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Gradients of salinity stress, environmental stability and water chemistry as a templet for defining habitat types and physiological strategies in inland salt waters

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Abstract

The search for pattern in the geographic occurrence of salt lake flora and fauna often reveals strong associations of specific taxa with certain types of water chemistry. Solute composition, along with salinity and habitat stability, may provide a templet shaping the distribution of many organisms inhabiting saline lakes. A review of studies demonstrating habitat associations, specific solute tolerance, and ionic and osmotic adaptations provide evidence of fidelity to particular conditions of environmental chemistry across a wide taxonomic spectrum. Under low salinity conditions, some species show osmoregulatory adaptability to varied solute composition but the capacity for such flexibility is reduced with increased salinity and only certain taxa are found in hypersaline waters dominated by a particular solute. Anionic ratios of chloride, bicarbonate–carbonate, and sulfate appear to be especially important determinants of distribution. Specific solute tolerance presents an alternative explanation to disrupted hydrographic connections in describing how biogeographic distributions may be restricted to certain aquatic habitats in arid regions. Physiological adaptations to chemistry, exemplified in the brine fly genus *Ephydra*, may be an integral part of the evolution, ecology and diversification of saline water organisms.

Introduction

A substantial body of work in environmental physiology has been dedicated to defining the range of adaptability to extreme conditions. Lethal limits of temperature, pH, oxygen availability and salinity, for example, have been determined for a variety of organisms – but why do such capabilities arise and how do these physiological strategies serve life under sublethal conditions? The thesis of this paper is that physiological tolerance to extreme physico-chemical conditions represents an avenue of escape from the adverse influences of predation and competition found in the more diverse communities of temperate environments. Susceptible organisms would be expected to be those that are most vulnerable as prey or as contenders for resources because they aggregate in local predictable habitat patches and/or have no specialized ability to exploit food resources. Physiological resistance to stress might be viewed as a means of establishing habitat refugia. Paths to these refugia in saline water environments form along gradients of chemical concentration (salinity), ionic composition and habitat permanence. These variables may form an ecological matrix for the evolution of clades or species complexes in differing saline environments depending on the geographic availability of chemical habitat niches and the physiological constraints inherent in different lineages. The objectives of this paper are to examine schemes for habitat classification, paths of geochemical evolution in salt lakes, some of the evidence for species associations with habitat chemistry, and an outline of integrated research needs for testing hypotheses.

Habitat classification and adaptive strategies

Schemes for organizing habitat types have often used gradients of the physical environment to arrange hab-

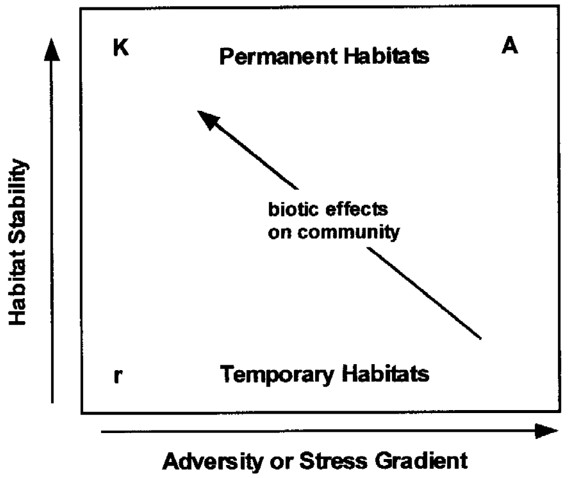

Figure 1. Southwood-Greenslade Habitat Templet (after Southwood, 1988). Letters indicate the classic adaptive syndromes to different combinations of stress and habitat stability: *K*-selected species are long-lived specialists, *r*-selected species are short-lived generalists, and *A*-selected species are tolerant of adverse environmental conditions. With reduced stress and more permanent habitat conditions the influence of biotic interactions (competition and predation) will become more important in structuring communities than physico-chemical forces.

itats. Holdridge (1967), for example, used humidity, precipitation and evapotranspiration to describe life zones supporting distinctive plant formations throughout the world. These, along with temperature, elevation, and maritime to continental gradients, have been used to broadly define the vegetation biomes of the world (Whittaker, 1975). Though often comprised of different plants on different continents, plants of each biome type share similar growth forms or physiognomy. Morphological and physiological traits unify the inhabitants of these similar environments. Since boundaries between habitats are often indistinct and changing, transitional zones are important sources of the spatial mosaics where different ecotypes may co-exist.

