

## BIOGEOGRAPHY AND PHYSIOLOGICAL ADAPTATIONS OF THE BRINE FLY GENUS *EPHYDRA* (DIPTERA: EPHYDRIDAE) IN SALINE WATERS OF THE GREAT BASIN

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**ABSTRACT.**—Four species of the genus *Ephydra* are commonly found in saline waters within the hydrologic Great Basin: *E. hians*, *E. gracilis*, *E. packardi*, and *E. auripes*. Though none of these brine flies is endemic (distributions also occur outside the Great Basin), they all inhabit distinctive habitat types and form the characteristic benthic insect fauna of inland saline-water habitats. The affinities of each species for different salinity levels and chemical compositions, and ephemeral to perennial habitats, appear to form the basis for biogeographic distribution patterns. Within any habitat, changing salinity conditions over time may impose physiological or ecological constraints and further alter patterns of population productivity and the relative abundance of co-inhabiting species.

Based on the physiology of salt tolerance known for these species, high salinity conditions favor *E. hians* in alkaline water and *E. gracilis* in chloride water. At lower salinities, based on limited habitat data, *E. auripes* and *E. packardi* are often more common, again showing respective preferences for alkaline and chloride chemical conditions. Specialized adaptations for alkaline carbonate waters are found in the larval Malpighian tubule lime gland of the alkali fly *E. hians*, while high salt tolerance in *E. gracilis* appears to be conferred by high hemolymph osmolality. Adaptation to ephemeral and low salinity conditions may be accomplished by swift adult colonizing ability and rapid larval development rates.

It is hypothesized that adaptive specializations in both physiology and life history and varied geochemistry of saline water habitats across the Great Basin produce the biogeographic pattern of distributions for species in this genus. This perspective on the genus *Ephydra*, and possibly other biota of mineral-rich Great Basin waters, suggests that interconnections among pluvial lakes may be less relevant to aquatic biogeography than chemical profiles developing in remnant lakes and ponds with the progression of arid post-pluvial climatic conditions.

*Key words:* *Ephydra*, saline lakes, Great Basin, osmoregulation, biogeography, salt tolerance.

Ever since the studies of Hubbs and Miller (1948), biogeographic studies of the aquatic fauna of the Great Basin have been dominated by a search for vicariance patterns. Distributions of fish species often revealed patterns suggesting pluvial interconnections among lake basins and provided evidence for post-pluvial hydrographic changes including isolation leading to extinctions and species differentiation (Miller 1946, Smith 1978). In addition to fish, other obligate aquatic species (e.g., spring snails, leeches, molluscs) have received an inordinate amount of attention because of the potential for endemic distributions arising out of the vicariance events of pluvial lake drying and recession, and the example set by Hubbs and Miller (Taylor 1960, Hershler 1989, Hovingh 1995). Insects with poor dispersal ability have also been studied in some depth in the Great Basin (e.g., Naucoridae; Polhemus and Polhemus 1994), but biogeographic patterns for most other aquatic invertebrates

within the Great Basin have been only incompletely described. Habitat affinities are poorly known, and collection records typically have no associated physical or chemical data.

In addition to geographic barriers, differentiation of populations may also result from differences in the physical and chemical features of aquatic habitats without producing geographic isolation and endemism. Selection for physiological adaptation may restrict species distributions to certain habitat types. Great Basin aquatic habitats often include waters with varied chemistry derived from high mineral content. The closed-basin drainages that define the Great Basin collect and evaporate water in saline lakes, ponds, and wetlands. Many springs (geothermal and otherwise) contain high concentrations of dissolved solutes and trace minerals. Streams in lower elevations of the basin and range also typically have relatively high conductivity and alkalinity. Physical conditions also may be quite varied

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in terms of thermal regime (hot springs) and ephemeral and episodic filling of playas and intermittent streams. Gradients of chemical and physical variation form a habitat template that sets the stage for adaptive syndromes determining the distribution and abundance of species (*sensu* Southwood 1977).

