

## NOTES

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### The onset of meromixis during restoration of Mono Lake, California: Unintended consequences of reducing water diversions

**Abstract**—Diversions of freshwater streams out of the Mono Lake basin since 1941 have led to a gradual decrease in size, an approximate doubling of lake-water salinity, and associated environmental impacts. To restore Mono Lake, the state of California amended Los Angeles' water rights by restricting diversions until the surface elevation rises 6 m above its 1982 low stand. Given the reduced volume of the lake, the cessation of diversions and an above average snowmelt runoff in 1995 led to an abrupt 1-m rise in surface elevation and the onset of persistent chemical stratification (meromixis). Long-term simulations using a one-dimensional vertical mixing model modified for application to hypersaline Mono Lake predict the current episode of meromixis is likely to persist for several decades, given the management policy of the state. A similar episode of meromixis in the mid-1980s following record snowmelt runoff in 1982–1983 and reduced diversions led to reductions in vertical mixing, recycling of nutrients, and primary productivity. That episode ended following an extended period of drought and the resumption of diversions. The ecological consequences of the predicted multidecade period of meromixis are largely unknown.

Saline lakes are widely recognized as highly productive aquatic habitats, which in addition to harboring unique assemblages of species, often support large populations of migratory birds. Saline lake ecosystems throughout the world are threatened by decreasing size and increasing salinity due to diversions of freshwater inflows for irrigation and other human uses (Williams 1993); notable examples in the Great Basin of North America include Mono Lake (Patten et al. 1987), Walker Lake (Cooper and Koch 1984), and Pyramid Lake (Galat et al. 1981). At Mono Lake, California, diversions of freshwater streams out of the basin beginning in 1941 led to a 14-m decline in surface elevation and an approximate doubling of the lake's salinity (Fig. 1).

In 1994, following two decades of scientific research, litigation, and environmental controversy, the State Water Resources Control Board (SWRCB) of California issued a decision to amend Los Angeles' water rights to "establish fishery protection flows in streams tributary to Mono Lake and to protect public trust resources at Mono Lake and in the Mono Lake Basin" (decision 1631). The decision limits water diversions until the surface elevation of the lake reaches 1,948 m. No diversions were allowed until a surface elevation of 1,943.7 m was reached, after which  $5.5 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$  were allowed to be diverted. A second increase to  $19.7 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$  was allowed after the surface elevation reached 1,944.6 m. This is the first time a large ( $>100 \text{ km}^2$ )

saline lake has been purposely enlarged to mitigate environmental impacts accompanying water diversions, and thus this action represents a unique restoration effort.

During this century, the large size, temperate latitude (38°N), declining lake level, and density characteristics of Mono Lake brine have resulted in a monomictic regime in which complete vertical mixing occurs throughout the winter. Because external inputs of nutrients to Mono Lake are low (Jellison et al. 1993a), the annual period of winter mixing is important for recycling nutrients, which accumulate in the hypolimnion during the summer, and for maintaining the high rates of primary productivity observed in Mono Lake (Jellison and Melack 1993a). During years of exceptionally high runoff, large freshwater inflows may initiate periods of persistent chemical stratification (meromixis) in which the vertical flux of nutrients is reduced (Jellison et al. 1993b).

The 1994 decision to restrict water diversions was immediately followed by the second highest runoff in the Mono Basin (182% of 50-yr average) since accurate records began in 1940. The large volume of freshwater inflows in 1995 resulted in significant chemical stratification throughout 1995. Field surveys in early 1996 verified that winter holomixis (complete vertical mixing) had been prevented, and chemical stratification increased through 1996 owing to continuous freshwater inflows and the curtailment of diversions. During our 1997 mid-February survey, usually a time within the period of winter holomixis, significant chemical and thermal stratification were present. A sharp gradient in both temperature and salinity between 17 and 19 m indicated the maximum depth of winter mixing. The near-surface ( $<4 \text{ m}$ ) salinities were  $76\text{--}77 \text{ g kg}^{-1}$  while those in the monimolimnion were  $\sim 87 \text{ g kg}^{-1}$ . The density stratification due to this salinity gradient is greater than that observed due to temperature during late summer at the annual maximum of the heating cycle (Jellison and Melack 1993b).

