Hydrobiologia **267**: 191–201, 1993.
S. H. Hurlbert (ed.), Saline Lakes V.

A population model for the alkali fly at Mono Lake: depth distribution and changing habitat availability

David B. Herbst & Timothy J. Bradley
Sierra Nevada Aquatic Research Laboratory, University of California, Star Route 1, Box 198, Mammoth Lakes, CA 93546, USA; Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717, USA

Key words: habitat conservation, *Ephydra hians*, Mono Lake, population model, saline lakes, tufa

Abstract

The densities of alkali fly larvae and pupae were measured in relation to depth and substrate type at six locations around Mono Lake. Samples representing a mixture of different bottom features were taken to a depth of 10 m (33 ft) using SCUBA. This is at or near the depth limit of fly larvae and pupae. The biomass of larvae and pupae on hard substrate were maximum and approximately equal at depths of 0.5 m and 1 m, substantially lower at intermediate depths of 3 m and 5 m, and over an order of magnitude further reduced at 10 m. Densities of flies on hard or rocky substrates (mainly calcareous tufa deposits), were significantly greater than those found on soft substrates such as mud or sand, at all but the greatest depth surveyed.

Bathymetric maps of the areas of hard and soft substrate occurring at different lake depths were used to estimate the fly population size over the whole lake, based on the density distribution of larvae and pupae with depth on different substrates. The mapped areas of soft and hard substrates were also calculated for different lake levels, and applying the same procedure, a population model comparing the abundance of flies at different lake levels was developed. This habitat-based population model predicts that the abundance of the alkali fly is maximized at 6380 ft (1945 m) lake surface elevation. Most of the tufa substrate submerged at this lake level will become exposed and unavailable as habitat as the lake declines to 6370 ft (1942 m). In late 1991, the lake level was just over 6374 ft (1943 + m).

Introduction

In the eastern Sierra Nevada of California, streams have been diverted from the Mono Lake Basin for 50 years. While these streams provide water and power to the city of Los Angeles, the deficit in freshwater supply to saline Mono Lake is lowering the level and increasing the salt concentration of this productive wildlife habitat. One of the ecological impacts originating from dropping lake level is exposure of littoral habitat that supports production of one of the major food organisms of the lake, the alkali fly *Ephydra hians* Say (National Academy of Sciences, 1987; Botkin *et al.*, 1988). This insect is a dietary staple for the many migratory shorebirds that use Mono Lake as a feeding and breeding site.

The objective of this research was to provide a predictive population model of the extent to which declining lake levels will alter the abundance of the alkali fly as its habitat becomes exposed. The model is based on surveys of the distribution of the aquatic larval and pupal stages of the fly on different bottom surface features over varied depths. It uses this information to provide a prediction of how the abundance of the alkali fly would change over a range of projected lake levels. The range of lake levels providing maximum habitat for flies could thus be identified.

Benthic aquatic organisms are often found associated with specific substrate types. Rocky and soft bottom environments have distinctive faunal assemblages, and these physical substrates circumscribe the habitats to which the epifauna or infauna are usually restricted. Since the substrate inhabited often serves as the template on which development and production occur, habitat area may be used to define distribution and abundance. Examples of methods that employ habitat-based estimates of population size or standing stock among aquatic invertebrates include habitat-stratified sampling (Elliot, 1977; Wrona *et al.*, 1986) and instream flow models (Gore, 1978; Gore & Judy, 1981). These methods have been used to predict population density based on usable physical habitat available. The present study follows this approach in modeling the lakewide population size of a benthic insect based on samples stratified by depth and substrate type.

Larvae and pupae of the alkali fly (*Ephydra hians* Say) are aquatic. Larvae hatch from eggs and develop through three instars before pupating. When mature, larvae attach to submerged, stable substrate, and form pupae. Adults emerge from the pupal case and float to the water surface in an air bubble. Adult flies (mainly females) re-enter the water by crawling down partly submerged rocks to feed on algal films and deposit eggs. Algae forms most of the diet for both larvae and adults.

Previous studies (Herbst, 1990; Little *et al.*, 1989, unpublished) established that tufa rock is the primary substrate on which larvae and pupae are found. This reef-like limestone has a complex surface, providing protected microhabitats and attachment sites for larvae and pupae. Since these earlier studies were restricted to shallow water sampling (0.5 m or less), it was not known to what depth larvae and pupae could occur, or whether tufa was still the predominant substrate used in deep water.

Other research on the alkali fly has established that larvae osmoregulate (Herbst *et al.*, 1988), using an unusual modification of the Malpighian tubule to regulate carbonate (Herbst & Bradley, 1989). Though osmotic and ionic regulation permit salt tolerance, these physiological adaptations are not without cost. Salinities above 10 g l^{-1} slow growth and development and reduce body size at maturity (Herbst, 1992), and those above 150 g l^{-1} are lethal to early instars.

