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SPATIAL AND TEMPORAL VARIABILITY OF TROPHIC RELATIONSHIPS AMONG AQUATIC MACROINVERTEBRATES IN A SEASONAL MARSH

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Abstract: We examined macroinvertebrate trophic relationships in stands of two emergent plants, pickleweed (*Salicornia virginica*) and alkali bulrush (*Scirpus robustus*), and in epiphytic and benthic habitats within pickleweed stands. Numbers of detritivores, predators, and herbivores were examined throughout the flooding season (October 1990–March 1991). Trophic structure of macroinvertebrate communities differed between epiphytic and benthic habitats; both herbivores and detritivores were abundant in epiphytic habitats, but detritivores alone were numerically dominant in benthic habitats. Macroinvertebrate communities also differed between pickleweed and alkali bulrush stands: (1) all trophic groups were abundant in pickleweed, but detritivores were numerically dominant in alkali bulrush; (2) pickleweed supported higher macroinvertebrate numbers than alkali bulrush. Species composition was similar in both vegetation types, and diversity decreased during the season. Macroinvertebrate trophic structure in the epiphytic habitats changed during the season; detritivores quickly colonized both vegetation types after flooding, and predator and herbivore numbers increased later. Herbivores were an important component of macroinvertebrate communities in these wetlands, indicating that algal herbivory may be more important than previously thought.

Key Words: macroinvertebrate, trophic structure, detritivore, predator, herbivore, seasonal wetland

INTRODUCTION

Aquatic invertebrates are an important component of seasonally flooded and tidal wetlands. They affect wetland processes such as energy flow (Teal 1962), and they serve as food resources for waterfowl (Swanson 1988) and game fish (Odum 1970). However, little is known about many of the factors that influence invertebrate community structure.

As in other aquatic systems (Downing 1991), habitat structure can affect the distribution of invertebrate taxa in seasonal wetlands. Abiotic factors such as soil and water nutrients, dissolved oxygen levels, and soil moisture are distributed unevenly throughout the wetland environment, leading to patchy distributions of plant species (Winchester et al. 1985, Patterson and Mendelssohn 1989, Scott et al. 1989). Distributions of plant species, in turn, can affect invertebrate distributions. For example, different invertebrate communities are associated with different types of wetland plants (Wrubleski and Rosenberg 1990), bare or vegetated areas (LaSalle and Rozas 1991), and different habitats within stands of vegetation (Findlay et al. 1989). Furthermore, as the distributions of abiotic factors change over time, so do plant distributions and their associated invertebrate communities (Voigts 1976).

The trophic structure of terrestrial invertebrate communities in wetlands is affected by food resource availability (Cameron 1972, Balling and Resh 1991), but the trophic relationships among aquatic macroinvertebrates are poorly understood. Apparently, herbivory of vascular macrophytes by aquatic invertebrates is low in most wetland ecosystems (Mason and Standen 1983, Cahoon and Stevenson 1986, but see Newman 1991), and the axiom that wetland food webs are detritus-based has been widely accepted (Teal 1962, Simpson et al. 1983). However, little research has been done to test this hypothesis, and efforts to regulate invertebrate populations by manipulating detrital food resources have produced ambiguous results (Stivens and Kuenzler 1979, Kaminski and Prince 1981, Murkin et al. 1982, Neckles et al. 1990). Although the extent that other trophic groups such as algal grazers and predators affect secondary production is virtually unknown, recent studies suggest that algal herbivory may be more important than was previously believed (Murkin 1989, Campeau et al. 1994, Rader and Richardson 1994), and predators are often abundant in seasonal wetlands (Neckles et al. 1990, Batzer et al. 1993).

This study compares spatial and temporal variation in trophic group composition of aquatic macroinvertebrates associated with two species of emergent plants, pickleweed (Chenopodiaceae: *Salicornia virginica* L.) and alkali bulrush (Cyperaceae: *Scirpus robustus* Pursh). We examined temporal changes of relative abundances of detritivores, predators, and herbivores in stands of these plants throughout one season. We also compared macroinvertebrate trophic structure found on plant stems (epiphytic habitats) and bottom substrates (benthic habitats) in stands of pickleweed.