To determine how long the current episode of meromixis is likely to persist, the vertical mixing model DYRESM (Imberger and Patterson 1981), which had been previously modified for use at Mono Lake (Romero and Melack 1996), was used in conjunction with 50 years of historical runoff data (1940–1990) and the allowable diversion schedule. Prior to performing long-term simulations, DYRESM was validated against field data collected from 1983 to 1996. Inspection of simulations of the mid-1980s episode of meromixis revealed that two modifications to the previously used model were necessary (Romero and Melack 1996). First, the constants  $a$  and  $b$  of the lake number formulation of eddy diffusivity were modified based on comparing simulated and observed

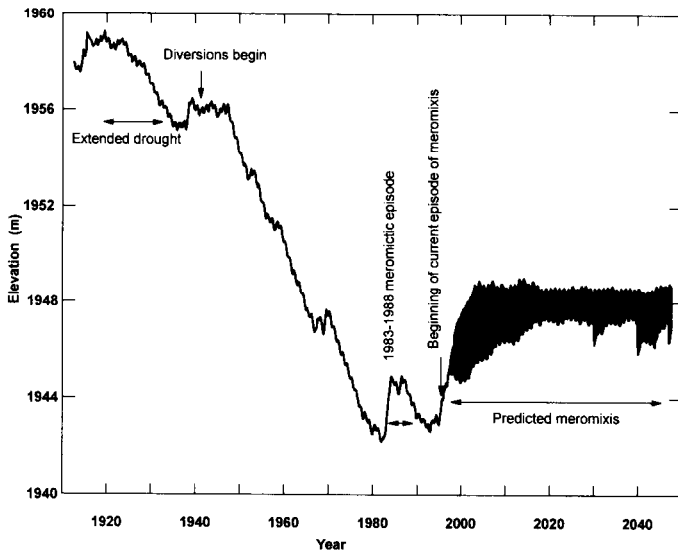


Fig. 1. Historical (1911–1997) and predicted (1997–2047) surface elevation of Mono Lake. The range of predicted surface elevation is from DYRESM simulations using 50-yr historical runoff sequences.

temperature and conductivity profiles taken during a previous episode of meromixis, 1983–1990 (Fig. 2). The constant  $b$  was set to  $-1$  and the multiplicative constant  $a$  was estimated to be 21. The uncertainty in the new parameterization was assessed by determining the entire range of the multiplicative constant ( $a = 17$ – $23$ ) over which the simulations

predicted the termination of meromixis during the appropriate winter (i.e. between September 1988 and March 1989). Second, the dissipation of turbulent kinetic energy was assumed to be constant below the pycnocline, whereas Romero and Melack (1996) assumed exponential decay with distance below the pycnocline. In addition to the 1980s episode of meromixis, this new parameterization also accurately simulated 1995–1996, the first 2 years of the current episode of meromixis.

Following validation, long-term simulations were conducted over the range of the new model parameterization by using historical freshwater inflow sequences, meteorological measurements collected on Paoha Island in the center of the lake from 1991 through 1996, and an initial salinity and temperature profile determined in the field on 4 July 1997 (Fig. 3). The persistence of meromixis is highly dependent on the actual sequence of wet and dry years, and thus a probability distribution for the duration of the current episode of meromixis was derived by performing simulations beginning with each of the 50 years of the historical runoff sequence. For instance, if the starting year was 1953, the runoff input to the model would consist of the 50-yr sequence 1953–1990, 1940–1952. Thus, 50 separate simulations were conducted for  $a$  values of 17, 21, and 23. This procedure eliminates the bias that would result from using a single historical sequence while preserving the various periodicities in the historical runoff data. Because there was a significant correlation between annual wind energy from our 6-yr meteorological dataset and runoff, the yearly meteorological data were randomly chosen from the 6-yr dataset

