Bull. Southern California Acad. Sci.
90(2), 1991, pp. 41–57

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Salinity Thresholds, Lake Size, and History: A Critique of the NAS and CORI Reports on Mono Lake

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Abstract.—These two reports usefully summarize and evaluate large amounts of information. They both suffer from and perpetuate, however, a deficient conceptual framework for analyzing changes in the Mono Lake ecosystem. Specifically, their assessments of the present and future state of this lake 1) use language implying that salinity-induced changes in the biota will begin to occur only at certain critical salinity thresholds, 2) neglect the significance of lake size as a determinant of bird food supplies, and 3) lack historical perspective in failing to consider what changes in the lake ecosystem may have been caused by historical changes in the salinity and size of the lake. The desirability of developing explicit models for the system is emphasized. Especially needed are models for: 1) the influence of salinity and lake size on the abundance of brine flies and brine shrimp, and 2) the influence of the abundance of these invertebrates on the bird populations that use the lake. To illustrate the heuristic value of such models, Rawson's models relating productivity and standing crop to lake mean depth are applied to Mono Lake. The results suggest some unusual consequnces of the lake's particular morphometry, especially for lake level changes between 6370 ft and 6380 ft.

In the last few years, two major reports on Mono Lake have been published. *The Mono Basin Ecosystem* (Patten et al. 1987) was prepared at the request of the U.S. Congress by a committee appointed by the National Research Council. It was published by the National Academy of Sciences in the summer of 1987 and will be referred to hereafter simply as the NAS report. The committee's mandate was to inventory and describe the Mono Lake ecosystem, its hydrology and its populations, to review historic changes in the system, to determine "the critical water level needed to support current wildlife populations," and to predict how the system would respond to continued diversions of water from the basin.

The Future of Mono Lake (Botkin et al. 1988) was prepared at the request of the California State Legislature by a committee assembled by the Community and Organization Research Institute (CORI) at the University of California, Santa Barbara. It was published in the spring of 1988 by the University of California Water Resources Center and is referred to hereafter as the CORI report. This committee's primary mandate was to "evaluate the effects of declining lake levels, increasing salinity and other limnological changes of Mono Lake upon" the various populations living in and near the lake, including human populations.

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The two studies overlapped greatly in their objectives, utilized mostly the same sources of information, and not unexpectedly have some similarities. They represent reasonable summaries of existing information and opinion on Mono Lake, and in that regard are useful. No other recent synthetic treatments on the ecology of Mono Lake exist.

Both reports, however, are based on and present to the reader deficient conceptual frameworks. The principal deficiencies are three and all relate to the central issue of how water diversions from the Mono Lake basin affect the organisms that live in or on Mono Lake.

First, in discussing salinity effects, both reports use language and graphical presentations that imply *thresholds*. They suggest that changes in the biota will begin to occur at certain critical salinity levels rather than occur continuously with salinity change. The latter is more likely to be the case.

Second, the importance of *lake size* is largely ignored. Obviously this will be a major factor in determining, for example, the total amount of food available to waterbird populations.

Third, the reports give a very incomplete framework for viewing *historical changes* in the Mono Lake ecosystem. Since biological data on the lake prior to the mid 1970s are very few, concrete conclusions about the past status of Mono Lake populations are not to be expected. But the reports do not even mention, for example, the likelihood that changes in the size and salinity of Mono Lake since 1941 have had effects on the lake's biota.

By neglecting the above, the NAS and CORI reports failed to provide a clear and coherent conceptual framework for management decisions, for legal decisions, and for the planning of future scientific research. The reports are less useful than they might have been and, especially for nonscientists, can be misleading.

Let me now document the above charges and in doing so suggest a broader conceptual framework for analyzing some of the anticipated effects of water diversions on the Mono Lake biota.

Certain issues will not be addressed here, such as nesting of the California Gull, substrate relations of brineflies, stream incision, tufa towers, and alkali dust problems. The focus will be on the trophic relationships among Mono Lake populations.

The benighted state of certain professions in the United States has resulted in use of the English system of measurement in most of the documents on Mono Lake. I follow this custom in my text. In my tables, however, I present values for lake dimensions in both English and metric units and values for productivity and standing crop only in metric units.

Salinity Thresholds?

There is every reason to believe that, both individually and collectively, the scientists preparing these reports were aware that the abundances or productivities of populations can be expected to change continuously as salinity is gradually increased over any given range. Changes that begin to occur only at particular salinity thresholds simply neither have been documented experimentally for any species nor are to be expected on physiological grounds. Sure, there will always be a point where a slight further increase in salinity from S_1 to S_2 will cause extinction of a population (Fig. 1A, species X_3). But under salinity S_1 the abundance or productivity of the population usually would already have been much lower than under optimal salinity conditions (e.g., a salinity $\ll S_1$). In the context of conservation, the battle has already been lost if salinities have increased to close to the extinction level for the species for which protection is sought. It is the other end of the curve that should occupy our attention. What kind of reduction in abundance is acceptable or tolerable? 0%? 5%? 10%? 20%? 40%? And at what increased salinity level will such a reduction be observed?

Regardless of the committees' understanding of the above points, the language of their reports fails to convey that understanding to the reader. Threshold salinity values are stated for every species or group.

Beyond those threshold values, effects are variously said to be "significant," "critical," "very slight," "severe," etc. In no case are the meanings of those terms defined either in terms of the magnitude of the expected effect, its importance to the rest of the ecosystem, or its societal acceptability. And below those threshold values, the usual implication is that salinity variations are without effect.