Methods

Sampling locations and procedures

Six locations around the lake, representing a mixture of different bottom features, were sampled to a depth of 10 meters (about 33 feet) using SCUBA (Fig. 1). This depth was determined to be at or very near the limit of fly larvae and pupae – below this, the thermocline is typically established and the water quickly becomes prohibitively cold and dark. Some 20 dives and a total of 40–50 hours of submerged sampling and observation time were logged. The diving began in early August and was completed in mid-October. There were 358 total samples taken: 210 on mixed hard substrates, including tufa, pumice and mineral-encrusted rock and wood; and 148 on soft substrates, including mixed mud, sand and detritus. Sites varied in the amount and type of substrate present and sampled (Table 1). Based on previous, more widespread surveys of the lake (Herbst, 1990), the six stations selected for this study were located in areas including the greatest range of alkali fly standing crop densities and substrate-habitat types.

Sampling was conducted along five depth contours at each location sampled – 10 m, 5 m, 3 m, 1 m, and 0.5 m (15 m was also examined initially but no larvae or pupae could be found and as this depth was usually below the thermocline, sampling was discontinued here). During the sampling period, depth of the thermocline varied be-

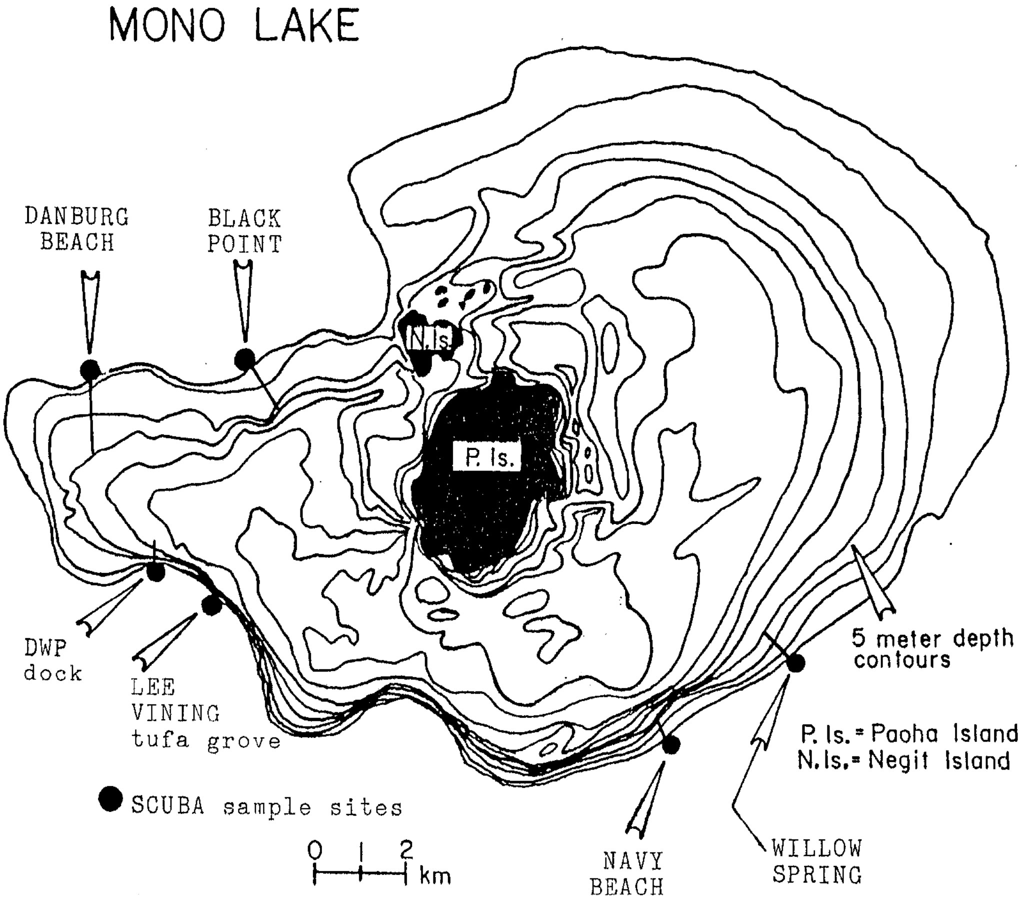

Fig. 1. Map of Mono Lake bathymetric contours and SCUBA sample sites and depth transects. Willow Springs and Navy Beach sites are predominantly sand and mud, Lee Vining tufa grove and Black Point tufa shoals both have high tufa cover over sand and mud, DWP dock and Danburg Beach possess mixed substrates with substantial encrusting tufa and gaylussite.

tween 12 and 20 m, and water temperature varied from 20 to 13.5 °C. The sampling procedure consisted of descending to the sample depth and searching for substrates of appropriate nature (conforming to size and consistency criteria), which were removed as encountered along a compass-guided course parallel to shore while swimming at a constant depth. Depth was maintained by the tension of a surface float line tied around the divers wrist. Hard substrates were

Table 1. Distribution of samples by depth and station site (hard substrate/soft substrate). Each sample represents an individual rock or core removal.