One of the most useful and general systems devised for habitat classification is in the form of a matrix termed the habitat templet (Southwood, 1977, 1988). In its simplest form, habitats are defined by levels of disturbance and adversity to which organisms respond with appropriate sets of traits such as short life spans and migratory ability in ephemeral environments, long life spans and resource specialization in stable environments, and physiological tolerance in adverse environments. This system for habitat classification has been used as a conceptual framework for predicting the types of life history traits organisms must possess to inhabit a particular type of habitat. Such a biological 'periodic table' of habitats and associated traits also provides a context for classifying inland saline water habitats (Fig. 1, the Southwood-Greenslade templet). In addition to life history traits related to habitat stability, physiological traits for salt tolerance adaptation to different types of chemical stress may form an important basis for habitat partitioning of salt lakes.

While diversity in growth form is often the most obvious feature associated with adaptation to different habitat types, physiological strategies may be most important in response to stress gradients. Character displacement is a well-known phenomenon in which divergent ecomorphs may arise in sequence from a common ancestor to exploit different resources by virtue of differing morphologies (e.g. Losos, 1992). By analogy, divergent physiological ecotypes for osmotic and ionic regulation may develop within a lineage when distinctive chemical environments present both the challenge and opportunity for colonization. For example, genotypes producing physiological variants with enhanced amino acid regulation of cell volume improved survivorship in the intertidal copepod *Tigriopus californicus* under hyperosmotic salinity stress (Burton & Feldman, 1983). Selection may operate to isolate such genotypes in the habitats where they function at best advantage.

The cost of homeostatic adjustment in the face of stressful conditions will likely be in the diversion of energy from other metabolic uses such as growth, development rate, defense or behavioral activity. That a trade-off exists between the cost of tolerance to stress and competitive ability has been well-stated by Southwood (1988): "By meeting these costs these species live in adverse habitats away from most biotic agents; they can survive and may even flourish in less adverse conditions, but only if given some protection from the increased levels or competition and predation". Experimental studies of lakeshore plants exposed to gradients of wave-disturbance and nutrient stress have demonstrated a negative correlation between tolerance and competitive ability (Wilson & Keddy, 1986). Slow metabolic and growth rates are often associated with stress resistance, often rendering such organisms poor competitors for limited resources under mild environmental conditions (Hoffmann & Parsons, 1991). Further tests of trade-offs in competitive ability are needed both between species with differing levels of tolerance and within tolerant species over varied levels of stress. Salinity stress tolerance could provide an easily manipulated experimental system for examining such relationships.

Classification of inland saline water habitats

Salt lake environments can be classified in the context of the habitat templet model. Inland saline waters range in stability from shallow temporary ponds to large permanent lakes, and in adversity from dilute salinities to the extreme stress of salt saturation. Before examining how these gradients may produce distinct habitats, I will first review some ideas that have previously been presented as themes for classifying inland saline waters.

Hedgpeth (1959) attempted an early provisional arrangement of inland mineral water habitats as part of a symposium on classification of brackish waters. These included (A) hypersaline lagoons with periodic connection to the sea dominated by a euryhaline marine biota, (B) relict marine waters once connected to the sea, but now isolated and harboring a biota of mixed marine and freshwater origins, (C) salterns and brines comprised of chloride-dominated waters including evaporation ponds, solar salt works and natural brines such as the Great Salt Lake, (D) other inland brines of primarily sulfate and/or carbonate composition, and (E) mineralized waters of thermal springs and groundwater origins. Supporting evidence of a biota with strict affinity to each habitat was presented for some cases but poor records on water chemistry and physical settings for collections were a problem then, as now, in understanding what features unify habitat types. At the same symposium, Beadle (1959) stated on physiological grounds that saline habitats might be defined according to organisms incapable of maintaining dilute body fluids above isotonic conditions, those capable of limited regulation, and those able to maintain hypotonic blood even at high salinities (corresponding to 0–15 ppt, 15–50 ppt and above 50 ppt salinity). Bayly (1967) first introduced the term athalassic to distinguish non-marine saline environments from those of thalassic (marine) origins. Athalassic waters were defined to encompass those that (A) have never been connected to the sea, and (B) those that have been connected in the past but became isolated, evaporated completely and lost all marine life prior to re-filling. Inhabitation by organisms with freshwater ancestry further distinguished truly inland saline habitats from those of marine origin such as the hypersaline lagoons listed by Hedgpeth (1959).