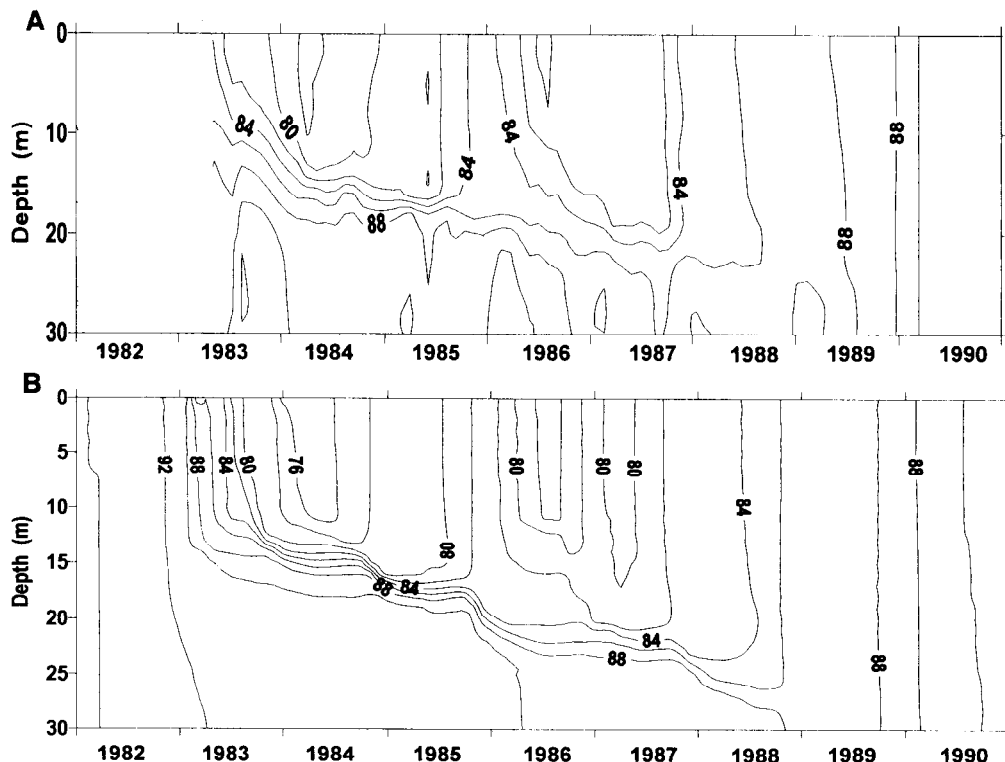


Fig. 2. Observed salinity ( $\text{g kg}^{-1}$ ) profiles during the mid-1980s episode of meromixis (A) vs. those predicted during validation by the vertical mixing model DYRESM (B).

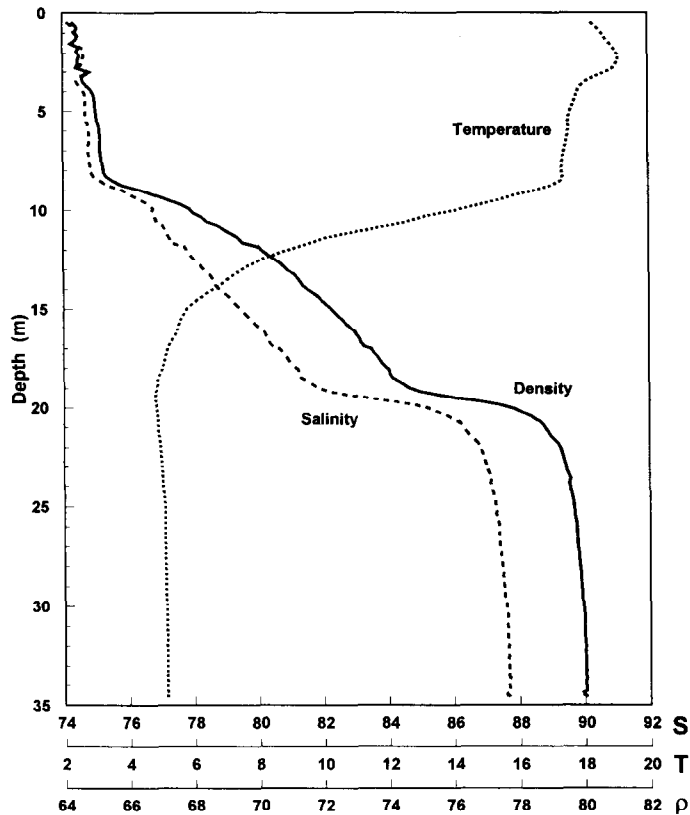


Fig. 3. Vertical profiles of salinity ( $S$ ,  $\text{g kg}^{-1}$ ), temperature ( $T$ ,  $^{\circ}\text{C}$ ), and density ( $\rho$ ,  $\text{kg m}^{-3} - 1,000$ ) collected on 4 July 1997 and used as initial conditions for long-term simulations.

based on whether runoff was low (1991, 1992), medium (1993, 1994), or high (1995, 1996).

