Demography and habitat use of the Badwater snail (*Assiminea infima*), with observations on its conservation status, Death Valley National Park, California, U.S.A.

Donald W. Sada
Desert Research Institute and University of Nevada, Reno, Biological Resources and Research Center, U.S.A.
Mailing address: 2215 Raggio Parkway, Reno, NV 89512-1095, U.S.A.

Key words: Assiminea ecology, Death Valley National Park, Mollusca, spring ecology, riparian management, playa, habitat use, disturbance

Abstract

Cultural use of spring-fed wetlands in Death Valley National Park, California has reduced populations of endemic macroinvertebrates. Studies were conducted during the spring and late autumn of 1994 to assess demography and habitat use by the Badwater snail (*Assiminea infima*), which is endemic to low-elevation, spring-fed habitats in Death Valley where its abundance is believed to be adversely affected by municipal diversions and habitat trampling by Park visitors. Effects on demography and habitat were examined at sites highly, lightly, and unaffected by these activities. Field experiments examined the response of its habitat and abundance to trampling.

Snail density ranged from 0 to 19 000 m^{-2} along the banks of seven springs sampled at Badwater and Cottonball Marsh. Springbrooks with high, steep, and overhanging banks were preferred *A. infima* habitat. Mean distance of snails from water ranged from 1 mm at Badwater to 39 mm at Cottonball Marsh, and distance from water was greater in autumn than spring. Frequency distributions of shell height showed each population was comprised of several cohorts during spring and autumn, suggesting that reproduction occurs several times a year.

Field experiments demonstrated that trampling reduces bank heights, angles and overhangs, and *A. infima* population density. Actions are required to manage public use at Badwater to arrest declines in abundance and distribution of *A. infima*, and to allow for recovery. Historical diversion of springs for irrigation and municipal uses have reduced and dried many aquatic and riparian habitats in the Funeral Mountains, causing current distribution in these springs to be approximately 15% of historical levels.

Introduction

Desert springs in North America support many endemic fishes and macroinvertebrates, with some relictual populations surviving since the Pleistocene (Smith, 1978; Taylor, 1985). Recent taxonomic studies revealed a surprising diversity of endemic aquatic invertebrates, particularly mollusks (e.g. Hershler & Sada, 1987; Hershler, 1989, 1998, 1999), but there is little knowledge of their ecology. Historical and recent extinctions and population extirpations indicate that additional ecological information is needed to protect this unique fauna by facilitating implementation of conservation programs (Williams et al., 1985; Shepard, 1993; Sada & Vinyard, 2002).

Like many aquatic habitats in the Great Basin, many permanent wetlands in Death Valley National Park are spring-fed and occupied by endemic fishes and macroinvertebrates (Sada et al., 1995). The Badwater snail (*Assiminea infima*) is endemic to some of these habitats. The genus *Assiminea* includes several North American species. With the exception of Fowler's (1980) study of *A. californica* reproductive biology, there is little known about *Assiminea* life history and ecology. *A. californica* inhabits mud substrate in salt marshes along the Pacific coast from Vancouver Island to Baja California (Fowler, 1980). Knowledge of *A. infima* ecology is limited to qualitative information accumulated during taxonomic studies by Berry (1947) and Hershler (1987) who described it as a semimoist soils lying beneath salt crust that borders valley-floor springs at Badwater and Cottonball Marsh, and the moist basal stratum of riparian sedges, grasses, and debris along Texas, Travertine and Nevares Springs in the Funeral Mountains (Hershler, 1987). Its habitats ranges in elevation from 100 m above sea level in the Funeral Mountains to 86 m below sea level at Badwater.

Even though Death Valley is a National Park, a variety of cultural activities have modified its springs over the past 100 years. Habitats at Badwater have been affected by visitors who inadvertently trample vegetation and salt crust. Badwater is the lowest point in North America, and it is a popular attraction that is visited by at least 700000 people annually (Death Valley National Park files). Visitation to Death Valley has increased by approximately 15% annually over the past decade, suggesting that increased public use of Badwater will continue. *A. infima* habitat at Badwater is highly localized along several small springs that cover less than 0.5 hectare, where visitor use is most concentrated. Diversions, which provide the only water to Death Valley visitors and residents, have decreased discharge from many Funeral Mountains springs occupied by *A. infima*.

In contrast to Badwater, Cottonball Marsh is a large (approximately 260 hectares), remote wetland that is visited infrequently (probably <5 people/year) and undisturbed. It lies at least 10 km from the nearest road in Death Valley National Park Wilderness where the climate is severe and there is no potable water. Borax mining during the 1920s disturbed dry portions of Cottonball Marsh but avoided wetlands occupied by *A. infima*. It is one of the few aquatic habitats in western North America minimally affected by cultural disturbance.

This study assessed *A. infima* demography by examining spatial and temporal variation in habitat use, distribution, abundance, and age structure at Cottonball Marsh and Badwater. Preferred habitat was quantified at the two wetlands by assessing relationships between snail abundance and salient features of springbrook bank morphology. Potential impacts of public use were examined during field experiments that tested the response of *A. infima* abundance and salt crust habitat to minimal trampling. Distribution and relative abundance of *A. infima* at springs in the Funeral Mountains were also assessed.

Habitats occupied by aquatic animals endemic to Death Valley are relictual wetlands that have persisted since the Pleistocene Epoch. Many of these habitats have been isolated since the most recent Holocene lake in Death Valley retreated approximately 2000 years ago (Miller, 1981). *Assiminea infima* occurs at low elevations where mean annual precipitation is less than 3 cm and temperatures range from a maximum of 55 °C during summer to a winter minimum of −5 °C (Hunt, 1975). When field studies were conducted, air temperatures recorded at Furnace Creek (which is on the Death Valley floor and approximately 30 km north of Badwater and 15 km southeast of Cottonball Marsh) ranged from 10 °C to 36 °C in March and 8 °C to 24°C, in December 1994.