Traditional classifications of the ontogeny of freshwater lakes have used trophic status to distinguish oligotrophic, eutrophic and dystrophic habitat types. Saline lakes may also be regarded as a terminal stage in the aging of endorheic lake basins (Whittaker, 1975). Por (1980) used changes in trophic structure (food chain length) with increased salinity as a means for classifying inland salt water habitats. Por restricted this classification scheme to hypersaline (above seawater) chloride-sulfate waters, claiming the biota of this chemical type to be different from those in carbonate waters. Based on reduced competitive ability and increased omnivory with increasing salinity, Por defined habitat categories corresponding to degrees of food-chain shortening as follows: (A) alpha-hypersaline waters have a reduced diversity of euryhaline taxa and reduced secondary productivity and include habitats of both marine and freshwater ('limnogenic') origin ranging from salinities in excess of seawater to about 100 g l^{-1}, and have intricate food webs of producers, grazers, and predators; (B) above 100 g l^{-1} diversity and primary production become severely restricted and these beta-hypersaline waters are characterized by an almost exclusively limnogenic biota with simple linear food chains and limited predation; (C) in gamma-hypersaline waters salinities in excess of 140 g l^{-1} become simple and imbalanced producer-grazer ecosystems (grazers exert limited control); and (D) delta-hypersaline waters in the realm of 200–300 g l^{-1} are basically producer-only systems comprised mainly of photosynthetic and chemosynthetic bacteria with little or no animal life and the lowest levels of diversity and productivity.

Based on a habitat templet approach to inland saline water classification (Fig. 2 and Table 1), the emphasis is placed on the traits that unify the biota in adaptation to physical and chemical gradients. As a simplified view, the habitat-adaptive strategy space can be divided into quadrants:

(1) Low to moderate salinity temporary ponds (lower left) represent one broad habitat type comprised of species with rapid development, migratory and/or dormant stages, limited osmoregulatory ability, broad or nonspecific ion regulation capacity, and poor competitive ability. Representative fauna include most branchiopod crustacea exclusive of *Artemia*, many Dipteran larvae including floodwater mosquitoes of the genus *Aedes*, some Coleoptera and Hemiptera. Two patterns of osmotic regulation (1) hyperosmotic

Table 1. Inland saline water habitat domains and syndromes of biotic adaptation. Examples drawn from invertebrates and habitats in the desert interior of North America

Low Salinity – Perennial *Physiological and Life History Traits*: • low salinity tolerance/osmotic and ionic regulation limited or none • resource competition/specialization • long-lived and larger body sizes • little dispersal/dormancy ability • slower growth, lower fecundity *Faunal Examples*: Diverse array of invertebrates including predators and trophic specialists. Vertebrates including endemic fish within isolated drainage basins. *Habitat Examples*: Early evaporative stages of large deep lakes such as Pyramid Lake and Walker Lake.	**High Salinity – Perennial** *Physiological and Life History Traits*: • high sality tolerance, extensive range of hypoosmotic regulation, anion preference often present • slower and flexible growth rates under stress, resulting in varied body sizes/fecundity at maturity • limited competitive/dispersal ability *Faunal Examples*: Brine flies (*Ephydra* & relatives) in benthic zone, planktonic brine shrimp *Artemia* (fish few to none). Few aquatic predators and little interspecific competition. *Habitat Examples*: Later evaporative stages of medium to large deep lakes of varied chemical composition such as Mono Lake, Great Salt Lake, Little Manitou Lake.
Low Salinity – Intermittent *Physiological and Life History Traits*: • rapid development • migratory/colonizing ability • limited osmoregulation: (a) hyperosmotic then conforming (b) hyper- then limited hypoosmotic • anion preference – some to none • resistant/dormant life stages *Faunal Examples*: Floodwater mosquitoes *Aedes*, fairy shrimp *Branchinecta*, water boatmen *Trichocorixa*. *Habitat Examples*: Playa environments, argillotrophic ponds, dispersed for instance over the Alvord and Black Rock Deserts, and the Carson Sink.	**High Salinity – Intermittent** *Physiological and Life History Traits*: • extreme resistance to high salinity via osmotic counter-solutes and cell structure (obligate halophiles) • rapid growth during hydrated phase followed by dormancy *Faunal Examples*: Metazoans absent or transient only, life restricted mainly to microbes such as halobacteria, come cyanobacteria, diatoms, methanogens, purple sulfur bacteria. *Habitat Examples*: Salt crust depressions and small astatic basins collecting and evaporating rainwater (dry lakebeds, e.g. Owens Lake).

regulation and limited conformity, and (2) hyperosmotic and limited hypoosmotic regulation, may further subdivide this category into low salinity and low to moderate salinity habitat types.

