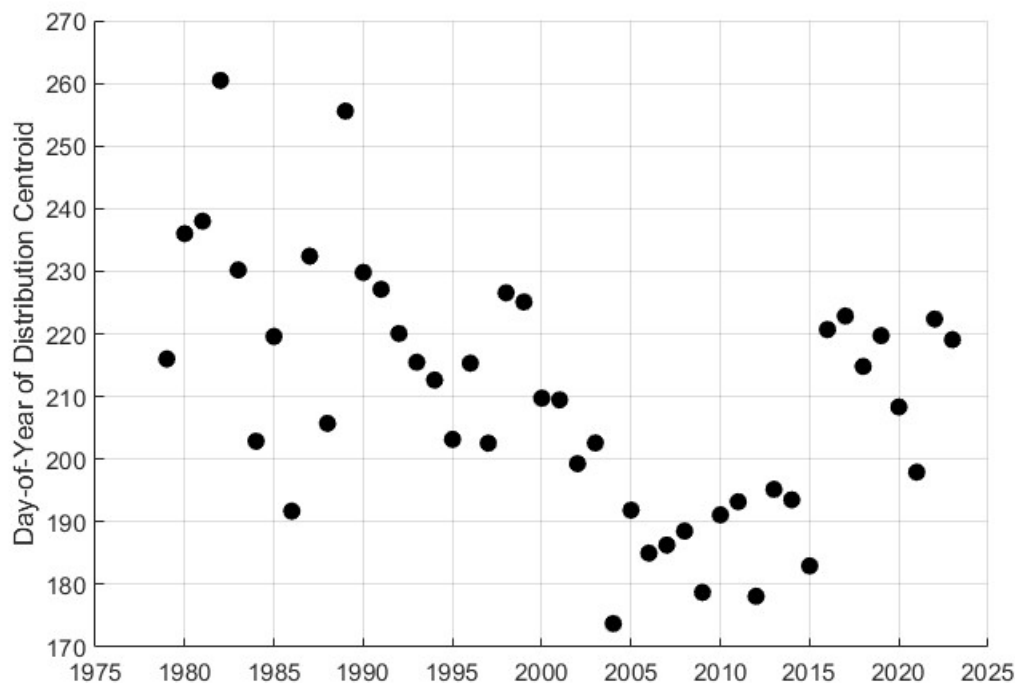


Fig. 12. Abundance-weighted centroid of adult *Artemia*, 1979–2023.

#### *Effects of Meromixis on Seasonal Mean Adult Artemia Abundance*

The effects of the onset, persistence, and breakdown of meromixis on ammonium recycling and primary productivity are well-documented (Jellison & Melack 1988, 1993, Jellison et al. 1993, Melack & Jellison 1998, 2017). However, the effects on the seasonal abundance of *Artemia* are still uncertain. Categorizing a year as meromictic or monomictic is inadequate for explaining the seasonal fluxes in nutrients and changes in primary productivity. Years of the onset, breakdown, and immediately following extended periods of meromixis are distinctly different. The spring and summer *Artemia* populations are likely to be little affected until late in the year when holomixis is prevented during the onset years. While the annual period of holomixis is absent during meromictic years and prevents the mixing of ammonium accumulated in the monimolimnion, the upward flux may be large during the last year of meromixis, when significant deepening of the mixed layer occurs. The year immediately following the breakdown of an extended period of meromixis experiences an increase in ammonium and primary productivity. The past 42 years can be divided into 5 categories: monomictic (11), onset of meromixis (6), meromictic (i.e., persistent stratification) (15), breakdown of meromixis (5), and post breakdown years (5) (Table 24).

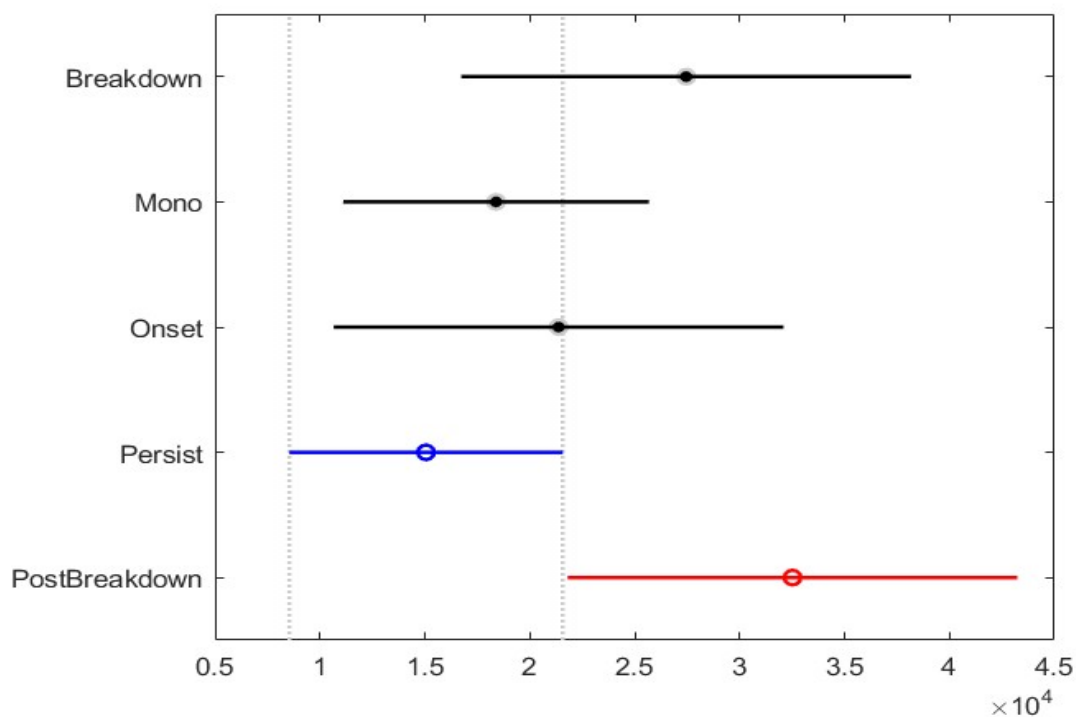
Table 3. Seasonal mean abundance of *Artemia* versus mixing status.