Simulations predict that the current management policy of rapidly raising the lake level by restricting diversions is likely to result in a multidecade period of meromixis at Mono Lake (Fig. 4). The median estimate of the duration of the current episode of meromixis ranges from 44 to 63 years due to uncertainty in the eddy diffusivity parameter coefficient (Table 1). However, the predicted duration is highly dependent on the starting year of the runoff sequence. With  $a$  of 21, starting with the high runoff observed in 1982 leads to a predicted duration of 62 years, while beginning with the drought conditions observed in 1987 predicts the breakdown of meromixis after 17 years.

The median prediction of the duration of meromixis using the best estimate of the eddy diffusivity parameter coefficient ( $a = 21$ ) began with the 1974 historical runoff. In this simulation the annual maximum depth of the mixed layer or mixolimnion, as defined by the first depth at which the density gradient exceeds  $0.25 \text{ kg m}^{-4}$ , increases during the first 4 years of the simulation but then decreases during a period of rising lake level (Fig. 5). The mixolimnion then gradually increases over several decades until meromixis is terminated in the year 2045. During July 1997, the depth of the top of the monimolimnion, defined as the depth from the bottom at which the density gradient exceeds  $0.25 \text{ kg m}^{-4}$ , was 24 m above the bottom. The top of the monimolimnion de-

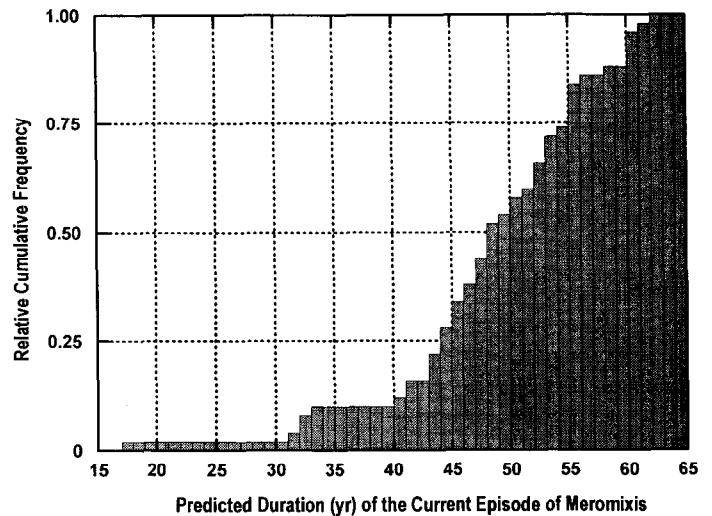


Fig. 4. Cumulative frequency distribution of the predicted number of years until the breakdown of the current episode of meromixis based on 50 different historical sequences of runoff and the DYRESM eddy diffusivity parameter coefficient,  $a$ , equal to 21 (see text).

scended during the first 11 years of the simulation to within 18 m of the bottom, after which it changed more slowly for several decades before descending prior to the breakdown of meromixis.

The onset and predicted persistence of meromixis represents a fundamental change in the annual mixing regime of Mono Lake, with potential long-term consequences for plankton. In the absence of winter mixing, nutrients that accumulate during the summer beneath the thermocline are not recycled into the euphotic zone as would normally occur during monomictic conditions. Following the low stand in 1982, a 6-yr period of meromixis was initiated by exceptionally high runoff (172% in 1982 and 193% in 1983) and reduced diversions. After the onset of meromixis, primary production dropped from an estimated  $700 \text{ g C m}^{-2} \text{ yr}^{-1}$  from mid-1982 to mid-1983 (1982–1983) to  $250 \text{ g C m}^{-2} \text{ yr}^{-1}$  during 1983–1984 and  $350 \text{ g C m}^{-2} \text{ yr}^{-1}$  during 1984–1985 (Jellison and Melack 1993a). However, resumption of diversions and an extended period of drought eventually led to the termination of meromixis in late 1988. Primary production increased in 1987–1988 as meromixis weakened, and was highest ( $900 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) in 1988–1989 when

Table 1. Predicted duration of current episode of meromixis and sensitivity of the prediction to uncertainty in a parameter coefficient ( $a$ ) of the eddy diffusivity formulation in vertical mixing model, DYRESM (see text). Fifty simulations using 50-yr historical runoff sequences were used for each value of  $a$ .