METHODS

Study Site

These studies were conducted at the California Department of Fish and Game's Grizzly Island Wildlife Area (GIWA) located in Suisun Marsh (Solano Co., CA). GIWA is managed to provide overwintering habitat for migratory waterfowl. This seasonally flooded, brackish-water marsh is subdivided into shallow (<100 cm depth) diked wetlands ranging in size from 15 to 200 ha. The majority of these wetlands are flooded via a network of channels in late summer and typically remain flooded until they are drawn down in early spring.

Pickleweed is the dominant vegetation in most of these wetlands. This perennial emergent plant grows in brackish to saline marshes and flats along the Atlantic and Pacific coasts (Hickman 1993). The succulent stems are woody at the base and are retained year-round. The stems can be highly branched and, when abundant, can form dense tangled stands.

Extensive stands of alkali bulrush also occur at GIWA. This perennial emergent plant grows in brackish to saline marshes along the Atlantic and Pacific Coasts (Hickman 1993). The aboveground rhizomes and leaves die and decompose in the winter months, and new growth resprouts from below-ground tubers in the following spring. The stems of alkali bulrush are not highly branched, and stands of this plant are structurally less complex than pickleweed stands.

Sampling Methods

To compare epiphytic and benthic macroinvertebrates in pickleweed, we selected three wetlands at GIWA (12A, 12B, 12D) with extensive (>1 ha) stands of this plant. We sampled a total of 12 sites in these wetlands on 13 November 1990, 8 January 1991, and 9 March 1991. On each sampling date, we generally collected an epiphytic and a benthic sample at each site. Not all sites were sampled on all dates because water levels in these wetlands fluctuated and were sometimes too shallow to sample.

We collected epiphytic samples with D-frame sweep nets (1-mm mesh size, 30-cm width). The net was drawn through the top 20 cm of the water column, and each sample consisted of the combined contents collected in four (1 m) sweeps through the emergent vegetation. Each sample was preserved with 95% ethanol in the field. In the laboratory, samples were rinsed through a 500-μ seive and hand-sorted.

We collected benthic samples with a hand-operated pump that had been modified to collect the sediments in a filter bag (350-μ mesh). Each sample consisted of the combined sediments collected with four pump strokes at each of four randomly chosen locations at each sampling site. The samples were preserved with ethanol, rinsed through a 300-μ seive in the laboratory, and hand-sorted.

To compare the macroinvertebrate communities in pickleweed and alkali bulrush, we selected two other wetlands (4B, 5) with extensive (>1 ha) stands of both pickleweed and alkali bulrush. In each wetland, we collected four epiphytic samples at random locations in each type of vegetation every two weeks throughout the sampling period. Sampling was initiated on 9 October 1990, about one week after these wetlands were flooded. Wetland 4B was sampled until 14 March 1991, after which it was drawn down. However, Wetland 5 was drawn down after 31 January 1991 and was not sampled after this date. We collected epiphytic samples with the same methods described above.

Because the epiphytic and benthic sampling devices had different mesh sizes, small invertebrate taxa could pass through the epiphytic sampler but were retained by the benthic samplers. In order to overcome this potential sampling bias, we excluded taxa that were smaller than 1 mm throughout their life cycle from analysis.

These sampling methods do not provide quantitative data (i.e., number of individuals/meter^2). Therefore, we compared relative abundances between habitats but did not estimate invertebrate densities.

We compared total numbers of epiphytic macroinvertebrates in pickleweed and alkali bulrush stands. Because we collected samples in each stand at different locations on each sample date, we used a two-factor (Vegetation by Date) ANOVA design. Macroinvertebrate numbers were $\mathrm{Log}10(x + 1)$ transformed prior to analysis to equalize variances.

We used Shannon's index of diversity (Zar 1984) to compare epiphytic macroinvertebrates collected in pickleweed and alkali bulrush samples. We used a linear regression model to assess the effect of sampling date on macroinvertebrate diversity.

We examined the trophic structure of the macroinvertebrate communities by grouping taxa into three categories: detritivores, predators, and herbivores

Table 1. Trophic category and percent of total number for epiphytic macroinvertebrates collected in pickleweed and alkali bulrush. Numbers collected were pooled over all sampling dates (9 October–14 March).