(2) Following a progression of increased salinity and habitat permanence (upper right) are large salt lakes of moderate to high salinity, exhibiting an evaporative sequence of mixed carbonate, to sulfate, to chloride waters. These classic saline lake environments are comprised of species with slower and flexible development rates, well-developed and specific osmotic and ionic regulation abilities, and poor-to-moderate competitive ability. The best-known examples are *Artemia* spp., *Ephydra* spp. and certain ostracods. This habitat type is further sub-divided according to the predominant anion chemistry, primarily as carbonate and chloride waters, with a more restricted province of sulfate water habitats. Stable spring-fed salt water pools may also fall in this category, notably including some of the pupfish of Death Valley (*Cyprinodon salinus* and *C. milleri*, Soltz & Naiman, 1978).

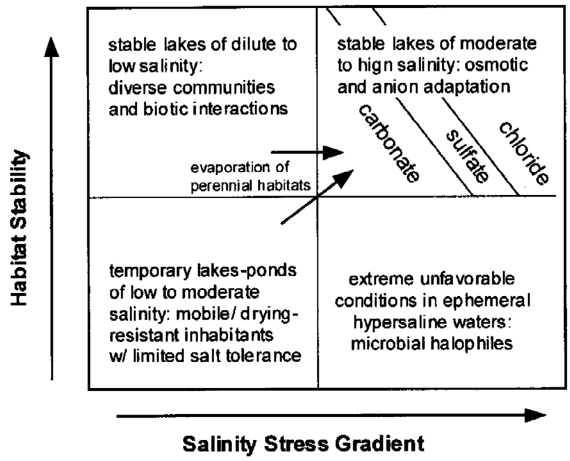

Figure 2. Habitat Templet for Inland Saline Waters. Simplified evaporative sequence of major anions shown for stable lakes of moderate to high salinity. Transition to more saline and stable habitats and geochemical evolution of anionic content (central arrows) selects for development of specialized physiological adaptations for osmotic and anionic tolerance. Low salinity permanent lakes are dominated by diverse biological interactions while highly saline instable environments are lifeless or inhabited only by halophiles.

(3) At the extreme of instable, ephemeral waters of high salinity (lower right) are generally uninhabited (except for microbial life) severe environments. Some category 1 organisms may be capable of ranging into such environments but the opportunities and examples are limited. Microbes such as halobacteria, certain methanogens, purple sulfur bacteria and cyanobacteria, and the green alga *Dunaliella* survive using osmotic counter-solutes to maintain cell integrity, and resistant stages to persist during dryness (including diatom auxospores).

(4) At the opposite extreme are large permanent lakes of dilute salinities in which biotic interactions dominate community organization. These waters are inhabited primarily by long-lived species with specialized abilities for resource utilization, poor tolerance of salinity stress (no hypoosmotic regulation), and reduced ability for migration or dormancy. A great diversity of flora and fauna, including a variety of fish, may live in such waters.

Geographic patterns of salt lake habitat chemistry

Descriptions of the geography and distribution of saline lakes have recognized sequences of chemical change along the evaporative series from sources to terminal lake sinks (Hutchinson, 1957; Cole, 1968). Using triangular plots of relative chloride, carbonate and sulfate anion composition, trends of brine evolution within drainage basins become apparent. Examining closed basins from throughout the world, the general pattern of geochemical change appears to follow a path from carbonate source waters to chloride most commonly, or sulfatochloride composition. If initial carbonate is sufficient the series will pass through mixed chemistry to carbonatochloride type waters. Geochemists have emphasized the importance of initial Ca+Mg/HCO_3 ratios in determining the solute branchpoints leading to terminal lakes of differing composition (Eugster & Jones, 1979). With Ca+Mg in excess, chloride or sulfatochloride waters will result. When the ratio is near equal, the level of Mg relative to Ca will affect mineral precipitation of calcite, gypsum or mirabilite and from these branchpoints shift the balance toward differing anion compositions. With bicarbonate in excess of Ca+Mg, alkaline soda lakes are formed. The nature of the geologic source material as the starting point also modifies the potential chemical pathway. A simplified view of this is that volcanic substrata promote carbonate chemistry, while inflows off sedimentary deposits favor chloride or sulfate dominant lake waters.