Here are some examples from the NAS report:

1. "[algal] productivity is likely to decrease gradually at salinities above about 100 g/l . . ." (p. 4).
2. "Brine shrimp are expected to gradually decrease in abundance if salinities exceed 120 g/l . . . reduction . . . would be large at salinities greater than 130 g/l . . ." (pp. 4–5).
3. "The decrease in availability of brine shrimp for food would begin to affect those birds relying on them . . . at a salinity of 120 g/l . . ." (p. 5).
4. "salinities above 133 g/l significantly depress [brine shrimp survival and growth]" (p. 89).
5. "algae . . . [and] brine shrimp and brine fly populations flourish [at salinities of] <50–89 g/l" (pp. 188–189).
6. "At salinities around 120 g/l, [the algae, brine shrimp, and brine fly] populations . . . would begin to show negative responses . . ." (p. 206).

And some examples from the CORI report:

7. "food for grebes and phalaropes declines significantly [at salinities >120 g/l]" (p. 9).
8. "Algal food supply for brine fly declines rapidly [at salinities >130 g/l]" (p. 10).
9. "a decline in status of lake ecosystem begins to occur . . . where salinity reaches a value of 97 g/l . . . the growth of brine shrimp and brine flies, and the abundance of certain algae, begins to decline" (p. 12; but see p. 10 where such decline is predicted to occur "before this").
10. "brine shrimp reproduction begins to decline at a salinity of 120 g/l" (p. 24).

Figure 1 contrasts the types of salinity effects models implicit in the NAS and CORI reports with the types of models that would be expected on the basis of physiological and ecological principles. Experimental data are not available, either for Mono Lake species or for other saline lake species, for rigorous empirical tests of which type of model most closely approximates reality. One would need *precise* estimates of population size (or productivity) at each of *many* salinities over a *wide* salinity range.

A further implication of the reports is that the threshold salinities are all higher than any salinities that have been experienced by the lake during historic times (quotes 1–10, above). Everything has "flourished" up to now or at least up to 89 g/l (quote 5). Salinity effects, if they are to occur at all, lie in the future. Such a notion is biologically indefensible. Every population in the lake surely has been affected by the rise in salinity from 51 g/l in 1941 to the 87–98 g/l experienced during the 1980s. Naturally we have little direct evidence as to what those effects have been.

The notion of "plateau and threshold" response curves and the notion that the thresholds all lie at higher than current salinities may subtly convey another idea to readers of the NAS and CORI reports: the idea that if, with increasing salinity, we are indeed approaching the edge of a "plateau," we should proceed extremely cautiously. Such a view suggests that we should consider with alarm the prospect of even small, temporary further increases in salinity, for the edge of the plateau may be a "cliff" (species X_1) or an extremely steep "slope" (species X_3, Fig. 1). The past may give no hint of the future. The levelness of the plateau behind us, the historical "flourishing" of the system, may be deceptive and provide no warning of the imminence of the "crash" of a population or of the whole system. And the crash may be irreversible.

Such an argument is perfectly sound on naive theoretical grounds. It is also the most rational and societally responsible position to take when little is known about system behavior or when some of the anticipated negative consequnces indeed seem likely to be irreversible.

I would argue, however, that we know enough about the Mono Lake ecosystem, about other alkaline saline lakes, and about the responses of organisms in general to salinity to be confident that such alarm is unwarranted. Population response curves such as those for species X_1 and X_3 in Fig. 1A are unknown in the biological literature. There is no reason to think that increasing salinity by, say, 10 percent over current levels would by itself cause large or irreversible changes to any Mono Lake population.

Two caveats should be offered here. I am saying that a small, temporary change is not cause for alarm; but I am not saying that a small, permanent change is necessarily societally acceptable. Also, as stated earlier, I am not discussing effects directly attributable to changes in water level, e.g., peninsularization of Negit Island, rather than to salinity *per se*.

Though the "plateau and threshold" models are implied by most of the language in the reports, one doubts that any of the biologist authors of those reports intended to advocate such models or their corollaries. All those authors most likely would agree that "smooth curve" models (Fig. 1B) are more realistic and that small (e.g., 10 percent) salinity increases are unlikely to cause population or system "crashes" of any sort. I infer this from a few rare and very general statements such as "Responses of various resources to changes in lake level will, for the most part, occur gradually over a range of levels" (NAS report, p. 7), though such statements neither refer explicitly to salinity effects nor exclude "plateau and threshold" models such as that for species X_2 (Fig. 1A).

If my suppositions are correct, the discrepancies between report language and

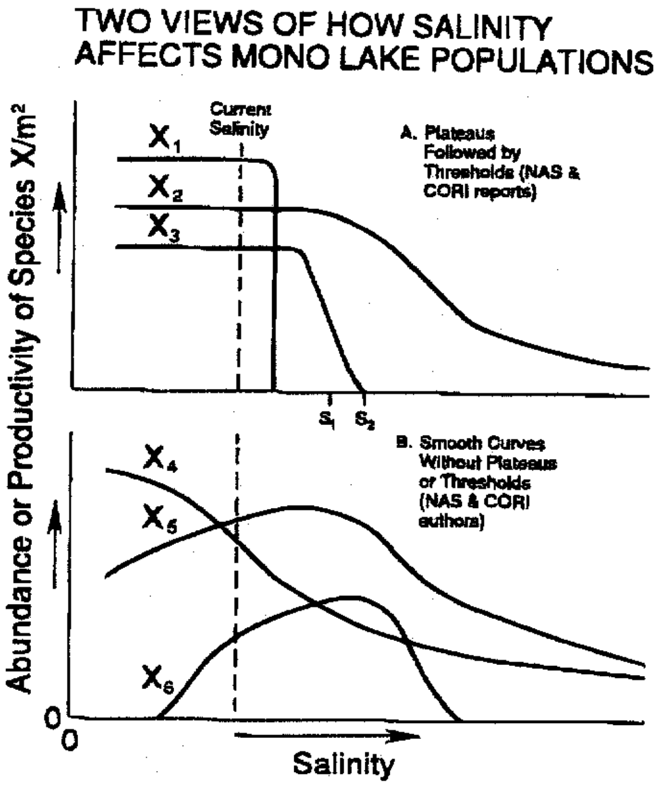

Fig. 1. Comparison of (A) the types of salinity effect models implicit in the NAS and CORI reports, and (B) those expected on the basis of physiological and ecological principles.

author opinion probably arose from failure to define terms (e.g., what is "significant" or "severe" or "critical?") and the lack of explicit models for salinity effects on populations.

