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A basal aquatic-terrestrial trophic link in rivers: algal subsidies via shore-dwelling grasshoppers

Abstract Rivers provide important resources for riparian consumers, especially in arid or seasonally arid biomes. Pygmy grasshoppers (*Paratettix aztecus* and *P. mexicanus*; Tetrigidae) graze river algae stranded along shorelines of the South Fork Eel River in northern California (39°44′N, 123°39′W) as the river recedes during the summer drought. Densities of tetrigids during the mid to late summer were highest (1 individual/m^2 in July) within 1 m of the river margin, and declined to near zero at 4 m from the margin, especially during peak temperatures in the afternoon. These observations suggested that the distribution of tetrigids was determined by the availability of algae, water, or both. We manipulated the presence/absence of water and beached algae (*Cladophora glomerata*) in a 2×2 factorial design. All treatments were positioned 2 m upslope from the river's edge (about 30 cm above the water table), where the cobble bar was naturally dry and devoid of algae and densities of tetrigids were lower than at the river margin (0.4 individuals/m^2 in July). Tetrigids responded only to the wet *Cladophora* treatment, which had 30× higher densities than other treatments. Stable isotopic signatures ($\delta^{13}C$) of tetrigids (–19.7‰) collected from the same cobble bars were more similar to those of epilithic algae (–20.4‰) than terrestrial plants (–28.2‰), and higher than those of acridid grasshoppers (–27.9‰) from the same habitats. Mixing models suggest that 88–100% of the C in tetrigid grasshoppers at our study site is derived from riverine algae. A preliminary analysis suggests that tetrigids ingested sufficient quantities of algae to easily meet their energetic demands during the summer. This study supports the idea that algae, produced in stream systems, can determine the distribution and relative abundance of a common terrestrial scavenger and provide an additional pathway for energy exchange between rivers and riparian food webs.

Keywords Subsidy · River-watershed exchange · Tetrigidae · Pygmy grasshopper · Riparian

Introduction

Food web dynamics in near-shore terrestrial habitats are often influenced by resource inputs from nearby aquatic ecosystems (Summerhayes and Elton 1923; Jackson and Fisher 1986; Polis and Hurd 1995, 1996). For example, the dynamics of shoreline communities on desert islands are driven by oceanic inputs to almost every trophic level, including top and intermediate predators, herbivores and scavengers (Polis and Hurd 1995, 1996; Rose and Polis 1998; Polis et al. 1997). Aquatic-terrestrial linkages are also important in river watersheds (Jackson and Fisher 1986; Gray 1989, 1993). While much work has focused on inputs of terrestrial detritus and insects to river food webs (Cummins et al. 1973; Goulding 1980; Vannote et al. 1980; Mason and MacDonald 1982; Wallace et al. 1997, 1999; Nakano et al. 1999), there are also riverine subsidies to riparian consumers (Jackson and Fisher 1986; Gray 1989, 1993; Henschel, in press; Power et al., in press; Sabo 2000; Power and Rainey 2000).

Insect herbivores are one of the main pathways by which riverine primary production enters terrestrial food webs. Although the winged adult forms of aquatic insects may account for much of this transfer (Jackson and Fisher 1986; Gray 1989, 1993; Power et al., in press; Henschel, in press; Sabo 2000), riparian scavengers (e.g., pygmy grasshoppers and beetles) may constitute a second link between aquatic and terrestrial food webs. For example, pygmy grasshoppers (Tetrigidae) feed on beached algae when this resource is available (Milne and Milne 1980). Ants (Formicidae) and ground beetles

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(Carabidae) have also been reported to feed opportunistically on beached algae (Hering and Platcher 1997). These insects make up a terrestrially based trophic link between river and riparian food webs, and may channel river energy to higher terrestrial trophic levels. The effects of algal export on the spatial distributions and energy budgets of riparian invertebrate scavengers remain largely unknown.

We studied the effect of stranded algae on the spatial distribution of two species of tetrigid grasshoppers (*Paratettix aztecus* and *P. mexicanus*). Tetrigids, or pygmy grasshoppers, are unusually small orthopterans that generally occur near water margins (Milne and Milne 1980). Along the South Fork Eel River, tetrigids are common within the first 5 m of the river, and aggregate on stranded mats of algae. Tetrigids may be attracted to moisture because their small size may make them more susceptible to dessication than other orthopterans. Stranded algae and moist micro-habitats are both more common near the river. As river base flow subsides during the summer drought of the region's Mediterranean climate regime, both resources become more restricted to the river's edge (Power 1990).