Cottonball Marsh

A. infima habitat lies along the west side of Cottonball Basin, which is a barren salt flat comprised mostly of sodium–calcium borate (Hunt, 1975). Observations during 12 visits between February 1993 and February 1996 indicated that *A. infima* occurs under salt crust that borders at least 60 springs where aquatic habitat is persistent. Most of these springs are inhabited by Cottonball Marsh pupfish (*Cyprinodon salinus milleri*) and Cottonball Marsh springsnails (*Tryonia salinus*); both are endemic to this wetland (La Bounty & Deacon, 1972; Hershler, 1989). These springs range from 5 cm to 1 m in depth, have an estimated mean wetted area of 40 m^2, and occur only within an area approximately 300 m wide and 1.5 km long. Many springs are connected during winter, but most are isolated during summer when evaporation decreases surface water coverage over the marsh by at least 90% (Hunt et al., 1966). Salt crust borders all springs, and pickleweed *(Allenfolfea occidentalis)* is the only vegetation present, which covers less than 1% of springbrook banks.

Maximum and minimum temperatures, recorded in snail habitat using a thermal probe (HOBO® thermograph, measurements every 72 min) placed beneath the salt crust along a south-facing springbrook bank, were 40 °C in July and 5 °C in January, respectively. Daily variation in habitat temperatures appeared to closely follow variation in ambient temperatures at Furnace Creek.

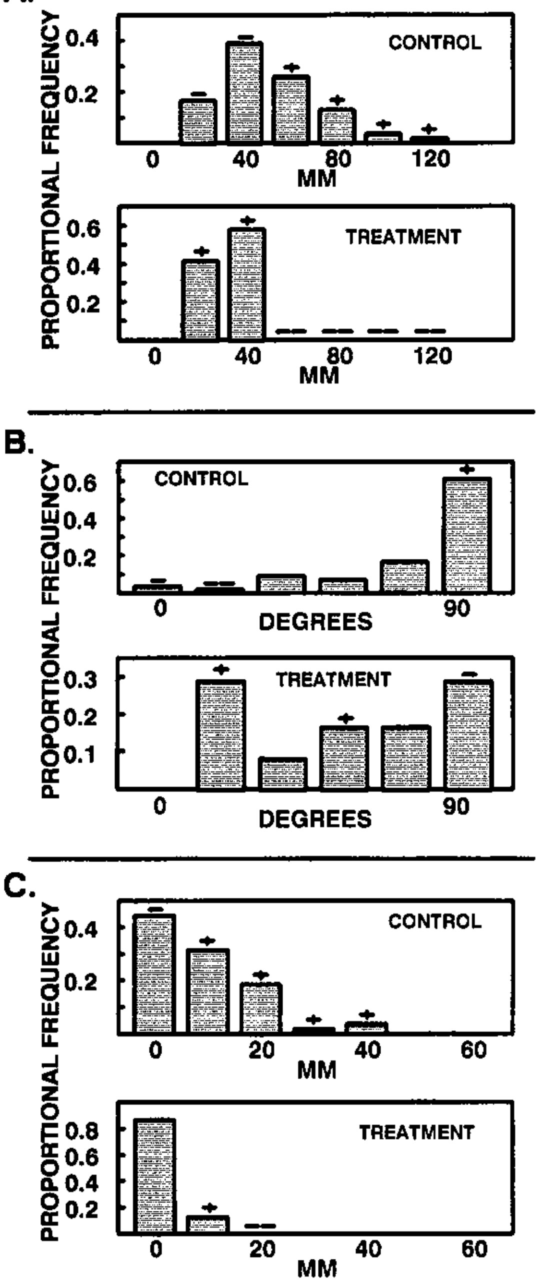

Figure 1. Frequency distributions of (A.) bank height, (B.) bank angle, and (C.) bank overhang occupied by *A. infima* in Cottonball Marsh control and treatment panels during autumn (following treatment). Positive electivity indicated by + for values between 0.1 and 0.5 and by ++ for values > 0.5. Negative electivity indicated by − for values −0.1 to −0.5 and by – for values <−0.5. Number of individuals observed for control and treatment blocks was 665 and 188, respectively.

Badwater is a small spring province covering approximately 0.5 ha of the eastern-most extent of the Badwater Basin, which is a barren salt flat composed of sodium, calcium, and magnesium salts (Hunt, 1975). Vegetation occurs peripherally in the basin and consists of widely dispersed patches of pickleweed, wire grass (*Juncus* spp.) and honey mesquite (*Prosopis glandulosa*). The basin is only wet during winters with high precipitation. Permanent aquatic habitat is limited to three small spring clusters at Badwater (referred to as South Pool, Middle Pool and North Pool). All of these springs are <3 cm deep during summer and total discharge from the province is estimated at 30 L min^{-1} (Hunt et al., 1966). Springs, vegetation (pickleweed and ditchgrass, *Ruppia maritima*) and *A. infima* are restricted to spring sources along the east side of Middle and North Pools. Snails do not occupy South Pool or the west banks of Middle and North Pools, where there are no spring sources. Snails occur under salt crust along springbrook banks, on moist pickleweed, and on ditchgrass. Ditchgrass is occupied only when shaded by vegetation, at night, or when Badwater is shaded by clouds or early morning and late afternoon shadows from surrounding topography. Snails quickly retreat into shadows provided by salt crust or vegetation when they are exposed to direct sunlight.

