

Comparative population ecology of *Ephydra hians* Say (Diptera: Ephydriidae) at Mono Lake (California) and Abert Lake (Oregon)

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Abstract

The population dynamics of *Ephydra hians* Say final instar larvae and pupae were compared over a two year period in rocky littoral habitats of two alkaline saline lakes in the western Great Basin. Relative abundance increased from 1983 to 1984 at Mono Lake (California), during dilution from ca. 90 to 80 g l⁻¹ TDS (total dissolved solids). In contrast, relative abundance decreased over the same period at Abert Lake (Oregon), accompanied by a dilution of salinity from ca. 30 to 20 g l⁻¹ and a marked increase in the number and abundance of other benthic macroinvertebrate species. These observations are consistent with a hypothesis that proposes biotic interactions limit *E. hians* abundance at low salinity, and physiological stress limits abundance at high salinity.

Oviposition extends from early spring to early fall. Mixed instars present throughout this period indicates multivoltine population dynamics with overlapping generations. The standing stock biomass of final instars increases exponentially in late spring and peaks in late summer or early fall. Pupae increase in proportional representation and abundance from a spring minimum to a fall maximum. The body size of adults and pupae cycle seasonally from a spring maximum to a fall minimum, and may be related to either or both food limitation, or water temperature.

Introduction

In contrast to the planktonic communities of salt lakes, benthic communities have received limited attention, despite their potential contribution to productivity, particularly in shallow lakes (Wetzel, 1964; Paterson & Walker, 1974a). Microhabitat and substrate heterogeneity usually produces aggregated distributions among the benthos, resulting in sampling variability that often precludes the quantitative studies possible in the more uniform open water of lakes. However, such studies are important because the high resource density at the benthic interface, and clumping of the benthos provide focal points for ecological processes and turnover to higher trophic levels. Benthic littoral habitat may be an important foraging location to shorebirds for ex-

ample (Winkler *et al.*, 1977). Saline lakes also combine a rigorous physical environment with low species diversity, and thus limited species interactions. These features make salt lakes useful ecosystems for contrasting the role of biotic interactions with physicochemical factors in regulating species distributions and abundances (Collins, 1977).

This study contrasts the benthic ecology of two large alkaline saline lakes in the western Great Basin. Sampling was confined to shallow, rocky littoral habitats. Abert Lake (Oregon, 42°35'N., 120°15'W.) is relatively shallow, and lower in salinity (20–30 g l⁻¹), than the deeper, more saline (80–90 g l⁻¹) Mono Lake (California, 38°00'N., 120°00'W.). This comparative study describes the population dynamics of the alkali fly *Ephydra* (*Hydropyrus*) *hians* Say, and examines the relation-

ship of salinity and macroinvertebrate diversity at these lakes to *E. hians* abundance.

The alkali fly occurs primarily in inland, alkaline saline water habitats (Wirth, 1971), and is usually the most common benthic macroinvertebrate in both Mono and Abert Lakes. All immature stages are aquatic and develop through the egg, 3 larval instars, and pupa. Larvae feed on benthic algae and detritus, and usually attach themselves to hard substrates at pupation. Adults also feed on algae. Larvae are capable of osmotic regulation over a wide range of salinities, but suffer high mortality at and above a range of $150\text{--}200\text{ g l}^{-1}$ (Herbst, 1981 and Herbst, 1986). The study by Collins (1980a) of *E. cinerea* Jones at the Great Salt Lake (Utah), provides a basis for interspecific comparisons.

Environments of Abert and Mono Lakes

Located in south-central Oregon, Abert Lake is at the northwestern extreme of the high altitude Great Basin desert, at an elevation of nearly 1300 meters (Fig. 1). It is a shallow remnant of Pleistocene Lake Chewaucan, which encompassed the present Abert and Summer Lake Basins, and left wave-cut terraces more than 60 meters above the lakebed (Phillips & VanDenburgh, 1971). The post-pluvial history of Abert Lake is characterized by fluctuating water levels and salinity, interspersed with periods of complete desiccation (Fig. 2). Hutchinson (1957) has cited Abert as a classic example of a fault scarp lake, with Abert Rim fault block rising abruptly from the eastern shore, up to 1000 meters above the lake.

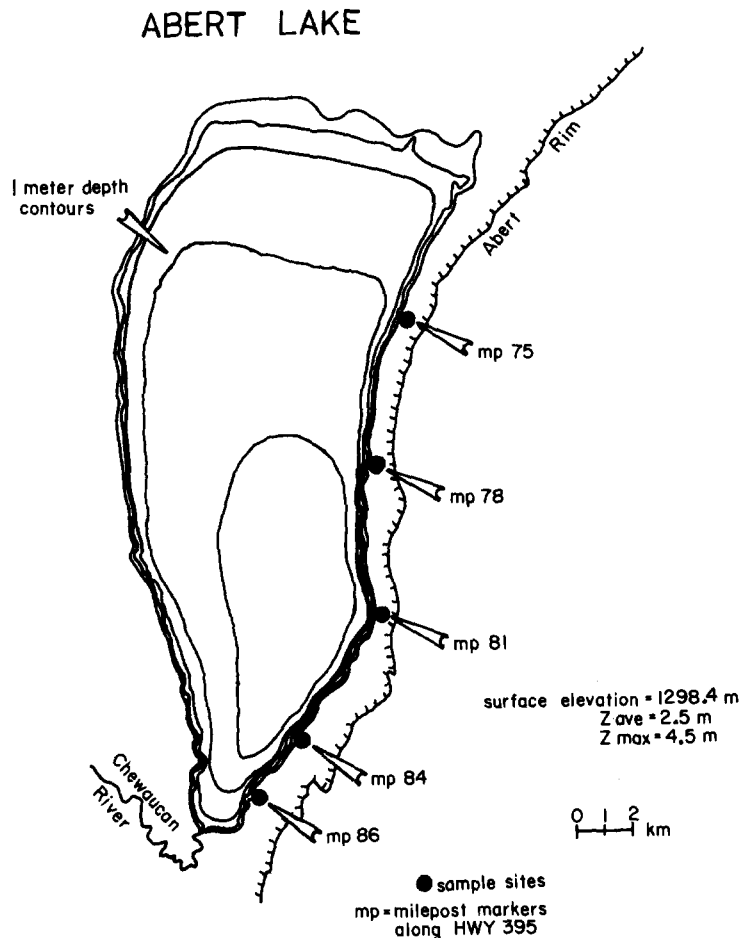


Fig. 1. Abert Lake basin morphometry and sample sites for benthic community studies. Depths and elevation based on Phillips & VanDenburgh (1971).

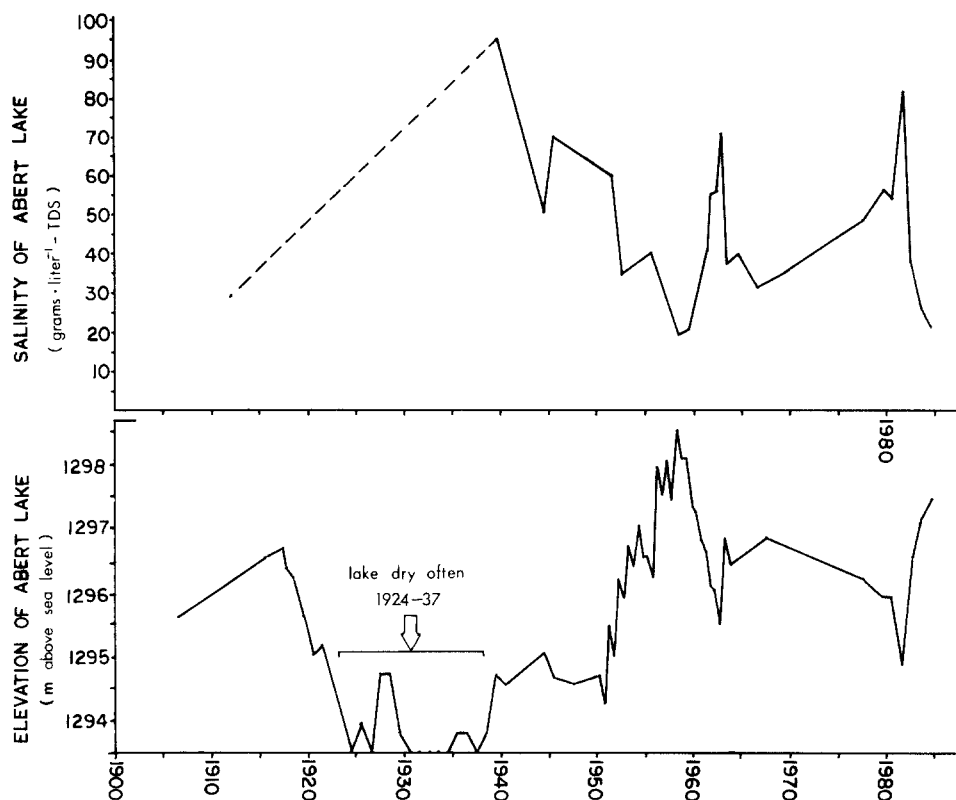


Fig. 2. Mono Lake basin morphometry and sample sites for benthic community studies. Depths and elevation based on Scholl et al. (1967), and Vorster (1985).

Along this shore, the lake bottom is dominated by rocky, basalt substrates. The northern and western shores consist mostly of alluvial clay and silt sediments, flocculent detritus, and some gravels and volcanic ash, without much rocky substrate.

The inorganic solutes present in Abert Lake are primarily chloride and bicarbonate-carbonate salts of sodium, with total dissolved solids (TDS) around 20–30 g l⁻¹ during the period of this study (Table 1). The Chewaucan River, entering at the southern end, is the only significant source of inflowing freshwater.

Mono Lake is an ancient, deep lake, located on the eastern side of the Sierra Nevada mountains in east-central California, at an elevation of almost 1950 meters (Fig. 3). Derived from Pleistocene Lake Russell, and isolated from the more extensive pluvial Lake Lahontan system, the Mono Basin has held a permanent body of water for at least a half-million years (Lajoie, 1968). Mono is thought to have origi-

Table 1. Water chemistry of Mono and Abert lakes.

Ion or Element	Mono	Abert
Na	51.9	53.4
K	1.6	1.0
Mg	0.070	0.012
Ca	0.004	0.003
Cl	20.1	30.2
HCO ₃	7.4	6.0
CO ₃	12.8	8.3
SO ₄	4.8	0.6
B	1.3	0.4
pH	10.0	10.0
TDS (g l ⁻¹) (1982–84)	ca 95–97	ca 40–20

Chemical composition expressed as molar-percent of major ions or elements. Mono Lake data based on 1974 and 1982 water chemistry analyses of the Department of Water and Power, city of Los Angeles (courtesy R.K. Kurimoto). Abert Lake data based on present results and 1961 USGS analysis (Phillips and VanDenburgh, 1971).