	% of Total Collected	
Taxa	Pickleweed[1]	Alkali Bulrush[2]
Detritivores		
Insects		
Ephemeroptera		
Callibaetis sp. (Baetidae)	<1	<1
Coleoptera		
Berosus ingeminatus d'Orchymont adults (Hydrophilidae)	2.5	1.8
Tropisternus sp. adults (Hydrophilidae)	<1	<1
Diptera		
Chironomus stigmaterus Say (Chironomidae)	2.0	1.1
Microtendipes sp. (Chironomidae)	1.1	1.9
Aedes melanimon Dyar (Culicidae)	4.0	2.2
Culex tarsalis Coquillett (Culicidae)	2.4	2.0
Culiseta inornata (Williston) (Culicidae)	<1	1.9
Odontomyia sp. (Stratiomyiidae)	<1	<1
Brachydeutera sp. (Ephydridae)	2.0	<1
Eristalis tenax L. (Syrphidae)	2.9	<1
Oligochaetes		
Unidentified species	2.4	8.1
Crustaceans		
Amphipoda		
Eogammarus confervicolus (Stimpson) (Gammaridae)	16.5	49.3
Decapoda		
Pacifastacus sp. (Astacidae)	0	<1
Total %	36.5	70.1
Predators		
Insects		
Odonata		
Ischnura sp. (Coenagrionidae)	0	<1
Aeshna sp. (Aeshnidae)	0	1.1
Libellula sp. (Libellulidae)	<1	<1
Hemiptera		
Trichocorixa verticalis Fieber (Corixidae)	28.2	6.1
Corisella sp. (Corixidae)	<1	<1
Notonecta sp. (Notonectidae)	<1	<1
Gerris sp. (Gerridae)	0	<1
Coleoptera		
Agabus sp. (Dytiscidae)	<1	1.9
Rhantus sp. (Dytiscidae)	4.1	1.6
Uvarus sp. (Dytiscidae)	<1	<1
Berosus ingeminatus d'Orchymont larvae (Hydrophilidae)	3.0	5.5
Diptera		
Culicoides sp. (Ceratopogonidae)	<1	<1
Crustaceans		
Mysidacea		
Mysis sp. (Mysidae)	0	<1
Total %	36.3	18.0

Table 1. Continued.

Taxa		% of Total Collected	
		Pickleweed[1]	Alkali Bulrush[2]
Herbivores			
Insects			
Coleoptera			
Enochrus sp. Adults (Hydrophilidae)		<1	<1
Diptera			
Cricotopus sylvestris Fabricius (Chironomidae)		12.7	4.4
Scatella sp. (Ephydridae)		14.4	7.2
	Total %	27.2	11.9

[1] Total number of macroinvertebrates collected in pickleweed = 9,284.
[2] Total number of macroinvertebrates collected in alkali bulrush = 4,838.

based on information in Pennak (1978), Merritt and Cummins (1984), and Thorp and Covich (1991). We supplemented this information by examining gut contents of some taxa. Taxa that feed on more than one food type were categorized by their predominant food source. Some taxa change feeding habits during their life cycle; for example, hydrophilid beetles are predatory as larvae, but detritivorous or herbivorous as adults. Therefore, we counted larvae and adults of such taxa separately. Insects that were collected in the nonfeeding pupal stage were not counted.

To compare the trophic structure of the macroinvertebrate communities between epiphytic and benthic samples and also between pickleweed and alkali bulrush stands, counts of macroinvertebrates in each trophic group were pooled on each sampling date. We constructed three-way contingency tables classifying counts by trophic group, date, and habitat (epiphytic versus benthic) and also trophic group, date, and vegetation (pickleweed versus alkali bulrush). We used log-linear models (Systat 1992) to test associations of these factors. Log-linear analysis creates a saturated model with all possible interaction terms, then interaction terms are tested by removing them in succession until the model's fit is significantly worse (Selvin 1995). The most complex interaction term (i.e., the three-way interaction term) was removed first, followed sequentially by less complex terms. We used Chi-square tests to examine the relationship of trophic group and habitat on each sampling date. Because we repeated the Chi-square tests for the three sampling dates, we used a critical value of $p < 0.017$ (i.e., 0.05/3) to maintain a procedure-wise error rate of $p < 0.05$.