It is possible that biological evolution tracks geochemical evolution along the series of habitats that become available within a drainage basin. As lakes evaporate or expand, altered chemistry forms a changing mosaic of habitats to which physiological specialists will have selective advantages in colonization and persistence. Branching of a lineage (formation of a clade) may occur as habitats arise over spatial and temporal gradients of chemical differences and provide opportunities for diversification.

Habitat associations of salt lake flora and fauna

The absence and incomplete gathering of physicochemical habitat data to associate with biological collections have impeded progress in the classification of distinct ecological communities in salt lakes. While early authors regarded hypersaline lakes as harboring a cosmopolitan biota because of the widespread occurrence of *Artemia* and *Ephydra*, these genera and relatives are now recognized as being comprised of a diversity of species including endemics and physiological specialists (Bowen et al., 1985; Barnby, 1987; Collins, 1977; Herbst, 1999). Data sets such as those collected by Blinn (1993) for benthic diatoms in North

American lakes permit classification and ordination analyses suggesting the key factors forming boundaries for habitats and distinctive species assemblages. Cluster analyses from Blinn's study found diatom assemblages formed groupings both along gradients of conductivity and anion composition. Extension of such an approach to broad geographic surveys of other taxa could provide the basis for further delineating the communities of saline water habitats.

Extensive sampling of ostracods in saline waters of North America has revealed distinct anionic associations within the genus *Limnocythere* (Forester, 1986). Anion diagrams show *L. staplini* is found in chlorosulfate waters (favoring high salinity sulfate), *L. sappaensis* in carbonate waters, and *L. ceriotuberosa* in mixed chemistry but most associated with high chloride salinity. Studies of populations of *Artemia* from lakes of diverse chemical backgrounds have demonstrated ecological isolation and nascent speciation owing to anionic specificity in nauplius to adult survival (Bowen et al., 1985). Even among strict halophilic bacteria there is preference in anionic content shown between alkalophilic and non-alkalophilic halobacteria (Javor, 1989). Many clades in the biota of inland saline waters may not yet be apparent because the habitat associations of congeneric species have been so poorly documented by collectors (viz. the county or township/sector data often given as the only locality information on museum labels), and because physiological diversity may be masked by morphological similarity (as in the sibling species of *Artemia*).

Examples of species with broad ionic tolerance (no apparent anionic preferences), and an osmoregulatory range limited to low salinities, often appear among inhabitants of shallow astatic habitats. These are species where development rate, migration and dormancy are critical traits to survival in low salinity temporary waters. Among the smallest of all corixids (water boatmen) are species in the genus *Trichocorixa*. Two species in particular, *T. verticalis* and *T. reticulata*, are of interest for their preference for living in saline waters, primarily associated with habitats marginal to the marine environment. While coastal locations are the most common habitats for these species (Gulf and Atlantic coasts of North America for *T. verticalis* and Pacific coast for *T. reticulata*), the subspecies *T. verticalis interiores* is found in the arid interior basins of North America from the southwest up into Saskatchewan (Sailer, 1948). Habitats appear to range from low to moderate salinities (dilute to somewhat in excess of 50 g l^{-1}) but encompass carbonate and chloride habitats in the south, and sulfate waters in the north (Canada). This subspecies is capable of limited hypoosmotic regulation, shows no anionic preference, and may escape competition from many other corixids that are capable only of living in dilute salinities because they can hyperosmoregulate but perish above isoosmotic conditions (Tones & Hammer, 1975). Another subspecies, *T. verticalis saltoni*, is found in the Colorado desert of southern California in the vicinity of Salton Sea. This region also harbors populations of *T. reticulata* that are distinguishable from coastal specimens by notably smaller body sizes, possibly related to selection for shorter development time. This species is also capable of hypoosmotic regulation but shows no anionic preferences, though comparative physiological studies among subspecies or geographic populations have not been done for either species. Adult corixids are well known for their migratory flight ability and may move out of habitats as they become physiologically unsuitable. As predators, these corixids may further influence the presence and abundance of vulnerable prey such as *Artemia* in saline habitats (Wurtsbaugh, 1992).

Floodwater mosquito larvae of the genus *Aedes* (several species) have been shown to be capable of osmoregulation and survival in saline waters and display no anionic preferences or requirements (Bradley & Phillips, 1977; Sheplay & Bradley, 1982; Bradley, 1987). Hyperosmotic regulation via transport mechanisms localized in the Malpighian tubules and hindgut permit some of these mosquitoes to live in salinities up to 100 g l^{-1} (though the concentration is usually lower than this and of only short exposure to larvae developing in evaporating floodwaters). Larval development is rapid and adults disperse as opportunistic colonizers of whatever habitats become available for oviposition.