Visitor parking facilities at Badwater are adjacent to Middle Pool, and visitors commonly walk around Middle and South Pool. North Pool lies 200 m north of Middle Pool and is infrequently visited.

Funeral Mountains Springs

Spring provinces at Texas, Travertine, and Nevares Springs historically discharged approximately 9600 L/min that flowed several kilometers before percolating into alluvium (Travertine and Nevares Spgs.) or spreading on the floor of Death Valley (Texas Spg.) (Hunt et al., 1966). Discharge from these provinces was first captured during the 1930s for mining and tourism industries and diversions continue to support residences and tourism. Prior to diversion, Texas, Travertine and Nevares Springs flowed an estimated, 7.5 km, 5 km (Threloff & Koenig, 1999) and 2 km, respectively, before seeping into alluvium or spreading on the playa. Characteristics of habitats supported by these springs were never documented. Surface discharge from Texas Spring is currently less than 10 L/min, from Nevares Springs it is approximately 15 L/min, and approximately 50 L/min flows from ter currently discharges from a single pipe at Texas Spring, from six springs and one pipe at Travertine Springs, and two spring provinces at Nevares Springs. Estimated length of existing aquatic habitat is approximately 1 km at Texas and Travertine Springs (Threloff & Koenig, 1999) and 0.5 km at Nevares Springs. Travertine and Nevares Springs are also occupied by an endemic springsnail (*Inobius robusta*) (Hershler, 1989), riffle beetle (*Microcylloepus formicoideus*) (Shepard, 1992), naucorid bug (*Ambrysus funebris*) (La Rivers, 1948), and two amphipods (*Hyalella sandra* and *H. muerta*) (Baldinger et al., 2000).

Methods

Population and habitat studies were conducted from April 11 to 14 and December 11 to 14, 1994. Habitat was evaluated by measuring bank height (distance from water to highest point located within 3 cm of water), bank overhang, and bank angle (estimated to nearest 10° from water surface). These parameters were selected following preliminary studies that indicated snails were most abundant close to water where springbrook banks were high and well developed. Badwater studies excluded vegetated habitats where sampling would have caused excessive resource damage.

Habitat parameters and snail abundance were recorded at evenly spaced points along springbrook banks. Snail abundance was estimated within a panel of 3 contiguous quadrats, measuring 7 cm wide × 3 cm deep. Quadrat 1 was aligned along the water's edge and quadrats two and three extended sequentially away from the water. Density within each quadrat was estimated by carefully lifting salt crust and counting all individuals. Density estimates and habitat measurements were made at the same sites; habitat measurements were made at the center point of each panel. At North Pool, panels were spaced every 1 m. To assure 10 replicate samples at each site, Middle Pool sites 1 & 3 were sampled every 75 cm, and at Middle Pool site 2 samples were made every 60 cm. Data from the three Middle Pool sites were pooled for analysis.

Sampling at Cottonball Marsh was designed to quantify the same parameters measured at Badwater and to experimentally examine the response of habitat and snail abundance to trampling. Studies were conducted at three isolated springbrooks with salt crust characteristics similar to each other and to Badwater.

40 panels organized into ten blocks of four panels each. Five blocks were spaced every 1.5 m along both banks of each springbrook, and panels within each block were spaced 30 cm apart. Populations and habitat characteristics of unimpacted Cottonball Marsh sites were quantified during April, after which one-half of the blocks at each site were randomly selected and trampled with a booted foot for 30 s. Remaining blocks served as untrampled controls. Treatment blocks were trampled again for 30 s during September. Effects of trampling were assessed by comparing snail density and habitat in treatment and control block panels during April and December. Care was taken during December to avoid placing panels at locations that were disturbed during April sampling.

Proximity to water was determined by measuring the distance from water (to the nearest 1.0 mm) for approximately 100 of the first snails encountered during density estimates at each springbrook. Size distributions of each population were compiled using digital calipers to measure shell height (to nearest 0.1 mm) of these individuals.

Effects of public use on salt crust were assessed at Badwater by comparing crust relief in an unused area to relief on a hiking trail encircling Middle Pool. From a randomly chosen point, twenty relief measurements were taken at 1.5 m intervals on the trail and in adjacent, untrampled salt crust (1.5 m from the trail). Relief in used and untrampled salt crust was quantified as the coefficient of variation of measurements from a horizontal plane to the crust surface (measurements were made on a grid of 13 evenly spaced points within a 38.5 cm^2 circle).

Distribution and abundance were estimated at Nevares Springs during August 1999 and Texas and Travertine Springs during June 2000 by counting snails in grab samples of riparian grasses and debris. Habitat use was described by recording vegetation types occupied by snails.

Data analysis

Habitat use was evaluated by prorating use in accordance to the abundance of snails in a panel. Habitat preference was calculated using the equation: $D = r - p / r + p - 2rp$, where p is the proportion of resource available and r is the proportion of the utilized resource (Jacobs, 1974). Niche breadth was calculated using the equation $B = 1 / \sum P_{ij}^2$ where P is the proportion of all resources in each category (Levin (A.) Cottonball Marsh and (B.) Badwater Middle (MP) and North (NP) Pools during spring and autumn. g_1 = skewness

	Distance from water (mm)						Snail height (mm)	
	Spring			Autumn			Spring	Autumn
A.								
Site	*N*	M (± 1SD)	g_1	*N*	M (± 1SD)	g_1	M (± 1SD)	M (± 1SD)
1	92	12.8(18.2)	2.97	104	23.2(24.3)	1.21	1.7(0.1)	1.3(0.1)
2	100	39.0(30.3)	0.573	99	37.6(34.9)	0.863	2.2(0.6)	1.8(0.6)
3	100	17.3(13.8)	1.549	98	38.2(30.7)	0.645	1.6(0.6)	1.3(0.4)
B.								
Site	*N*	M (± 1SD)	g_1	*N*	M (± 1SD)	g_1	M (± 1SD)	M (± 1SD)
MP	164	3.7(8.4)	2.706	98	1.0(4.5)	5.660	1.9(1.4)	2.0(1.3)
NP	138	4.5(5.6)	1.265	99	4.0(4.0)	0.853	2.1(0.6)	2.1(0.9)