RESULTS

Of 29 macroinvertebrate taxa collected, 14 taxa were categorized as detritivores (Table 1). These included species that feed on fine particulate organic matter either suspended in the water column (filterers) or deposited on the substrate (collector gatherers), as well as those that feed on coarse particulate organic matter (shredders). Thirteen taxa were categorized as predators, including those that feed by piercing or engulfing their prey. Only three taxa were categorized as herbivores, and these feed primarily on algae.

Comparisons of Epiphytic and Benthic Macroinvertebrates

The log-linear model without the three-way interaction term fit the data worse than the saturated model ($Y^2 = 9.7$, d.f. = 4, $p < 0.05$) indicating that the three-way interaction (trophic group by habitat by date) was significant. Therefore, the relationship of trophic group and habitat changed during the season.

On the earliest sampling date (13 November), there was no relationship between trophic group and habitat ($\chi^2 = 1.71$, d.f. = 2, $P = 0.426$). In both epiphytic and benthic samples, detritivores were numerically dominant, followed by predators and herbivores, respectively (Table 2).

On 8 January, macroinvertebrate trophic structure differed between epiphytic and benthic samples ($\chi^2 = 31.14$, d.f. = 2, $p < 0.001$). Although detritivores were only 49.6% of the total number collected in epiphytic samples, they comprised 87.9% of the total in benthic samples.

On 9 March, macroinvertebrate trophic structure again differed between epiphytic and benthic samples ($\chi^2 = 308.72$, d.f. = 2, $p < 0.001$). In epiphytic samples, the majority of invertebrates collected were herbivores (84.2% of the total number collected). In benthic samples, numbers of detritivores were slightly higher than herbivores (50.4% and 48.7% of the total number collected, respectively).

Table 2. Percent of total macroinvertebrates in each trophic group collected on 13 November 1990, 8 January 1991, and 9 March 1991. N is the total number collected in epiphytic or benthic samples on each sample date. Pooled is the percent of total number collected in epiphytic or benthic samples pooled over the entire season.

Trophic Group	13 November		8 January		9 March		Pooled	
	Epiphytic N = 650	Benthic N = 20	Epiphytic N = 575	Benthic N = 58	Epiphytic N = 4003	Benthic N = 226	Epiphytic	Benthic
Detritivore	66.9%	80.0%	49.6%	87.9%	10.6%	50.4%	21.9%	59.6%
Predator	30.6%	20.0%	37.2%	8.6%	5.2%	0.9%	11.8%	3.6%
Herbivore	2.5%	0%	13.2%	3.5%	84.2%	48.7%	66.3%	36.8%
Total	100%	100%	100%	100%	100%	100%	100%	100%

When we pooled numbers of invertebrates in the epiphytic samples over all three sampling dates, herbivores, detritivores, and predators comprised 66.3%, 21.9%, and 11.8%, respectively, of the total number collected. When we pooled numbers collected in the benthic samples, detritivores, herbivores, and predators comprised 59.6%, 36.8% and 3.6%, respectively, of the total.

Comparisons of Macroinvertebrates in Pickleweed and Alkali Bulrush

Most species were collected in both pickleweed and alkali bulrush (Table 1). The five species collected in alkali bulrush and not found in pickleweed were all relatively rare (<1.1% of the total collected in alkali bulrush samples). As a result, macroinvertebrate diversity values in these plants were similar (mean Shannon's index [S.E.]: H′ = 0.683 [0.041] in pickleweed; H′ = 0.705 [0.053] in alkali bulrush). In both types of vegetation, diversity values declined with time (pickleweed: r^2 = 0.345, P < 0.05; alkali bulrush: r^2 = 0.863, P < 0.0001) (Figure 1).

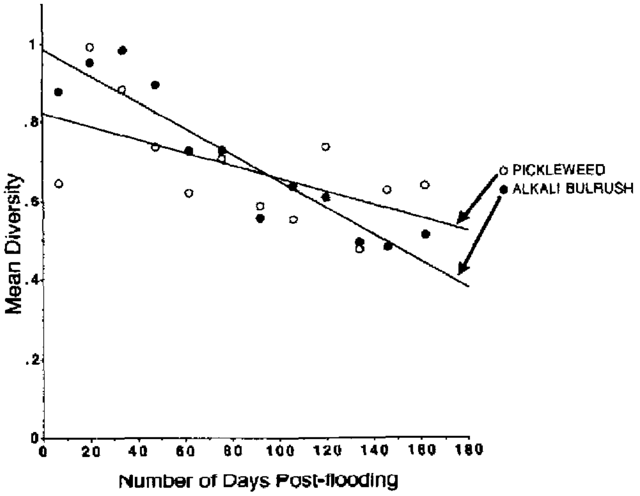

Figure 1. Mean Shannon's diversity values of macroinvertebrates collected in pickleweed and alkali bulrush samples from 9 October 1990–14 March 1991. Wetlands were first flooded on 2 October.