Geochemical evolution of major solutes in closed-basin saline lakes (e.g., Eugster and Jones 1979) may be a useful model for following progression and patterns in the biological evolution and distribution of saline water biota throughout the Great Basin. Water chemistry is determined primarily by the following factors:

- drainage basin lithology of inflowing waters (especially igneous vs. sedimentary);
- mineral precipitation pathways depending on the initial ratio of bicarbonate to calcium and magnesium and resulting in lake brines with differing contents of the major cations  $\text{Na}^+/\text{Ca}^{+2}/\text{Mg}^{+2}$  and major anions  $\text{Cl}^-/\text{SO}_4^{-2}/\text{CO}_3^{-2}$  (high bicarbonate generally evolves into alkaline brines and low bicarbonate into chloride-sulfate brines, and low salinity conditions may retain similar content of bicarbonate and Ca/Mg without forming precipitates);
- fractionation processes which enrich highly soluble (conservative) ions such as Na and Cl and deplete others through carbonate mineral formation, release of carbon dioxide gas, and biogenic reduction of sulfate for example.

Progressive enrichment from carbonate to sulfatochloride to chloride waters appears to occur with the concentration of inflowing waters over time and distance along interconnected evaporation basins of varied volume (Hutchinson 1957). Spatial and temporal components of variation in water chemistry form a habitat template that may be the foundation for shaping the distribution of saline water organisms.

Four species of the genus *Ephydra* are commonly found in saline waters within the hydrologic Great Basin: *E. hians*, *E. gracilis*, *E. packardi*, and *E. auripes*. Though none of these brine flies is endemic (distributions also occur outside the Great Basin), they inhabit distinctive habitat types and form the characteristic benthic insect fauna of inland saline water habitats. Wirth (1971) first suggested

that some *Ephydra* had particular chemical preferences. The objective of this paper is to present evidence for the hypothesis that affinities of each species for different salinity levels and chemical compositions, and ephemeral to perennial habitats, form the basis for biogeographic distribution patterns.

## METHODS

Contrasts of physiological specializations for habitat chemistry are presented here as evidence of adaptations that determine biogeographic patterns. Data for comparisons of osmoregulatory physiology and salt tolerance in *Ephydra* were derived from published research (Nemenz 1960, Herbst et al. 1988). Calculations of relative costs of osmoregulation were determined by applying the known osmotic gradients to calculations of the relative energy required for the work of active transport. Data on the range of known development times in *Ephydra* were also summarized from published sources (Ping 1921 for *E. packardi*, reported as *E. subopaca*; Collins 1980a for *E. gracilis*, reported as *E. cinerea*; and Herbst 1986 for *E. hians*). Distribution data were derived from Wirth (1971) and further supplemented by collection records and habitat chemistry data of the author.

## RESULTS

Ecological and physiological limitations under changing salinity conditions in salt lakes appear to result in varied distribution and productivity of *Ephydra* spp. Distribution maps (Figs. 1, 2) and limited habitat data suggest high salinity conditions (usually  $>25 \text{ g}\cdot\text{L}^{-1}$ ) favor *E. hians* in alkaline water and *E. gracilis* in chloride water. In low salinity ( $<25 \text{ g}\cdot\text{L}^{-1}$ ) and ephemeral waters, *E. auripes* and *E. packardi* are often more common, again showing respective preferences for alkaline and chloride chemical conditions. The general prevalence of *E. gracilis* in the eastern, and *E. hians* in the western, Great Basin correspond to the trend in lake geochemistry being derived from eastern sedimentary vs. western igneous lithology in the generation of chemical profiles (Jones 1966, Fiero 1986). Habitats in which I have collected *E. auripes* and *E. packardi* are typically small, shallow seep and spring outflows onto saline playas, whereas *E. hians* and *E. gracilis* habitats are often large, deep

perennial lakes or ponds. Within the Owens–Death Valley system of the southwest Great Basin, *E. auripes* is common in alkaline seeps around Owens Lake, while at the Death Valley terminus of these once-interconnected basins, *E. packardii* dominates the chloride waters of small seeps.