Table 2. Niche breadth values for bank height (BH), bank angle (BA), and bank overhang (BOH) for *A. infima* populations at Cottonball Marsh and Badwater during spring (SP) and autumn (AU) of 1994. *N* = number of snails observed

Site	BH	BA	BOH
Cottonball Marsh			
SP (*N* = 854)	3.362	2.894	2.713
AU (*N* = 665)	3.520	2.430	3.082
Middle Pool			
SP (*N* = 198)	3.127	3.597	1.471
AU (*N* = 98)	1.746	1.924	1.705
North Pool			
SP (*N* = 702)	4.550	6.815	3.834
AU (*N* = 602)	4.196	3.429	3.203

Table 3. Two-way ANOVA testing differences in *A. infima* density at Cottonball Marsh in control and treatment panels during spring before treatment (A.) and during autumn, following 60 seconds of trampling (B.) that occurred eight months before

Source of variation	df	Q1		Q2		Q3	
		F	*p*	F	*p*	F	*p*
A.							
Sites	2	1.035	0.36	0.28	0.76	5.68	.004
Treatment	1	0.461	0.5	0.44	0.51	0.93	0.34
Interaction	2	0.102	0.9	2.14	0.12	0.42	0.66
Error	115						
B.							
Sites	2	5.71	0.004	3.91	0.02	6.80	0.002
Treatment	1	14.00	0.00	23.34	0.00	23.89	0.000
Interaction	2	0.61	0.55	0.33	0.72	1.28	0.28
Error	115						

ins, 1968). To normalize data, density, habitat, shell height, and distance to water measurements were log (i.e. ln +1) transformed prior to statistical analysis, except for angular estimates, which were converted by arcsine transformation. All data were tested for normality; normal distributions were compared using a *T*-test and other distributions compared using a Kruskal–Wallis non-parametric test. Statistical analyses were conducted using Systat v. 6.0. Habitat use was calculated from habitat measurements made

Results

Cottonball Marsh

Habitat use

At Sites 1, 2 and 3, *A. infima* occupied both banks of springbrooks that were 41 m, 120 m and 63 m long, respectively, during spring and autumn. Mean distance from water was greatest during autumn at Sites 1 and 3 and greater in spring at Site 2, but not significantly (Table 1A; temporal differences within Sites 1 and 3 highly significant, $p<0.001$, ns within Site 2, $p=0.253$,

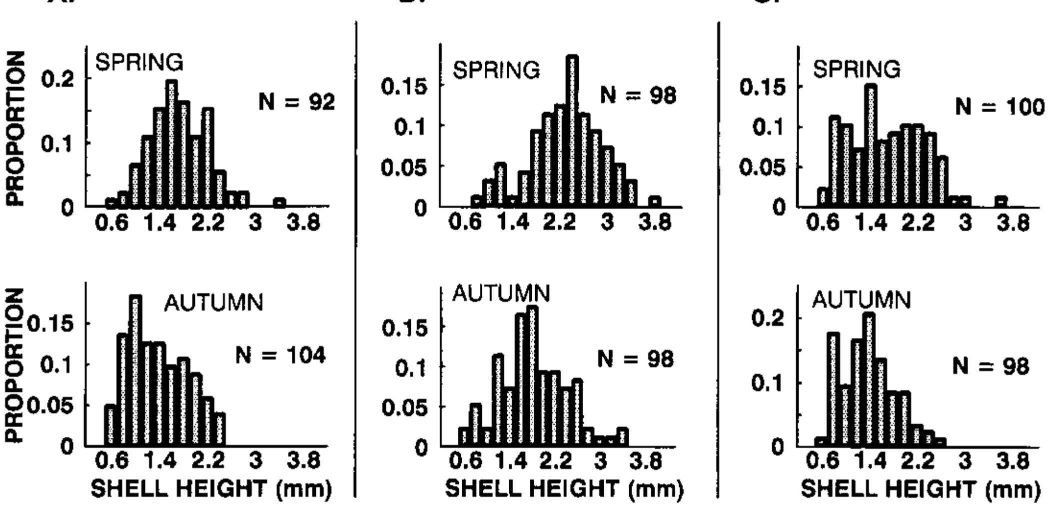

Figure 2. A. infima shell height frequency distributions at three Cottonball Marsh sites during spring and autumn 1994. Spatial differences among sites and temporal differences within sites were all highly significant ($p < .001$, T-test).

ficant for spring and autumn, $p < 0.001$, Kruskal–Wallis test). These seasonal differences indicate that habitat use may be broader when air temperatures are cool and water covers most of the marsh. In addition to springbrook banks, individuals were also occasionally found more than 5 m from springbrooks in protected areas of well developed salt crust that were next to water that persisted through summer.

Snails generally preferred habitats with high, steep, and undercut banks (Fig. 1). There was little difference in occupied habitat during both spring and autumn, even though availability of aquatic habitat was extensive during autumn. Niche breadth values indicated that temporal differences in habitat use were small (Table 2).