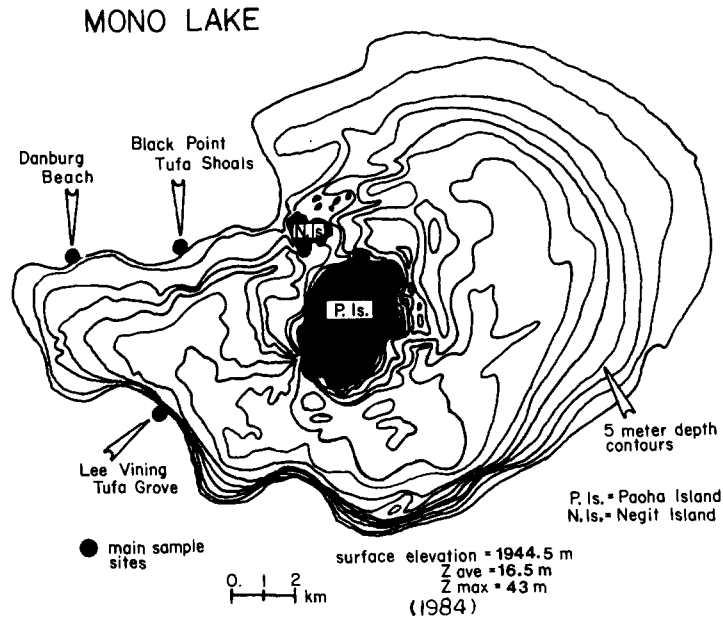


Fig. 3. Historical elevations and salinity of Abert Lake. Based on Phillips & VanDenburgh (1971), and salinity from 1977 onward based on personal observation.

nated as a tectonic-volcanic depression (Pakiser, *et al.*, 1964), or through broad structural downwarping associated with the eastern Sierra fault zone (Gilbert *et al.*, 1969). The profundal lake bottom consists primarily of fine detrital sediments of autochthonous origin (anaerobic much of the year), and alluvium. Localized around sublacustrine springs and seeps (mainly found along the western lake margins) there are extensive formations of the main hard substratum, porous limestone deposits known as tufa (Dunn, 1953). On the south and southeast lakeshore, the bottom is covered by wind-blown volcanic sands. East and northeast shores are composed almost entirely of soft detrital muds, with some areas having a surface veneer of sand.

The level of Mono Lake fell rapidly at the end of the Wisconsin glaciation, about 10–12000 years ago, and eventually came to a minimum sometime during the altithermal (5000–9000 ybp, somewhat below the present level of Mono Lake). Since then the lake has fluctuated considerably in elevation, between this altithermal minimum, and levels more than 30 meters higher. Recent evidence (Stine, 1979) suggest, however, that during the past thousand years the lake level has been relatively constant, at

a level that would correspond to a salinity of approximately 50 g l^{-1} . During the past 40 years, the lake has been declining rapidly due to the diversion of streams that supplied about 75% of the freshwater inflow. Extremely wet winters immediately preceding the present study reversed this trend, with salinity of surface waters becoming diluted from ca. 100 g l^{-1} in 1981–82, to ca. 75 g l^{-1} in 1983–84 (Fig. 4). The solutes of Mono Lake water consist mainly of chloride, bicarbonate-carbonate, and sulfate salts of sodium (Table 1).

Methods

Sample sites.

Benthic organisms were censused at about 1–2 month intervals over 18 months, from April 1983 to September 1984. Sample sites were chosen based upon expected physicochemical gradients associated with freshwater inflows into the saline lake waters. At Abert Lake, 4 sites (5 in 1984) were located south to north along the eastern shore of the lake at approximately 3 mile (ca. 5 km) intervals along US

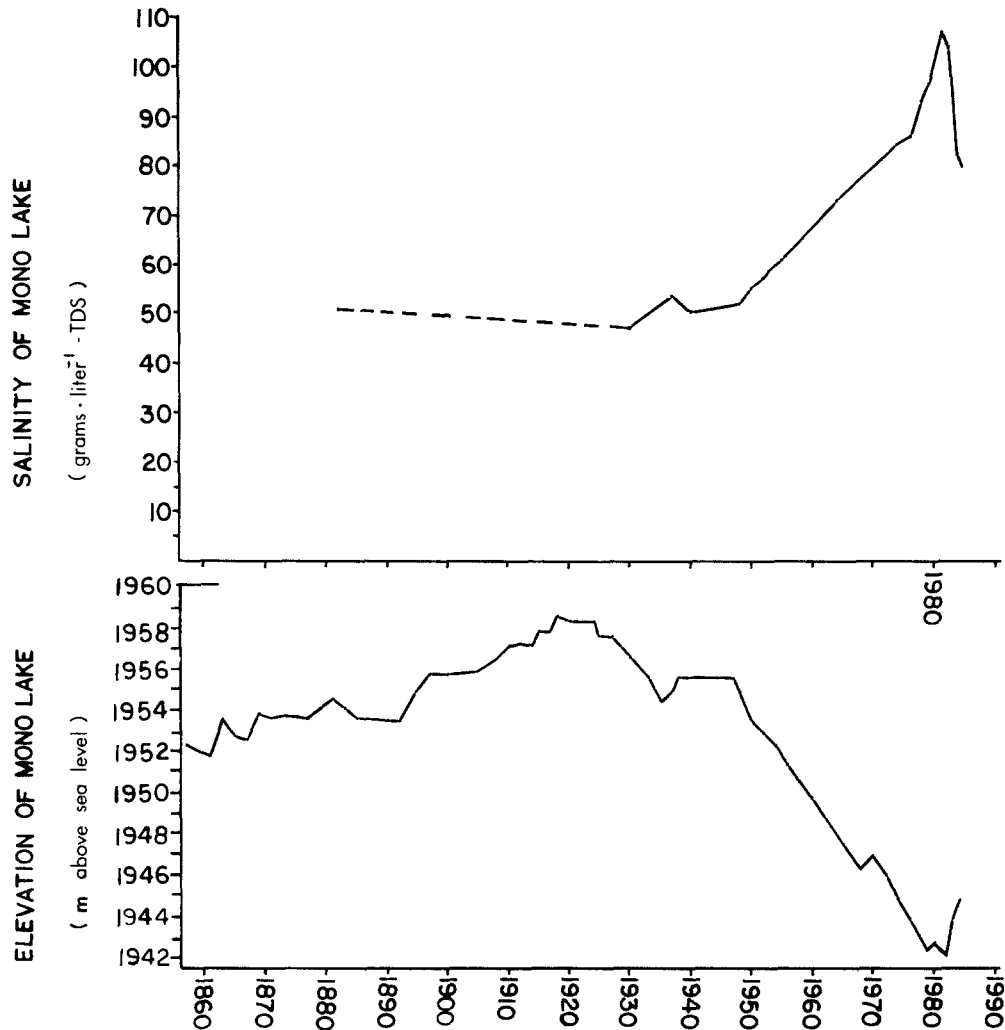


Fig. 4. Historical elevations and salinity of Mono Lake. Based on Vorster (1985), and salinity from 1976 onward based on personal observation.

HWY 395 (mileposts 86 to 75; Fig. 1). This series corresponds to a decreasing influence from Chewaucan River inflow at the south end of the lake. Substrates at all sites consisted of rocky cobble, mixed flocculent detritus, and sand. All these eastern shore locations were exposed to the prevailing southwesterly winds, and often heavy wave action.

At Mono Lake, there is no consistent point source of freshwater, due to diversions and intermittent stream flow, but numerous springs and seeps may create local differences in salinity. All 3 sample sites of Mono were in the western portion of the lake (Fig. 2). Black Point tufa shoals is an extensive, shal-

low tufa shelf, permeated by onshore and sublacus-trine seepage and springflow, largely protected from wave action, and containing accumulated organic sediments and tufa fragments. Lee Vining tufa grove is a long, shoreline belt of tufa towers located at the edge of a relatively steep littoral incline. Substrate is mixed sand, tufa fragments, and some detritus. Springflow is also intermittently present here, but originates mostly onshore. Danburg Beach was selected because of similarity in exposure and substrate features to the sites at Abert Lake. Stones at this site were mainly rounded to angular cobbles with fairly smooth surfaces, unlike the porous, reef-like tufa

found at the other Mono Lake sampling locations. In addition, this is an exposed, wave-swept site, with little detritus accumulation or freshwater seepage.

Temperature and salinity

For each sampling, temperature and specific gravity were measured at the benthic interface in 50 cm of water and at the surface. Standard mercury thermometers were used to measure temperature, and salinity was measured as specific gravity using a hydrometer floated in a transparent plastic cylinder. Specific gravity was converted to total dissolved solids (TDS, in g l^{-1}) by an empirically determined regression equation for each source of lake water. TDS was determined for different specific gravities by evaporation of known volumes (1–10 ml) at 60 °C for 4 days, followed by 110 °C for 2 days; samples were then cooled in a desiccator and weighed.

Relative abundance censusing

Benthic collections for all abundance estimates were accomplished using the semi-quantitative method of kicknet sampling. This involved vigorously disturbing an area approximately 50 cm in diameter by repeated kicks and swirling of water above the sample area. Sediment and organisms suspended in the vortex of overlying water were then removed with two successive rapid passes (in both horizontal directions) of a circular dip net 25 cm in diameter with 1 mm mesh. The area sampled would cover roughly between one quarter and one half square meter. Samples were taken at a 30–50 cm depth strata in approximately evenly spaced locations within any study site, and only when calm wind conditions prevailed. Sampling was restricted to cobble-size rocks or those easily moved. The number of kicks/sample at any site for a given collection date varied according to invertebrate density, fewer kicks being taken as abundance increased. Samples were sorted and counted on site as 3rd instar *E. hians* larvae (first and second instars were not effectively retained by mesh), viable (buoyant) pupae, and all other retained macroinvertebrates regardless of size or

life stage. The number of individuals of *E. hians* in a sample was converted to ash-free dry weight (AFDW) biomass estimates based on separate correction factors for larvae and pupae from each lake, and presented as biomass/kick sample standing stock abundance. Conversion equations were based on mean weights of third instar larvae and pupae randomly collected from both lakes during spring and summer. The data obtained for *E. hians* population dynamics thus represent seasonal relative abundance estimates for third instar larvae and pupae only.