Comparisons of osmoregulation in *E. gracilis* and *hians* (Fig. 3) show that *E. gracilis* regulates hemolymph osmolality at an unusually high level for insects (700–1000 mOsm; Nemenz 1960), and about 3 times that found in *E. hians* (Herbst et al. 1988). The energetic cost of osmoregulation against this gradient may be calculated as shown by Potts and Parry (1964):

$$\text{Calories} = \sum_{\text{all solutes}} PA \cdot RT \cdot \ln \frac{C_h}{C_l} + nFE$$

where  $P$  and  $A$  refer to integumentary permeability and area,  $R$  is the gas constant,  $T$  is temperature,  $C_h$  and  $C_l$  are the high and low concentrations of the concentration gradient (external or internal),  $n$  is ion valence,  $F$  is Faraday constant, and  $E$  is the electrical poten-

tial difference. As a first approximation, the osmotic concentration gradient can be used to estimate energetic costs assuming cuticular permeability ( $P$ ) and surface area ( $A$ ) and electrical gradient ( $E$ ) are similar for both species and chemical conditions, and all other units are constants; the relative cost becomes proportional to the natural log of the osmotic gradient  $C_h/C_l$  (Fig. 4). The cost functions shown indicate that *E. gracilis* may inhabit more saline waters because high hemolymph osmolality reduces the gradient, and relative cost is only about half that for *E. hians* at an equivalent external salinity. Chloride waters tend to be more hyperosmotic than carbonate because the osmotic concentration is higher for an equivalent TDS ( $\text{g}\cdot\text{L}^{-1}$ ) concentration.

While *E. gracilis* possesses physiological adaptation for life in high salinity chloride water, *E. hians* shows much greater tolerance for life in carbonate waters (alkaline soda lakes) than in chloride waters. LC-50 toxicity values occur at lower concentrations in chloride water than carbonate water (Figs. 5A, 5B). *E. hians* is adapted to alkaline carbonate lakes by virtue of the lime gland (Herbst and Bradley

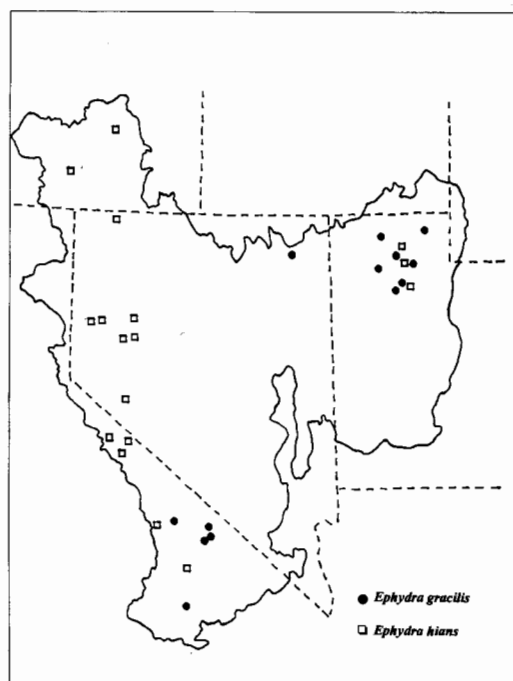


Fig. 1. Distribution of *Ephydra gracilis* and *Ephydra hians* within the hydrographic Great Basin. Based on Wirth (1971) and supplemental collections.

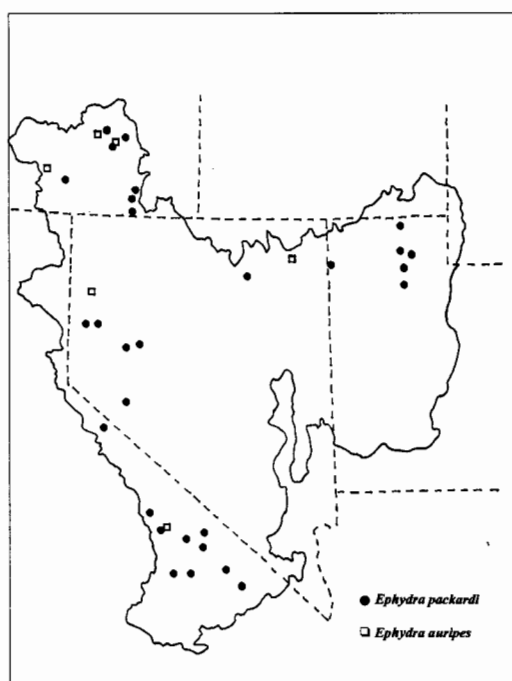


Fig. 2. Distribution of *Ephydra packardii* and *Ephydra auripes* within the hydrographic Great Basin. Based on Wirth (1971) and supplemental collections.