Some scientists may also argue that it was desirable to use the "threshold" terminology in the NAS and CORI reports so as to make them intelligible to lawyers, engineers, managers, politicians, and other non-scientists. The notion is without merit. Both lawyers and engineers have told me that, at least on good days, they are capable of understanding the concept of gradual, continuous change. They also have stated that if biologists, for example, state or imply that the pattern of expected biological change is likely to follow a "plateau and threshold" model, then that is exactly what they will assume represents the best collective biological judgment on the matter, in the absence of clear arguments to the contrary.

Among academics this matter might be considered only a minor one of semantics. In the larger politico-legal context of the Mono Lake controversies, however, the details on language can be very consequential. There is no better evidence of this than the "Memorandum of points" that accompanied the National Audubon Society's (1989) recent successful petition for a writ of injunction against the Los Angeles Department of Water and Power. Among the first statements that the court found in that well-crafted document are:

> "we are *now* [my emphasis] faced with the imminent and irreversible injury to Mono Lake [p. 1] . . . the lake is poised on the *threshold* [my emphasis] of substantial and irreversible environmental damage [p. 7]."

Whether or not Audubon's attorneys actually believed this "threshold" scenario is irrelevant. The fact remains that they were able to cite the CORI and NAS reports in support of it, and that became a factor influencing the judge's decision in their favor.

Lake Size

Lake size is a major determinant of the abundance of aquatic organisims in Mono Lake or any other lake. Yet, with one minor exception, its importance in this regard was largely neglected by both the NAS and CORI reports.

In the CORI report, not only is the importance overlooked, data on lake size are omitted completely. Not a single datum for the area of Mono Lake, past, present, or future, is presented in its text, table or figures. Figure 1 in the report gives a map showing the lake's 1987 shoreline and a second, higher shoreline which is unlabeled.

The NAS report gives adequate information on lake area in its Figs. 3.1 and 6.2. Slight confusion is introduced by Fig. 6.1, however, which shows, in 4 separate maps, the shoreline and size of the lake at elevations of 6340, 6360, 6380, and 6400 ft. This figure is visually deceptive. It gives the impression of a smaller decline in lake area with decrease in lake elevation than would actually be the case. Two elements produce the illusion: as the lake shrinks in dropping from 6400 ft to 6340 ft (1) the width of the shaded band around the lake remains approximately constant in width, the outer edge of the band being whittled away as the inner edge follows the receding shoreline, and (2) the scale bar representing 30,000 ft gradually increases in length by about 18 percent. The latter causes the decrease in lake area between 6400 ft and 6340 ft to *appear* to be about 27 percent when in fact the actual decrease would be about 48 percent.

The importance of lake area derives from the simple fact that the amount of solar radiation received by the lake ecosystem is directly proportional to that area. Total solar radiation received, in turn, should be a major determinant of the total primary and secondary production that takes place in the lake. Specifically, as lake area decreases the total amount of brineflies and brine shrimp potentially available to the grebes, phalaropes, gulls, and other waterbirds at Mono Lake should be expected to decrease, even if the concomitant increase in salinity has no effect.

Whether the numbers of these birds that feed at Mono Lake is currently limited by these food supplies is a complex and unanswered question (see below). But surely our main concern should be for the *numbers* of birds that utilize the lake and not their *densities,* i.e., not the numbers per unit area. The aesthetic and ecological value of Mono Lake should be a function of, *inter alia,* the numbers of birds it supports. Also, for any given species, the number of individuals that utilize the lake is a measure of the extent to which the lake contributes to the survival and health of that species as a whole. If the lake were to decrease in area by 50 percent, there would be strong cause for concern even if the density (number/km^2) of birds on the lake remained unchanged.

It is not clear that the same argument is valid for the algal and invertebrate populations. A 50 percent decrease in total phytoplankters or total brine shrimp numbers might be of little concern, so long as it had no effect on the numbers of birds that utilized the lake.

The relationship between lake area and total lakewide productivity of Mono Lake's populations is complicated by another relationship, that between productivity and depth. Among lakes, productivity per unit area is widely considered to increase with decreasing mean depth at least in part because of increased nutrient fluxes between sediments and the euphotic zone. Unfortunately the exact nature of the depth-productivity relationship has never been determined for any set of lakes in a way that separates the effects of depth from those of all the lake morphometric and hydrologic parameters that tend to covary with mean depth.

A Modelling Approach

Rawson (1952, 1955) developed a simple, tentative approach to this problem that may be usefully applied to Mono Lake. It entails using mean depth as a general index of lake morphometry and size determining the mathematical relationships between mean depth and various measure of productivity *per unit* area. (I use 'productivity' here in a broad sense to include standing crop as well as productivity *sensu strictu*). The products of lake area and these productivities then give whole lake productivity estimates that reflect both the positive relationship between lake area and total insolation and the negative relationship between lake depth and nutrient cycling rates. Calculation of these whole lake estimates is actually an extension of Rawson's approach. It assumes that productivity per unit area is independent of lake area when mean depth is held constant.

Using data from 11–20 lakes in western and central Canada (that ranged from 11 m to 249 m in mean depth), Rawson used regression analysis to deduce the following three relationships:

$$\mathrm{FP/U} = 14.71\,(\mathrm{D}^{-0.7029}) + 0.56 = \text{fish production (kg/ha/y)} \qquad \text{Eq. 1}$$

$$\mathrm{PS/U} = 3765\,(\mathrm{D}^{-1.5337}) + 8.0 = \text{plankton standing crop (kg/ha)} \qquad \text{Eq. 2}$$

and

$$\mathrm{BS/U} = 69.2\,(\mathrm{D} - 5)^{-0.788} = \text{benthos standing crop (kg/ha)} \qquad \text{Eq. 3}$$

where D = mean depth (m).