The abundance of other benthic macroinvertebrate species were recorded as numbers of individuals only. Small organisms (less than 1 mm) such as larvae of the biting midge *Culicoides occidentalis occidentalis* Wirth and Jones at Mono Lake, and the thread-like oligochaetes at Abert Lake could not be accurately counted due to incomplete retention by the net. These species, when found, were present in every sample, and so were assigned a minimum abundance of 1 individual/kick sample. Relative species abundance on each sample date was calculated as a fraction of the mean number of total individuals of all species, averaged over all sites sampled for each lake.

Ephydra hians body size

Adults and pupae were collected for morphometry and dissections on most sampling dates from the study sites. Thorax length and total body length of dry, pinned adult specimens were measured with an ocular micrometer (to 0.01 mm) and steel calipers (to 0.05 mm), respectively. Pupal dorso-ventral width between the third and fourth prolegs was measured on preserved specimens to 0.01 mm with an ocular micrometer.

Ephydra hians reproductive condition

Adult females were collected along shores using a sweep net, and preserved immediately in 80% ethanol. These flies were measured for thorax length and the abdomens and ovaries dissected to evaluate

the vitellogenic status of presumptive oocytes, and count chorionated eggs. Flies were first separated as vitellogenic (yolk production present) or non-vitellogenic (no yolk production, with oocytes and eggs entirely absent, or as presumptive oocytes without yolk). Vitellogenic flies were further subdivided into those which had produced complete, chorionated eggs, representing an advanced stage of oogenesis, and those with only incomplete yolk deposition in the follicles (an early stage). Ovipositional activity in nature was inferred from the proportions of eggs in each developmental stage. Presence of chorionated eggs was presumed to indicate the capability for egg deposition. Conversely, non-vitellogenic oocytes and/or non-chorionated eggs were assumed to indicate the absence of oviposition in those flies.

Benthic flora

Algal standing crops on epilithic and soft sediment substrates were estimated as extracted chlorophyll from samples in the marginal shallows (5–10 cm depth), and at kick-sampling depth (30–50 cm). Samples were taken at most sites during late winter, spring, early summer, and early fall of 1984 only. Collections of rocks (usually in triplicate) at each sample site and depth, were taken arbitrarily, though size had to conform to dimensions of not more than 7.5×10 cm width \times length, to fit in half-pint glass jars. These epilithic samples were preserved in 3–4% formaldehyde in natural lake water in the field, and stored in cold and darkness until extraction (within two weeks). Storage in formaldehyde did not degrade chlorophyll because the slight acidity of this preservative was neutralized both by addition of magnesium carbonate, and by storage in the strongly alkaline lake water. The surface area of rocks was determined by wrapping that portion exposed to light (about 75% of total surface, as top and sides of most rocks) with pieces of aluminum foil that were unfolded and measured by outlining the combined areas on a grid. Sediment core samples were taken regularly only at Black Point tufa shoals (Mono Lake). A glass tube, 22 mm in diameter (3.8 cm² area), was pushed into the soft, coherent detrital mud and clay, to a depth of about 20 mm,

and plugged with a rubber stopper, permitting the core to be withdrawn intact. These samples were preserved in plastic vials and stored as above.

Preservative was decanted from stored samples, and the remaining rocks or sediment frozen at -20°C for 48 hours to break cell walls and facilitate extraction. Thawed substrates were subsequently extracted for 24 hours in 90% alkaline (magnesium carbonate added) acetone, and the absorption of centrifuged samples read at 750 and 663 nm. Concentrations of chlorophyll were determined from a monochromatic equation using an extinction coefficient of 87.7 (Jeffrey & Humphrey, 1975). A qualitative survey of algal species diversity was made from the identification of algae present in fresh, unpreserved substrate collected from several sites at both lakes in the spring of 1984.

Results

Salinity and temperature

Salinity during the study period decreased by about $5-10 \text{ g l}^{-1}$ among sites at both lakes (Figs. 5a and 6a). Seasonal cycles in salinity had a low amplitude, with decreases coinciding with spring run-off, and increase with summer-fall evaporation. At Abert Lake, the southernmost site was the least saline of all sites, and changed little during 1983–84 (Fig. 5a). Although streamflow has a diluting influence at the south end of the lake, Abert is well mixed, and only slight increases in salinity occur toward the northern sites. At Mono Lake, extensive seepage and wave protection produced the lowest and most variable salinity conditions at Black Point tufa shoals (Fig. 6a). Transient changes in salinity occurred at certain locations but were usually confined to surface waters and probably originated as stratified stream flow during calm periods (e.g. Danburg Beach in autumn 1983, Fig. 6a; and mp 84 in spring 1983, Fig. 5a). Dilution of Mono Lake surface waters since 1982 has been enhanced due to high run-off and formation of a meromictic condition. TDS increases from 84 to 94 g l^{-1} near the bottom, with the chemocline at about 12 meters in 1984 (R. Jellison, personal communication).

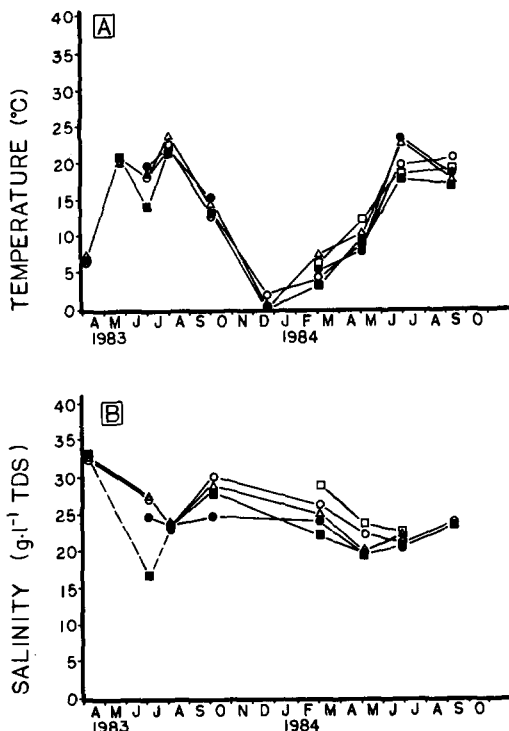


Fig. 5. Seasonality of temperature (A) and salinity (B) at the benthic interface of Abert Lake sample sites during 1983-84. Symbols indicate different sites (● = mp86, ■ = mp84, △ = mp81, ○ = mp78, □ = mp75; refer to Fig. 1).

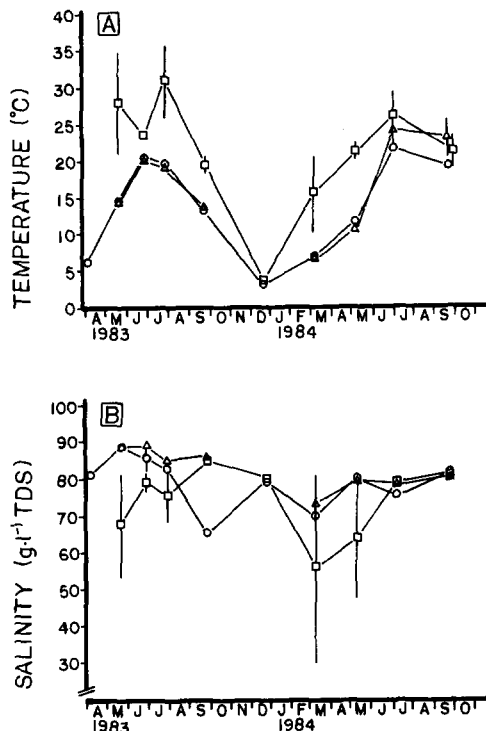


Fig. 6. Seasonality of temperature (A) and salinity (B) at the benthic interface of Mono Lake sample sites during 1983-84. Vertical lines show range of observations on each sample date. Symbols indicate different sites (□ = Black Point tufa shoals, △ = Lee Vining tufa grove, ○ = Danburg Beach; refer to Fig. 3).

The relationship of specific gravity to total dissolved solids is shown in Fig. 7. The correspondence is linear over the full salinity range examined (10–250 g l⁻¹), with Abert Lake water having a slightly higher density for the same dissolved salt concentration than Mono Lake water.

Water temperature increased most rapidly in May and declined most rapidly in September, delineating the growing season at both lakes (Figs. 5b and 6b). At Black Point tufa shoals, this shallow, wave-protected tufa shelf permitted earlier and prolonged seasonal warming, resulting in a longer growing season. At this site, daily temperatures in late winter could range between 10–21 °C while ambient lake temperature was less than 8 °C, and in spring, between 20–35 °C while other Mono Lake sites were below 15 °C. All other sites generally followed lake surface water temperatures except under calm summer conditions when afternoon heating of the shallows could occur.

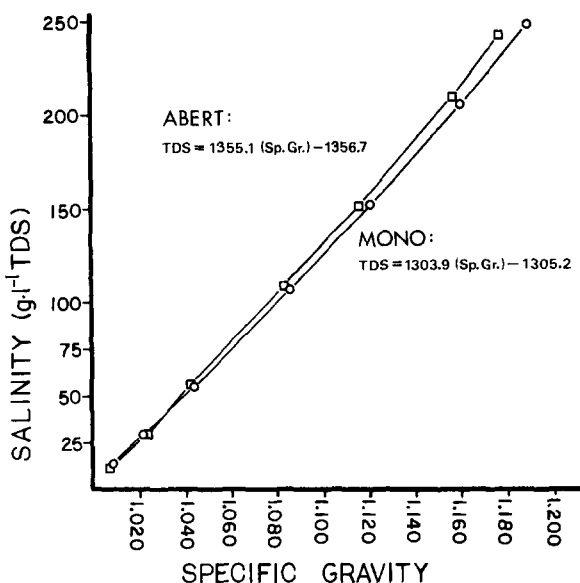


Fig. 7. Relationship between total dissolved solids (as evaporated residue) and specific gravity (as measured by hydrometer at 20 °C) of Mono (circles) and Abert (squares) Lakes waters.

Table 2. Benthic macroinvertebrates and algae from Mono and Abert Lakes.