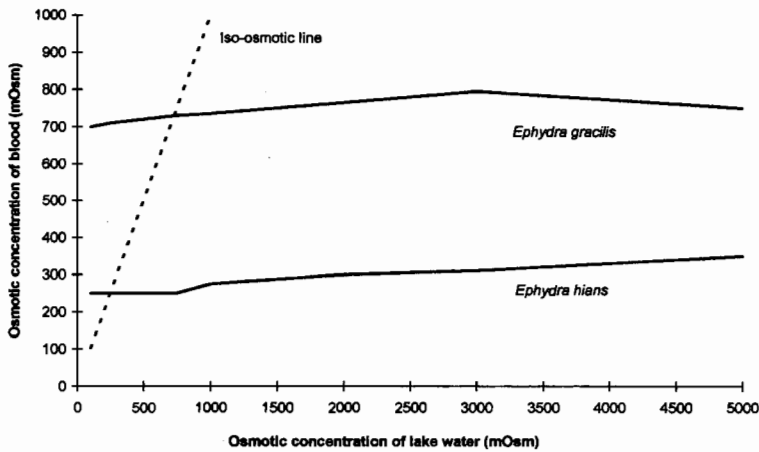


Fig. 3. Osmotic regulation in *Ephydra hians* (from Herbst et al. 1988) and *Ephydra gracilis* (from Nemenz 1960). Iso-osmotic line indicates where internal equals external concentrations.

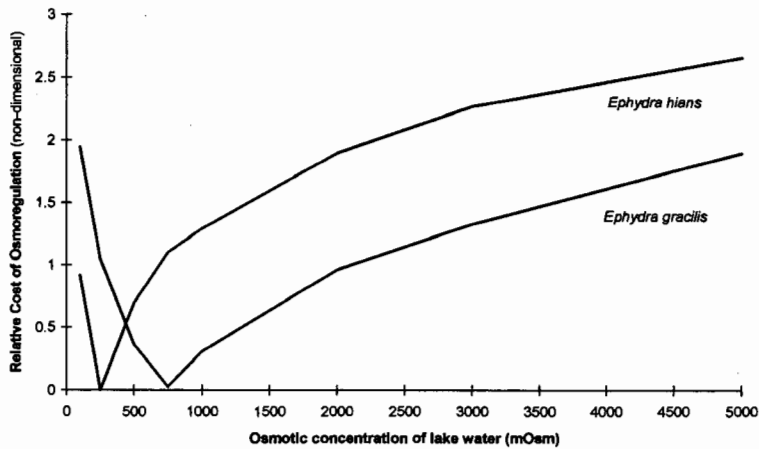


Fig. 4. Relative cost of osmoregulation in *Ephydra hians* and *Ephydra gracilis* based on osmotic gradient (cost is minimum where hemolymph and lake water are iso-osmotic).

1989). The lime gland is a modification of one pair of the Malpighian tubules in this species wherein calcium is concentrated and bicarbonate/carbonate are removed from the blood by forming a calcium carbonate precipitate within the tubules ("lime"). The intolerance shown by *E. hians* for chloride waters may indicate reduced capacity for regulating this anion though this species can survive in lower salinities of chloride water as suggested by the convergence of toxicity data for longer exposure times and lower salinities (Fig. 5).

Completion of a life cycle in ephemeral aquatic habitats involves such adaptations as

resting stages or diapause, colonizing ability, and rapid development (Williams 1987). A comparative summary of ephydrid development rates in ephemeral vs. perennial habitats is given in Table 1. *E. packardi* has a short development time, comparable to *Scatella picea* from ephemeral ponds. This contrasts with the longer and more flexible development times seen in *E. gracilis* and *E. hians*, which may extend larval growth over long periods when exposed to the stress of reduced food availability or increased salinity. Species of temporary waters, without resting stages, do not have this option and must develop

TABLE 1. Duration of larval development in selected Ephydriidae.