Depth (m)	DWP dock	Lee Vining tufa grove	Danburg Beach	Navy Beach	Willow Spring	Black Point	No. sites (N_{sd})	No. samples ($\Sigma_j N_{jsd}$)
0.5	15/5	10/0	10/0	0/8	0/8	8/8	4/4	43/29
1.0	20/0	10/0	10/0	0/8	0/8	8/8	4/3	48/24
3.0	19/0	10/0	6/10	0/8	0/5	10/8	4/4	45/31
5.0	14/0	20/0	3/8	0/8	5/9	4/8	5/4	46/35
10.0	15/0	10/0	0/8	0/7	0/8	0/8	2/4	25/31

any loose rock of 5–25 cm diameter, sampled by wrapping the substrate with fine mesh netting and enclosing the sample in a sealable plastic bag. For soft substrates, a coring tube (8 cm diameter) was pushed into undisturbed sediment, capped and withdrawn and the intact core put into a plastic storage bag. For sediments that were not cohesive enough to permit this, the substrate within the emplaced coring tube was removed with a large suction pipet into fine mesh bags. Successive cores were taken at least 5 meters apart to avoid diver-disturbed areas.

Samples were processed by placing sediments or rock substrates in buckets of saturated salt solution, separating larvae and pupae by flotation. The low density organisms float to the surface where they can be skimmed and collected, while the substrate material sinks to the bottom. Following flotation, rock substrates were also submerged in hot tap water to drive any remaining larvae from crevices. The surface area of hard substrates was determined in two ways: (1) by outlining the projected upper surface onto a grid (2 dimensional cover area) and (2) by wrapping the entire exposed upper surface with aluminum foil and measuring the area of the foil used (3 dimensional surface area). Processed samples were preserved in 80% ethanol with 5% glycerol and counted into life stage age classes (three larval instars and pupae).

Stations were selected not to represent a particular region of the lake, but to represent the most varied physical habitat types and alkali fly densities found around the lake (Herbst, 1990). Since sampling of both hard and soft substrate types within each station was conducted over a wide and uneven geographic area, at different times within the season of production, and included unequal mixtures of different types of rock, mud and sand substrates, variability is probably exaggerated.

Modeling procedures

The goal of this project was to produce a model of alkali fly abundance in relation to changes in benthic substrate area at different lake elevations. These changes in habitat availability provide one approach to predicting the abundance of insect food supply to birds at varied lake levels. The model derived is probably a conservative assessment of the potential impact of dropping lake level on alkali fly abundance at Mono Lake because it does not incorporate the growth-limiting effects of increased salinity.

The steps followed in constructing this predictive population model were as follows:

(1) Determine the density of alkali fly larvae and pupae on hard and soft substrates at depths to the limit of distribution.
(2) Calculate the total area of both hard and soft substrates within depth zones centered on the depth contours sampled in (1) for lake levels from 6360 ft to 6390 ft (1939 m to 1948 m). The data of Stine (1988), who determined by planimetry the area of hard and soft substrates from bathymetric and aerial surveys, were used to calculate the amount of substrate habitat available within the zone between the surface and 15 m depth for each lake level.
(3) Population abundance at a given lake level (P_L) was estimated as the product of density and the area occupied by each substrate type, summed over all depth intervals for a given level:

$$P_L = \sum_d \sum_s D_{sd} A_{sd} ,$$

where

D_{sd} = density (no. or g/m^2) of larvae and pupae on substrate s at depth d

and

A_{sd} = area (m^2) of substrate type s within depth interval d;
d = depth interval (5 intervals);
s = substrate type (2 types).

Depth intervals were delimited by the mid-point between sample depths: 0–0.75 (represents 0.5 m), 0.75–2 (= 1 m), 2–4 (= 3 m), 4–7.5 (= 5 m), and 7.5–15 (= 10 m). No estimates are available for the areas that would be occupied by different substrate types at elevations above 6390 ft (1948 m), so estimates of P_L were not possible above this lake elevation. Elevation is reported in feet (though metric equivalents will also be given) because of the widespread convention of reference to these units in water management planning (e.g. in the environmental impact report in preparation for the California State Water Resources Control Board).