Population studies and field experiment
Spatial and temporal differences in mean shell height of populations at Sites 1, 2 and 3 were highly significant (Table 1A; $p < 0.001$, T-test). Mean height of each population was greatest during spring, indicating that reproduction may occur more in late summer than winter. Height-frequency distributions also indicate that two or three cohorts comprised each population, suggesting that reproduction occurs several times during the year (Fig. 2). Regressions between shell height and distance to water were not significant ($p > 0.08$) for all sites and samples with the exception of Site 1 during spring ($p = 0.005$). Weak correlation ($r^2 = 0.0827$) suggests that conclusions based on this regres-

that snails of all sizes use habitats both near and far from water.

Snail density Mean density ranged from 5.75 to 13.45 snails during spring and autumn in control panels (range 0–38 snails). Mean density was highest in quadrat 1 (located nearest water), and decreased through quadrats 2 and 3 at all sites (Fig. 3). There was little difference between control panel densities during spring and autumn in quadrat 1, suggesting that abundance varied little in habitats nearest water (Fig. 3). Although densities in control panels were frequently greater during autumn than spring, these differences were significant only for quadrat 3 (Table 3). Minimal spatial and temporal variability in mean densities within quadrats 1and 2 (where snails are most abundant) indicates that there may be little temporal variation in *A. infima* abundance at Cottonball Marsh.

Field experiments Differences between densities in quadrats 1 and 2 of control and treatment panels, and between sites, were not significant during spring, prior to treatment (Fig. 3, Table 3). Spatial differences in quadrat 3 densities were significant during spring, but differences between control and treatment densities within each site were not significant (Fig. 3, Table 3). Following treatment by trampling, differences between sites and between control and treatment panels during autumn were significant for all quadrats (Table 3). Differences between mean snail density in

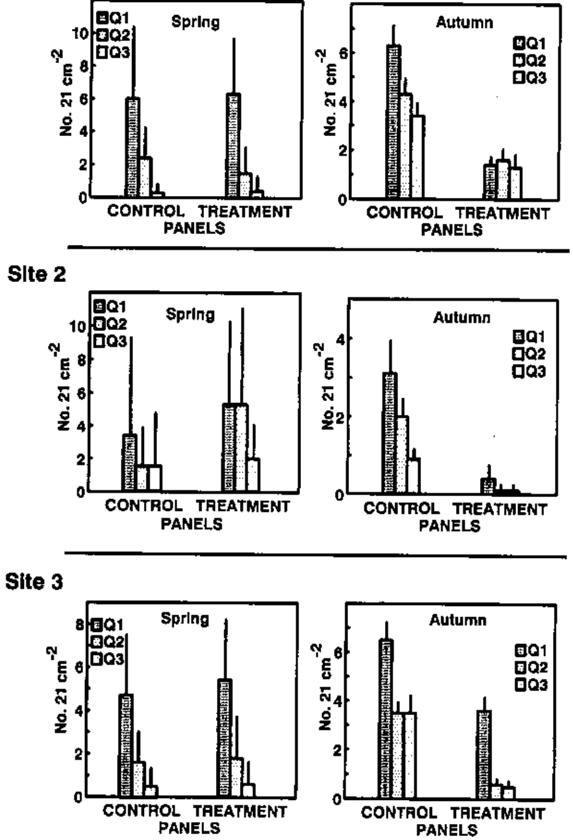

Figure 3. Mean (vertical bar = 1 SD) snail density during spring (before treatment) and autumn (following treatment) in control and treatment panels at Cottonball Marsh Sites 1, 2 and 3. Differences between abundance within quadrats 1, 2 and 3, respectively, of control and treatment samples ns during spring and highly significant during autumn (see Table 3). Q1 = quadrat 1, Q2 = quadrat 2, Q3 = quadrat 3.

brook habitats at three Cottonball Marsh sites occupied by *A. infima* April (Spring) and December (Autumn), 1994. *N* = the number of habitats sampled. SpringC refers to values from control panels during spring (prior to experimental treatment), SpringT refers to spring time values from treatment panels. AutumnC refers to values from control panels during autumn, AutumnT refers to values from autumn treatment panels

Site	*N*	Bank height (mm)	Bank angle (degrees)	Bank overhang (mm)
Site 1[a]				
SpringC	20	43.8 (13.4)[c]	64.5 (21.8)[c]	4.0 (8.4)
SpringT	20	66.9 (27.4)	83.5 (10.8)	2.7 (7.1)
AutumnC	20	43.7 (4.2)[d]	75.3 (5.4)	5.3 (1.6)[d]
AutumnT	20	22.4 (1.6)	48.6 (7.4)	0.0 (0.0)
Site 2[a]				
SpringC	20	42.3 (13.4)	56.5 (29.1)	2.3 (4.8)
SpringT	20	34.6 (13.5)	49.0 (31.9)	0.5 (2.2)
AutumnC	20	26.5 (2.8)[d]	56.8 (7.1)[d]	1.8 (0.0)[d]
AutumnT	20	11.3 (1.7)	11.0 (3.4)	0.0 (0.0)
Site 3[a]				
SpringC	20	44.0 (9.6)[b]	51.3 (30.0)	8.5 (10.8)
SpringT	20	51.6 (12.8)	55.3 (26.2)	7.5 (9.4)
AutumnC	20	52.5 (12.1)[d]	82.0 (4.8)	13.8 (2.8)[d]
AutumnT	20	29.0 (1.4)	82.3 (3.1)	2.8 (1.0)

[a] Spatial differences among habitats for all parameters at three sites prior to treatment very highly significant ($p<0.001$, *T*-test df = 119 for each parameter). [b] Within site difference among control and treatment panels significant ($p<0.05$, df = 38, *T*-test). [c] Within site difference among control and treatment panels highly significant ($p<0.01$, df = 38, *T*-test). [d] Within site difference among control and treatment panels very highly significant ($p<0.001$, df = 38, *T*-test).

during autumn were 8.15 vs. 4.3, 12.5 vs. 0.55, and 7.7 vs. 4.6, respectively.