	Range of larval development time for instars 1-3 (days)	Habitat type	Reference
<i>Ephydra packardii</i>	11-13	ephemeral saline pools	Ping 1921
<i>Ephydra gracilis</i>	16-30 >100*	saline lakes	Collins 1980a
<i>Ephydra hians</i> **	15-58 >120*	saline lakes	Herbst 1986
<i>Scatella picea</i>	4-11	ephemeral ponds	Connell and Scheiring 1982

\*Under food limitation or salinity stress

\*\*Range for populations from Mono and Abert lakes at 50 g L<sup>-1</sup> salinity and excess food

rapidly to reach maturity and disperse to new habitat. *E. packardii* exhibits this type of life history. In addition, *E. packardii* exhibits best growth at 40-50 g L<sup>-1</sup> and cannot survive above 90 g L<sup>-1</sup> (Ping 1921), well below the limits for *E. gracilis* or *E. hians*.

#### DISCUSSION

Based on the physiology and expense of salt tolerance, high salinity conditions favor *E. hians* in alkaline water and *E. gracilis* in chloride water. At lower salinities, based on limited habitat data, *E. auripes* and *E. packardii* are often more common, again showing respective preferences for alkaline and chloride chemical conditions. Specialized adaptations for alkaline carbonate waters are found in the larval Malpighian tubule lime gland of the alkali fly *E. hians*, while high salt tolerance in *E. gracilis* appears to be conferred by high hemolymph osmolality. Adaptation to ephemeral and low salinity conditions may be achieved by rapid larval growth rates as seen in *E. packardii*. Biogeographic patterns of association with chemical and regional differences in habitat types correspond with differing abilities of these *Ephydra* species.

While water chemistry may broadly define the distribution of *Ephydra* spp. among different habitat types, salinity changes within a habitat appear to control population production of species and the relative abundance of co-existing species. The intermediate salinity hypothesis (Herbst 1988) proposes that abundance of salt-tolerant organisms is limited by physiological stress at high salinities and by ecological factors, such as predation and competition, in more diverse communities at low salinities (Fig. 6). Field observations have provided evidence of changing population dynamics

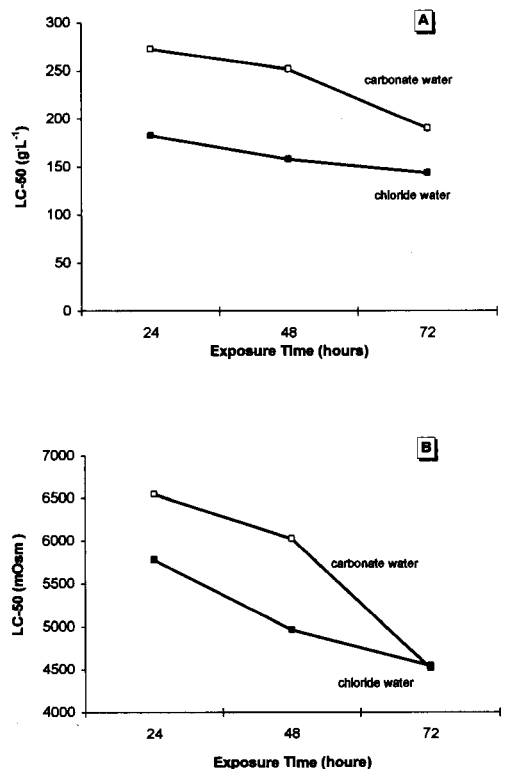


Fig. 5. Salt tolerance in third instar larvae of *Ephydra hians* exposed to saline waters where either carbonate or chloride are the dominant anions (from Herbst et al. 1988). LC-50 values are lethal concentrations at which half the exposed population dies as determined in mortality bioassays: A, expressed as total dissolved solids external salinity (g L<sup>-1</sup>); B, expressed as external osmotic concentration (mOsm = milliosmolar).

in fluctuating salt lakes. Increased abundance of *E. hians* at Mono Lake (California) and *E. gracilis* at Great Salt Lake (Utah) occurred during periods of salinity dilution (Winget et al. 1972, Herbst 1988). During a period of dilution of already low salinity at Abert Lake