Densities on hard or soft substrates are expressed both as the numerical density (total number of individuals m^2) and as biomass density (grams dry weight of all life stages m^2). Station means showed positively skewed distributions, with some zero values, and so were log-transformed to normalize distributions and equalize variances. The unweighted geometric mean density for a given substrate (s) at a given depth interval (d) was calculated as:

$$D_{sd} = \text{antilog}\left[\frac{\sum_j \log(M_{jsd} + k)}{N_{sd}} + (1.15)(V_M)\right] - k$$

where

N_{sd} = no. stations with substrate s present at depth d,

M_{jsd} = arithmetic mean density per m^2 on substrate s at depth d, for station j,
$= \sum_i X_{ijsd}/N$

V_M = variance of the log $(M_{jsd} + k)$ values; 1.15 V_M is a correction factor to make D_{sd} closer to the arithmetic mean (Elliot, 1977, p. 33),

X_{ijsd} = density (per m^2) in ith sample from substrate s and depth d at station j,

N_{jsd} = no. samples taken at station j for substrate s at depth d,

and

k = minimum non-zero value of M_{jsd} possible. For biomass density (mg dry wt/m^2), $k = 0.13$ on hard, 0.4 on soft; for numerical density (no./m^2), $k = 7$ on hard, 20 on soft (assuming 10 cores of 50 cm^2 each, or 20 rocks of 75 cm^2 each, per station). Biomass conversions (mg dry wt ind^{-1}) were as follows: instar 1- 0.02, instar 2- 0.16, instar 3- 2.5, and pupae- 2.0.

Results

Depth distribution of larvae and pupae

On hard substrates, biomass and numerical densities of larvae and pupae were greatest at depths of 0.5 and 1 m (about 100 g m^2), lower at 3 and 5 m (about 30–40 g m^2), and more than an order of magnitude lower at 10 m (less than 1 g m^2) (Fig. 2). Soft substrates harbored far lower densities of larvae and pupae than hard substrates at any depth except 10 m (Fig. 2). Biomass on soft substrates was somewhat higher at the most shallow depth (5 g m^2 at 0.5 m), and more uniform in deeper water (1.5 to 2.5 g m^2 from 1 to 10 m depth). The distribution of sampling by station, depth and substrate type are given in Table 1.

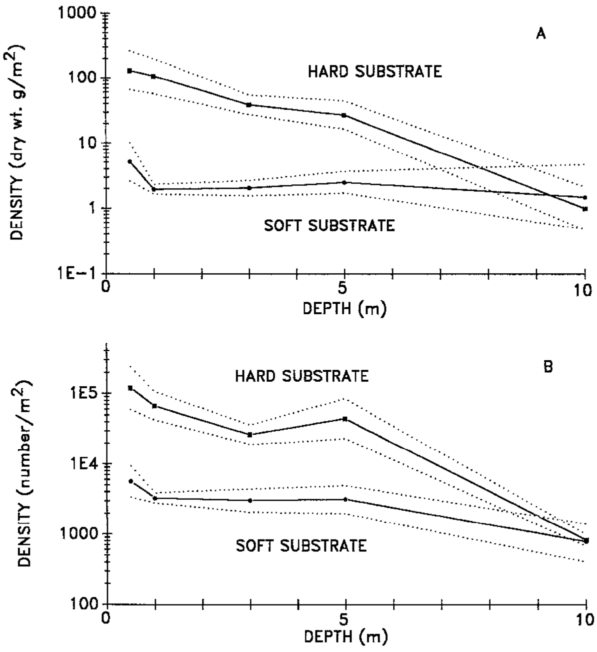

Fig. 2. Depth distribution of biomass density (A) and numerical density (B) for *Ephydra hians* larvae and pupae on hard and soft substrates. Dashed lines connect values representing $D_{ds} \pm 1$ SE. Sample size equal to the number of stations sampled for that depth and substrate type (N_{sd}, Table 1).

Eggs were also collected in samples, but not quantified. A few eggs were found even as deep as 10 m, but they were far more common on shallow substrates. Though eggs appear to be deposited by adult females crawling underwater, eggs can also be found in the water column, presumably dislodged by wave action or perhaps laid by adults on the water surface. In any case, eggs may drift down into deeper water, as may larvae, but subsequent survival is probably poor.

The condition of pupae also deteriorates with increased depth. Fully formed pupae found at depths of 5 m or more often contained unemerged adults in a decomposed condition. Few healthy pupae or eclosed pupa cases were found, suggesting pupae forming in deep water often fail to complete development and emerge.

Substrate area at elevations between 6360 ft and 6390 ft

The total lake bottom area of Mono Lake is reduced by about 33% for a drop in lake level from 6390 ft to 6360 ft elevation (Fig. 3). However, 83% of the hard substrate area is exposed by the same drop in lake level, and nearly half of the area of this habitat is lost when the level drops from 6380 ft to 6370 ft. This restriction of most hard substrate within a narrow range of elevation contours is a prominent feature of the physical environment of Mono Lake. The association of fly larvae and pupae with tufa and other hard substrates portends the importance of this elevation interval as habitat for the production of *E. hians*.