Although species composition of the epiphytic macroinvertebrate communities in pickleweed and alkali bulrush stands were similar, total macroinvertebrate numbers were higher (two-factor [Vegetation by Date] ANOVA, F = 21.70, d.f. = 1, P < 0.0001) in pickleweed than alkali bulrush (mean number of macroinvertebrates/sample [S.E.] from 9 October–14 March: 110.5 [11.4] in pickleweed; 57.6 [5.8] in alkali bulrush). There was also a significant effect of sampling date (F = 4.53, d.f. = 11, P < 0.0001). Total numbers fluctuated during the season, with three conspicuous peaks in November, January, and February in pickleweed (Figure 2) and two peaks in November and February in alkali bulrush (Figure 3). No Vegetation by Date interaction was found (F = 0.88, d.f. = 11, p = 0.558).

The log-linear model without the three-way interaction term fit our data worse than the saturated model (Y^2 = 1610.6, d.f. = 22, p < 0.001), indicating that the three-way interaction (trophic group by vegetation by date) was significant. Therefore, the relationship of trophic group and vegetation changed during the season.

In pickleweed stands, detritivores were numerically dominant on three of the twelve sampling dates, including the first two sampling dates (Figure 2). Their numbers declined after the fourth sampling date and increased again later in the season. Detritivores comprised 36.5% of the total number collected (Table 1).

Predators were numerically dominant on five sampling dates and comprised 36.3% of the total number collected. Predator numbers were low at the beginning of the season, increased until late November, then maintained a fairly constant level except for a conspicuous peak in mid-January.

Herbivores were numerically dominant on four sampling dates and comprised 27.2% of the total number collected. Herbivore numbers were low at beginning of the season, increased until the fourth sampling date,

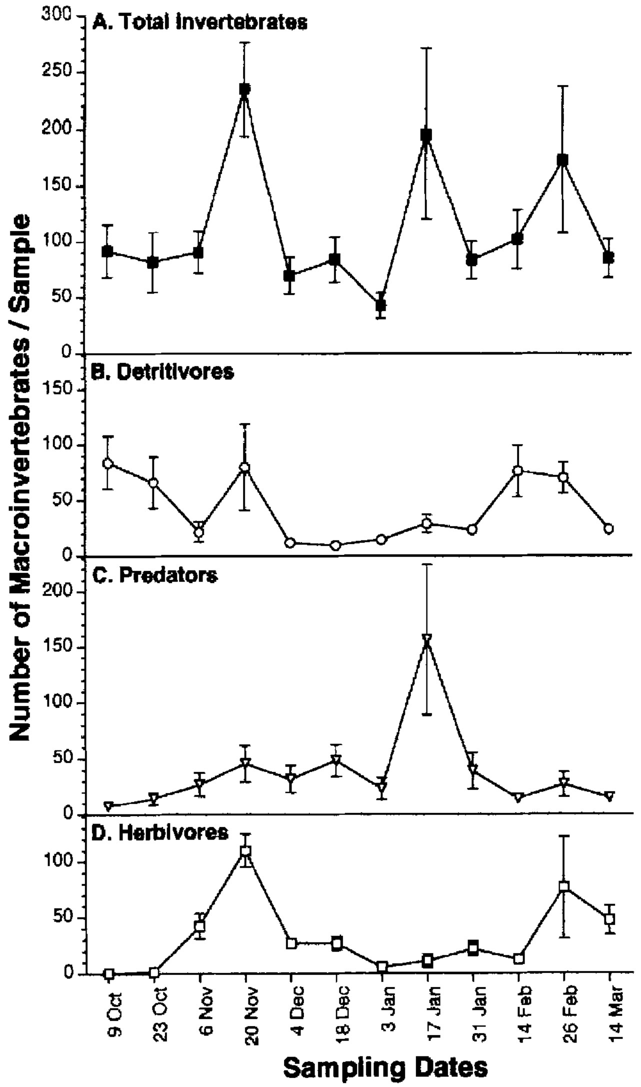

Figure 2. Mean number of macroinvertebrates per sample collected in pickleweed. Error bars are ± one S.E. (9 October–31 January, n = 8; 14 February–14 March, n = 4) A. Total number of macroinvertebrates collected in pickleweed samples. B–D. Number of macroinvertebrates collected in each trophic group (detritivore, predator, and herbivore).

then decreased to low levels until increasing again on the last two dates.