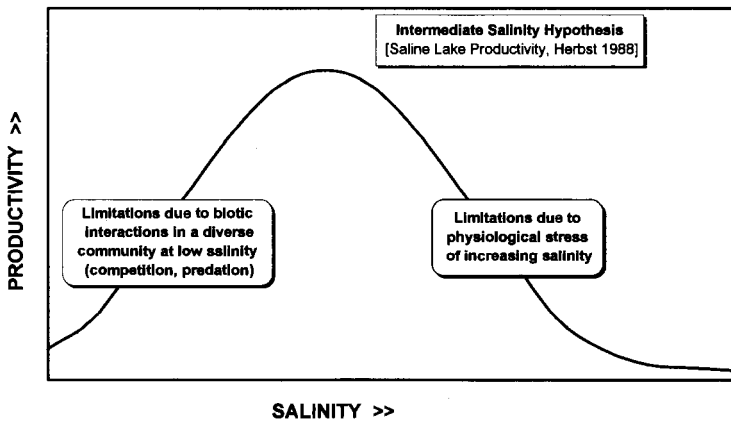


Fig. 6. Intermediate salinity hypothesis (Herbst 1988).

(Oregon), *E. hians* abundance was reduced in the presence of increasing numbers of other benthic invertebrates (Herbst 1988). Preliminary results of mesocosm salinity gradient experiments also support the intermediate salinity hypothesis (Herbst in preparation). Dilution of the chloride-rich waters of the Great Salt Lake has been followed by colonization and increased abundance of *E. hians*, where otherwise only *E. gracilis* was present (Welker and Havertz 1973, Collins 1980b). This last example suggests coexistence can occur within transitional regions of the physiological tolerance zones of *Ephydra* species.

Saline water habitats appear to be partitioned among the 4 species of Great Basin *Ephydra* along gradients of chemical composition, salinity, and stability (Fig. 7). This habitat template model (*sensu* Southwood 1977) predicts expected species distributions and potential changes in range and coexistence in space and time under varied environmental conditions. As a test of this conceptual model, further research on *Ephydra* spp. should include relating zoogeographic distributions to ionic tolerance and habitat chemistry using triangular anion diagrams, and comparisons of colonizing ability, life history traits, and population abundance along environmental gradients. For *E. auripes*, for which little data are available, the conceptual model predicts that this species has short development time, rapid colonization of new habitats, lower salt tolerance than *E. hians*, greater survival in carbonate than chloride chemistry, and poor competitive ability in coexistence with *E. hians*.

These data also might be applied to understanding other zoogeographic patterns in the Great Basin. Brine flies play a central trophic role in saline lakes as consumers of benthic algae, in turn providing one of the principal food sources used by migratory and breeding shorebirds and waterfowl (Jehl 1994, Rubega and Inouye 1994). The historical development of avian migratory routes and breeding colonies along the Pacific Flyway within the Great Basin during the Holocene may therefore be linked to salinity-related changes in the population production of *Ephydra* in different saline lake basins. Assuming that optimum production for *E. hians* is in the 25–100 g·L<sup>-1</sup> range, and for *E. gracilis* in the 100–200 g·L<sup>-1</sup> range, probable historical locations and changes of feeding grounds may be reconstructed from paleosalinity records alone.

Physiological and life history traits related to the selection regime of saline water habitats could provide distinctive characters for cladistics analysis and permit further investigation of the phylogenetic relationships in the genus *Ephydra* and other Ephydrinae (Mathis 1979a). Mathis separates *Haloscatella* from other subgenera of *Lamproscatella* partly on the basis of saline water habitat preferences, and it would be useful to examine further whether chemical tolerances among the species of the subgenus correspond to the cladogram presented (Mathis 1979b). The 5 Nearctic species of *Lamproscatella* (*Haloscatella*) spp. can be found within the Great Basin, and Mathis suggested that this is the zoogeographic origin of this group. Isolation through physiological adaptation to