Each site provided different *A. infima* habitat. Prior to treatment, differences between sites were significant for bank height, angle, and overhang (Table 4), and differences between control and treatment blocks within sites were significant for bank height (Sites 2 & 3) and estimated mean bank angle (Site 1). Treatment effects resulted in significantly decreased bank heights, angles, and overhangs at all sites, with the exception of bank angle at Sites 1 & 3. Control banks were also consistently higher, steeper, and more deeply overhanging than trampled banks following treatment. These differences suggest that salt crust relief is fragile and susceptible to substantial change even when trampled for only 60 sec over an eight month period.

Badwater

Crust relief

Salt crust relief in untrampled areas exceeded relief in the path surrounding Middle Pool by approximately 2.5 times (untrampled relief index = 27.9 ± 13.8 1SD, trampled relief index = 10.8 ± 4.0 1SD). Evidence of tourist activity effects on Badwater salt crust are also noticeable when current conditions are compared with conditions shown by National Park Service archival photographs taken during the 1930s and 1940s (e.g. photos DEVA 22093, DEVA 23245 and DEVA 30485).

Snail distribution was similar during spring and autumn; snails consistently occupied only habitat along the east shoreline of both Middle Pool and North Pool. Occupied shoreline at Middle Pool extended for 68.5 m and 68.3 m and at North Pool for 120.0 m and 136.5 m during April and December, respectively. Examination of archival photographs suggests that trampling has reduced salt crust relief along approximately 30 m of springbrook at Middle Pool, which is a reduction of approximately 30% of historical habitat these springs. There had been no apparent habitat loss at North Pool.

Habitat use patterns were similar at Cottonball Marsh and Badwater. Regressions between shell height and distance to water were not significant ($p > 0.08$) for both sites and samples with the exception of Middle Pool during autumn ($p = 0.004$). Weak correlation ($r^2 = 0.08$) suggests that conclusions based on this regression may have little biological importance. It appears that snails of all sizes also use habitats both near and far from water at Badwater. Similar to Cottonball Marsh, snail distribution was highly skewed to water (Table 1). However, distance to water at Badwater was considerably less than at Cottonball Marsh and snails were closest to water at Middle Pool (Table 1B; temporal differences highly significant, $p < 0.001$, at Middle Pool, and ns, $p = 0.336$ at North Pool, Kruskal–Wallis test). Spatial differences between Badwater sites were highly significant ($p < 0.001$) and significant ($p = 0.02$) during autumn and spring, respectively. It appeared that public use around Middle Pool had diminished salt crust relief, which may relegate snails to habitats nearest water. At North Pool, public use was lower, salt crust relief higher, which allowed snails to occupy habitat further away from water. Snails did not occupy habitats where banks gently sloped into the water at either pool. This habitat type typified bank morphology at Middle Pool where visitors frequently walk closest to springs and it was uncommon at North Pool where vertical, overhanging banks were more extensive. Niche breadth values indicated that habitat use at Middle Pool consistently was more restricted than use at North Pool (Table 2). This may be attributed to snails being abundant in very few quadrats at Middle Pool, and more abundant and widespread at North Pool. The amount of utilized habitat at Middle Pool was usually less than what was observed at Cottonball Marsh (Table 2).

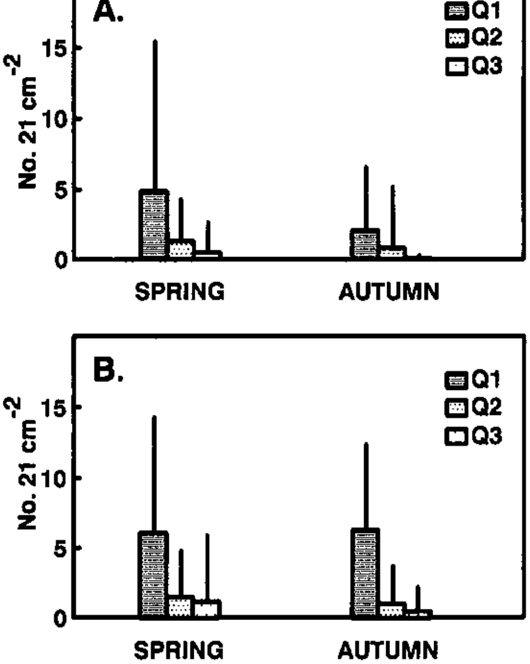

Figure 4. Mean (vertical bar = 1 SD) snail density during spring and autumn at Badwater Middle (A.) and North (B.) pools. Q1 = quadrat 1, Q2 = quadrat 2, Q3 = quadrat 3. Temporal differences within quadrats at each pool ns ($p > 0.23$, T-test), spatial differences between pools ns ($p > 0.24$, T-test).

Population studies

Shell height distributions at Badwater were similar to those observed at Cottonball Marsh, where each population also included several cohorts during spring and autumn. Contrary to Cottonball Marsh populations, there were no significant spatial or temporal differences ($p > 0.05$, T-test) in height distributions at Badwater (Table 1B).

Abundance of snails at Middle Pool and North Pool ranged from 0 to 19 000 m^{-2} (0–40 snails/21 cm^{-2} at both sites) (Fig. 4). Mean snail density in quadrats 1, 2 and 3 was always lower at Badwater than at Cottonball Marsh. Spatial and temporal variations in densities were small. Approximately 75% of the population consistently occupied quadrat 1 (located nearest water) and densities decreased sequentially in quadrats 2 and 3 as distance from water increased.