In alkali bulrush stands, some temporal changes in numbers of detritivores, predators, and herbivores (Figure 3) were similar to those observed in pickleweed stands. Detritivores colonized the wetlands immediately after flooding and were numerically dominant on all twelve sampling dates. Predator numbers were low at the beginning of the season, peaked in late November, and decreased afterwards. Herbivore numbers were low at the beginning of the season, increased until the fourth sampling date, and decreased afterwards. Detritivores, predators, and herbivores comprised 70.1%, 18.0%, and 11.9%, respectively, of the total number collected (Table 1).

DISCUSSION

Comparisons of Epiphytic and Benthic Macroinvertebrates

In pickleweed stands, the trophic structure of macroinvertebrate communities was markedly different in epiphytic and benthic habitats: detritivores and herbivores were numerically important in epiphytic habitats, whereas detritivores were dominant in benthic habitats. This pattern may reflect food availability. In wetlands, fine particulate organic matter settles out, providing a rich detrital food resource that supports high numbers of benthic detritivores (Teal 1962, Berrie 1976). Furthermore, epiphytic algae are an important food resource for grazers (Cattaneo 1983, Mihuc and Toetz 1994), and benthic algal biomass in wetlands can be low because of shading by emergent vegetation (Crumpton 1989). This may explain why herbivores were more important in epiphytic samples and detritivores were more important in benthic samples.

Comparisons of Macroinvertebrates in Pickleweed and Alkali Bulrush

In this seasonal marsh, macroinvertebrates colonized the wetlands within one week of flooding (i.e., 9 October). Aquatic invertebrates of intermittently flooded wetlands are well-adapted to colonize newly created habitats, and populations quickly reestablish after flooding (Wiggins et al. 1980, Robert and Matta 1984).

Although total numbers of macroinvertebrates stayed relatively high throughout the season, species diversity declined with time. The reasons for this were not clear. However, seasonal decreases in diversity have been observed in other wetland habitats (Campbell and Denno 1978).

Pickleweed stands supported higher numbers of macroinvertebrates than did alkali bulrush stands. We believe that plant architecture may have caused this difference. Pickleweed stands are structurally more complex and provide greater epiphytic surface area than alkali bulrush stands (Collins and Resh 1989). Although this is not the only factor determining macroinvertebrate abundance (e.g., Cyr and Downing 1988), higher invertebrate densities are often associated with plants that have highly branched stems or finely dissected leaves (Krecker 1939, Dvorak and Best 1982, Schramm et al. 1987, Wrubleski and Rosenberg 1990). Although we did not examine other potentially important factors such as biomass and turnover rate of ma-