I have used the first two of these to calculate the expected "fish" production and plankton standing crop for Mono Lake at different elevations between 6330 ft and 6430 ft. Results are expressed on both a per unit area basis and a lakewide basis in Tables 1 and 2 and Figure 2. The salinity, lake area, and mean depth corresponding to each elevation are also given, as tabulations of the values for these variables neither were presented in the NAS and CORI reports nor are available elsewhere in the open scientific literature.

Of course there are no fish in Mono Lake, but perhaps the production of (or consuption by) their trophic counterpart, the invertebrate-eating waterbirds, is a rough analogue. And of course we do not know how reliable these particular expressions are as predictors of even the relative, let alone the absolute, degrees

Table 1. Variation of the surface area, mean depth and salinity of Mono Lake as a function of the elevation of its surface. Data from tables and models in LADWP (1986, 1987). Predicted salinity values assume no net loss of salts via precipitation or other processes.

Elevation		Surface area		Mean depth		Predicted salinity		Observed salinity
(ft)	(m)	(sq. mi.)	(sq. km)	(ft)	(m)	(g/l)	(g/kg)	(g/l)
6428	1959.3	89.7	232.2	86.1	26.2	42.4	41.0	
6427	1958.9	89.3	231.2	85.6	26.1	42.9	41.5	
6426	1958.6	88.9	230.2	84.8	25.9	43.4	42.0	
6425	1958.3	88.5	229.1	84.3	25.7	43.9	42.4	
6424	1958.0	88.0	227.8	83.7	25.5	44.4	42.9	
6423	1957.7	87.7	227.1	83.0	25.3	45.0	43.4	
6422	1957.4	87.4	226.3	82.2	25.1	45.6	44.0	
6421	1957.1	87.1	225.5	81.7	24.9	46.1	44.5	
6420	1956.8	86.7	224.5	80.9	24.7	46.7	45.0	47.0
6419	1956.5	86.3	223.4	80.4	24.5	47.3	45.5	
6418	1956.2	86.1	222.9	79.5	24.2	47.9	46.1	
6417	1955.9	85.8	222.1	78.7	24.0	48.5	46.6	51.3
6416	1955.6	85.6	221.6	77.9	23.8	49.0	47.1	
6415	1955.3	85.2	220.6	77.4	23.6	49.7	47.8	
6414	1955.0	84.8	219.5	76.7	23.4	50.3	48.4	54.0
6413	1954.7	84.6	219.0	75.8	23.1	51.0	49.0	
6412	1954.4	84.4	218.5	75.0	22.9	51.7	49.6	
6411	1954.1	84.1	217.7	74.5	22.7	52.4	50.3	56.3
6410	1953.8	83.7	216.7	73.6	22.4	53.0	50.9	
6409	1953.5	83.3	215.7	73.1	22.3	53.9	51.6	
6408	1953.2	83.0	214.9	72.2	22.0	54.6	52.3	
6407	1952.9	82.7	214.1	71.5	21.8	55.4	53.0	58.1
6406	1952.5	82.4	213.3	70.8	21.6	56.1	53.6	58.6
6405	1952.2	82.0	212.3	70.2	21.4	56.9	54.4	
6404	1951.9	81.6	211.3	69.5	21.2	57.8	55.2	
6403	1951.6	81.2	210.2	68.9	21.0	58.6	56.0	60.2
6402	1951.3	80.9	209.5	68.0	20.7	59.4	56.7	
6401	1951.0	80.6	208.7	67.2	20.5	60.4	57.6	
6400	1950.7	80.0	207.1	66.8	20.4	61.2	58.3	
6399	1950.4	79.5	205.8	66.3	20.2	62.2	59.2	
6398	1950.1	79.1	204.8	65.6	20.0	63.3	60.2	
6397	1949.8	78.8	204.0	64.9	19.8	64.1	61.0	
6396	1949.5	78.4	203.0	64.1	19.6	65.3	62.0	
6395	1949.2	77.9	201.7	63.6	19.4	66.1	62.8	
6394	1948.9	77.3	200.1	63.0	19.2	66.9	63.5	
6393	1948.6	76.9	199.2	62.4	19.0	68.3	64.7	
6392	1948.3	76.5	198.1	61.7	18.8	69.3	65.6	
6391	1948.0	76.1	197.0	61.0	18.6	70.5	66.7	
6390	1947.7	75.5	195.5	60.5	18.4	71.5	67.6	
6389	1947.4	74.8	193.7	60.0	18.3	72.9	68.8	
6388	1947.1	74.4	192.6	59.4	18.1	73.9	69.7	
6387	1946.8	74.0	191.6	58.7	17.9	75.4	71.1	
6386	1946.5	73.5	190.3	58.1	17.7	76.5	72.0	
6385	1946.1	72.6	188.0	57.7	17.6	78.0	73.4	
6384	1945.8	71.4	184.9	57.8	17.6	79.6	74.9	
6383	1945.5	70.9	183.6	57.1	17.4	80.8	75.8	
6382	1945.2	70.4	182.3	56.6	17.2	82.1	77.0	
6381	1944.9	69.8	180.7	56.1	17.1	83.7	78.4	
6380	1944.6	68.7	177.9	55.9	17.1	85.2	79.7	89.3
6379	1944.3	66.8	172.9	56.4	17.2	86.7	81.0	

Table 1. Continued.