The dormant eggs produced by the diverse branchiopod crustacean fauna of temporary desert ponds appear to be the key adaptation of these organisms to this environment (Belk & Cole, 1975). Studies of osmoregulation in *Branchinecta campestris*, *B. mackini* and *B. gigas* (Broch, 1969, 1988) have shown hyperosmotic regulation up to isoosmotic conditions followed by osmotic conformity and eventual mortality when the blood reaches about twice this concentration.

Evidence that physiological tolerance can provide chemical refugia other than along salinity gradients can also be found in some freshwater invertebrates. For example, thin-shelled snails (*Physella*) may avoid predation by tolerance of low oxygen and high sulfide levels (Covich, 1981). Tolerance of high dissolved carbon dioxide by the spring snail *Pyrgulopsis montezumensis* has been proposed as a chemical refuge from competition and predation for this endemic species from Montezuma Well, Arizona (O'Brien & Blinn, 1999).

Distribution of *Ephydra* in Nearctic and Palaearctic habitats

Of 28 described species in the genus *Ephydra* in the Holarctic, only one, *Ephydra riparia*, is found in both the Old and New World (Wirth, 1971, 1975, 1976). This species is capable of limited hypoosmotic regulation and survives in low to moderate salinities in both inland and coastal environments (Sutcliffe, 1960; Zack et al., 1976). Given its distribution and modest salt tolerance, *E. riparia* may represent a potential ancestral type for the halotolerant members of this genus. Dendrograms based on limited habitat data for some of the Nearctic and Palaearctic species of *Ephydra* are presented in Figures 3 and 4. These are not intended to imply phylogenetic relationships but are ecological traits to be tested and incorporated into cladistic analysis. Excluding *E. riparia*, Nearctic *Ephydra* (Fig. 3) are most diversified in inland water environments of varied salinity and chemistry (including thermal mineral springs), with 12 of 15 species found in these habitat types and only 3 associated primarily with coastal habitats (usually in the supralittoral splash zone). In contrast, in all the Palaearctic and Afrotropical Regions, only 5 of 13 species occur mainly in inland habitats and all others are associated with coastal marine-derived saline habitats (Fig. 4). These patterns suggest that in general, the Old World has more geographically diverse coastal environments and less varied continental salt-water habitat relative to the Nearctic Region. The taxonomy and distribution of saline habitat ephydrids in the Neotropics has yet to be adequately described but this would be a good region to test the correspondence between the chemical diversity of inland waters and the inhabitant brine flies.

Physiological investigations of this genus have demonstrated the capacity for hyper- and hypoosmotic regulation in all species examined (*E. riparia*, Sutcliffe, 1960; *gracilis* as *cinerea*, Nemenz, 1960; *hians*, Herbst et al., 1988; and *geodeni*, Barnby, 1987). Contrasts of *E. hians* and *E. gracilis*, the two most saline tolerant species, reveal physiological specializations for life in alkaline waters and hypersaline chloride waters, respectively (Herbst, 1999). The Malpighian tubules of *E. hians* permit carbonate excretion (Herbst & Bradley, 1989), while homeostasis of hemolymph osmotic concentration at high levels allows *E. gracilis* to survive in high chloride salinities. The rapid development rate of *E. packardi* (as *E. subopaca*, Ping, 1921) suggests this species has undergone selection for life in temporary saline waters. Using the habitat templet, it is possible to generate hypotheses regarding other expected associations between physiological and life history traits and habitat types. Herbst (1999) predicted that *E. auripes* and *E. packardi* should be found in temporary habitats, have more limited osmoregulatory ability relative to *E. hians* and *E. gracilis*, poorer competitive ability, but show more rapid development, colonization ability, and some anionic preference. Physiological tolerance of sulfate might be expected in *E. pectinulata* given its northern distribution, but no anion specificity in *E. riparia*. In addition to trade-offs between tolerance and competitive ability, anion affinity in some species implies that there is reciprocal loss of the capacity to adapt to high concentrations of other anions. Predictions of patterns in osmotic and ionic regulation, life history traits and habitat relations are all amenable to experimental test through comparative studies of these and other congeneric species complexes. Stress tolerance along thermal gradients appears to be another strategy for escape from biotic influences in the genus *Ephydra*, and for the Yellowstone endemics *E. thermophila* and *E. bruesi*, hot spring habitats appear to be further partitioned along a pH gradient (Collins, 1977).