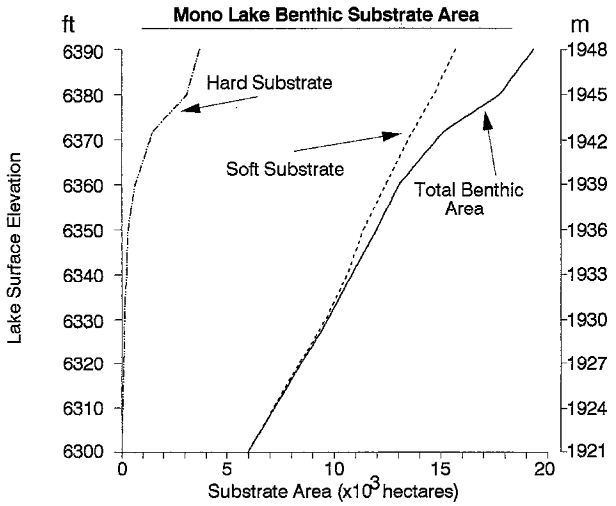

Fig. 3. Estimated areas of benthic hard and soft substrates for Mono Lake between elevations 6300 ft to 6390 ft. Hard substrate assumed to be absent when lake elevation at 6300 ft. Data from Stine (1988, Table 2).

Population model: density × substrate area

A model of alkali fly abundance was derived by combining the results of the density distribution with depth and the area of substrate available at different lake levels (Fig. 4). The model varies with physical habitat availability and predicts that the abundance of the alkali fly is maximized at 6380 ft lake surface elevation. This population maximum at 6380 ft coincides with the elevation where there is the greatest area of hard substrate in shallow water, where densities were found to be highest and most variable. Above and below this level, abundance is projected to decrease in association with the limits of hard substrate habitat availability. Below an elevation of 6372 ft the mean abundance is projected to drop to less than half that predicted for maximum abundance at 6380 ft.

Discovery of the mineral gaylussite

During early dives into deep water sampling locations, large crystals of an unknown mineral were discovered encrusting the surface of a variety of substrates. Subsequently, it was determined from mineralogical tests that these crystals were the evaporite mineral gaylussite [$Na_2Ca(CO_3)_2$ $5H_2O$]. After further diving and observation, it became clear that the crystal size and extent of gaylussite deposited varied with depth. With increasing depth, crystals were both larger and more extensive in coverage on rock surfaces such as pumice. In addition, encrustation on pumice in shallow water (0.5 and 1 m) consists mainly of tufa rather than gaylussite. This, coupled with the observation of large aragonite tufa crystals in deep

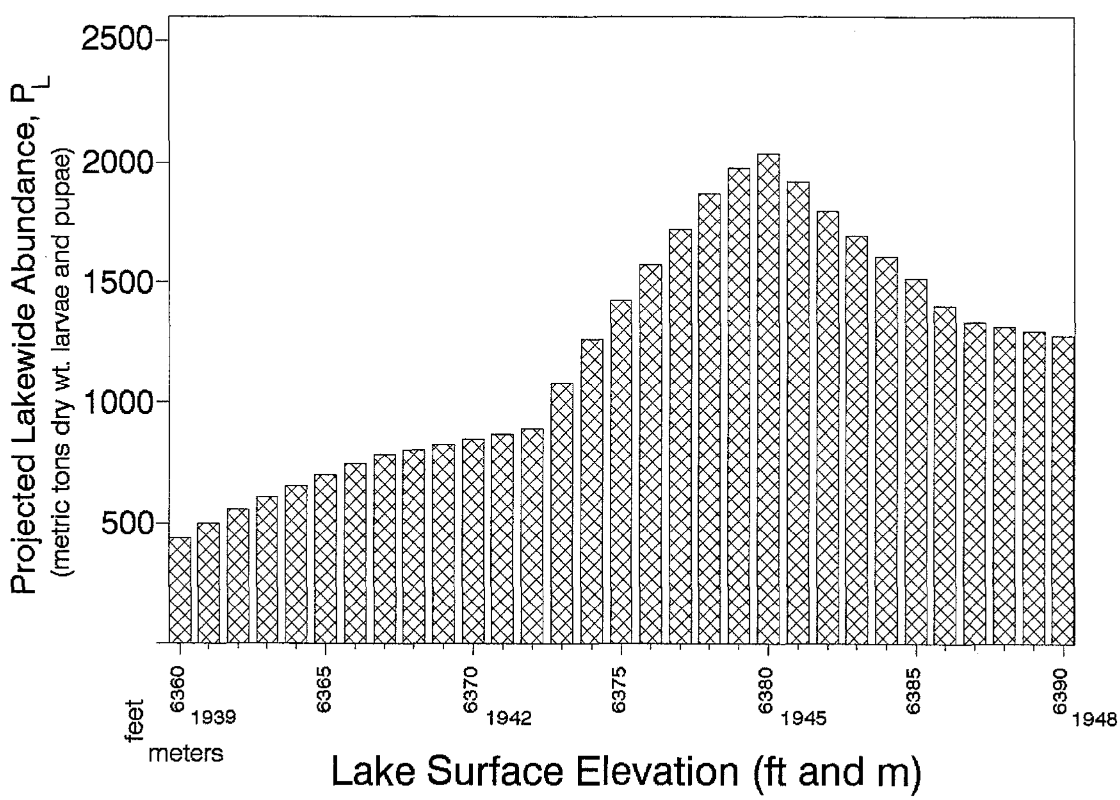

Fig. 4. Predicted lakewide standing stock of the alkali fly at Mono Lake for different lake elevations.