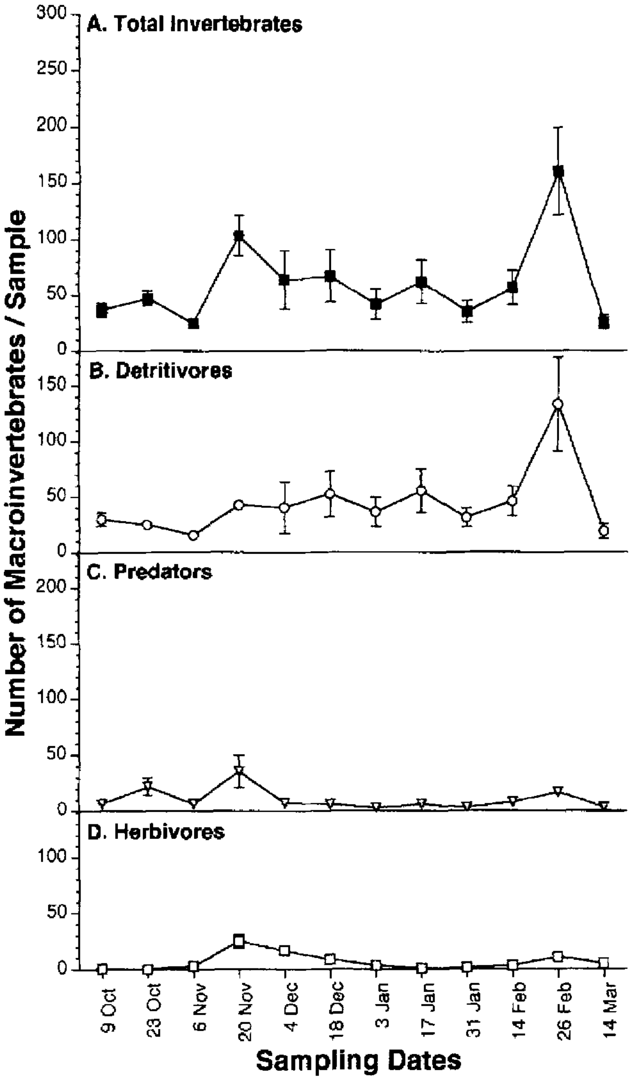

Figure 3. Mean number of macroinvertebrates per sample collected in alkali bulrush. Error bars are ± one S.E. (9 October–31 January, n = 8; 14 February–14 March, n = 4) A. Total number of macroinvertebrates collected in alkali bulrush samples. B–D. Number of macroinvertebrates collected in each trophic group (detritivore, predator, and herbivore).

croinvertebrates, pickleweed stands may support higher macroinvertebrate production than alkali bulrush.

Macroinvertebrate trophic structures also differed between pickleweed and alkali bulrush; all trophic groups were numerically important in pickleweed stands, but detritivores dominated alkali bulrush stands. Unlike pickleweed, the aboveground stems of alkali bulrush decompose during winter, and more detritus may be available in alkali bulrush stands. Furthermore, pickleweed has more epiphytic surface area and could support greater algal biomass. Therefore, macroinvertebrate communities in alkali bulrush stands should support proportionally more detritivores and fewer herbivores than pickleweed.

The trophic structure of the macroinvertebrate community also changed throughout the season. In both pickleweed and alkali bulrush, the earliest colonizers were detritivores. Predator and herbivore abundances increased slowly after flooding. Some of these patterns also occur in other seasonal wetland habitats; for example, predator populations typically are low immediately after flooding and increase as prey populations become more abundant (Wiggins et al. 1980). Furthermore, decaying plant matter colonized by microbes during the non-flooded period provides a rich food source for aquatic detrivores immediately upon flooding (Bärlocher et al. 1978, Campeau et al. 1994). In seasonal wetlands, algal populations increase gradually after flooding (Hooper-Reid and Robinson 1978), and herbivore densities are correlated with epiphytic biomass (Cattaneo 1983). At Suisun Marsh, algal populations become established after flooding and decrease in the winter months (Meyer et al. 1982, Batzer and Resh 1991). Therefore, the temporal pattern of herbivores that we observed correlates with predicted availability of their food resources.

Secondary production in wetlands has often been characterized as dominated by detritus-based food chains, and it was surprising that herbivores were sometimes the dominant trophic group in our macroinvertebrate communities. However, the perception that algal herbivores are relatively unimportant in wetland macroinvertebrate communities may be based on a lack of knowledge of feeding ecology of these taxa. For example, many trophic studies in wetlands do not distinguish between those taxa feeding on detritus and algae (e.g., Teal 1962, Murkin and Kadlec 1986). Our herbivore group was composed primarily of larvae of two taxa, the midge *Cricotopus sylvestris* and the brinefly *Scatella* sp. We examined the gut contents of these taxa and found they contained substantial amounts of filamentous algae and diatoms. Moreover, in past studies, *C. sylvestris* populations at Suisun Marsh were strongly affected by periphyton biomass (Batzer and Resh 1991), suggesting that they are limited by algal food resources. Other field studies examining gut contents of these taxa found that most *Scatella* species feed entirely on algae (Blair and Foote 1984), and algae is a major portion of *C. sylvestris* diets (Mackey 1979). Therefore, our results show that herbivores feeding on algae can be an important component of the macroinvertebrate community in wetland habitats.

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