Mono Lake	Abert Lake
Benthic Macroinvertebrates	
Diptera	Diptera
Ephydriidae	Ephydriidae
<i>Ephydra hians</i> Say	<i>Ephydra hians</i> Say
Dolichopodidae	Dolichopodidae
<i>Hydrophorus plumbeus</i> Aldrich	<i>Hydrophorus plumbeus</i> Aldrich
Tabanidae	Tabanidae
<i>Chrysops</i> sp.	<i>Chrysops</i> sp.
Stratiomyidae	Stratiomyidae
<i>Odontomyia (Catatasina)</i> sp.	<i>Stratiomys</i> sp.
<i>Odontomyia (Odontomyia)</i> sp.	<i>Odontomyia (Odontomyia)</i> sp.
<i>Nemotelus</i> sp.	<i>Nemoteles</i> sp.
Ceratopogonidae	
<i>Culicoides occidentalis occidentalis</i> Wirth and Jones	
	Coleoptera
	Dytiscidae
	<i>Hygrotus masculinus</i> (Crotch)
	<i>Hydroporus</i> cf. <i>striatellus</i> LeConte
	Hydrophilidae
	<i>Berosus fraternus</i> LeConte
	Hemiptera
	Notonectidae
	<i>Notonecta spinosa</i> Hungerford
	Corixidae
	<i>Corisella decolor</i> (Uhler)
	Odonata
	Coenagrionidae
	<i>Enallagma clausum</i> Morse
	Amphipoda
	<i>Hyallela azteca</i> (Saussure)
	Oligochaeta
	unidentified spp.
Benthic Algae (spring collection 1984 only)	
Bacillariophyceae	Bacillariophyceae
<i>Nitzschia frustulum</i> Kutzing	<i>Nitzschia frustulum</i> Kutzing
<i>Nitzschia epithemoides</i> Grun.	<i>Nitzschia epithemoides</i> Grun.
<i>Amphora coffaeformis</i> Ag. (Kutz.)	<i>Amphora coffaeformis</i> Ag. (Kutz.)
<i>Anomoeoneis sphaerophora</i> (Kutz.)	<i>Anomoeoneis sphaerophora</i> (Kutz.)
<i>Anomoeoneis costata</i> (Kutz.) Hustedt.	<i>Anomoeoneis costata</i> (Kutz.) Hustedt.
<i>Synedra fasciculata</i> (Ag.) Kutz.	<i>Synedra fasciculata</i> (Ag.) Kutz.
<i>Navicula</i> sp.	<i>Navicula</i> sp.
Chlorophyceae	Chlorophyceae
<i>Ctenocladus circinnatus</i> Borzi	<i>Ctenocladus circinnatus</i> Borzi
Cyanophyta	Cyanophyta
<i>Oscillatoria</i> cf. <i>guttulata</i> vanGoor	<i>Aphanocapsa</i> cf. <i>salina</i> (Woronichin)
<i>Oscillatoria</i> cf. <i>amphibia</i> Ag.	<i>Phormidium</i> cf. <i>tenue</i> (Menegh.) Gom.
<i>Spirulina</i> cf. <i>subsalsa</i> Oersted.	<i>Oscillatoria</i> cf. <i>guttulata</i> vanGoor
<i>Spirulina</i> cf. <i>major</i> Kutz.	
<i>Phormidium</i> cf. <i>tenue</i> (Menegh.) Gom.	
<i>Anabaena</i> sp.	

Benthic fauna

Fourteen species of benthic macroinvertebrates were collected at Abert Lake, compared to only seven from Mono Lake (Table 2), with *Ephydra hians* usually being the most numerous species at both lakes. Only dipteran larvae are found in the Mono Lake benthos, and all are shared in common with the Abert Lake fauna, except the biting midge *Culicoides occidentalis occidentalis*, and possibly a rarely occurring stratiomyid larva. In addition to dipteran larvae, Abert Lake contains a variety of other benthic insects, an amphipod, an oligochaete, and occasionally an aquatic parasitoid on alkali fly pupae (*Urolepis rufipes*) (Ashm.): Pteromalidae).

Relative abundance phenologies are shown for the common macroinvertebrates (>5–10% of total, excluding *E. hians*) for pooled sample sites in each lake

over the study period (Figs. 8 and 9). At both lakes an increase in abundance and numbers of species occurred in the summer of 1984 compared to 1983. In 1984, overall abundance at Abert Lake increased by nearly an order of magnitude, associated with a shift from the dolichopodid *Hydrophorus plumbeus* Aldrich, to the cosmopolitan amphipod *Hyallela azteca* (Saussure) being the numerically codominant species to *E. hians*. In 1983, only 3 species were commonly encountered in Abert Lake (i.e. present in at least 2 sites), being *H. plumbeus*, deer fly larvae *Chrysops* sp., and oligochaetes. In 1984, 6 species were commonly encountered, including *H. azteca*, the predatory diving beetle *Hygrotus masculinus* (Crotch) (larvae and adults), and the water boatman *Corisella decolor* (Uhler), in addition to those listed for 1983. In 1985, a set of samples on 17 June showed that the large-bodied, predatory damselfly nymph,

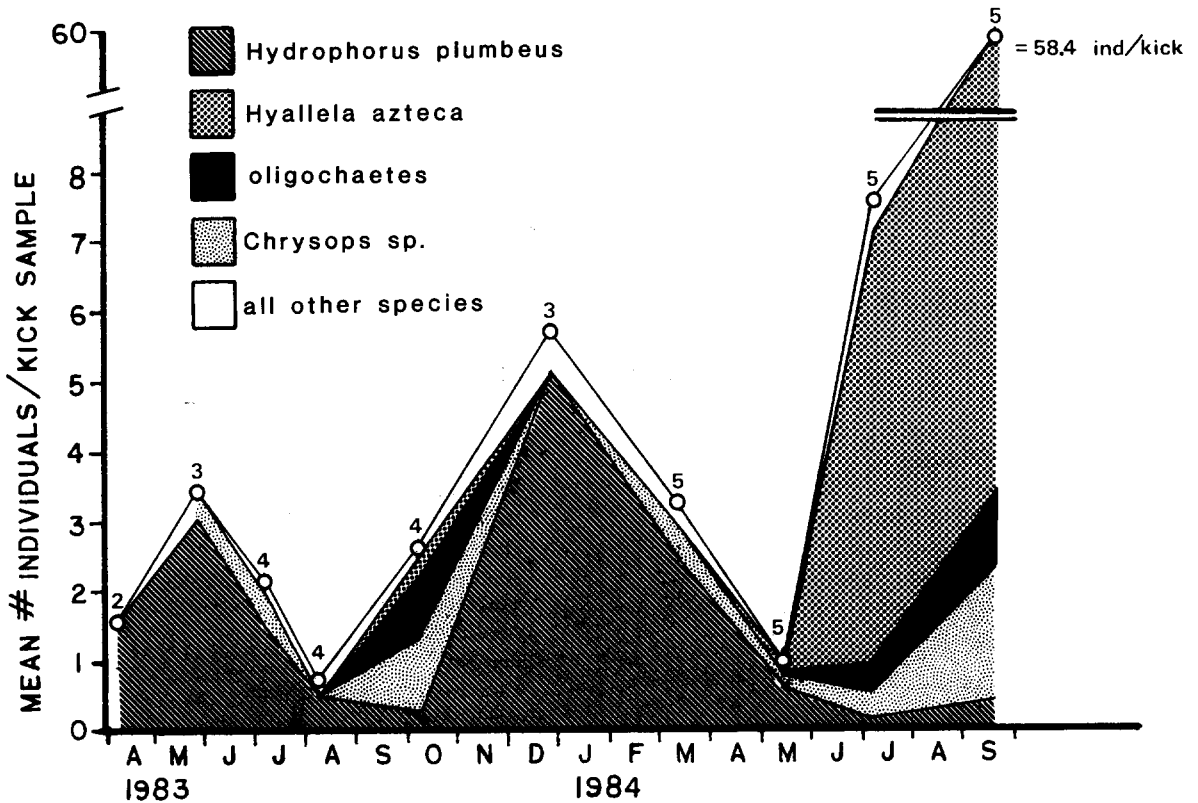


Fig. 8. Abundance dynamics of benthic macroinvertebrates (excluding *Ephydra hians*) at Abert Lake. Open circles indicate cumulative numerical abundance of all species as a composite average of all sample sites. Number of sites sampled shown above these points. Coefficient of variation averages over 60% between sites over all sample dates. Note scale increase by nearly an order of magnitude at final sample date. Refer to Table 2 for species list.

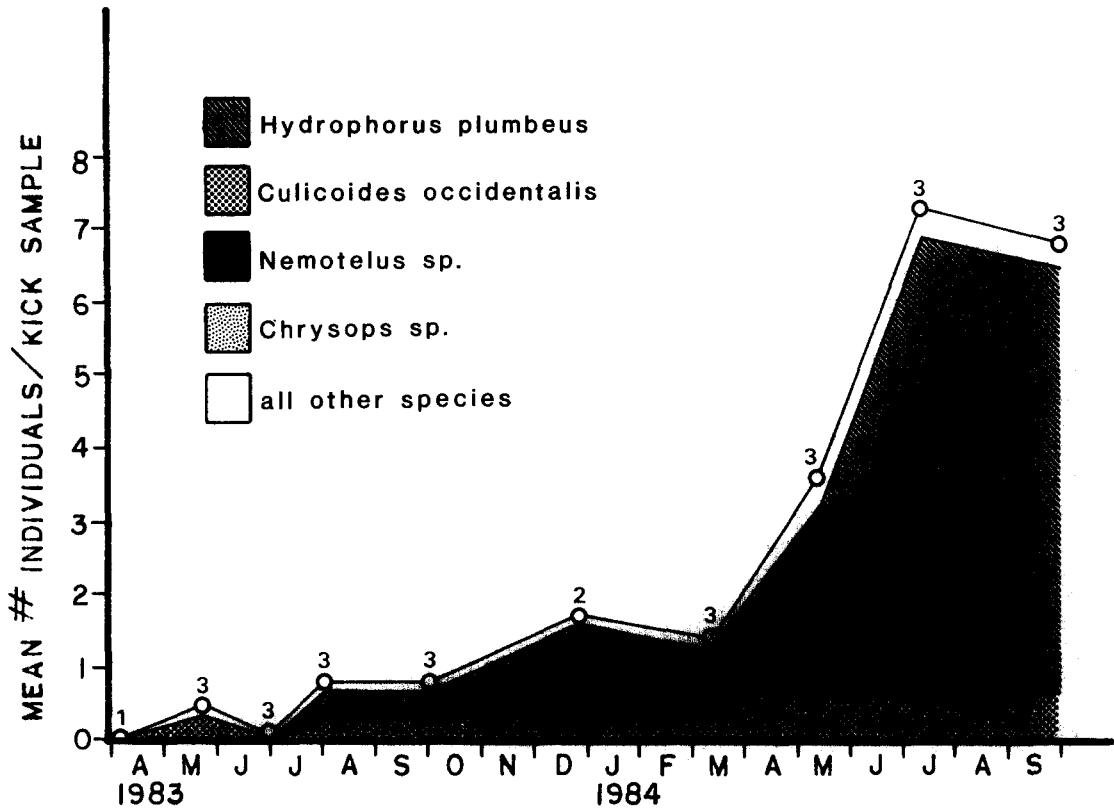


Fig. 9. Abundance dynamics of benthic macroinvertebrates (excluding *Ephydra hians* at Mono Lake. Open circles indicate cumulative numerical abundance of all species as a composite average of all sample sites. Number of sites sampled shown above these points. Coefficient of variation averages over 100% between sites over all sample dates. Refer to Table 2 for species list.