water, occurring inside gaylussite crystals of identical shape, suggests that much of the encrusting tufa formed in Mono Lake originates through the process of pseudomorphism from gaylussite (Bischoff *et al.*, 1991).

Discussion

As depth increases, habitat conditions were expected to become more unfavorable, so it is not surprising that we observed a decrease in the density of larvae and pupae with depth. Among the factors limiting this distribution are decreased light and thus decreased algal production, decreased temperature and oxygen availability, and reduced area of tufa available as habitat. Using vertical temperature profiles, Herbst (1990) constructed a degree-day model for alkali fly development that predicted sufficient heating for one or more generations per year at depths down to 5 m, but cumulative temperature usually did not permit production of even one generation at 10 m depth.

Hard substrates clearly harbor the highest densities, usually 10–20 times those found on soft substrates, and are particularly important for the attachment of the sessile pupa stage. Even considering the greater area of soft substrates found in the lake, the biomass present on soft substrate comprises less than 10% of the total at all but the lowest lake level projected (6360 ft), where it approaches only 20% of the total.

An evaluation of the model developed here to project alkali fly abundance over varied lake levels would be possible if past census information on flies, or diets of their avian predators were available. Unfortunately, earlier observations of the numbers of flies or birds at Mono Lake are largely anecdotal. Entomologists and naturalists visiting the lake in the 19th and early 20th century reported wide bands of adult flies and vast windrows of pupae along the shore (Brewer, 1930; Aldrich, 1912). These observations provide no quantitative basis on which comparisons can be made however. Herbst (1988) observed an increase in the abundance of *Ephydra hians* larvae and pupae from 1983 to 1984 coinciding with a period of rising lake levels and reduced salinity. Lake level rose from 6377 ft to 6380 ft over this period and salinity declined by about 5 to 10 g l^{-1}. The model developed here predicts that the increased habitat availability produced by a rise from 6377 ft to 6380 ft, would increase fly population size by 15 percent. Salinity reduction would further enhance production of fly larvae and their algal food sources.

The California Gull, nesting on islands in Mono Lake, feeds both on brine shrimp and alkali flies (all life stages). Records of the proportion of flies in the gull diet (D. Shuford, pers. comm.) show that from 1976 until 1982, while lake level and lake bottom habitat area had been declining, gull diet was never more than about 5% flies. With a dramatic rise in lake level beginning in 1982 and persisting through 1988, the proportion of flies in the diet increased to between 20–50% of the total, and was about 20% in 1989 when the lake level began dropping again (still well above the low in 1982). Bird diets may provide a useful sampling tool for evaluating the availability and quality of prey. Both my own observations between 1983–1984 and the records of gull diet changes over a longer time period are consistent with the predictions of the population model developed here.

The model makes some simplifying assumptions about the relation between physical substrate availability and population abundance. In order to define limitations and identify refinements to the model, an explicit examination of assumptions is necessary.

(1) Substrate is limiting to population density, and as tufa availability changes with fluctuating lake level, population size will respond proportionately. The question is, can crowding occur on the limited hard substrates as lake level declines, without harming survival or growth rate? The model assumes that the present density is at some constant equilibrium carrying capacity. An alternative assumption, that population size remains constant, would require that as lake level rises above or falls below elevation 6380 ft, densities increase as larvae and pupae crowd onto limited areas of shallow hard substrate. Between the reference elevation of 6375 ft and 6380 ft, density would actually have to decrease for a lake level rise over this range if population size were to remain constant.

(2) No salinity effect has been incorporated over the elevation range examined by the model. Salinity is 73.8 g l^{-1} at 6390 ft and 127.2 g l^{-1} at 6360 ft (Vorster, 1985). This is a wide salinity range, over which impaired growth and survival have been observed (Herbst, 1992), so this is not a valid assumption. The effect of salinity over this range could be added as a refinement to the population model by considering relative larval survival and other developmental effects. Since densities measured at 6375 ft (the elevation during this study) were taken as the reference point of the model, a model incorporating the effects of salinity would predict total population size to be lower at elevations <6375 ft, and higher at elevations >6375 ft relative to the predictions in Fig. 4. The further the lake level is from the reference elevation, the greater is the disparity between the two models. The net effect of such a refinement would be to elevate the lake level at which the predicted population size would be maximized.