Elevation		Surface area		Mean depth		Predicted salinity		Observed salinity
(ft)	(m)	(sq. mi.)	(sq. km)	(ft)	(m)	(g/l)	(g/kg)	(g/l)
6378	1944.0	66.2	171.4	56.0	17.1	88.8	82.9	86.8
6377	1943.7	65.6	169.8	55.8	17.0	89.9	83.8	91.6
6376	1943.4	64.8	167.8	55.3	16.8	90.8	84.5	89.3
6375	1943.1	63.3	163.9	55.5	16.9	92.7	86.3	93.4
6374	1942.8	61.1	158.2	56.5	17.2	94.7	87.9	
6373	1942.5	59.3	153.5	57.1	17.4	96.5	89.5	97.7
6372	1942.2	57.0	147.6	58.5	17.8	98.2	91.0	99.4
6371	1941.9	56.4	146.0	58.1	17.7	99.9	92.4	
6370	1941.6	55.7	144.2	57.9	17.6	101.5	93.8	
6369	1941.3	54.9	142.1	57.7	17.6	103.3	95.4	
6368	1941.0	54.1	140.1	57.5	17.5	104.9	96.7	
6367	1940.7	53.6	138.8	57.1	17.4	107.0	98.5	
6366	1940.4	53.1	137.5	56.6	17.3	109.7	100.8	
6365	1940.1	52.6	136.2	56.1	17.1	110.9	101.8	
6364	1939.7	52.1	134.9	55.7	17.0	113.0	103.5	
6363	1939.4	51.7	133.9	55.1	16.8	114.9	105.2	
6362	1939.1	51.2	132.6	54.6	16.7	116.5	106.4	
6361	1938.8	50.7	131.3	54.1	16.5	119.2	108.7	
6360	1938.5	50.2	130.0	53.7	16.4	121.3	110.5	
6359	1938.2	49.7	128.7	53.1	16.2	123.7	112.5	
6358	1937.9	49.3	127.6	52.7	16.1	126.3	114.6	
6357	1937.6	48.9	126.6	52.2	15.9	128.5	116.4	
6356	1937.3	48.5	125.6	51.5	15.7	131.3	118.7	
6355	1937.0	48.1	124.5	50.8	15.5	133.6	120.6	
6354	1936.7	47.8	123.8	50.3	15.3	136.2	122.7	
6353	1936.4	47.4	122.7	49.9	15.2	139.0	125.0	
6352	1936.1	47.0	121.7	49.1	15.0	142.8	128.0	
6351	1935.8	46.5	120.4	48.5	14.8	144.8	129.6	
6350	1935.5	46.2	119.6	47.9	14.6	147.7	132.0	
6349	1935.2	45.8	118.6	47.4	14.3	151.0	134.6	
6348	1934.9	45.4	117.5	46.8	14.3	154.2	137.2	
6347	1934.6	45.0	116.5	46.2	14.1	157.5	139.8	
6346	1934.3	44.5	115.2	45.7	13.9	160.6	142.1	
6345	1934.0	44.1	114.2	45.3	13.8	164.6	145.3	
6344	1933.7	43.6	112.9	44.6	13.6	168.0	147.9	
6343	1933.3	43.1	111.6	44.3	13.5	172.1	151.1	
6342	1933.0	42.6	110.3	43.6	13.3	175.8	153.9	
6341	1932.7	42.1	109.0	43.3	13.2	180.1	157.3	
6340	1932.4	41.7	108.0	42.6	13.0	184.8	160.9	
6339	1932.1	41.2	106.7	42.0	12.8	188.8	163.9	
6338	1931.8	40.8	105.6	41.5	12.6	193.7	167.6	
6337	1931.5	40.3	104.3	41.0	12.5	198.2	170.9	
6336	1931.2	39.9	103.3	40.4	12.3	203.2	174.6	
6335	1930.9	39.4	102.0	39.9	12.2	208.0	178.1	
6334	1930.6	39.0	101.0	39.3	12.0	213.5	182.2	
6333	1930.3	38.6	99.9	38.7	11.8	219.1	186.2	
6332	1930.0	38.2	98.9	38.1	11.6	225.0	190.3	

Table 2. Variation of the predicted "Fish" production and plankton standing crop of Mono Lake as a function of the elevation of its surface.

Elevation (ft)	"Fish" production FP/U (kg/ha/y)	"Fish" production FP/L (1000 kg/lake/y)	Plankton standing crop PS/U (kg/ha)	Plankton standing crop PS/L (1000 kg/lake)
6428	2.04	47.4	33.1	769
6426	2.06	47.3	33.7	775
6424	2.07	47.2	34.2	779
6422	2.09	47.2	34.9	790
6420	2.11	47.3	35.6	799
6418	2.13	47.4	36.4	810
6416	2.15	47.6	37.2	825
6414	2.17	47.5	38.0	834
6412	2.19	47.9	39.0	852
6410	2.21	47.9	39.9	864
6408	2.23	48.0	40.8	877
6406	2.26	48.2	41.9	893
6404	2.28	48.2	42.9	906
6402	2.31	48.3	44.0	921
6400	2.33	48.2	45.0	932
6398	2.35	48.2	46.1	944
6396	2.38	48.3	47.4	962
6394	2.40	48.1	48.5	970
6392	2.43	48.1	49.8	987
6390	2.46	48.0	51.1	999
6388	2.48	47.8	52.3	1008
6386	2.51	47.8	53.9	1025
6384	2.52	46.6	54.2	1003
6382	2.55	46.4	55.7	1016
6380	2.56	45.6	56.6	1006
6378	2.56	43.9	56.4	967
6376	2.58	43.3	57.5	965
6374	2.55	40.3	55.8	883
6372	2.50	36.9	53.3	787
6370	2.52	36.3	54.1	781
6368	2.52	35.4	54.5	764
6366	2.55	35.0	55.7	766
6364	2.57	34.7	56.9	768
6362	2.60	34.4	58.4	774
6360	2.62	34.1	59.7	776
6358	2.65	33.8	61.3	782
6356	2.68	33.7	63.1	792
6354	2.72	33.7	65.2	807
6352	2.76	33.5	67.3	819
6350	2.79	33.4	69.6	832
6348	2.83	33.3	71.9	846
6346	2.87	33.1	74.3	855
6344	2.91	32.8	76.7	866
6342	2.95	32.5	79.1	872
6340	2.99	32.3	81.9	884
6338	3.03	32.0	84.8	896
6336	3.08	31.8	88.0	909
6334	3.13	31.6	91.5	923
6332	3.18	31.5	95.5	944