Enallagma clausum Morse, had also become common (>1 individual/kick sample).

At Mono Lake, *H. plumbeus* became common at Black Point tufa shoals in summer and fall of 1984, accounting for most of the observed increase in overall abundance. This and other species found at Mono Lake are localized in distribution however, so abundance did not increase uniformly. Moreover, numbers of individuals seldom approached those found for *E. hians*.

The two southernmost sites at Abert Lake were least saline, and closest to the colonization source represented by the Chewaucan River and its resident freshwater invertebrate fauna. These locations had the greatest number of species of all sites at Abert Lake (12 and 11 total species collected, respectively). Sample sites also showed a cline in diversity progressing toward fewer species in the north, with 9, 6, and 5 total species collected at mp 81, 78, and 75, respectively.

Black Point tufa shoals and Lee Vining tufa grove at Mono Lake both have more species (both with 5–6 species) than the wave-swept Danburg Beach site, which is monospecific for *E. hians* at most collections (only a few individuals of 2 other species were ever found here). Between-site differences at Mono were also apparent in that dolichopodid and tabanid larvae were common at Black Point tufa shoals and stratiomyid larvae (esp. *Nematelus* sp.) rare, while the reverse was true for the Lee Vining tufa grove site. The coefficient of variation for total macroinvertebrate density (excluding *E. hians*) exceeds 100% of the mean among sites at Mono Lake, and is over 60% at Abert Lake, for most collection dates.

Population dynamics of *Ephydra hians*

Standing stock biomass of *E. hians* decreased sig-

nificantly from 1983-84 at most Abert Lake sample sites, and increased significantly at Mono Lake sample sites over the same period (Table 3).

Late spring and early summer is generally the time of most rapid population growth, with the abundance of third instars and pupae increasing by 1–2 orders of magnitude or more (Figs. 10 and 11). At Black Point tufa shoals this same rapid growth phase occurs in April and then maintains higher standing stock over a longer period than any other site at either lake (Fig. 11). Danburg Beach in spring 1984 also had an April peak in growth rate. Population size increases to summer maxima at Abert, and usually early fall at Mono, then decline gradually through autumn into winter, with minimum abundance levels in late winter to mid-spring.

Abert Lake sites generally had a higher standing stock biomass than the Mono Lake sites in 1983 (ex-

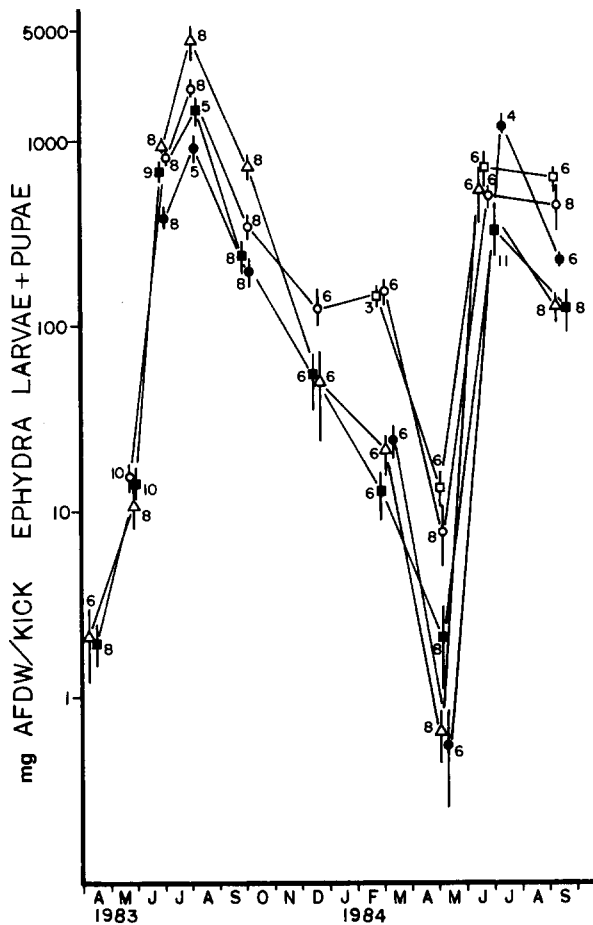


Fig. 10. Seasonality of *Ephydra hians* standing stock abundance of larvae and pupae at Abert Lake. Expressed as log biomass in milligrams ash-free dry weight (AFDW) per kick sample. Numbers beside each point are the sample size, and vertical lines are one standard error on either side of the mean. Symbols refer to sample sites on Fig. 1: ● = mp86, ■ = mp84, ▲ = mp81, ○ = mp78, □ = mp75.

Table 3. Comparison of *E. hians* abundance between years.

Site	Period compared	Cumulative Standing Stock (g AFDW/kick)		p-value
		1983	1984	
Mono Lake				
Danburg Beach	April–Sept. (18 w)	3.23	7.35	***
Lee Vining tufa grove	May–Sept. (15 w)	2.18	4.35	***
Black Point tufa shoals	May–Sept. (15 w)	14.81	21.90	**
Abert Lake				
mp 86	June–Sept. (10 w)	5.34	5.38	ns
mp 84	April–Sept. (18 w)	8.20	2.23	***
mp 81	April–Sept. (18 w)	17.23	2.82	**
mp 78	May–Sept. (15 w)	10.70	4.95	*
mp 75	April–Sept. (18 w)	–	7.71	–

Standing stock (ash-free dry weight) values are the cumulative sum for weekly intervals over the period of comparison. These were derived from the curve connecting actual sampled abundance means (Figures 10 & 11), with weekly values obtained by interpolation, and compared over the same time spans between 1983 and 1984. Note that no sampling was conducted at mp 75 (Abert) in 1983. p-values indicate significant differences by Wilcoxon’s matched-pair test (for Nw = number of weekly intervals compared): p < 0.05 (*), p < 0.01 (**), p < 0.001 (***).

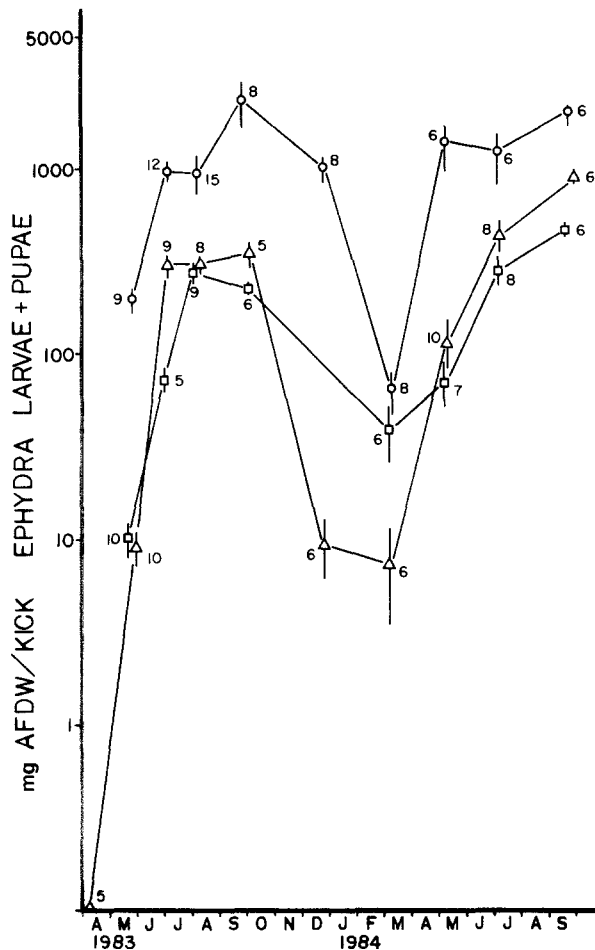


Fig. 11. Seasonality of *Ephydra hians* standing stock abundance of larvae and pupae at Mono Lake. Expressed as log biomass in milligrams ash-free dry weight (AFDW) per kick sample. Numbers beside each point are the sample size, and vertical lines are one standard error on either side of the mean. Symbols refer to sample sites on Fig. 3: \circ = Black Point tufa shoals, \square = Lee Vining tufa grove, \triangle = Danburg Beach.

cluding the Black Point tufa shoals), with the reverse true in 1984 (Table 3). This is particularly evident in relation to the Danburg Beach site, the most comparable to Abert sites in terms of substrate and wave exposure. The more northerly sites at Abert Lake tend to harbor a greater cumulative alkali fly biomass than southern sites. In 1985, the sample set on 17 June comparing mp 87, 86, and 78, showed several species of predatory benthic insects (*H. masculinus* and *E. clausum*) were quite common at the southern sites (mp 87 & 86), but occurred only rarely at the northern mp 78. The abundance of *E. hians*,

however, was over an order of magnitude greater at this northern site compared to the southern locations.

The proportion of pupae was at a minimum in winter-spring at both lakes, increasing in summer and peaking in autumn of both years (Fig. 12). Pupae are thus most numerous in autumn when larval and pupal biomasses are highest (Figs. 10 and 11).

Body sizes of all life stages of Abert Lake *E. hians* are larger than those of the Mono Lake population by both morphometric and gravimetric measures (Figs. 13 and 14, and Herbst, 1986). Seasonal cycles in body size at maturity (pupae and adults) at both lakes suggests some environmental control of this trait. Adult body size is at a maximum in spring, declining gradually through summer to an autumn minimum (Fig. 13). Body size is usually intermediate between these levels in winter. Although the data on pupa size variations are not as complete and may be biased by microhabitat effects at the collection locale, the same general trends were found (Fig. 14).