Eddy diffusivity parameter coefficient	Predicted duration of current meromixis (yr)		
	Min.	Median	Max.
$a = 17$ ; minimum reasonable value	37	63	73
$a = 21$ ; best fit value	17	49	62
$a = 23$ ; maximum reasonable value	17	44	57

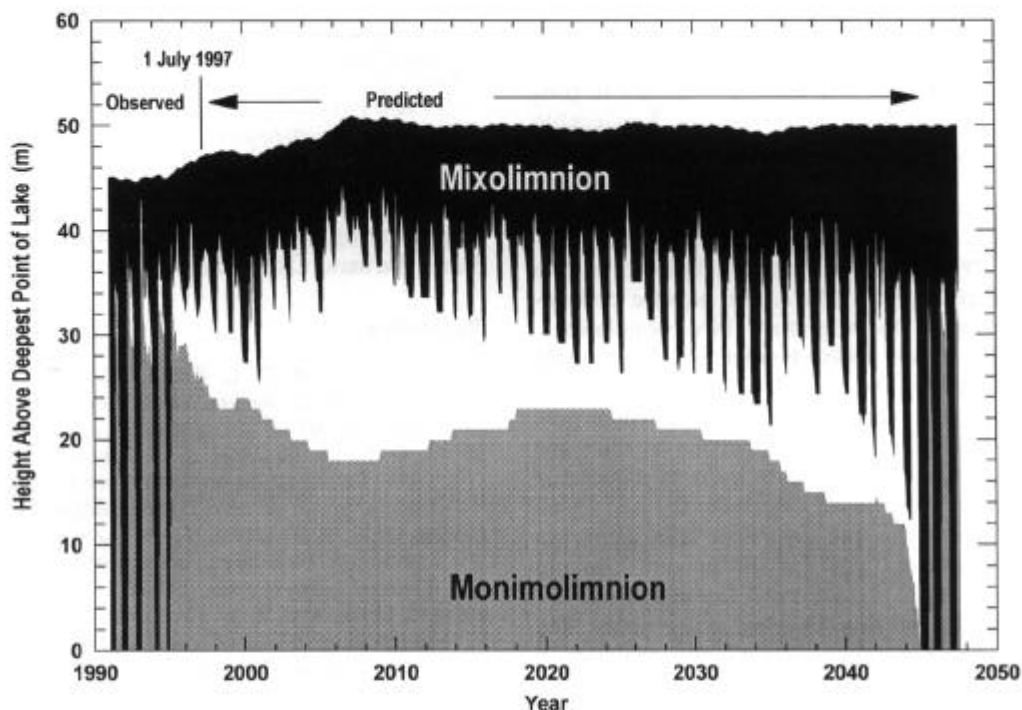


Fig. 5. Vertical extent of monimolimnion and mixolimnion for the simulation in which meromixis ended after 37 years, the median value of 50 simulations with  $a$  equal to 21. Vertical scale is distance above the lowest point of the basin (1,898 m). Simulation begins with data from the 1972 runoff year. Gray region between mixolimnion and monimolimnion indicates region of strong salinity stratification.

meromixis broke down and nutrients that had accumulated for 6 years beneath the chemocline were injected into the euphotic zone.

In addition to altering the internal recycling of nutrients, several other changes accompany meromixis. The water column beneath the chemocline becomes permanently anoxic, and methane and dissolved sulfide accumulate (Miller et al. 1993). The existence of permanent oxy- and chemoclines creates new habitats for various bacterial populations, which are likely to further reduce the upward flux of nutrients and shift productivity away from algal photosynthesis. Conditions at the sediment-water interface are also changed, with the higher salinity likely to increase losses of nitrogen due to burial (Jellison et al. 1996). *Artemia* cysts, which only hatch under oxygenated conditions, are also permanently buried.