Year	Category	Spring	Summer	Autumn
1982	Onset	3,500	43,700	68,300
1983	Persist	2,900	25,400	29,000
1984	Persist	15,400	28,700	14,800
1985	Persist	14,800	30,100	17,700
1986	Persist	23,300	22,100	5,800
1987	Persist	14,600	39,300	23,000
1988	Breakdown	37,100	36,200	19,500
1989	Post Breakdown	7,100	43,100	62,800
1990	Mono	13,600	27,800	23,800
1991	Mono	11,400	30,200	18,100
1992	Mono	19,100	27,400	15,600
1993	Mono	16,300	19,100	13,600
1994	Mono	18,400	23,100	14,200
1995	Onset	18,000	21,100	13,300
1996	Persist	14,600	30,500	15,200
1997	Persist	15,800	24,800	9,400
1998	Persist	12,200	31,400	20,800
1999	Persist	10,700	35,400	22,800
2000	Persist	9,600	19,600	7,300
2001	Persist	18,200	35,900	15,200
2002	Persist	13,600	22,600	4,000
2003	Breakdown	15,800	23,300	6,500
2004	Post Breakdown	64,800	41,500	5,700
2005	Onset	31,300	29,400	8,800
2006	Persist	37,200	31,600	6,200
2007	Breakdown	31,500	30,400	3,700
2008	Post Breakdown	19,300	18,900	3,600
2009	Mono	52,300	31,800	6,200
2010	Mono	21,000	27,900	2,900
2011	Onset	31,600	33,100	9,300
2012	Breakdown	36,900	12,800	8,100
2013	Post Breakdown	35,900	49,200	10,900
2014	Mono	18,300	28,200	3,200
2015	Mono	14,100	12,400	1,900
2016	Mono	9,500	18,100	10,200
2017	Onset	12,800	26,100	14,600
2018	Persist	12,400	19,000	11,200
2019	Persist	10,500	24,600	12,700
2020	Breakdown	16,000	20,600	10,600
2021	Post Breakdown	35,500	29,800	12,100
2022	Mono	8,300	30,800	16,200
2023	Onset	13,200	34,800	18,600

One-way analysis of variance of mean adult abundance during spring (May-June), summer (July-August), and autumn (September-October) revealed only one significant (95% confidence level) difference between the means of the five categories. Adult abundance was

significantly higher during May–June of the year following the breakdown of meromixis than during meromixis (Fig. 69).

Fig. 13. Mean spring (April–May) lakewide abundance of adult *Artemia* during different mixing regimes.



The high variability within the five categories prevents further conclusions. This variability may arise due to the different nature of the meromictic episodes or the importance of other factors on the *Artemia* population. The degree and timing of freshwater inflows during the onset of meromixis, the length of the meromictic episode, the nature of the deepening mixed layer during the meromictic episode and breakdown are all likely important and will require measures of ammonium flux, primary productivity, and hydrodynamic modeling to fully characterize. Each of these factors in addition to changing salinity and annual climatic variation likely affect cyst hatching, growth, survivorship and reproduction of *Artemia*.

#### *Naupliar and Cyst Production*

The annual production of encysted embryos (cysts) and ovoviviparously produced embryos (naupliar eggs) depends on seasonal variation in the number of ovigerous females, the mode of reproduction (cyst versus naupliar), fecundity, and brood interval. Both naupliar and

cyst production are highly variable. Annual naupliar production which leads to the 2<sup>nd</sup> and sometimes a small 3<sup>rd</sup> late summer generation has varied from 5 to 634 ( $10^3 \text{ m}^{-2}$ ) with a 41-yr mean of 183 ( $10^3 \text{ m}^{-2}$ ). The total cyst production is much larger and has varied from 1.9 to 5.7 ( $10^6 \text{ m}^{-2}$ ) with a mean of 3.7 ( $10^6 \text{ m}^{-2}$ ). While there is no significant longterm trend in naupliar production, a linear regression of cyst production on year yields a significant ( $r^2=0.286$ ,  $p\text{-value}=0.0003$ ) decline of 47.2 ( $10^3 \text{ m}^{-2} \text{ yr}^{-1}$ ) or a 40% decline over 40 years (Table 25, Fig. 70). The five mixing categories cannot explain a statistically significant portion of this variation (1-way Anova  $p\text{-value}=0.814$ ).

Fig. 14. Long-term variation in annual cyst and nauplii production, 1983–2023.