(3) There is no new hard substrate forming (or disappearing) as lake level either rises or falls. Tufa formation from springs may occur only around the shallow margins of the lake according to a recent model suggesting that dense interstitial saline water in lake sediments prevents fresh water from entering via sublacustrine springs in all but the shallows where the gradient is more favorable (S. Dreiss & D. Rogers, pers. comm.). Springs would migrate with the changing shoreline and deposit new tufa at lower or higher lake levels.

During these studies, primary formation of the mineral gaylussite was discovered in Mono Lake. This may have important implications for both the origin of tufa habitat and brine evolution in alkaline lakes (Bischoff *et al.*, 1991). Through a process of mineral transformation known as pseudomorphism, the sodium and water are lost from the gaylussite parent mineral and the calcium and carbonate redistributed without loss of the original structure, to form aragonite tufa crystals. Because tufa has been shown to be the most important physical habitat feature for the alkali fly, this process of formation from gaylussite may play an important role in determining where and how tufa substrate becomes available in Mono Lake. Furthermore, precipitation of gaylussite requires the removal of dissolved ions from solution into the solid phase crystal form. This could affect the proportions of different dissolved salts present as the salt concentration of Mono Lake changes.

The rate at which gaylussite transformation and tufa encrustation occurs is unknown. It is uncertain that enough new habitat would ever be created to be make a significant addition to that already mapped. Furthermore, gaylussite precipitation requires that some hard substrate already be present to provide a nucleation surface, and would only add layers to formations already present.

Submerged vegetation can also serve as 'hard' substrate in that it provides attachment sites for pupae (Herbst, 1990). At high lake levels where tufa becomes less abundant in shallow water areas, substantial areas of vegetation could become submerged (e.g. *Distichlis spicata*), contributing to habitat enhancement. From the middle of the last century until about 1920, the level of Mono Lake was rising (Herbst, 1988), inundating large areas of dense vegetation, and providing extensive alternative habitat for the attachment of pupae.

(4) The area of hard and soft substrate above 6390 ft is unknown. This could be determined from aerial photographs (as Stine did for 6375 ft to 6390 ft), and would permit the population model developed here to be extended to elevations above 6390 ft. Such expanded mapping could also incorporate the zones of vegetation that would become submerged.

(5) Standing stock abundance (the population index of the model) is representative of productivity. Productivity, the annual sum of biomass produced by a population, is the most useful measure against which changes in a population should be compared. Standing stock may not represent how productivity is changing. A productivity model algorithm would be based on factors affecting rates (e.g. salinity, food and temperature affects on growth) rather than density. Physical habitat availability is appropriately modeled here as the driving variable for density, yielding standing stock as a relative indicator of population size. A productivity model should be developed for forecasting the effects of factors affecting population growth rates. Density could remain constant while the productivity varied, if turnover rates change with salinity.

(6) Lake surface area is an adequate representation of actual lake bottom area. The planimetered contours of lake surface area at different elevations is the basis for lake bottom area estimates (this is a 2-dimensional projection onto an inclined surface – the lake bottom). The steeper the lake bottom, the closer together are contour lines, and the greater the underestimate of the actual surface area of the lake bottom. This is actually a simple trigonometric problem that could be corrected (the actual area is the hypotenuse rather than the surface leg of the right triangle). However, the underestimate may not affect absolute values much (1.5% for the steepest slopes of 10 degrees), and are otherwise negligible because slopes are similar over the 6360 ft to 6390 ft elevation range.

(7) Maps indicating an outlined area is covered entirely by one substrate type may not be accurate. A map showing a certain area as 'tufa' is unlikely to be 100% tufa, and mud/sand areas are also unlikely to consist entirely of that substrate class. Finer resolution of actual area covered by different substrates could be provided by transect surveys of these areas.

The standing stock densities found in this study are similar to previous estimates (Herbst, 1990), and place *Ephydra hians* density at Mono Lake among the highest of any saline aquatic ecosystem known (Herbst, 1988). An important ecosystem management question that remains however, is how do these densities and overall abundance compare with those that are limiting to bird feeding? This issue, and refinement of the population model presented here, will be addressed in an environmental impact assessment being prepared for the California State Water Resources Control Board.

A balancing of resource values, including both the ecological and economic values of water, will underly the development of a management plan for Mono Lake. The results of the present study may be used to determine the water needed to sustain the ecological value of Mono Lake as a wildlife habitat. Though other refinements to the lake bottom habitat model developed here should be incorporated (such as the effect of salinity), the lake level predicted in the absence of salinity effects to provide habitat conditions maximizing fly abundance, and therefore food abundance for birds, is 6380 ft. Outside the elevation range 6373 ft to 6385 ft little population change is predicted. These levels provide one guideline for balancing management policy.