Although periods of meromixis may have occurred at previously higher lake levels, both their frequency and duration are expected to have been less. From February (the annual water temperature minimum) 1993 to February 1994, the net rise in surface elevation of Mono Lake of 0.4 m was less than required to initiate meromixis. The larger increase of 1.0 m from February 1995 to February 1996 initiated the current episode of meromixis. Although interactions among freshwater inflows, wind, insolation, and air temperatures affect the details of stratification, this indicates that the annual surface elevation increment required to initiate meromixis is between 0.4 and 1.0 m. As the lake expands and salinity decreases, the annual surface elevation increment required

to initiate meromixis will become larger. Also, as the lake volume increases, surface elevation fluctuations become smaller as the incremental volume associated with a unit surface elevation change increases.

Other than the recent 1983–1988 and current episode of meromixis, there are only two prior instances in the 20th century in which meromixis could have been initiated. These are following exceptionally high runoff in 1938 (runoff not recorded) and 1969 (173%) when the surface elevation rose 1.0 and 0.7 m, respectively. Because the lake water was less saline during both of these periods, meromixis, although possible, was probably not initiated. If meromixis did result, it would have lasted for only a year as both events were followed by declining lake levels.

Accurate estimates of annual fluctuations in surface elevation during the 19th century are not available. However, based on a variety of geomorphological and other techniques, Stine (1990) calculated an average annual rise of  $0.17 \text{ m yr}^{-1}$  over the 22-yr period from 1889 to 1911. Because the lake was significantly less saline during this period and the largest annual rise was estimated to be 0.9 m, meromixis was unlikely to have occurred.

Under natural conditions when the lake is near its equilibrium size for a given climatic water balance, periods of meromixis are likely to be brief as normal climatic variation will invariably result in alternating periods of rising and declining lake levels. Also, the chemical stratification established at the onset of meromixis will typically be less than that observed in the 1983–1988 and current episode when

the lake was highly saline (90–100 g liter<sup>-1</sup>) and far from equilibrium. In contrast, the current management policy of raising the lake level by limiting diversions is likely to prolong the current episode of meromixis into the foreseeable future and thus change many limnological aspects of Mono Lake.

The decision to restrict diversions and raise the surface elevation of Mono Lake was based on a number of considerations, including air quality, gull nesting habitat, stream fisheries, scenic and recreation values, and aquatic productivity and its importance to migratory bird populations. Many studies (Herbst et al. 1988; Herbst and Castenholz 1994; Jellison et al. 1993a; Dana et al. 1993; Melack et al. 1985) suggest that the lake was more productive under previously less saline conditions, and the decision to raise the lake was, in part, an attempt to mitigate impacts associated with increasing salinity. The chosen target elevation of 1,948 m, which is well below the pre-diversion lake elevation (~1,954 m) and equilibrium size for the current climatic water balance (Vorster 1985), represents a compromise between public trust values and Los Angeles' water rights. The onset of meromixis immediately following the decision in the state resulted from the combined effects of no diversions and high runoff. While the full impacts of prolonged meromixis on the Mono Lake ecosystem are not known, basic characteristics of the lake are changed and declines in aquatic productivity are predicted. Given these facts and the observation that the lake level can be raised at least 0.4 m per year as observed in 1993 without initiating meromixis, a more conservative course of action would have been to restrict diversions based on surface elevation and predicted runoff.

Resumption of moderate diversions could be implemented to hasten the breakdown of meromixis should monitoring reveal significant adverse impacts of extended meromixis. Given a diversion rate of about half the previous unrestricted rate ( $49 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$ ), the median estimate for the duration of meromixis would be decreased by 29 years. The surface elevation at which meromixis ended in these high-diversion simulations was 1,946.5 m, or 1.5 m below the target elevation. Following termination of the current episode of meromixis, resumption of the current diversion restrictions would easily allow the lake level to rise to the target elevation of 1,948 m. Based on the historical record, the likelihood of another high runoff year capable of initiating meromixis is low and becomes even less likely as the lake level rises. However, the impacts of resumed diversions on active stream restoration efforts would have to be considered.

In many cases the restoration of ecosystems requires a better understanding of the functioning of natural ecosystems than is currently available. In the case of Mono Lake, the negative impacts of raising the lake level over the next several decades were deemed minimal by the SWRCB of California in 1994 (decision 1631). However, the onset of long-term meromixis represents a fundamental change in the mixing regime of this productive ecosystem with largely unknown consequences. Although large variations in runoff are natural and short periods of meromixis may have occurred in the past, the prediction of a multidecade period of mer-

omixis is largely a function of the expected continually rising lake levels accompanying restrictions on diversions.