Seasonal reproductive activity (Figs. 15 and 16), assessed from dissection of ovaries, showed that the capability for oviposition was lowest in fall and early winter. Abert flies showed very little vitellogenic activity during this period, while Mono flies were vitellogenic in early winter but possessed no chorionated eggs (December 1983). Although most flies continued to show vitellogenic activity through the sum-

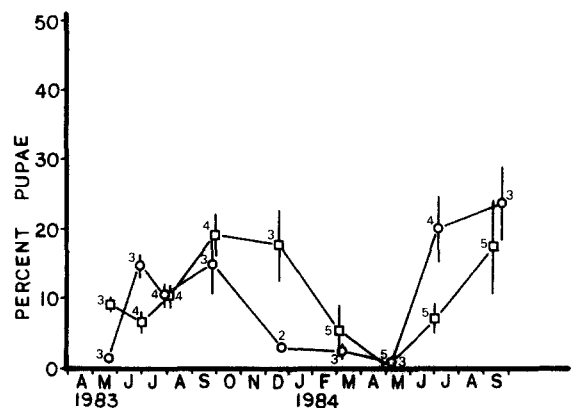


Fig. 12. Percentage of *Ephydra hians* pupae (relative to larvae) in benthic kick samples at Mono Lake (circles) and Abert Lake (squares). Number of sites sampled for each date indicated next to data point, and vertical lines are one standard error on either side of the mean. Sandy sites excluded from Mono lake samples.

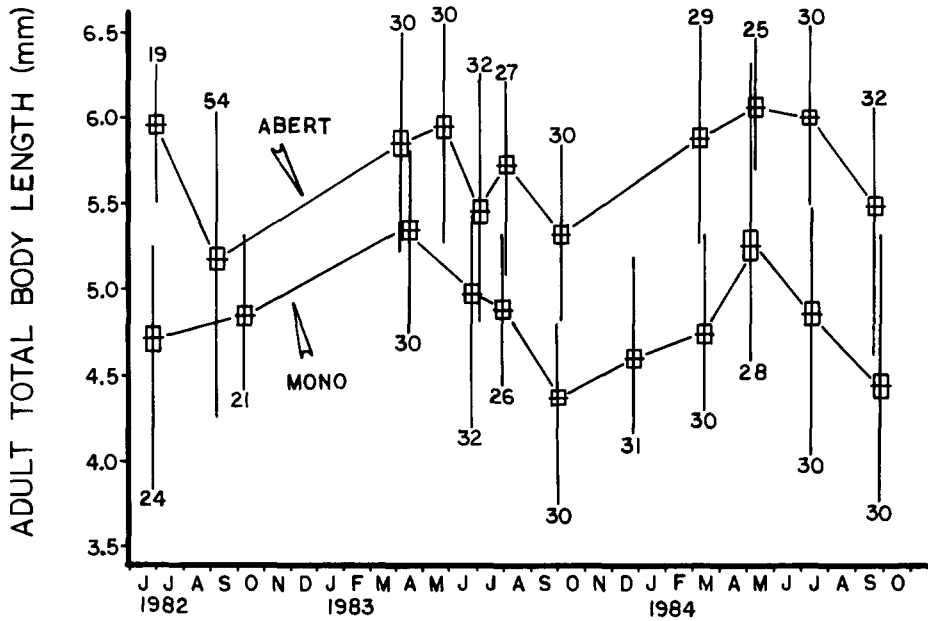


Fig. 13. Seasonal variation in adult body size of *Ephydra hians* from Abert Lake and Mono Lake. Vertical bars are one standard error on either side of the mean (horizontal lines), and vertical lines are the range. Number of adults measured indicated at top (Abert) or bottom (Mono) of range lines.

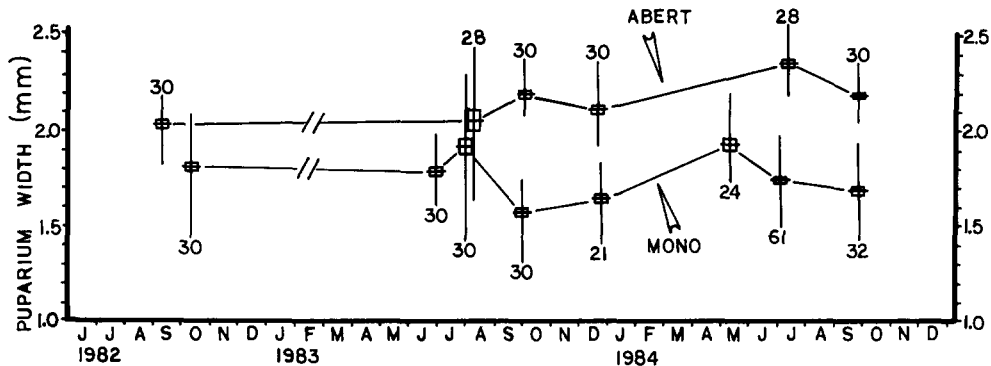


Fig. 14. Seasonal variation in puparium size of *Ephydra hians* from Abert Lake and Mono Lake. Vertical bars are standard errors, and vertical lines are ranges. Number of pupae measured indicated at top (Abert) and bottom (Mono) of range lines.

mer, the number of chorionated eggs present were invariably lower than in spring, indicating either or both a decrease in fecundity, or more rapid turnover (oviposition) of those eggs produced. The decline in autumn egg inputs to the population, attributable to vitellogenic inactivity, may be related to the decreased reproductive capacity and success associated with reduced body size in autumn. Only a

few flies collected as adults in the field in early autumn of both 1983 and 1984 produced eggs in the lab, while most of those collected in spring or summer did so readily. However, if provided with high quality algal food, flies reared in the lab from pupae collected in the field at any time were usually capable of active reproduction and oviposition.

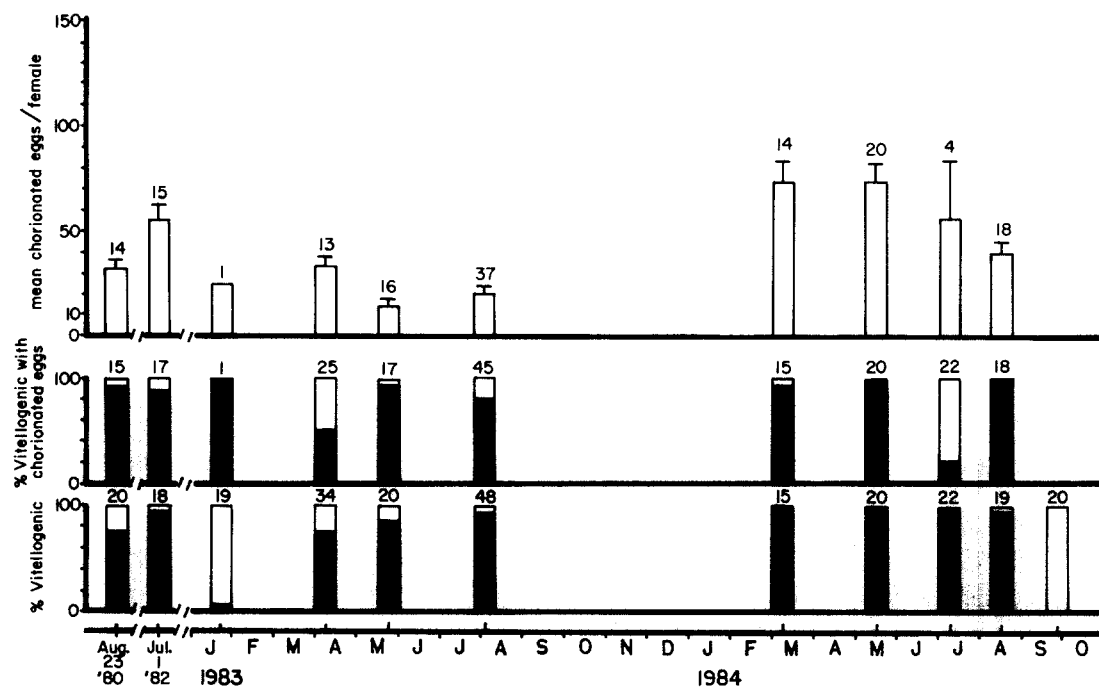


Fig. 15. Seasonal reproductive activity of *Ephydra hians* at Abert Lake. Bottom panel shows percent of females vitellogenic (producing yolk), middle panel shows the percent of these that possess fully developed, chorionated eggs, and top panel shows the mean number of chorionated eggs in the ovaries of those having such eggs (bars). Standard error of the mean number of eggs is indicated by lines on top of bars. Numbers above bars in each category are the sample size.

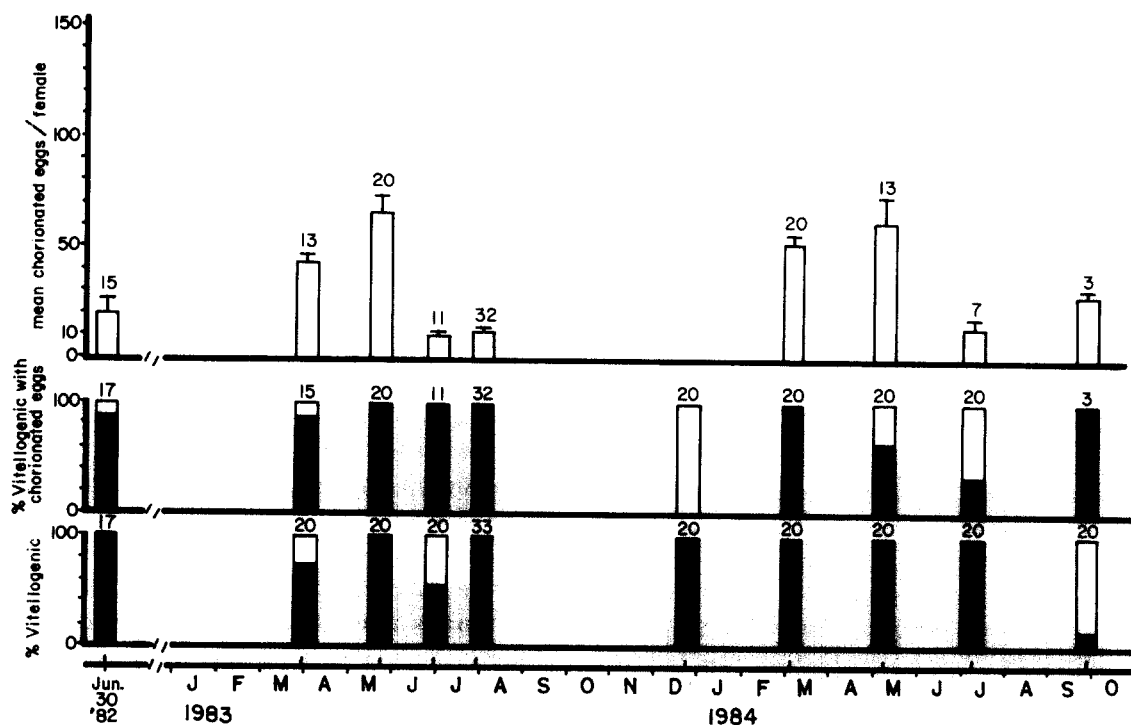


Fig. 16. Seasonal reproductive activity of *Ephydra hians* at Mono Lake. Bottom panel shows percent of females vitellogenic (producing yolk), middle panel shows the percent of these that possess fully developed, chorionated eggs, and top panel shows the mean number of chorionated eggs in the ovaries of those having such eggs (bars). Standard error of the mean number of eggs is indicated by lines on top of bars. Numbers above bars in each category are the sample size.