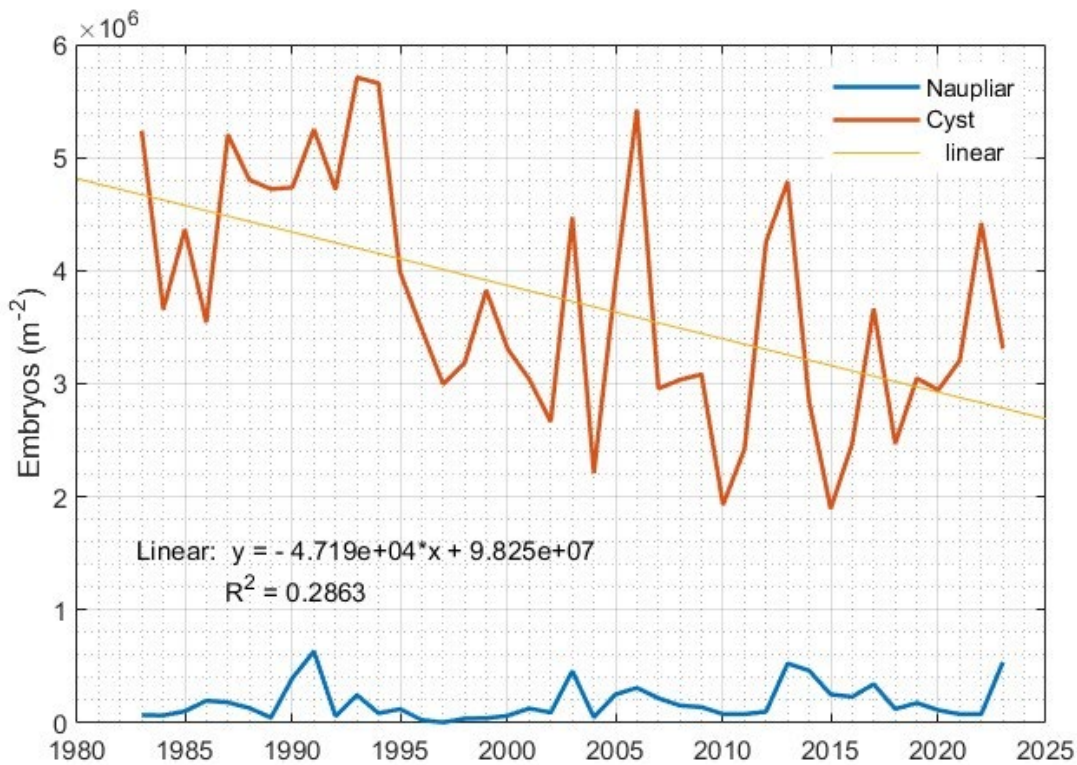


Table 4. Annual nauplii and cyst production, 1983–2023.

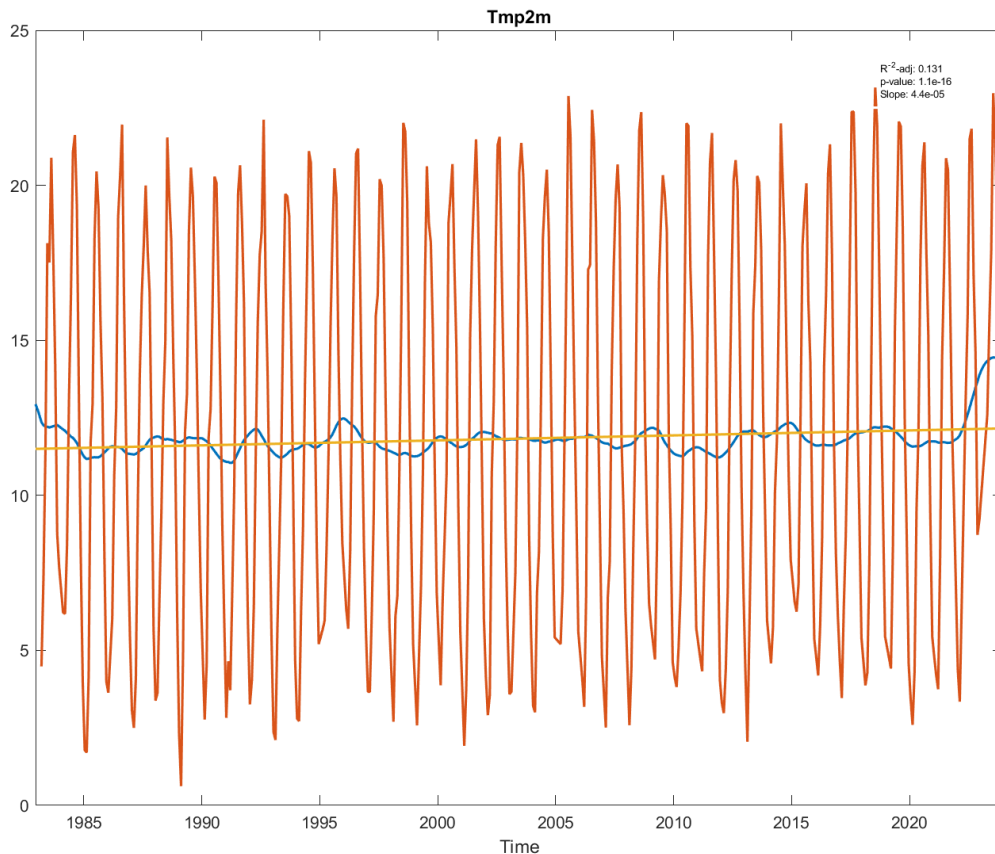
Year	Mixing Category	Nauplii (x 10 <sup>3</sup> m <sup>-2</sup> )	Cyst (x 10 <sup>6</sup> m <sup>-2</sup> )
1983	Persist	70	5.2
1984	Persist	67	3.7
1985	Persist	104	4.4
1986	Persist	197	3.5
1987	Persist	183	5.2
1988	Breakdown	132	4.8
1989	Post Breakdown	47	4.7
1990	Mono	398	4.7
1991	Mono	634	5.2
1992	Mono	60	4.7
1993	Mono	247	5.7
1994	Mono	86	5.7
1995	Onset	123	4.0
1996	Persist	27	3.5
1997	Persist	5	3.0
1998	Persist	40	3.2
1999	Persist	42	3.8
2000	Persist	64	3.3
2001	Persist	128	3.0
2002	Persist	92	2.7
2003	Breakdown	460	4.5
2004	Post Breakdown	51	2.2
2005	Onset	252	3.9
2006	Persist	311	5.4
2007	Breakdown	219	3.0
2008	Post Breakdown	155	3.0
2009	Mono	140	3.1
2010	Mono	79	1.9
2011	Onset	79	2.4
2012	Breakdown	100	4.3
2013	Post Breakdown	526	4.8
2014	Mono	464	2.8
2015	Mono	252	1.9
2016	Mono	232	2.5
2017	Onset	344	3.7
2018	Persist	124	2.5
2019	Persist	177	3.0
2020	Breakdown	114	2.9
2021	Post Breakdown	78	3.2
2022	Mono	79	4.4
2023	Onset	537	3.3

To understand the decline in cyst production further, the abundance-weighted mean of each of the factors contributing to the cyst production calculation (ovigerous females, oviparity, fecundity) was examined. A linear regression of the number of oviparous (nauplii producing) females on year shows no significant change. However, fecundity (eggs per female) declined significantly over time ( $r^2=0.264$ ,  $p\text{-value}=0.0006$  (Fig. 74). The long-term trend line ranged

from 51.2 eggs brood<sup>-1</sup> in 1983 to 29.5 eggs brood<sup>-1</sup> in 2023, a 42% decrease, and can explain the estimated long-term decrease in cyst production of 40%. Fecundity is known to vary with adult female length. A linear regression of the abundance-weighted adult female length also showed a significant long-term decrease ( $r^2=0.317$ ,  $p\text{-value}=0.0001$ ) from 10.89 mm to 9.66 mm, an 11% decrease (Fig. 75). Means of abundance-weighted fecundity or female length did not vary significantly across the five mixing categories.