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### References

- COOPER, J. J., AND D. L. KOCH. 1984. Limnology of a desertic terminal lake, Walker Lake, Nevada, U.S.A. *Hydrobiologia* **118**: 275–292.
- DANA, G. L., R. JELLISON, J. M. MELACK, AND G. L. STARRETT. 1993. Relationships between *Artemia monica* life history characteristics and salinity. *Hydrobiologia* **263**: 129–143.
- GALAT, D. L., E. L. LIDER, S. VIGG, AND S. R. ROBERTSON. 1981. Limnology of a large, deep, North American terminal lake, Pyramid Lake, Nevada, U.S.A. *Hydrobiologia* **82**: 281–317.
- HERBST, D. B., AND R. W. CASTENHOLZ. 1994. Growth of the filamentous green alga *Ctenocladus circinnatus* (Chaetophorales, Chlorophyceae) in relation to environmental salinity. *J. Phycol.* **30**: 588–593.
- , F. P. CONTE, AND V. J. BROOKES. 1988. Osmoregulation in an alkaline salt lake insect, *Ephydra (Hydropyrus) hians* Say (Diptera: Ephydriidae) in relation to water chemistry. *J. Insect Physiol.* **34**: 903–909.
- IMBERGER, J., AND J. C. PATTERSON. 1981. A dynamic reservoir simulation model: DYRESM 5, p. 310–361. In H. B. Fischer [ed.], *Transport models for inland and coastal waters*. Academic.
- JELLISON, R., R. F. ANDERSON, J. M. MELACK, AND D. HEIL. 1996. Organic matter accumulation in sediments of hypersaline Mono Lake during a period of changing salinity. *Limnol. Oceanogr.* **41**: 1539–1544.
- , AND J. M. MELACK. 1993a. Algal photosynthetic activity and its response to meromixis in hypersaline Mono Lake, California. *Limnol. Oceanogr.* **38**: 818–837.
- , AND J. M. MELACK. 1993b. Meromixis in hypersaline Mono Lake, California. 1. Vertical mixing and density stratification during the onset, persistence, and breakdown of meromixis. *Limnol. Oceanogr.* **38**: 1008–1019.
- , ———, AND G. L. DANA. 1993a. A modeling analysis of *Artemia* dynamics in Mono Lake. (Mono Basin EIR auxiliary report No. 13.) Report to the California State Water Resources Control Board, Sacramento.
- , L. G. MILLER, J. M. MELACK, AND G. L. DANA. 1993b. Meromixis in hypersaline Mono Lake, California. 2. Nitrogen fluxes. *Limnol. Oceanogr.* **38**: 1020–1039.
- MELACK, J. M., S. D. COOPER, AND P. H. LENZ. 1985. The ecology of Mono Lake, California. *Nat. Geographic Soc. Res. Rep. 1979 Projects*, p. 461–470.
- MILLER, L. G., R. JELLISON, R. S. OREMLAND, AND C. W. CULBERTSON. 1993. Meromixis in hypersaline Mono Lake, Cali-

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- fornia. 3. Breakdown of stratification and biogeochemical response to overturn. *Limnol. Oceanogr.* **38**: 1040–1051.
- PATTEN, D. T., AND OTHERS. 1987. The Mono Basin ecosystem: Effects of changing lake level. National Academy Press.
- ROMERO, J., AND J. M. MELACK. 1996. Sensitivity of vertical mixing in a large saline lake to variations in runoff. *Limnol. Oceanogr.* **41**: 955–965.
- STINE, S. 1990. Late holocene fluctuations of Mono Lake, eastern California. *Palaeogeog. Palaeoclimatol. Palaeoecol.* **78**: 333–381.
- VORSTER, P. 1985. A water balance forecast model for Mono Lake, California. Earth resources monograph. Forest Service Region 5, USDA.
- WILLIAMS, W. D. 1993. The worldwide occurrence and limnological significance of falling water-levels in large, permanent saline lakes. *Verh. Internat. Verein. Limnol.* **25**: 980–983.