Benthic flora

Qualitative surveys of the algal flora at both lakes (for spring collections only), show equivalent species richness (see species list, Table 2). Epilithic substrates are dominated by thick mats of the filamentous green alga *Ctenocladus circinnatus* Borzi and epiphytic diatoms (mainly *Nitzschia frustulum* Kutzing) at Abert Lake. Mono Lake benthic algae are composed almost entirely of this same diatom, along with a variety of other less common diatoms, filamentous blue-green algae, and *Ctenocladus circinnatus*.

Standing crop of benthic algae for each season is presented in Fig. 17. There was no consistently significant difference in chlorophyll between shallow (5–10 cm) and kick-sampled (30–50 cm) epilithic substrates at either lake, so these data were pooled. Algal standing crops among sites at Abert were also pooled because of their uniformity. At Mono Lake however, the distinctly more productive substrates at Black Point tufa shoals are graphed separately from the other sites (combined as Lee Vining tufa grove and Danburg Beach).

Standing crops at Abert Lake were generally much higher than at Mono, particularly if compared to

Danburg Beach, where benthic substrates and local habitat is most similar to Abert sample sites. This occurred despite incomplete pigment extraction from the thick mats of *Ctenocladus* on Abert Lake rocks (green filaments remained on some of these rocks after extraction). The standing crops of epilithic algae at Black Point tufa shoals were similar to those at Abert Lake, and on sediment substrates were at times even greater than those at Abert.

Discussion

Ecological studies of saline lakes suggest that salinity and biotic interactions may combine to determine species distribution and abundance. Biological surveys of saline lakes in Canada (Rawson & Moore, 1944; Scudder, 1969; Hammer *et al.*, 1983) and Australia (Bayly & Williams, 1966; Timms, 1983) have shown that floral and faunal diversity decreases with increasing salinity, presumably because few species tolerate high salinities. However, productivity or standing stock of halobiont species in saline lakes often reach maximum values at salinities intermediate between physiologically limiting high salinity and ecological limitations imposed by a diverse community of predators and competitors at low salinity. The range defining these moderate salinities varies among studies, and may be related to differences in the salt tolerance of native species. Less salt-tolerant organisms will become physiologically limited at relatively lower salinities, and the competitors, predators, and parasites that act to reduce the abundance of the salt-tolerant dominant species may not colonize until salts become considerably diluted. In addition, the varied water chemistry of different lakes and differential ion toxicity may further exert an important influence on species composition of saline lakes and thus alter the relative range defining 'moderate' salinities.

In the present study, dilution of two alkaline salt lakes during a two year period is accompanied by decreasing standing stock of the dominant benthic macroinvertebrate population in the less saline lake, and increasing standing stock in the more saline lake. These trends are consistent with a general model for the role of salinity in salt lake productivity (Fig. 18).

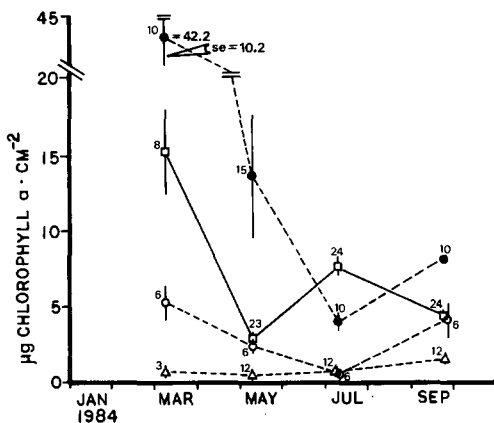


Fig. 17. Seasonality of algal standing crops (as chlorophyll) at Abert Lake and Mono Lake, on epilithic substrates (except where noted) in 1984. Squares and solid line show the average for all Abert Lake sites. Dashed lines show the less uniform Mono Lake sites (Δ = Danburg Beach & Lee Vining tufa grove combined; \circ = epilithic and \bullet = soft sediment cores at Black Point tufa shoals). Vertical lines are one standard error above and below means. Numbers indicate sample size. Note scale extension.

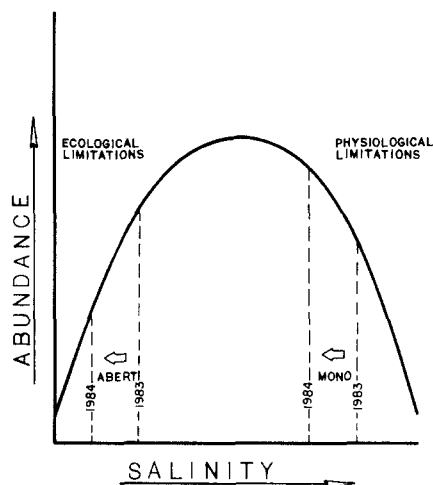


Fig. 18. Model of hypothetical relationship between salinity and abundance of *Ephydra hians*. Abundance is proposed to be maximized at salinities intermediate between the physiological limitations of high salinity stress, and the ecological limitations imposed by biotic interactions (e.g. predation and competition) at low salinity. Salinity dilution at Mono Lake was accompanied by increased abundance of *E. hians*, while dilution at Abert Lake was accompanied by a decrease in abundance.

Specifically, I hypothesize that ecological limitations reduced *E. hians* abundance during dilution of Abert Lake, and that dilution of Mono Lake reduced physiological stress, promoting higher standing stock *E. hians* biomass. Between site contrasts within lakes are also qualitatively consistent with this hypothesis. Black Point tufa shoals, at Mono Lake, is exposed to more seepage and moderated salinities than any other site sampled, and contains the greatest standing stock of alkali fly larvae and pupae. Probably other features of this habitat also contribute to the abundance of *E. hians* there (e.g. longer and warmer growing season, wave-protection, organic sediments, and algal mats). At Abert Lake, a decreasing cline in species richness at sites from south to north is associated with a general trend of increasing *E. hians* abundance. Predators such as dytiscids and coenagrionids, and competitors such as the amphipod *Hyallela* were becoming increasingly abundant, especially at southern sites, and could be important biotic agents regulating the abundance of *E. hians*. Though *Hyallela* had never been collected as recently as 1981–82, and only appeared in substantial numbers in late summer 1983,

this species, along with dolichopodid larvae, equalled or exceeded the abundance of *E. hians* by late 1984. A browser on algal periphyton and detritus, *Hyallela* has been shown to be competitively dominant, depressing abundance of all other species in experimental microcosms (Neill, 1974). High ingestion rates, inefficient digestion, compaction of available biomass into fecal pellets, and the rapid growth and reproduction of *Hyallela* (Hargrave, 1970) are likely to have a strong negative impact on other benthic grazers or detritivores such as the alkali fly. In addition, increasing abundance of predaceous dytiscids (*Hygrotus*) and damselfly nymphs (*Enallagma*) at Abert Lake also are likely to introduce losses. At Mono Lake, increased abundance of dolichopodid larvae in 1984 is localized and not of the same magnitude observed for *Hyallela* at Abert. Thus, biotic interactions at Mono Lake are probably insignificant with regard to population regulation because salt concentrations remain prohibitive to most invertebrates. Increasing abundance of *E. hians* at Mono Lake might also result from enhanced growth of algae at lower salinity, thus increasing algal food available to the alkali fly (Herbst, 1986 and unpublished data), in addition to a lessening of osmotic stress on larvae. Collins (1980a) also notes that the abundance of *E. cinerea* at Great Salt Lake appears to be inversely related to salinity, but over a relatively high range (130 to 250+ g l⁻¹ TDS).

An alternative interpretation of population abundance dynamics is that high sampling variability results in chance differences among sites. However, chance differences should result in random changes among sites. The uniformity of decreasing biomass at Abert, and increasing biomass among Mono sites, argues against such an explanation.

Although the data presented here are suggestive, test of this intermediate salinity hypothesis requires an experimental approach. Microcosm tanks in which salinity and species composition of benthos could be manipulated and replicated would provide a means of examining the relative effects of these factors on the survival, production dynamics, and size at maturity of the alkali fly.

While the numbers of algal taxa are approximately equivalent between lakes, Abert has higher epilithic standing crops compared to Danburg Beach

at Mono Lake (selected for physical similarity to Abert sample sites). This is due to the greater abundance of the filamentous green alga *Ctenocladus* at Abert. The scarcity of *Ctenocladus* at Mono Lake is probably related to inhibition of growth by the present salt concentration of this lake (Herbst, 1986). In contrast to the low standing crops found at other Mono Lake locations, algal biomass at Black Point tufa shoals may equal or exceed that at Abert Lake. A combination of favorable physicochemical conditions at this site appears to permit rapid algal growth, and organic detrital sediments in particular provide an excellent substrate for the development of an extensive algal-microbial mat (Herbst, personal observations).

In a quantitative survey of Canadian salt lakes, Rawson & Moore (1944) found highest standing stock of benthic invertebrates in a lake at 2.5 g l^{-1} , and of zooplankton in another lake with 8 g l^{-1} TDS. Although numbers and biomass declined at either more dilute or more concentrated salinities, this is impossible to evaluate over a wide range of TDS since no lakes were examined between 20 g l^{-1} and the most saline lake at 120 g l^{-1} . Timms (1983) found peak benthic abundance among 24 shallow saline Australian lakes at 7 g l^{-1} , with a subsidiary peak around $25\text{--}30 \text{ g l}^{-1}$. Again, this represented an incomplete series because it did not include any lakes over the salinity range $40\text{--}80 \text{ g l}^{-1}$. Paterson & Walker (1974a) reported a detailed study of the productivity of a benthic midge in Lake Werowrap, one of the lakes sampled by Timms. An extremely productive population (ranking among the highest recorded for any benthic lentic invertebrate) of the midge *Tanytarsus barbitarsis* Freeman was found while this lake was at a salinity between $36\text{--}56 \text{ g l}^{-1}$. Data in Timms (1983) showed Lake Werowrap to be considerably more dilute (21 g l^{-1}) in 1980 than when Paterson & Walker studied the lake (ten years previous in 1969–70), and had a far lower abundance of this midge. Paterson & Walker (1974b) suggest from fossil sediment remains of other chironomids that *T. barbitarsis* abundance is restricted at lower salinities due to an inability to compete with other tube-building sediment feeders, rather than a physiological intolerance of dilute salinities. However, salinities above 50 g l^{-1} severely reduced survival and development.