The mean lakewide temperature at 2 m estimated using the STL method increased from 11.5°C to 12.2°C over the 41-yr period (Fig. 71) and may contribute to slightly shorter brood intervals and higher cyst production. Neither annual abundance-weighted fecundity or female length were significantly correlated with changes in the summer (1 June - 30 September) average temperatures at 2 m.

Fig. 15. Trend line of lakewide temperature at 2 m with seasonal component removed, 1983–2023.



Salinity of the mixolimnion (upper mixed layer) varies due to lake level changes and seasonal changes in salinity stratification associated with the annual thermal regime during the 6 episodes of meromixis. Summer mixolimnetic salinities are more likely to affect the *Artemia* population dynamics than overall lake mean salinity. Routine conductivity measurements using high resolution conductivity-temperature-depth profilers began in 1991. For the period 1991 through 2023 there was a positive correlation of both fecundity and adult female length with the mean 1 June–30 September conductivity at 2 m. The mean conductivity at 2 m ranged from 74 to 92 mS cm<sup>-1</sup> (69 to 91 g kg<sup>-1</sup>). The overall best fit trend line of fecundity decreased 40% from 51 eggs ind<sup>-1</sup> in 1991 to 30 eggs ind<sup>-1</sup> in 2023. The best fit trend line of adult female length decreased 9% from 10.7 mm in 1991 to 9.7 mm in 2023.

This positive correlation with salinity is opposite to what is expected based on well-established osmoregulatory costs and energy constraints, and salinity bioassays using Mono Lake *Artemia* (Dana et al. 1990, 1993). This suggests that mixolimnetic salinity is inversely covarying with some other aspect of episodic meromixis that negatively effects growth and fecundity.

Fig. 16. Long-term variation in abundance-weighted fecundity, 1983–2023.

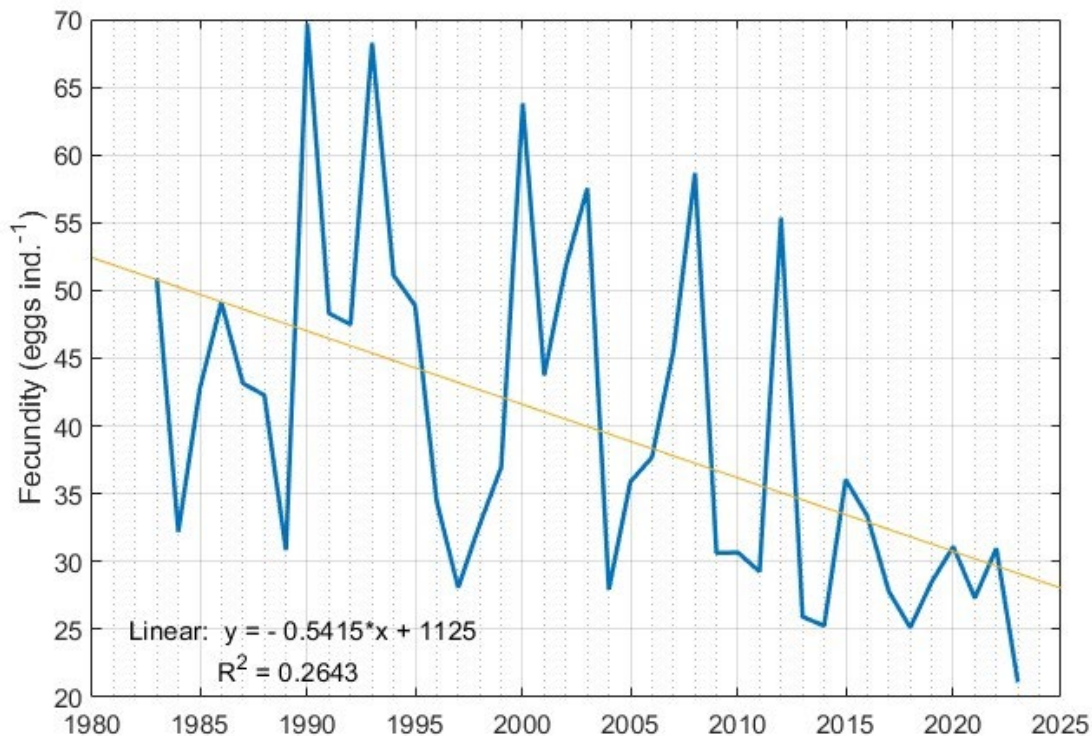


Fig. 17. Long-term variation in abundance-weighted adult female length, 1983–2023.