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## Selective predation by the mosshead sculpin *Clinocottus globiceps* on the sea anemone *Anthopleura elegantissima* and its two algal symbionts

**Abstract**—The mosshead sculpin *Clinocottus globiceps* (Girard, 1857) feeds on the sea anemone *Anthopleura elegantissima* that contains two different algal endosymbionts, zooxanthellae and zoochlorellae. During laboratory feeding experiments, the sculpin selectively fed on the tentacles of zooxanthellate anemones over those of zoochlorellate and algae-free anemones. Zoochlorellae passed through the fish gut unharmed while zooxanthellae were degraded. The productivity of zooxanthellae in the fish feces ( $0.20 \pm 0.13 \text{ pg C cell}^{-1} \text{ h}^{-1}$ ) was significantly lower (93% less) than that of zooxanthellae freshly isolated from anemones ( $3.14 \pm 0.52 \text{ pg C cell}^{-1} \text{ h}^{-1}$ ), whereas the productivity of fecal zoochlorellae was the same as that of freshly isolated zoochlorellae ( $1.21 \pm 0.15 \text{ pg C cell}^{-1} \text{ h}^{-1}$ ). The chlorophyll content (Chl *a* and *c*) of zooxanthellae was reduced by 50% after passage through the fish gut while the chlorophyll content of zoochlorellae (Chl *a* and *b*) did not change. Selective predation on zooxanthellate anemones confers several ecological advantages to zoochlorellate anemones and to zoochlorellae, most notably predator avoidance and dispersal of viable zoochlorellae that may serve as a source of symbionts for other anemones. By influencing the outcome of predator–prey interactions involving their hosts, symbiotic algae may have broader ecological roles in benthic communities than previously described.

The sea anemone *Anthopleura elegantissima* is an ecologically important member of the rocky intertidal community, occurring on the North American Pacific Coast from Alaska to Baja California, Mexico (Hand 1955). Photosynthesis by zooxanthellae (*Symbiodinium californium*) in this anemone contributes substantially to primary production of the rocky intertidal zone in southern California (Fitt et al. 1982). Besides dinophyte zooxanthellae, anemones in the northern part of the anemone's range harbor green chlorophyte algae known generally as zoochlorellae (Muscatine 1971; O'Brien 1978). Zooxanthellae and zoochlorellae symbionts occur in both *A. elegantissima* and its congener *A. xanthogrammica* (O'Brien 1978). Anemones that harbor mostly zoochlorellae are green, anemones with mostly zooxanthellae are brown, and anemones that lack algae are white (algae-free or non-

symbiotic). All three types, as well as mixed anemones containing both zooxanthellae and zoochlorellae, are found in the vicinity of one another in the Puget Sound region (pers. obs.).

The primary role ascribed to symbiotic algae is provision of photosynthetic carbon to the animal host (Muscatine 1990). Carbon budgets derived for zooxanthellate and zoochlorellate *A. elegantissima* during summer months suggest that zooxanthellae are able to provide substantially more carbon to their anemone host than are zoochlorellae (Verde and McCloskey 1996). The presence of zoochlorellae in addition to zooxanthellae in anemones is puzzling if the only function of the algal partner is to provide photosynthetic carbon to the animal. Algal symbionts may have other roles in the symbiosis, especially in temperate regions, where anemone hosts may not rely on carbon provided by their symbiotic algae (Davy et al. 1997). *A. elegantissima* is an active carnivore that feeds on plankton and small invertebrates (Sebens 1981). The presence of two distinct algae in one host anemone allowed us to explore the possibility of multiple roles for symbiotic algae.

In this study we determined that symbiosis with one or the other alga affects the outcome of predation on the host anemone. A variety of fishes and invertebrates, including the mosshead sculpin *Clinocottus globiceps* (Hand 1996; Yoshiyama et al. 1996b), the nudibranch *Aeolidia papillosa* (Waters 1973; McFarland and Muller-Parker 1993), and the leather star *Dermasterias imbricata* (Sebens 1977) consume both *A. elegantissima* and *A. xanthogrammica*. We consider whether the presence of one symbiotic alga or the other provides an associational defense (sensu Hay 1992) for the animal host. Associational defenses, where a palatable partner is protected by its association with an unpalatable species, have been described for seaweed–herbivore interactions (Hay 1992; Wahl and Hay 1995). If predation on the anemone host is influenced by its algal endosymbiont complement, the benefit of associating with the deterrent algal species will be significant when grazing pressure is high.

We used intertidal/tidepool *C. globiceps*, which has the