Scudder (1983) explained the distribution of two species of water boatmen (*Cenocorixa*) as resulting from a combination of physiological and ecological factors. The more salt tolerant of the species occurs in greatest abundance over a moderate range of salinities from ca. $5\text{--}25 \text{ g l}^{-1}$, with the upper limit set by osmotic stress, and the lower imposed by parasitic water mites tolerant only of salinities below 5 g l^{-1} . The less salt tolerant species is not found in lakes with a salinity of more than ca. 18 g l^{-1} but does occur in freshwater and low salinity lakes due to lower water mite parasite loads.

Wiederholm (1980) documented changes in benthic fauna abundance at Lake Lenore (Washington, USA) over the period 1950–75 while this alkaline carbonate lake was undergoing a dilution from ca. 17 to 1.5 g l^{-1} TDS. While salinities were still relatively high ($6\text{--}17 \text{ g l}^{-1}$) two midges (*Tanytarsus nubifer* Coquillett and *Cricotopus ornatus* (Meigen)) were extremely abundant, but following dilution below 6 g l^{-1} , were virtually eliminated from the benthos while other midges and the amphipod *Hyallela azteca* colonized. *C. ornatus* was reported as having a low productivity in meromictic Waldsee Lake, Canada (ca. $5\text{--}20 \text{ g l}^{-1}$) by Swanson & Hammer (1983). However, Mg-Na sulfate chemistry, seasonally fluctuating salinities, limited favorable littoral habitat, and presence of fish and insect predators appear to limit production of what otherwise was known to be an abundant species at similar salinities in Lake Lenore. Soap Lake (17 g l^{-1}) also harbors abundant *C. ornatus* and *T. nubifer*, and, as in nearby Lake Lenore before its dilution, is without predatory fish.

Continued changes in levels of Mono and Abert Lakes should lead to predictable qualitative changes in the abundance of *E. hians* if this intermediate salinity hypothesis is correct. It is interesting to note that huge pupal windrows and dense larval abundance occurred at Abert Lake in 1981 when salinity was $50\text{--}80 \text{ g l}^{-1}$, but were not observed in subsequent years. Moreover, historical accounts of Mono Lake in the 19th and early 20th centuries indicate the same vast accumulation of pupae cast ashore (salinity was about 50 g l^{-1} during these periods), although I have never observed these at Mono from 1976 to the present. Future studies of benthic productivity in the context of this model also need to distinguish

between the overall abundance of benthic fauna, and that contributed by what is often the dominant, halobiont population.

Body size or weight of adults among higher dipterans are typically reduced by larval food stress (e.g. Haupt & Busvine, 1968; Robertson, 1960). Increases in salinity or temperature in the rearing of brine mosquito larvae have also been shown to reduce body size in adult mosquitoes (Parker, 1982). Collins (1980b) has demonstrated that decreased algal food quality reduces body size in *E. cinerea*. Density manipulations of larvae in the field also showed that pupae were significantly larger in low density enclosures than in high density enclosures (Collins, 1980a), suggesting density-dependent interspecific food limitation may have occurred. The seasonal cycles in body size of *E. hians* adults and pupae at both Mono and Abert Lakes (Fig. 13), may also be related to algal food limitations, but this cannot be evaluated from the field data on algal standing crops (productivity data are needed). However, laboratory studies (Herbst, 1986) demonstrated that food deprivation or increased salinity can reduce body size, and that a heritable component for this trait also exists, with Abert flies consistently larger than Mono flies when reared under the same conditions.

An alternative explanation of seasonal cycles in body size is that these are inversely related to temperature, such that colder spring conditions promote larger sizes, declining as temperatures warm into summer. However, if cooler conditions produce increased body size, then flies should be relatively large in fall as well as in spring. Although this is not the case, temperature effects on larvae may be the critical determinant of size at maturity, and small autumn pupae may be derived primarily from summer-developing larvae.

Collins (1980a) found larvae of *E. cinerea* from Great Salt Lake to be at minimum densities in June, while pupae were at maximum densities. This situation was suggested to result from a synchronization of overwintering development among larvae, followed by pupation and mass adult emergence when temperatures increased in June. Egg inputs were low in early summer and reached maximum levels by mid-summer. In contrast, the relative abundance of *E. hians* pupae is minimum in spring and increases

through the summer to an early autumn peak (Figs. 10, 11, and 12). Oviposition probably begins in late winter to spring, with third instar larval abundance increasing exponentially by late spring and early summer. This suggests that the population is composed primarily of larvae in spring, developing to pupae in summer while continued generations of larvae appear, with larval recruitment ending in late summer or early fall as these summer generations develop into pupae and oviposition ceases. Decreasing temperatures in autumn may also contribute to an increased proportion of pupae in samples due to the slowing of development and consequent increased residence time of this stage in the lake. Pupal abundance in this study coincides with the late summer-autumn 'Koo-cha-be' (dried *E. hians* pupae) harvest of Kuzedika Paiute legend (Davis, 1965).

Although Collins does not report on population dynamics beyond late August, it is apparent that *E. hians* population growth begins earlier than *E. cinerea* and probably has a longer growing season. This follows also from the fact that pupal development rate for *E. cinerea* is substantially slower than that of *E. hians* at the same temperatures, and thus will delay adult emergence, and curtail growth earlier in fall (Herbst, 1986). Thus *E. cinerea* appears to have a residual winter-spring generation that develops synchronously and emerges in early summer to produce 1–2 generations (Collins, 1980a). Although the abundance of early instar *E. hians* larvae and adults were not quantified, they were present throughout the study period, suggesting (1) there is no single life stage in which an overwintering phase is passed (low temperatures appear only to slow metabolism and prolong the development of any stage in the life cycle), and (2) prolonged oviposition results in multivoltine population dynamics, with mixed instars and overlapping generations.

A considerable amount of benthic research in freshwater ecosystems has been directed at quantifying the secondary production of invertebrate fauna (Waters, 1977). Although the relative abundance census data collected in this study are not reliable for calculating annual productivity, a minimum estimate of mean annual standing stock may be derived for comparative purposes, using conservative as-

Table 4. Abundance of benthic invertebrates in some saline lakes.

Lake	Salinity (g l ⁻¹)	Mean Annual Standing Stock (dry wt. g m ⁻²)	Dominant species	Reference
Purrumbete	0.4	0.82	oligochaetes	Timms, 1981
Last Mountain	2.5	8.55*	midges	Rawson & Moore, 1944
Waldsea	5–20	0.01–0.02	<i>Cricotopus ornatus</i> (Meigen)	Swanson & Hammer, 1983
Pyramid	5.5	ca. 1.0	oligochaetes and midges	Robertson, 1978
Bullenmerri	8	1.24	oligochaetes and midges	Timms, 1981
Lenore & Soap	17	ca. 14.9 (max.)*	<i>C. ornatus</i> & <i>Tanytus nubifer</i> Coquillett	Lauer, 1963
Abert	20–30	0.7–1.5 (1.4–5.1)*	<i>Ephydra hians</i> Say	This study
Werowrap	36–56	8.07	<i>Tanytarsus barbitarsis</i> Freeman	Paterson & Walker, 1947a
Gnotuk	58	0.26	<i>T. barbitarsis</i>	Timms, 1981
Mono	80–90	0.4–3.6 (0.8–4.6)*	<i>E. hians</i>	This study
Little Manitou	118	0.18*	<i>Ephydra</i> sp.	Rawson & Moore, 1944
Great Salt	130	3.8–49*	<i>E. cinerea</i> Jones	Collins, 1980a

* = mean summer biomass only.

sumptions. Means weighted by the proportion of the year represented by the interval between successive samples were summed and converted from ash-free dry weight to dry weight for samples taken from spring 1983 to spring 1984, and multiplied by 2 (assuming the maximum area represented for a kick sample was a half-meter square) to convert biomass/kick to biomass/square meter. The weighted mean annual standing stock biomass so obtained ranges from 0.4–0.5 g m⁻² at Danburg Beach and Lee Vining tufa grove respectively to 3.6 g m⁻² at Black Point tufa shoals for Mono Lake, and from 0.7–1.5 g m⁻² at mp 86 and mp 81 respectively for Abert Lake. The average summer biomass for *E. cinerea* at Great Salt Lake (Collins, 1980a) range from 3.8 g m⁻² on sand, to 49 g m⁻² on rock and mud substrates, with a whole-lake mean of 7.9 g m⁻². These values probably overestimate annual mean biomass. However, comparable summer figures at Mono and Abert are nonetheless lower, at 0.8–4.6 g m⁻² and 1.5–5.1 g m⁻² respectively (for the littoral zone at 30–50 cm sample depth only). Considering the incomplete sampling method (certainly missing many larvae in the kick-net census, not even considering first and second instars), overestimation of sampling area per kick (probably not as much as a half-square meter encompassed by each

kick sample), and multivoltine population dynamics, these numbers might underestimate biomass by as much as an order of magnitude or more. Comparisons with other saline lakes for which benthic standing stock biomass has been determined are compiled in Table 4. These lakes represent some of the most productive habitats for benthic fauna known from any aquatic habitats.

While the results of the preceding ecological comparisons suggest that biotic interactions may be important in *E. hians* population regulation at low salinities, and that physiological limitations may operate at high salinity, the validation of the predictions of this hypothesis will require further data from other habitats to fill in the salinity range. In addition, experimental studies of water chemistry, food resource, and predation and competition effects on life history are needed to separate and quantify the consequences of variation in these abiotic and biotic factors to survival, development, reproduction, and population growth potential.

Acknowledgement

This research was supported by grants from the U.S. Fish and Wildlife Service, the Mono Lake Founda-

tion, Los Angeles Department of Water and Power, The American Museum of Natural History, and Sigma Xi. I thank the following individuals for suggestions and improvements in this manuscript: N. C. Collins, F. P. Conte, V. J. Brookes, P. B. McEvoy, J. M. Melack, and an anonymous reviewer. The research collection of pinned adult flies from this study is housed in the Entomology Museum at Oregon State University.

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