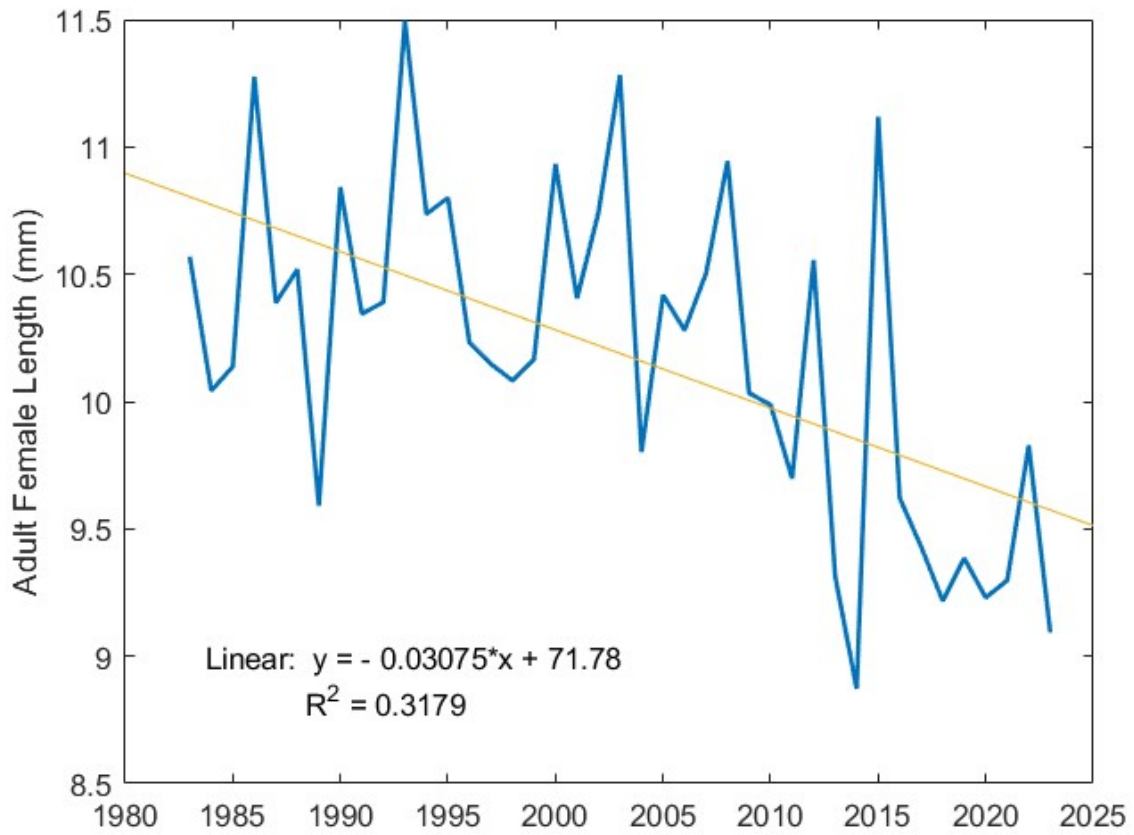


Fig. 18. Mean adult female weighted fecundity versus summer (1 June– 30 September) mean lakewide conductivity at 2 m depth.

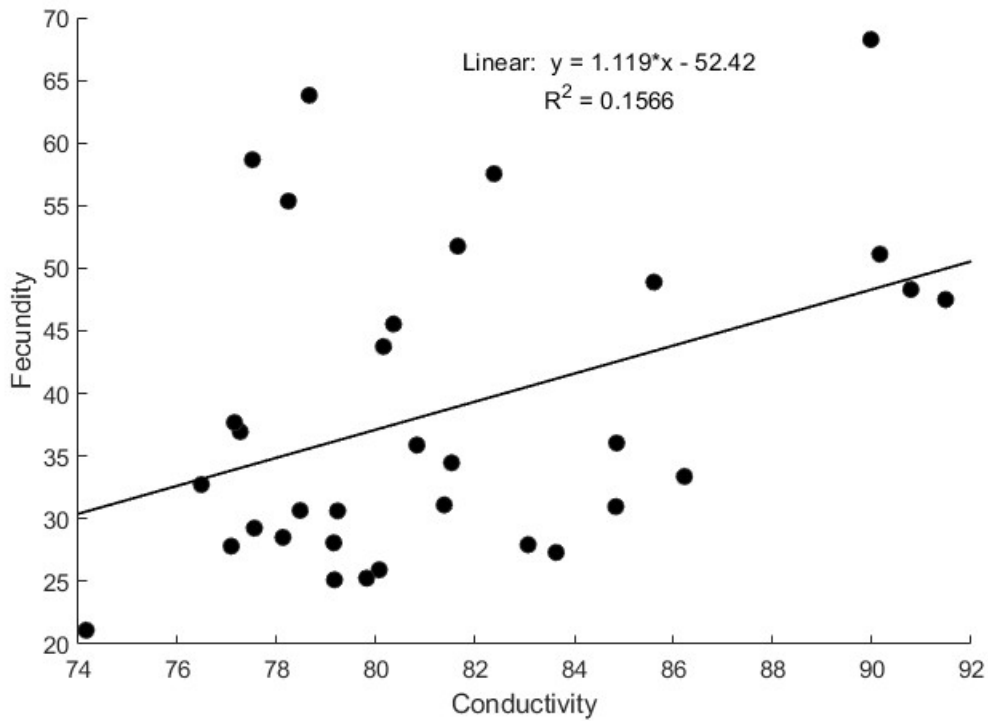
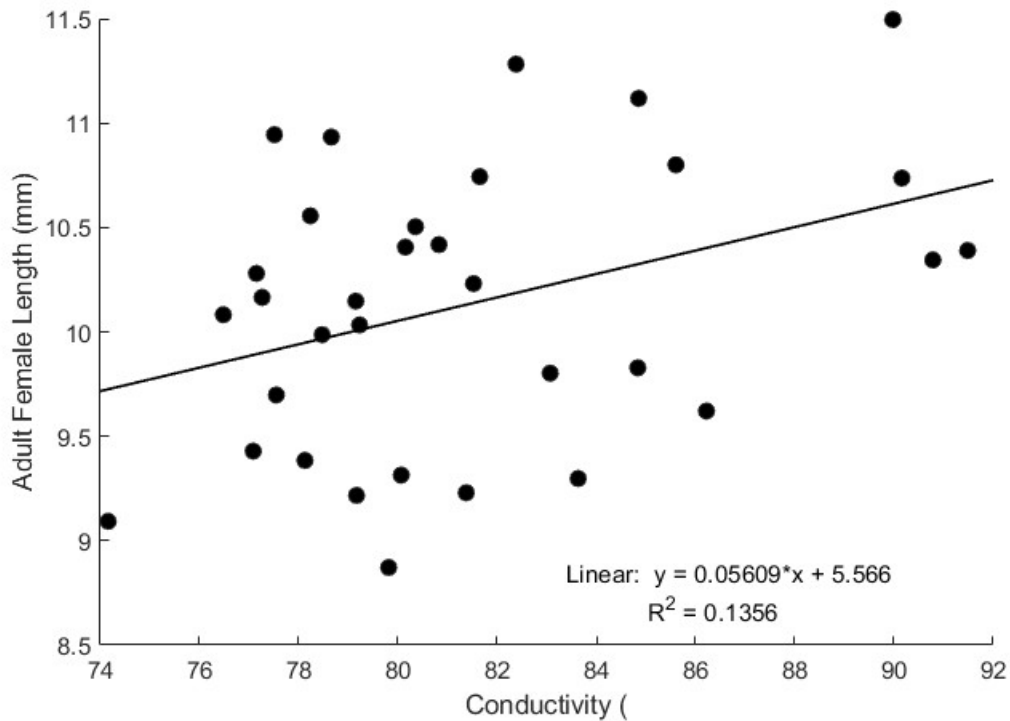