We hypothesized that grasshopper distributions were influenced by the spatial and seasonal availability of both water and algae. To test this hypothesis, we used a combination of observation, stable isotope analysis and field experiments. First, we surveyed the distribution of two species of tetrigids, *P. aztecus* and *P. mexicanus*, on three cobble bars, using transect surveys to document diel and seasonal patterns in the distribution of these grasshoppers with respect to the river. Second, we experimentally subsidized low density riparian plots located 2 m from the river with algae, water or both to evaluate the effect of these resources on local grasshopper densities. Third, we quantified ingestion rates of *Cladophora* by captive tetrigids. Finally, we used analysis of stable isotope ratios of C (δ^{13}C) to determine the overall contribution of algal based resources to the diets of riparian pygmy grasshoppers.

Materials and methods

Study site

Experiments and surveys took place on three rock bars along the South Fork Eel River in Mendocino County, California (39°44′N, 123°39′W). The South Fork Eel has a forested watershed in the California coastal range. The bars differ in substrate size, area and in their orientation within the channel, which affects the amount of sun they receive. Two of them, Wilderness Lodge and Merganser, are cobble bars, whereas the third site (Globus) is composed of finer pebbles and gravels. The Wilderness Lodge cobble bar is 0.41 ha in area (of which 64 m^2 was surveyed for tetrigids), and is intermittently sunny for 7 h a day during the summer. In contrast, Merganser and Globus are smaller, 0.21 ha in area each (78 and 89 m^2 were surveyed, respectively). Merganser receives direct sunlight for 10 h a day, while Globus is sunlit for 8 h a day. These sites appear to be typical habitat for *P. aztecus* and *P. mexicanus*. Both grasshoppers are generally found near running water. *P. aztecus* reportedly prefers rocky or gravelly substrate, while *P. mexicanus* is more associated with muddy substrate, but they are often found together (Rehn and Grant 1961). Both species occurred at Globus, while only *P. aztecus* was found at the other two sites.

The climate of the study site is Mediterranean, with rainy winters (November–March) and dry summers (April–October). Average annual rainfall exceeds 150 cm, resulting in winter flooding of the river channel. Cobble bars along the South Fork Eel River are periodically submerged during the winter. This suggests that tetrigids, which over-winter as adults (Borror et al. 1989), move to upland habitats to avoid winter floods. In these habitats they may feed on terrestrial detritus, mosses, fungi and lichen (Paranjape and Bhalerao 1985; Bhalerao and Paranjape 1986). The cobble bars become exposed in April and May as the water level drops. A film of mud and epilithic algae is left behind, and this may serve as food for the tetrigids. In mid July, algal mats, made up predominantly of *Cladophora glomerata*, begin to wash ashore (Power 1992). Tetrigids are often found on these algal mats when they are available in the late summer. In addition to tetrigids, we also commonly observed a band-winged grasshopper (Acrididae, Oedipodinae) at all three sites. In contrast to tetrigids, this grasshopper feeds on terrestrial vegetation, and is rarely found on algal mats (J. Bastow, personal observation).

Potential predators of tetrigids are diverse and abundant. These include toad bugs (Gelastocoridae), carabid beetles, several lycosid spiders, and the western fence and sagebrush lizards (*Sceloporus occidentalis* and *S. graciosus*). Toad bugs, which are very abundant within the first meter of the river, were observed preying on tetrigids on occasion, but seemed to feed predominantly on shore flies (Ephydridae) (J. Bastow, personal observation). *Pardosa* spp. and *Arctosa* spp. wolf spiders are also quite common at the study sites, and probably prey on smaller tetrigid nymphs. *Sceloporus* aggregate along the river as a result of the higher availability of aquatic insects in these microhabitats, but diet analyses showed only occasional consumption of tetrigids (Sabo 2000).

Transect surveys

We surveyed tetrigids along transects laid out parallel to the river at 1-m intervals within the first 7 m, at all three study sites on 15–16 June, 13–17 July and 14–17 August 1999. We also carried out 24-h surveys at two sites in June to establish tetrigid activity patterns. After these initial surveys, our sampling efforts consisted of hourly counts for 12 h, from 0800 to 2000 hours. Tetrigids were counted in adjacent 1-m-wide band transects parallel to the water's edge and extending at least 7 m away from the river. We walked transects sequentially starting at the river's edge, so that any fleeing tetrigids subsequently recounted would inflate the observed densities further away from the river. In this way, our estimates of aggregation at the water's edge are conservative. In recording the observed tetrigids in each transect at each hour, we distinguished nymphs and adults, and, in the July and August surveys, distinguished *P. mexicanus* at the site where it occurred. The locations of seasonal transects were adjusted according to the receding river level. We also measured the substrate temperature each hour during the surveys with an alcohol thermometer placed on the ground, 2.5 m from the river, at roughly the mid-point of where tetrigids were found.