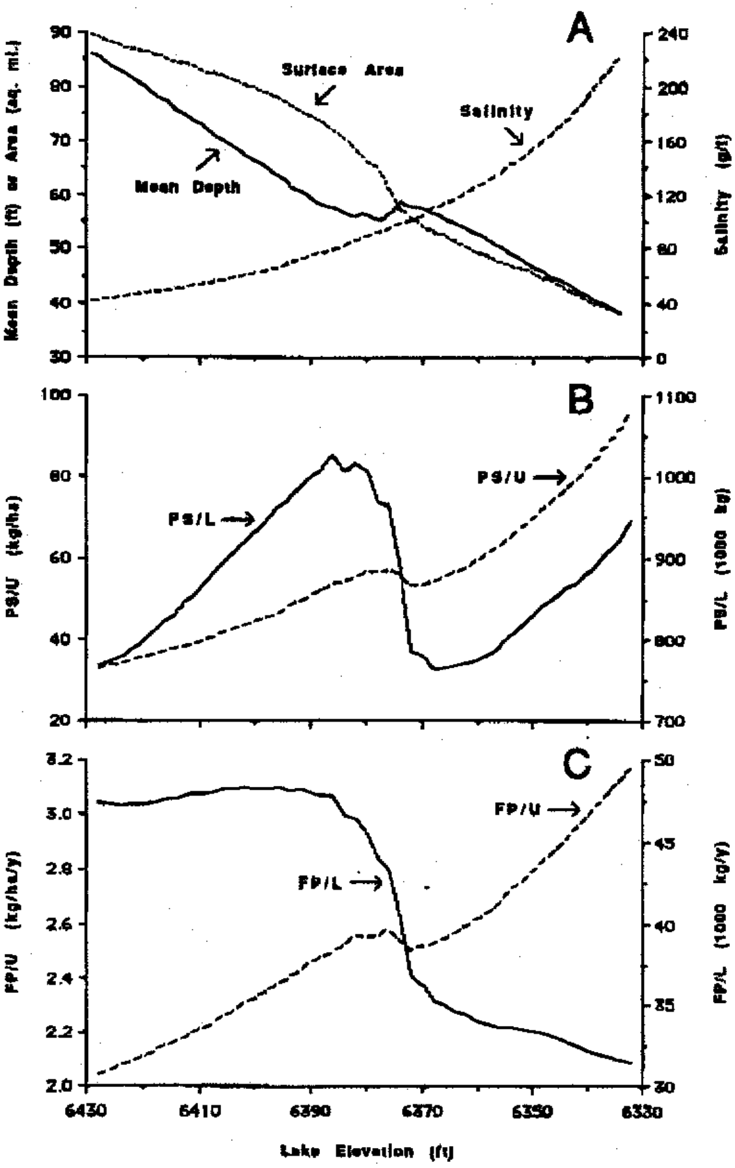

Fig. 2. Predicted variation of various properties of Mono Lake as a function of the elevation of its surface. PS/U = plankton standing crop per unit area; PS/L = plankton standing crop for entire lake; FP/U = fish production per unit area; FP/L = fish production for entire lake.

of change to be predicted for a change in Mono Lake's level. Nevertheless these results at least define a neglected issue in terms of a concrete example.

Analysis of the Predictions of the Models

The predicted variations of plankton standing crop and fish productin are complex and quite different from each other. They illustrate well the potential influence of lake morphometry. They illustrate how the relative importance of lake area

(A) vs. lake mean depth (D) is a function of the power to which D is raised and thus can be very different for different biological variables.

Both FP/U and PS/U generally are predicted to increase as lake level drops (Figs. 2B, C). The general trend is reversed, however, when lake level drops from 6376 to 6372. That drop brings about declines of 3 percent for FP/U and of 7 percent for PS/U.

These 'bumps' in the curves are produced by a corresponding 'bump' in the curve relating mean depth to lake elevation (Fig. 2A). When lake elevation drops from 6376 ft to 6372 ft, lake maximum depth naturally decreases by 4 ft but lake mean depth *increases* by 3.2 ft (Table 1)! The apparent anomaly is due to the broad wave-cut platform, the Scholl terrace, that exists between roughly 6385 and 6370 ft around at least 75 percent of the lake's margin (Scholl et al. 1967; Pelagos 1987; Stine 1991). The lower boundary of this terrace is the so-called nick-point at 6368 ft. As the lake retreats across the gently sloped central portion of the terrace, lake volume decreases more slowly than does lake area and so mean depth increases.

Predicted values for total lake fish production (FP/L) and total lake plankton standing crop (PS/L) were obtained by multiplying FP/U and PS/U values by the corresponding values for lake area (A). The FP/L and PS/L curves are similar in some repects and dissimilar in others (Fig. 2)

Both FP/L and PS/L actually increase, PS/L quite substantially, as lake level drops from 6438 ft (its historic high stand, attained in 1919; Stine 1991) to about 6406 ft (FP/L) or 6386 ft (PS/L). For both variables the negative influence of declining lake area is more than offset by the positive influence of declining mean depth, over this range of lake elevations.

Then, starting at elevations around 6380 ft to 6384 ft, both FP/L and PS/L begin to decline rapidly with further declines in lake level. At 6380–6384 ft, lake level reaches the upper margin of the Scholl terrace, where the rate of decline in lake area per 1 ft drop in elevation begins to increase. The rates of decline of FP/L and PS/L are greatest as lake level drops from 6376 to 6372 ft and the negative influences of decreasing lake area and increasing mean depth reinforce each other.