Fig. 19. Mean adult female weighted length versus summer (1 June– 30 September) mean lakewide conductivity at 2 m depth.



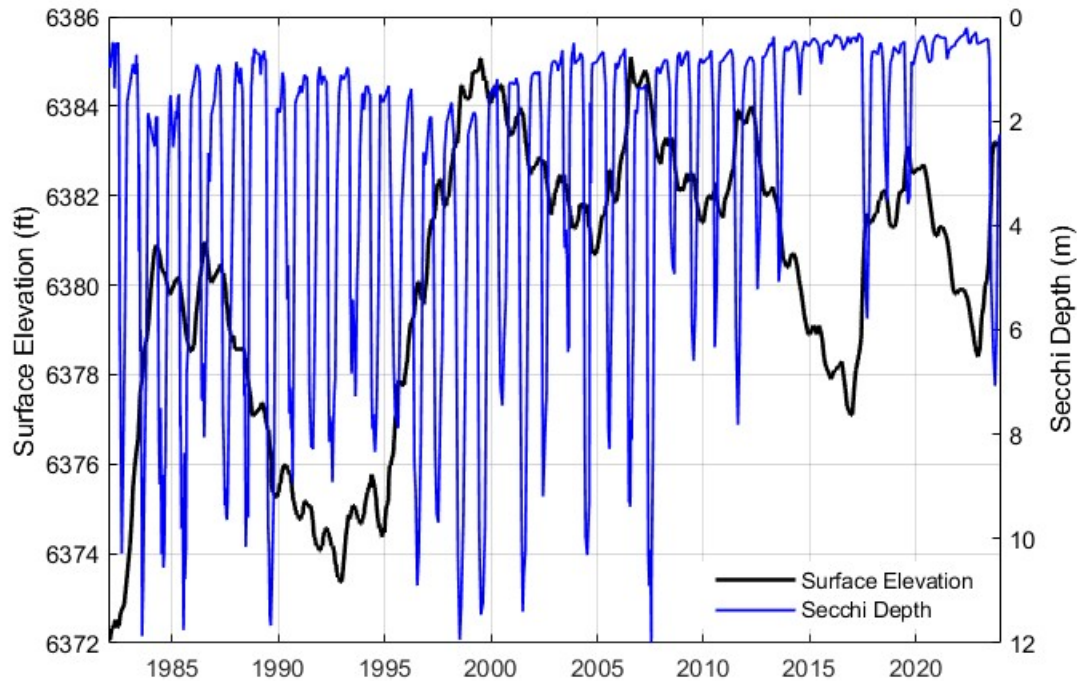
### *Transparency*

For more than three decades (1982–2014), the plankton community of Mono Lake exhibited a regular seasonal variation of abundant phytoplankton and low transparency during winter-spring followed by decreased phytoplankton and high transparency during the summer due to grazing by abundant *Artemia*. High summer transparencies (>6 m, as measured by Secchi depth) due to *Artemia* grazing were a perennial seasonal feature. Winter transparency was generally 0.5–2 m during winter and summer values were 5–12 m (Fig. 76). During this period winter transparencies increased during periods of meromixis due to the lack of autumn turnover and mixing of nutrient-rich hypolimnetic waters throughout the water column. This increase in winter transparency was observed during three episodes of meromixis: 1983–1988, 1997–2005, and 2006–2007.

In 2014, the lake entered a state unseen during the previous thirty years as midsummer transparencies remained less than 2 m. These low transparencies continued through 2015 and 2016. Summer transparencies increased to 3–6 m during a period of meromixis, 2017–2019, but returned to the low levels during 2020–2022. Changes in transparency in Mono Lake is primarily a function of phytoplankton abundance. Unfortunately, chlorophyll measurements from 2013–2022 were improperly analyzed and have limited utility in examining the changes in transparency (see Chapter 4).