An integrated program for research

Unifying features among saline lake habitats and their biota may provide the basis for developing a system of classification. Verifying the predictions of the habitat templet model will require the coordinated efforts of an interdisciplinary research plan (Table 2). Quantitative measurement of the environmental settings in terms of salinity and stability are a priority need to test and place limits on the domains of the habitat matrix. From collectors and naturalists, sampling should include associated water chemistry data (major anion and cation content, salinity, pH) from the habitat of origin. Hydrologists and geochemists can provide measures of habitat stability in terms of response time and coefficient of variation in area (*sensu* Langbein,

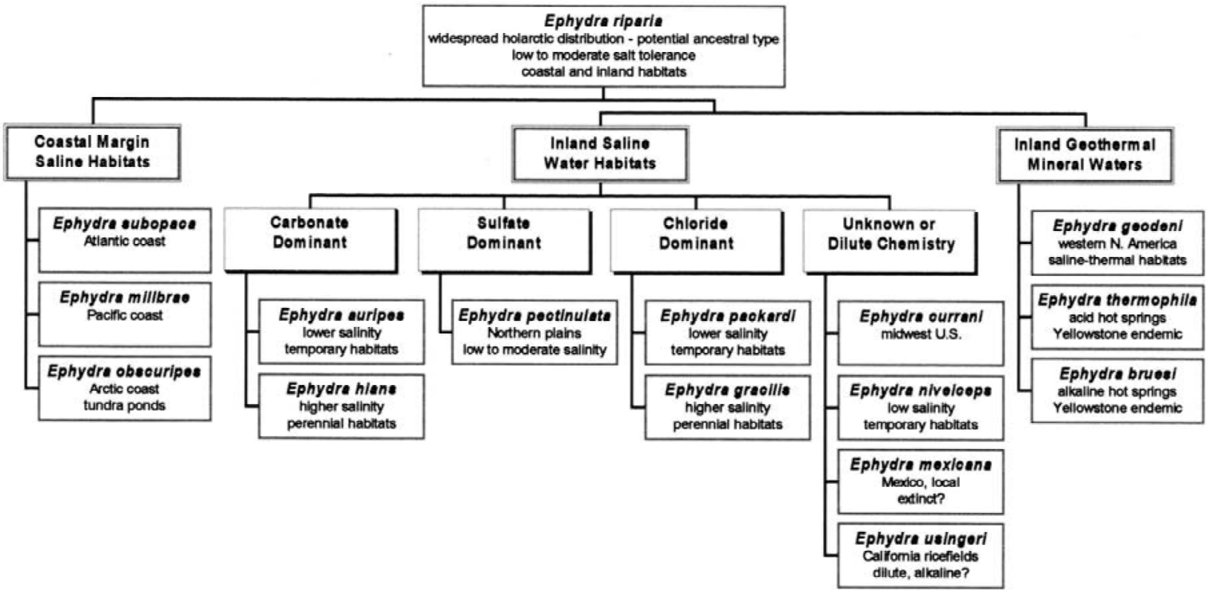

Figure 3. The genus *Ephydra* in Nearctic saline water habitats. Contrasts inland from coastal marine habitat preferences and potential origins or relationships of these species based on habitat chemistry (based on Wirth, 1971).