The major differences between the FP/L and PS/L curves reflect the empirical fact that, at least among Rawson's (1952, 1955) Canadian lakes, FP/U is less strongly a function of mean depth than is PS/U. FP/U varies linearly with $D^{-0.7}$ and PS/U linearly with $D^{-1.5}$ (Eqs. 1, 2). Thus as lake level drops from 6428 to 6332 ft and mean depth decreases by 56 percent, FP/U increases only 56 percent while PS/U increases by 189 percent.

As lake level drops below 6370 ft, PS/L begins to increase again, the strongly positive effect of increasing shallowness overwhelming the negative effect of decreasing lake area (Fig. 2B). FP/L, on the other hand, continues to decline as elevation drops below 6370 ft, the influence of area dominating that of depth.

Despite the hypothetical nature of these calculations (Figs. 2B, C), I believe they provide insight into how the general productivity of Mono Lake, including the availability of invertebrate food for bird populations, may respond to changes in the depth and area of the lake. If depth or morphometry influences productivity at Mono Lake in a manner at all similar to that implied by Rawson's regression equations, the following conclusions are likely to hold for Mono Lake:

1) Over certain elevation ranges, a decrease in lake area will cause an increase in total lake productivity (TP/L);
2) TP/L may have increased for many years as water diversions caused lake level to drop from its 1940 pre-diversion elevation of 6416 ft;
3) With a particular change in lake level one index or component of TP/L may decrease (e.g., FP/L) while another may increase (e.g., PS/L);
4) TP/L will decline abruptly as lake level drops from 6380 to 6370 feet. A decline of 19 percent is expected solely from the 19 percent decrease in lake area; the 3.4 percent increase in mean depth and 19 percent increase in salinity both will increase the magnitude of this decline.
5) Salinity effects will depress the lefthand portions of the curves in Figs. 2B, C. Certainly no curve representing total invertebrate abundance or productivity will have a rising righthand limb.

These conclusions should be robust. They derive primarily from the particular morphometry of Mono Lake, and not from the specific form or coefficients of Rawson's equations. Many other functions representing a negative relationship between productivity per unit area and mean depth would yield the same conclusions.

Area and Brineflies

Though neither of the reports discusses the general importance of decrease in lake area, both did give specific attention to how the amount of hard, mostly tufaceous substrate in the littoral zone may decrease very abruptly when lake level drops from 6380 ft to 6370 ft. This hard substrate is strongly preferred by brine fly larvae and pupae over soft substrates. In the NAS report the expected reduction is repeatedly stated to be one of 40 percent (pp. 5, 189, 207), though the report's own Table 6.5 (p. 190) shows that the expected reduction would actually be either 61 percent or 57 percent, depending on whether the littoral zone is considered to extend to a depth of 10 ft or 30 ft. In any case, the magnitude of this decrease is more a consequence of the shallow water location of most of the lake's hard substrates than of the 19 percent decrease in lake area as it drops from 6380 ft to 6370 ft.

Need for a Reference Lake Level

A general and important question is, 'For any given past or future change in lake level, how do the salinity effects and lake size (area-depth) effects compare?' A great deal of attention is given in the NAS and CORI reports to defining at what salinity levels various negative impacts will "begin to occur." By the time such salinities are reached, however, marked reductions in the lakewide productivity or abundance of particular populations already may have occurred as a result of reduction in lake area. Naturally such assessments will depend on what lake level is taken as the baseline condition. This is another matter not explicitly addressed by the NAS and CORI reports, so a few comments on it may be appropriate.

The selection of a reference lake level must be partially arbitrary, but can also be partially objective. At least two lake elevations—6417 ft and 6376 ft—might usefully be selected to define reference conditions. The former is the approximate mean lake elevation (June values) for the decade prior to the initiation of water diversions from the Mono Lake basin. We have, of course, no biological data for the lake during that decade. The second elevation, 6376 ft, is the approximate mean lake elevation for the decade (1977–1986, June values) prior to the establishment of the NAS and CORI panels. The charge to the NAS panel, and perhaps implicitly to the CORI panel, was to assess the consequences of lake level changes for "current wildlife populations" (NAS report, p. vii). Given the high year-to-year variability of Mono Lake populations and the unusual meromictic state of the lake at the time of the NAS and CORI panel deliberations, it seems reasonable to take as a reference point the mean lake level during the decade when large amounts of ecological data began to be collected at the lake. Arguments could also be advanced for using whatever lake level was just sufficient to keep coyotes off Negit Island. In any case it should be apparent that *the magnitude of effects of lowered lake cannot be estimated until a reference lake level is specified and a 'baseline state' of the lake ecosystem defined.*

Historical Perspective

Both the NAS and CORI reports provide inadequate analysis of the historical changes in the salinity and size of Mono Lake and their possible effects on the ecosystem. Very complete historical records of these variables were available to the committees. Their failure to give them more explicit consideration may explain why the possible effects of *future* changes in lake size were ignored and why the possible effects of *future* changes in salinity tended to be discussed in "plateau and threshold" terminology.

Both reports present graphs showing the full historical record for lake elevation, but neither report does this for salinity or lake size. For most populations at the lake, however, salinity and lake size will be the more important direct determinants of abundance. Lake elevation itself is of significance primarily as a determinant of size and salinity.

It was implicit in a NAS report (pp. vii–viii) that future changes, observed or projected, in Mono Lake populations were to be judged against the "current" status of those populations. However, the mandate to the NAS panel also called for consideration of "historic . . . populations levels . . . of all terrestrial and acquatic species" (NAS report, p. vii). Moreover, even if the sole objective were to estimate the future trajectory of the Mono Lake ecosystem, would not the best foundation for that exercise be an analysis of the historic trajectory of the ecosystem? In no way does the lack of validated models or the paucity of biological information for the system prior to the mid-1970's reduce the need for explicit consideration of how past changes in salinity and lake are may have altered the Mono Lake ecosystem.