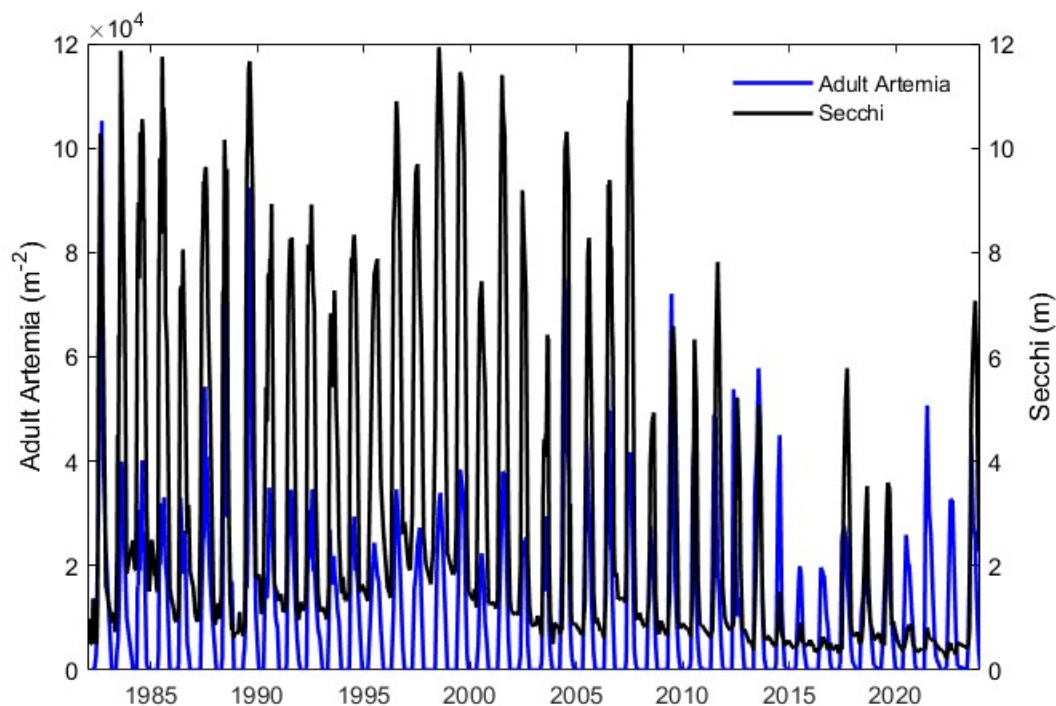
Individual filtering rates of adult *Artemia* are high (150 ml d<sup>-1</sup>, Lenz 1982; 170 ml d<sup>-1</sup>, Jellison, unpublished data) and, when abundant, *Artemia* can graze the standing biomass of phytoplankton daily. Thus, phytoplankton abundance in Mono Lake is a dynamic balance between growth and loss processes (grazing, sinking, senescence). This balance markedly changed in 2014–2016 and 2020–2022 due to yet undetermined causes.

Fig. 20. Long-term changes in transparency (Secchi depth) and surface elevation. Secchi depth is plotted vertically to illustrate the coincidence of adult *Artemia* and midsummer clearing of the upper water column.



The abundant summer generation of adult *Artemia* is primarily responsible for the marked seasonal changes in transparency and phytoplankton abundance (Fig. 77). Adult *Artemia* were the lowest observed during 2015 and 2016 and coincide with the unusually low transparency and high phytoplankton abundance. However, *Artemia* were only slightly more abundant in some other years (e.g., 1996, 2001, 2008), when midsummer transparency was higher. *Artemia* were more abundant during the second period (2020–2022) of low midsummer transparency than other years of high midsummer transparency.

Fig. 21. Long-term changes in transparency (Secchi depth) and adult *Artemia* abundance. Secchi depth is plotted increasing upward to visualize the coincidence of adult *Artemia* midsummer clearing of the upper water column more easily.



### Summary

The recurring episodes of meromixis are likely to continue given the current management regime. While the short-term effects on nutrient recycling, and algal productivity have been documented, long-term effects of this change on the lake's biota and nesting and migratory bird populations, if any, are not yet known.

The five previous episodes of meromixis of varying duration and beginning of the sixth in 2023 have introduced additional components of variability to those due to climatic variation and changing management regimes. Long-term trends in the *Artemia* population and their effect on breeding and migrating bird populations are not well understood.

The long-term trend in adult *Artemia* is driven largely by two years of a large second generation associated with a very low spring hatch at the lake's highest salinity and historic low in 1981 and 1982 and a couple years of high abundance associated with the breakdown of two long periods of meromixis. Without these years, a long-term trend in the 44-yr record is obscured

by high interannual variability. *Artemia* biomass measurements, begun in 2000, show no statistically significant long-term trend.

A significant (40%) decrease in annual production of over-wintering cysts (1983–2023) did occur and is not associated with conditions during years post-breakdown of meromixis. The decrease is a result of a 42% decline in abundance-weighted fecundity. A significant, but smaller (11%), decrease in adult female length occurred. The reasons for the decline in fecundity are not known.

The changing physical, nutrient, and biotic regimes associated with episodic meromixis over the past 44 years cannot be divided into simple categories. Characterizing years as monomictic, onset of meromixis, meromictic, breakdown of meromixis, and post meromixis provided limited insight into causal explanations of observed seasonal and interannual variation. The only statistically significant difference of adult mean abundance was smaller May–June values during meromictic compared to post-meromictic years. Further understanding will require better characterization of the mixing regimes with estimates of nutrient fluxes and hydrodynamic modeling of stratification regimes.

In 2014–2016 and again in 2020–2022 summer transparencies were <2 m. These low midsummer transparencies associated with high phytoplankton abundance had not been observed from 1979 to 2013, or in earlier studies (Mason 1967, Winkler 1977). These conditions represent a significant shift from the previous balance between growth and loss of phytoplankton extending to at least 1965. The 2014–2016 period of high summer phytoplankton abundance was terminated by the onset of meromixis in 2017, and the 2020–2022 period terminated by the onset of meromixis in 2023,

The monitoring program will continue to collect a full suite of limnological data. In addition, several components have been added to address questions raised by the analysis of the long-term data. Deployment of moored arrays of temperature, salinity, chlorophyll fluorescence and dissolved oxygen sensors will provide continuous records to better characterize vertical mixing regime, nutrient fluxes and algal abundance. The design and implementation of laboratory experiments and models to examine the dynamic balance between phytoplankton growth and loss processes in relation to *Artemia* dynamics and physical condition is recommended.