Funeral Mountains Springs

A. infima were limited to habitat within approximately 15 cm of water, and they were most common in decaying cattail (*Typha* sp.), sedges (*Scirpus* sp.), and fallen fan palm (*Washingtonia felifera*) leaves. They were rare in decaying salt grass (*Distichlis spicata*) and wire grass (*Juncus* spp.). At Nevares Springs, 11 were found in 83 grab samples taken along a total of 370 m of the largest spring in the province. It was absent in 37 grabs taken from all other springs and seeps in the area. Absence from seeps can be attributed zeric conditions caused by small discharge and periodic drying. Reasons they did not occur at flowing springs are not clear, however, evidence of dredging at these springs suggests that existing habitat conditions have naturalized from past disturbance that may have extirpated populations.

At Travertine Springs, 28 were observed in 162 grabs along approximately 1 km of springbrook. It was absent from 56 grabs taken from springbrooks without vegetation or debris, from Texas Spring, and all seeps in the area. Absence from Texas Spring can be attributed to dry conditions caused by total diversion of its outflow for many years. Threloff & Koenig (1999) estimated that diversion has eliminated approximately 85% of historical springbrooks at Travertine and Texas springs, which suggests that *A. infima* habitat has been reduced by a similar amount at these springs.

Discussion

Even though desert wetlands are comparatively small they provide the only persistent water over expansive landscapes of most continents. In the Death Valley region of North America, persistent water is additionally distinguished by providing habitat for at least 60 endemic plants and animals (Sada et al., 1995). A number of studies have examined fish ecology and fish and invertebrate taxonomy in these systems, but invertebrate ecology has received little attention.

Characteristics of the semi-aquatic habitat occupied by *A. infima* suggests that its demography may be highly influenced by seasonal conditions affecting soil temperature and water availability. Its demography and habitat use indicate, however, that seasonal variation in abundance, size class structure, and habitat use is small. Size class structure of all Badwater and Cottonball Marsh populations were similar during spring and autumn, and there was little spatial and temporal variation in population size. Snail abundance at Badwater was consistently less than at Cottonball Marsh. It is difficult to determine if this is attributable to impacts of human disturbance, the small size of Badwater springs, or differences in chemical composition of salts at the two areas. Results of trampling experiments indicate, however, that snail abundance and habitat may be detrimentally impacted by visitors.

Preferred habitat for *A. infima* at Badwater and Cottonball Marsh consisted of high banks, high bank angles and bank overhangs. There was little seasonal variation in habitat use, but the amount of available habitat during autumn at Cottonball Marsh appeared to be greater than during spring. This was indicated by densities in quadrats 2 and 3 that were highest in all three sites during autumn and lowest in spring. Increased abundance in habitats more distant from water may result from seasonal changes in water availability and temperature that expand habitat availability during periods when air temperatures are low and the amount of water greatest. Snails may be excluded from these habitats during spring and summer when air temperatures are highest and soil moisture is lowest.

On the Death Valley floor, *A. infima* relies on persistent water and high-relief salt crust that forms when evaporation draws moisture and salts from soils deposited during pluvial periods. Its preferred habitat occurs along springbrooks where salt crust banks are high, steeply angled and deeply undercut. Experimental manipulations indicated that trampling decreased bank heights, angles, undercuts, and snail abundance. The comparatively large declines that were caused by only 60 s of trampling suggest that populations can be easily extirpated with similar, but more extended, activities. The specificity of *A. infima* habitat use also suggests that it is poorly suited to occupy other habitat types, and that populations can be eliminated when habitats are altered. Reliance on persistent water and their absence from habitats without undercuts, and with low bank angles and height also indicates that populations may be extirpated when springbrooks are physically modified. These impacts are similar to effects to riparian and aquatic habitats that are caused intensive livestock grazing (Fleischner, 1994). Sada & Vinyard (2002) concluded that these types of impacts have resulted in extinctions and population extirpations of many aquatic taxa endemic to the Great Basin region of North America.

Impacts of human trampling on salt crust relief, examination of recent and historical photographs, and the influence of trampling on *A. infima* habitat and abundance all indicate that public use has altered physical and biological characteristics of Badwater. Death Valley National Park archival photographs indicate that Badwater remained in comparatively natural condition until the first road was constructed into the area during 1933 (Lingenfelter, 1986). Photographs taken over the past 30 years show the extent of high-relief salt crust dwindling over much of Badwater. It is difficult to compare extant and historical *A. infima* populations at Badwater without knowledge of its abundance and distribution prior to human disturbance. However, historical changes in the extent of flattened salt crust indicates that little habitat has been lost at North Pool and that approximately 30 m has been lost at Middle Pool. This represents a reduction of approximately 30% of historical habitat at Middle Pool.

Abundance and distribution of *A. infima* has also been affected by diversions that dried aquatic and riparian habitats supported by Texas, Travertine and Nevares Springs. Influence of these diversions on *A. infima* is also difficult to determine because there were no studies documenting its historical abundance and distribution. Its present occurrence in all spring-fed riparian areas with persistent water unaffected by frequent flood events suggests, however, that diversions eliminated several kilometers of habitat that may have been occupied by millions of individuals. Other aquatic macroinvertebrates endemic to Funeral Mountain springs have also been affected by these diversions. It is likely that continuation of historical use patterns at Badwater and future springbrook diversions will cause additional declines in abundance and distribution of many aquatic macroinvertebrates endemic to Death Valley. Fortunately, *A. infima* populations at Cottonball Marsh appear to occupy its historical habitat and to be comparatively unaffected by cultural uses.