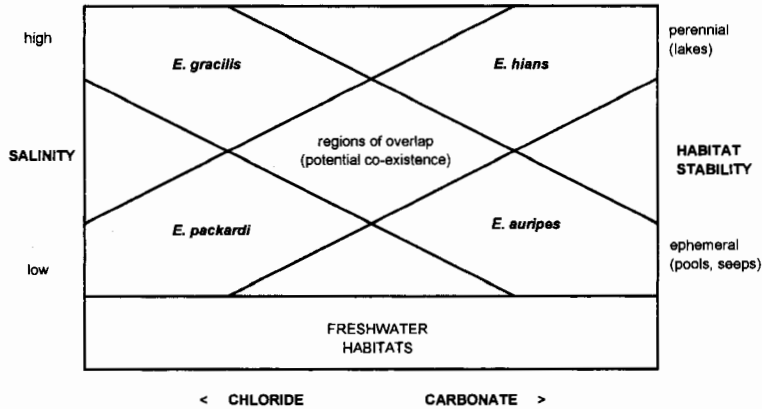


Fig. 7. Saline water habitat template for the distribution of Great Basin *Ephydra*. Each corner of environmental template inhabited primarily by a single species.

varied water chemistry may in fact be a more likely explanation for speciation and distribution in this group than through repeated vicariance through glaciation events as proposed by Mathis.

Other species in the genus *Ephydra* exhibit thermal adaptation. *E. geodeni* inhabits hot springs in freshwater to moderate salinities (Barnby 1987). *E. thermophila* and *E. bruesi* are endemics of acidic and alkaline thermal springs, respectively, in Yellowstone National Park (Collins 1977). Physiological adaptation and habitat partitioning along thermal, conductivity, and pH gradients may contribute to the origins and zoogeographic distribution of these species.

Other Ephydridae found in athalassic saline water habitats of the world may also exhibit biogeographic associations with geochemistry. Physiological adaptation to varied habitat geochemistry may exist in homologous ephydrid fauna in isolated desert regions such as the *Dimecoenia* spp. of the South American Altiplano, *Ephydrella* spp. of the Australian interior, and *Ephydra* spp. of the Old World (Wirth 1975).

Use of biological proxies as indicators of water chemistry of closed-basin lakes is well illustrated by the distribution of certain ostracode taxa in saline waters (Forester 1986). Species in the genus *Limnocythere* appear to have varied anionic preferences, with *L. staplini* found in chloride and sulfate waters, *L. sappaisensis* in alkaline waters, and *L. ceriotuberosa* in waters of mixed chemistry. Another species, *Candona rawsoni*, is found only in low salinity

alkaline water but can live in moderate salinities of sulfate water. These distributions suggest adaptations to different chemical conditions allow habitat partitioning. Fossil preservation of ostracodes permits their use as paleosalinity indicators. Other taxa with probable specific chemical-habitat affinities and potential for biogeographic interpretation through geochemistry include diatoms (Blinn 1994), corixids (Scudder 1976), and branchiopod crustacea (Bowen et al. 1985). Resh and Sorg (1983) have shown that lithium tolerance in the shore bug *Saldula usingerina* permits survival in certain thermal springs and can be used to predict local habitat distribution.

The remnants of pluvial Great Basin lakes are primarily saline bodies of water. Only a few perennial saline lakes remain (including Mono Lake, Abert Lake, Great Salt Lake, and Pyramid and Walker lakes), and many ephemeral ponds, wetlands, and spring seeps are also disappearing. Habitat loss has resulted primarily from stream diversion and spring development. Perennial lakes and ponds and other habitat refugia are threatened and must become part of a program of aquatic systems protection in the Great Basin to ensure the mosaic of habitats is available that has permitted the diversification of life such as is represented in the Ephydridae.

In conclusion, the following general syndromes of biogeographic patterns in the Great Basin are presented to reflect the importance of both vicariance and geochemical variation:

- obligate aquatic species (or those with poor dispersal ability) having restricted

or endemic distributions (habitat isolation through vicariance);

- obligate aquatic species with widespread distributions (wide tolerance);
- vagile species with widespread distributions and wide habitat tolerance;
- vagile species with restricted distributions due to specialized adaptations for certain chemical or physical habitat conditions (e.g., *Ephydra*, others).

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