## REFERENCES

- Arar, E. J., and G. B. Collins. 1997. Method 445.0 In vitro determination of chlorophyll *a* and pheophytin *a* in marine and freshwater algae by fluorescence, *In* U.S. Environmental Protection Agency.
- Blevins, M. 1984. Background report on Mono Basin geology and hydrology. Los Angeles Department of Water and Power, Aqueduct Division.
- Bower, C. E., and T. Holm-Hansen. 1980. A salicylate–hypochlorite method for determining ammonia in seawater. *Canadian Journal Fisheries Aquatic Sciences* 37: 794–798.
- Boyd, W., N. Clyde, A. Breault, R. Di Paolo, and M. McAdie. 2021. Abundance, distribution and migration patterns of North American Eared Grebes (*Podiceps nigricollis*). *Waterbirds* 44: 76–85.
- California State Water Resources Control Board. 1994. Final environmental impact report for the review of Mono Basin water rights of the city of Los Angeles. California Environmental Protection Agency.
- Chapman, D. V. 1996. Water quality assessments: a guide to the use of biota, sediments, and water in environmental monitoring, 2nd ed. E & FN Spon.
- Dana, G., R. Jellison, and J. Melack. 1995. Effects of different natural regimes of temperature and food on survival, growth, and development of *Artemia monica* Verrill. *J. Plankton Res.* 17: 2117–2130.
- Dana, G., R. Jellison, J. Melack, and G. Starrett. 1993. Relationships between *Artemia monica* life history characteristics and salinity. *Hydrobiologia* 263: 129–143.
- Dana, G. L., and P. H. Lenz. 1986. Effects of increasing salinity on an *Artemia* population from Mono Lake, California. *Oecologia* 68: 428–436.
- Elphick, C., and M. Rubega. 1995. Prey choices and foraging efficiency of recently fledged California Gulls at Mono Lake, California. *Great Basin Naturalist* 55: 363–367.
- Golterman, H. L., and R. S. Clymo. Methods for chemical analysis of fresh waters. IBP Handbook No. 8.
- Heath, H. The external development of certain phyllopods. *J. Morphology* 38: 453–483.
- Herbst, D. 1990. Distribution and abundance of the alkali fly (*Ephydra hians*) Say at Mono Lake, California (USA) in relation to physical habitat. *Hydrobiologia* 197: 193–205.
- Holmes, R. M., A. Aminot, R. Kerouel, B. Hooker, and B. J. Peterson. 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. *Canadian Journal Fisheries Aquatic Sciences* 56: 1801–1808.
- Holm-Hansen, O., and B. Riemann. 1978. Chlorophyll *a* determination: improvements in methodology. *Oikos* 30: 438–447.
- Jehl, J. 2007. Why do Eared Grebes leave hypersaline lakes in autumn? *Waterbirds* 30: 112–115.

- Jellison, R., S. MacIntyre, and F. J. Millero. 1999a. Density and conductivity properties of Na-CO<sub>3</sub>-Cl-SO<sub>4</sub> brine from Mono Lake, California, USA. *Int. J. Salt Lake Research* 8: 41–53.
- Jellison, R., S. MacIntyre, and F. J. Millero. 1999b. Density and conductivity properties of Na-CO<sub>3</sub>-Cl-SO<sub>4</sub> brine from Mono Lake, California, USA (erratum). *Int. J. Salt Lake Research* 8: 384.
- Jellison, R., and J. Melack. 1988. Photosynthetic activity of phytoplankton and its relation to environmental factors in hypersaline Mono Lake, California. *Hydrobiologia* 158: 69–88.
- Jellison, R., and J. Melack. 1993. Meromixis in hypersaline Mono Lake, California. 1. Stratification and vertical mixing during the onset, persistence, and breakdown of meromixis. *Limnology and Oceanography* 38: 1008–1019.
- Jellison, R., L. Miller, J. Melack, and G. Dana. 1993. Meromixis in hypersaline Mono Lake, California. 1. Nitrogen fluxes. *Limnology and Oceanography* 38: 1020–1039.
- Lenz, P. H. 1982. Population studies on *Artemia* in Mono Lake, California. PhD Dissertation. University of California, Santa Barbara.
- Lenz, P. H. 1984. Life-history analysis of an *Artemia* population in a changing environment. *Journal of Plankton Research* 6: 967–983.
- Los Angeles Department of Water and Power. 2012, 2013, ...,2023. Annual Compliance Reports to State Water Resources Control Board.
- Mason, D. T. 1967. *Limnology of Mono Lake, California*, University of California Press.
- Melack, J., and R. Jellison. 1998. Limnological conditions in Mono Lake: contrasting monomixis and meromixis in the 1990s. *Hydrobiologia* 384: 21–39.
- Melack, J., R. Jellison, S. MacIntyre, and J. Hollibaugh. 2017. Mono Lake plankton dynamics over three decades of meromixis or monomixis, p. 325–351. *In* R. Gulati, E. Zadereev, and A. Degermendzhi [eds.], *Ecology of Meromictic Lakes*.
- Patten, D. T., F. Conte, W. E. Cooper, and others. 1987. *The Mono Basin ecosystem: effects of changing lake level*, National Academy Press.
- Solorzano, L. 1969. Determination of ammonia in natural waters by the phenol-hypochlorite method. *Limnology and Oceanography* 14: 799–801.
- Strickland, J. D. H., and T. R. Parsons. 1972. *A practical handbook of seawater analysis*. Bull. Fish. Res. Bd. Canada.
- Taylor, B. W., C. F. Keep, R. O. Hall, B. J. Koch, L. M. Tronstad, A. S. Flecker, and A. J. Ulseth. 2007. Improving the fluorometric ammonium method: matrix effects, background fluorescence, and standard additions. *Journal of the North American Benthological Society* 26: 167–177.
- Weber, C. I., L. A. Fay, G. B. Collins, D. E. Rathke, and J. Tobin. 1986. A review of methods for the analysis of chlorophyll in periphyton and plankton of marine and freshwater systems. OHSU-TB-15. OHSU-TB-15.
- Winkler, D. W., ed. 1977. *An ecological study of Mono lake, California*, University of California, Davis.

- Winkler, D. W., and S. D. Cooper. 1986. Ecology of migrant Black-necked Grebes (*Podiceps nigricollis*) at Mono Lake, California. *Ibis* (London, England) 128: 483–491.
- Wrege, P., W. Shuford, D. Winkler, and R. Jellison. 2006. Annual variation in numbers of breeding California Gulls at Mono Lake, California: The importance of natal philopatry and local and regional conditions. *CONDOR* 108: 82–96.
- Zadorojny, C., S. Saxton, and R. Finger. 1973. Spectrophotometric Determination of Ammonia. *Journal - Water Pollution Control Federation* 45: 905–912.