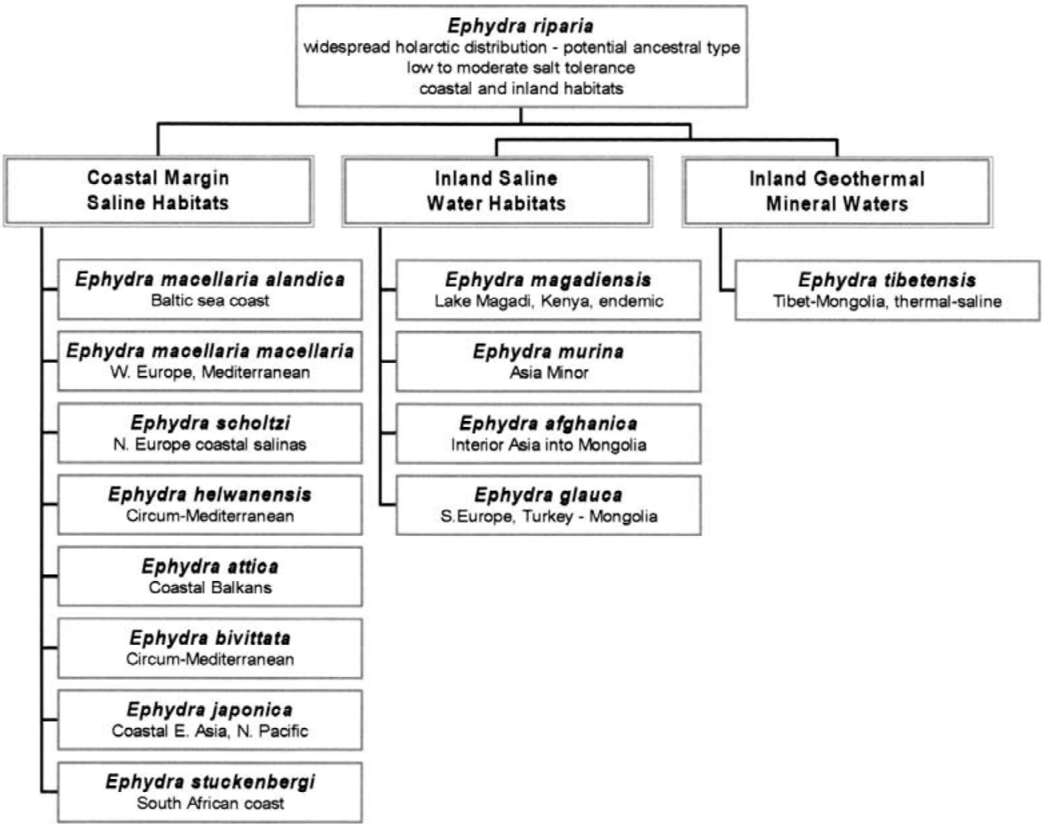

Figure 4. The genus *Ephydra* in Palaearctic and Old World saline water habitats. Contrasting inland from coastal marine habitat preferences (based on Wirth, 1975).

Table 2. An integrated research plan for defining the habitat templet of saline lakes

Discipline	Data contribution needed	Purpose
Collectors and naturalists	Associated habitat salinity, stability, solute chemistry for collections of flora and fauna	Provide data for defining the relationship of species distributions to the chemical and physical setting of habitat locales
Hydrologists and geochemists	Measures of the spatial and temporal components of salinity gradients, and the stability of habitats (e.g. response time and coefficient of variation in lake area)	Develop a basis for quantifying the distribution of biota along gradients of habitat salinity and stability
Physiologists	Comparative ion tolerance within and between congeneric species complexes of saline water biota; tests of trade-offs between tolerance and competitive ability, and between ion regulating mechanisms	Test hypotheses that suites of traits enabling adaptation to particular environmental conditions result in obligate fidelity to that habitat, and even define habitat types according to the unifying traits of the biota
Systematists	Phylogenies and cladograms developed from habitat associations and physiological phenotypes to supplement or contrast with results using traditional morphological data	Examine the question of biological diversification in terms of the opportunity for specialization in the diverse geochemical environments of saline waters
Stratigraphers, palaeolimnologists	Correlation of sediment core communities with data from experimental calibrations of biological proxy responses to salinity and solute variation	Improve the accuracy of reconstructions of ancient environments, lake ecosystems, and regional climatic histories

1961), and historical geographic information on the spatiotemporal distribution of lakes of varied composition. Comparative physiologists should investigate more thoroughly the differences in salinity and ionic tolerance between and within congeneric species, the regulatory mechanisms for coping with chemistry, and develop experiments to test for predicted trade-offs among physiological and life history traits. Systematists may complement conventional cladograms based on morphology with data on discrete traits of physiological phenotype and habitat associations. Plesiomorphic traits are expected to be associated with low salinity mixed chemistry adaptations and apomorphic derived traits with the terminal branchpoints of solute evolution and anion predominances. This approach to cladistic analysis might be used along with molecular methods to construct phylogenies related to the sequential evolution of species complexes in saline water environments.

An integrated research approach may provide insight not only to current biogeographic patterns of habitat utilization but also to the past. Palaeolimnologists and stratigraphers might be able to improve the accuracy of historical reconstructions through calibration of biological proxy responses to experimental variation of salinity and/or solute composition (e.g.

Herbst & Blinn, 1998). Differences in regional geochemical evolution also become a viable alternative explanation to geographic isolation by glacial vicariance events as has been often used to explain the distribution of aquatic fauna (Herbst, 1999). Through coordinated surveys and experimental studies, the variety that characterizes saline lake environments may find unifying themes for the outline of an ecological templet for organizing these habitats.

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