Birds and Their Food Supplies

A few further comments on this topic are warranted as it is a central one. From the viewpoint of conservation, an understanding of the factors influencing the productivities of algal and invertebrate populations is valuable primarily in allowing prediction of the food supply available to the birds using Mono Lake. We must then be able to understand how the bird populations would respond to

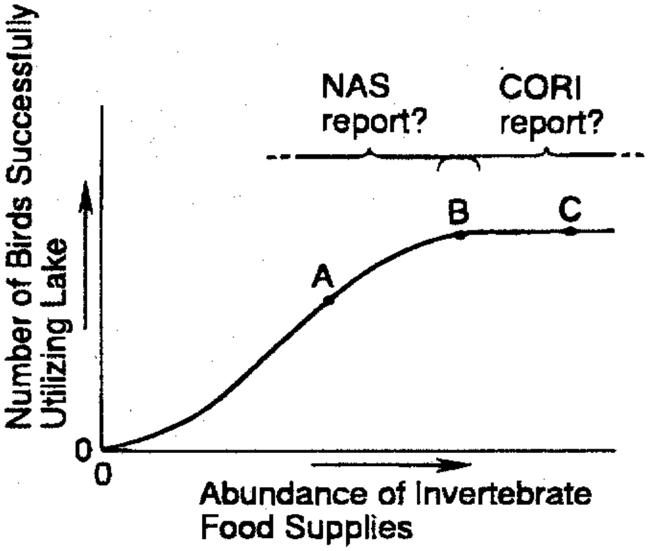

Fig. 3. A model of the relationship between invertebrate-eating birds and their food supply at Mono Lake. Points A, B, and C represent three possibilities for the present status of the system, as implied by the NAS and CORI reports.

changes in this food supply. And on that point somewhat uncertain but divergent conclusions seem to be reached by the two reports.

If brine shrimp and brine fly abundances were to decrease below a certain threshold, the birds that depend on them for food would be affected. Various effects can be imagined: reduced residence time at Mono Lake and movement to other lakes; reduced weight gain and survival on the lake; increased mortality following departure from Mono Lake, and so on. As J. Wiens points out in the CORI report (Appendix B), primarily in reference to the Eared grebe: "Unfortunately, we have no firm indication of the level of this threshold for Mono Lake bird populations with respect to either brine shrimp or brinefly abundances. It seems likely that, during recent years, summer and early fall shrimp and fly populations have been superabundant to the birds." The NAS report (p. 5), on the other hand, concludes that "If the lake fell to levels at which the birds' food sources were adversely affected, the bird populations would be reduced." In other words we are at or below the threshold now—*any* "adverse effect, *any* reduction in shrimp or fly abundance will have negative effects on the bird populatons." "At" seems the intended idea. At least there is no intimation in the NAS report that more grebes and phalaropes, for example, would visit the lake if invertebrate densities were higher or the lake larger.

Both reports neglect, as indicated earlier, the role of lake size in determining total prey abundance and instead concern themselves only with the effects of salinity and, in the case of the brine flies, substrate availability. Discussion of bird energetics and physiology appropriately focuses on prey densities which in turn relate to per unit area productivity, but clearly for a given initial prey density a large lake can support birds in greater numbers and/or for a longer period of time than can a small lake. This is especially germane given the opinion of some (Cooper et al. 1985) that grebe predation contributes to the autumnal decline of the brine shrimp population.

A threshold model for bird number-food supply relationships is depicted in Fig. 3, together with an indication of the differing viewpoints of the NAS and CORI reports. Note that a population at point B is consistent with the language of both reports. If the current status of a population at Mono Lake is accurately represented by point B or C, then the numbers that use Mono Lake are limited by some factor other than Mono Lake food supplies—such as habitat or nest site availability on the breeding range, for example. If the current status of the population is represented by point A, then food availability is indicated to be the prime factor limiting numbers of brids that use the lake. If there was a sustained increase in invertebrate productivity, we would expect eventually to see more birds using the lake.

Both reports failed to consider seriously that the current status of some Mono Lake bird populations might be represented by point A in Fig. 3. The omission was perhaps a consequence of the panels' failure to use explicit models or to wonder how bird food supplies might have been affected by the post-1940 25 percent decrease in lake area and 80 percent increase in salinity.

I am arguing neither that point A *does* represent the status of any particular species nor that the model in Fig. 3 *is* the most appropriate one, but only that those were and are important questions meriting deliberate consideration.

Conclusion

The criticisms offered here of the NAS and CORI reports have been put forward in an attempt to provide a broader perspective for the analysis of some aspects of the Mono Lake ecosystem. Discussions of the ecological, conservation, and water management issues will be clearer, more fruitful, and more appropriately focused if two things are done. First, all discussion of effects of changing lake levels should involve explicit models, even if these initially are only in the form of graphs with unscaled axes (e.g., Figs. 1 and 3). Such models are particularly needed 1) for expressing the presumed effects of salinity and lake size on the densities and sizes of invertebrate populations, and 2) for expressing the presumed effects of the invertebrate food supply on the number, behavior, and physiological state of certain bird species at Mono Lake. Second, explicit consideration should be given to how historical changes in salinity and lake area may have affected invertebrate and bird populations, even if, as is almost certain, firm conclusions cannot be reached on the topic.

Acknowledgments

My understanding of the Mono Lake ecosystem has benefitted from discussions with many scientists who have worked at the lake, including especially T. Bradley, G. Dana, D. Herbst, J. Jehl, and J. Melack. Many of these discussions have taken place under the auspices of the Los Angeles Department of Water and Power and benefitted from the participation of LADWP's scientists, engineers, and lawyers. Calculation of the data in Table 1 was carried out by Randall Neudeck of LADWP. N. Sjaarda and J. Ferrara prepared the figures. T. Hammer, D. Herbst, J. Jehl, P. Richerson, and two anonymous reviewers are thanked for their comments on the manuscript.

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Accepted for publication 24 July 1990.