Although information is needed to design recovery programs for Badwater populations of *A. infima*, observations at Cottonball Marsh indicated that trampled salt crust can regain its relief when protected from trampling. Growth rates were comparatively slow, approximately 2 cm yr^{-1} in trampled areas, and considerable time may be required to allow the crust to mature and provide *A. infima* habitat. Water rights granting diversions from Funeral Mountain Springs may preclude restoration of these systems, but diversions should be curtailed as much as possible to prevent additional losses and restore as much *A. infima* habitat as possible. Public use of aquatic and riparian resources in Death Valley National Park should consider biological integrity of these spring resources. These uses should be allowed only when management programs result in functional conditions at these springs that are more similar to those at Cottonball Marsh than to those currently existing at Badwater and in the Funeral Mountains.

Acknowledgements

Funding and assistance with this work was provided by the U.S. National Park Service, Death Valley National Park. D. Threloff, B. Davenport and B. Thornburg assisted with field work. S. Smith, D. Herbst and J. Wehausen, D. Blinn and an anonymous reviewer provided helpful comments to early manuscripts.

References

Baldinger, A. J., W. D. Shepard & D. L. Threloff, 2000. Two new species of *Hyalella* (Crustacea: Amphipoda: Hyalellidae) from Death Valley National Park, California, U.S.A. Proc. Biol. Soc. Wash. 113: 443–457.

Berry, S. S., 1947. A surprising molluscan discovery in Death Valley. Leaflets in Malacology 1: 5–8.

Fleischner, T. L., 1994. Ecological costs of livestock grazing in western North America. Cons. Bio. 8: 629–644.

Fowler, B. H., 1980. Reproductive biology of *Assiminea californica* (Tyron, 1865) (Mesogastropoda: Rissoacea). Veliger 23: 163–166.

Hershler, R., 1987. Redescription of *Assiminea infima* Berry, 1947, from Death Valley, California. Veliger 29: 274–288.

Hershler, R., 1989. Springsnails (Gastropoda: Hydrobiidae) of Owens and Amargosa River (exclusive of Ash Meadows) drainages, Death Valley system, California-Nevada. Proc. Biol. Soc. Wash. 102: 176–248.

Hershler, R., 1998. A systematic review of the hydrobiid snails (Gastropoda: Rissooidea) of the Great Basin, western United States. Part I. Genus *Pyrgulopsis*. Veliger 41: 1–132.

Hershler, R., 1999. A systematic review of the hydrobiid snails (Gastropoda: Rissooidea) of the Great Basin, western United States. Part II. Genera *Colligyrus*, *Eremopygrus*, *Fluminicola*, *Pristinicola* and *Tryonia*. Veliger 42: 306–337.

Hershler, R. & D. W. Sada, 1987. Springsnails (Gastropoda: Hydrobiidae) of Ash Meadows, California–Nevada. Proc. Biol. Soc. Wash. 100: 776–843.

Hunt, C. B., 1975. Death Valley Geology, Ecology, and Archaeology. U. California Press, Berkeley, CA: U.S.A., 234 pp.

Hunt, C. B., T. W. Robinson, W. A. Bowles & A. L. Washburn, 1966. Hydrologic basin, Death Valley, California. U.S.G.S. Prof. Pap., 494-B: B1-B138.

Jacobs, J., 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia (Berlin) 14: 413–417.

La Bounty, J. F. & J. E. Deacon, 1972. *Cyprinodon milleri*, a new species of pupfish (Family Cyprinodontidae) from Death Valley, California. Copeia 1972: 769–780.

La Rivers, I., 1948. A new species of *Ambrysus* from Death Valley with notes on the genus in the United States (Hemiptera: Naucoridae). Bull. S. Calif. Acad. Sci. 47: 103–110.

Levins, R., 1968. Evolution in Changing Environments. Princeton U. Press, Princeton, NJ, U.S.A.: 120 pp.

Lingenfelter, R. E., 1986. Death Valley and the Amargosa. A Land

Cyprinodon) in the American southwest. In Naiman, R. J. & D. L. Soltz (eds), Fishes in North American Deserts. John Wiley & Sons, NY, U.S.A.: 39–94.

Sada, D. W. & G. L. Vinyard, 2002. Anthropogenic changes in biogeography of Great Basin aquatic biota. Smiths. Contr. Earth Sci.: in press.

Sada, D. W., H. B. Britten & P. F. Brussard, 1995. Desert aquatic ecosystems and the genetic and morphological diversity of Death Valley system speckled dace (*Rhinichthys osculus*). In Nielsen, J. L. (ed.), Evolution and the Aquatic Ecosystem. Defining unique units in population conservation. Am. Fish. Soc. Sym. 17: 350–359.

Shepard, W. D., 1993. Desert springs – both rare and endangered. Aq. Conser.: Mar. and Freshwat. Ecol. 3: 351–359.

Shepard, W. D., 1992. Riffle beetles (Coleoptera: Elmidae) of Death Valley National Monument, California. Great Basin Natur. 52: 378–381.

Basin Natur. Mem. 2: 17–42.

Taylor, D. W., 1985. Evolution of freshwater drainages and molluscs in western North America. In Smiley, C. J. (ed.), Late Cenozoic History of the Pacific Northwest. Amer. Ass. Adv. Sci. San Francisco, CA, U.S.A.: 265–321.

Threloff, D. L. & S. Koenig, 1999. Effects of water diversion activities on stream lengths in the Travertine–Texas Spring complex, Death Valley National Park, summer 1999. Unpublished U.S. National Park Service report, Death Valley National Park, CA, U.S.A.: 7 pp.

Williams, J. E., D. B. Bowman, J. E. Brooks, A. A. Echelle, R. J. Edwards, D. A. Hendrickson & J. J. Landye, 1985. Endangered aquatic ecosystems of North American deserts, with a list of vanishing fishes of the region. J. Arizona-Nevada Acad. Sci. 20: 1–62.