Over the short-term, the exposure of lake bottom habitat by dropping lake levels is likely to be a more significant impact than the more slowly developing long-term effects of increased salinity. Five feet above or below 6375 ft for example, would increase or decrease the availability of hard substrate habitat by 40 percent. Over the same range, salinity would decrease or increase by only about 10 percent. For this reason, the results of the depth distribution population model may provide useful short-term management objectives for defining the optimum range of lake levels that will sustain a productive wildlife habitat.

A study commissioned by the California Legislature concluded that an elevation of 6382 ft would protect ecosystem values at Mono Lake (Botkin *et al.*, 1988). The US Forest Service, in its management plan for the Mono Basin Scenic Area (1989), recommends a lake level range of 6377 ft to 6390 ft be maintained. The results of the present study are consistent with, and provide independent support of these conclusions and recommendations. This is the first model to simulate population changes at different levels of Mono Lake and establishes a conceptual basis for further defining the conditions that will preserve ecological values.

Acknowledgements

This research was supported by grants from the Policy Research Program of the California Policy Seminar (University of California), and the Mono Lake Foundation.

Without aid of the following dive partners and helpers, research into this unknown realm could not have been completed: Joel Axelrad, Dave Carle, Larry Ford, Larry Miller, Curtis Milliron, Stephen Osgood, and Richard Perloff. For use and handling of boats we thank Dave Carle and the State Tufa Reserve, Chuck Culbertson, Gayle Dana, Lee Dyer, and Curtis Milliron and the California Department of Fish and Game. Helpful assistance in several shallow water dives was provided by Melanie Findling, Cindy Findling, and Dan Tolson. Stuart Hurlbert contributed valuable advice on data analysis.

References

Aldrich, J. M., 1912. The biology of some Western species of the dipterous genus *Ephydra*. J. N.Y. ent. Soc. 20: 77–99.

Bischoff, J. L., D. B. Herbst & R. J. Rosenbauer, 1991. Gaylussite formation at Mono Lake, California. Geohim. Cosmochim. Acta 55: 1743–1747.

Botkin, D. B., W. S. Broecker, L. G. Everett, J. Shapiro & J. A. Wiens, 1988. The Future of Mono Lake. Water Resources Center, University of California, Riverside. Report no. 68.

Brewer, W. H., 1930. Up and Down California in 1860–1864. Berkeley: University of California Press. Repr. 1966.

Elliot, J. M., 1977. Some methods for the statistical analysis of samples of benthic invertebrates. 2nd edition. Freshwater Biol. Assoc. publication no. 25. Ambleside, England. 160 pp.

Gore, J. A., 1978. A technique for predicting in-stream flow requirements of benthic macroinvertebrates. Freshwat. Biol. 8: 141–151.

Gore, J. A. & R. D. Judy, 1981. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. Can. J. Fish. aquat. Sci. 38: 1363–1370.

Herbst, D. B., 1988. Comparative population ecology of *Ephydra hians* Say (Diptera: Ephydridae) at Mono Lake (California) and Abert Lake (Oregon). Hydrobiologia 158: 145–166.

Herbst, D. B., 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.

Herbst, D. B, 1992. Changing lake level and salinity at Mono Lake: Habitat Conservation Problems for the Benthic Alkali Fly. In: C. Hall (ed.) History of Water in the Eastern Sierra. Volume 4 of the White Moutain Research Station Symposia. University of California, Los Angeles 4: 198–210.

Herbst, D. B., F. P. Conte & V. J. Brookes, 1988. Osmoregulation in an alkaline salt lake insect, *Ephydra* (*Hydropyrus*) *hians* Say (Diptera: Ephydridae) in relation to water chemistry. J. Insect Physiol. 34: 903–909.

Herbst, D. B. & T. J. Bradley, 1989. A Malpighian tubule lime gland in an insect inhabiting alkaline salt lakes. J. exp. Biol. 145: 63–78.

National Academy of Sciences, 1987. The Mono Basin Ecosystem: Effects of Changing Lake Levels. National Academy Press, Washington D.C. 272 pp.

Stine, S., 1988. Geomorphic and geohydrographic aspects of the Mono Lake controversy. Appendix report to The Future of Mono Lake. D. Botkin *et al.* (eds). Report No. 68, Water Resources Center, University of California.

US Forest Service, 1989. Mono Basin National Forest Scenic Area – comprehensive management plan. Inyo National Forest. 58 pp.

Vorster, P. 1985. A water balance forecast model for Mono Lake, California. US Forest Service Region 5. Monograph No. 10, 350 pp.

Wrona, F. J., P. Calow, I. Ford, D. J. Baird & L. Maltby, 1986. Estimating the abundance of stone-dwelling organisms: a new method. Can. J. Fish. aquat. Sci. 43: 2025–2035.