We tested for bias in observed tetrigid densities related to our routine census sequence by comparing data from several hours of surveys taken systematically up slope from the river's edge (the regular survey sequence) with data from surveys on the next day taken at the same time of day, but in a random spatial order. If there were a significant effect of tetrigids being flushed and recounted in adjacent sites, we would have expected all transects >1 m from the river to have higher densities when the transects were walked in order. After excluding the first meter and transects which happened to be walked consecutively with their adjacent transect in the random series, we compared the paired observations using a Wilcoxon matched-pairs signed ranks test. This test revealed no significant effect of transect survey sequence at either of the two sites (T=13.5, df=44, P<0.71).

We also counted two other riparian insects during some of our transect surveys. In July we counted numbers of band-winged grasshoppers at all three sites. In August we counted toad bugs (Gelastocoridae) at one site.

Resource manipulation

In August 1998 we set up a field experiment to evaluate the relative influence of algal and moisture gradients in determining the local distribution of grasshoppers. We added *Cladophora* and water to plots (25×35 cm) on two cobble bars (Wilderness Lodge and Merganser) in a 2×2 factorial design randomized within two experimental blocks (cobble bars). Each plot received either: (1) dry algae; (2) water; or (3) water and wet algae. Undisturbed plots served as unsubsidized controls. Plots were all set at distances of 2 m from the river (about 30 cm above the water table), where the tetrigids were not normally encountered after 1000 hours in August. Plots were separated by at least 1.25 m of undisturbed habitat. All treatments were replicated 3 times on each cobble bar.

Watered plots (water only and with wet algae treatments) were hydrated constantly with water from 19-l buckets. Each bucket was fitted with five 2-m rubber tubes capped with drip nozzles. The buckets were set ca. 1 m behind the plots, so they would not shade them, and raised 10–20 cm on cobble pedestals. The nozzles were set to drip at the rate of 840 ml/h. In order to keep their drip rates relatively constant, the watering buckets were refilled every 2 h, so that the water level never dropped below half. To assess the efficacy of the slow-drip buckets, we took soil samples from each of the water-only treatments at 0900, 1300 and 1700 hours, and compared the percent water by mass of these samples with those of soil samples taken from outside the plots at the same times at four distances (0, 2, 4 and 8 m) from the river.

Algal addition treatments were supplemented with 60 g (±0.01 g, wet weight) of *Cladophora*. We used *Cladophora*, a macroalgae, because it was easy to manipulate the abundance of *Cladophora* mats on the cobble bar. Epilithic algal detritus may be a more important food source for tetrigids, but manipulating its abundance was less feasible. Tetrigids are readily observed on algal mats, although it is unclear whether they feed on *Cladophora* or epiphytic diatoms growing on the *Cladophora*. If in fact it is epiphytic diatoms that tetrigids graze from beached *Cladophora* mats, then this food source may be effectively quite similar to epilithic algal detritus, as many diatom genera in the Eel grow on both stones and macroalgae (J. C. Marks and M.E. Power, unpublished data).

We collected and damp weighed the *Cladophora* for both wet and dry algal treatments at each site at the same time. Damp weights were measured after clumps of fresh algae were spun 100 times in a salad spinner. We then dried the *Cladophora* for dry algae treatments at 65°C for at least 24 h. The algae for the wet algae treatments were stored in Ziploc bags during this time.

We made hourly counts of tetrigids between 0800 and 1800 hours the day before resource manipulation to determine natural densities at each site. Treatments were then set up the night before data were taken, so that the tetrigids would encounter the plots when they first became active in the morning. We replaced the algae with new algae, prepared in the same manner, an hour before data collection began in the morning to ensure uniformity between plots. Hourly counts were once again taken for a day, from 0830 until 1630 hours. Counts were taken in three passes of every third plot in order to avoid flushing tetrigids between plots. Treatment effects on grasshopper densities were analyzed in pre- and post-manipulation censuses using a 2×2 ANOVA with algae and water as the independent variables, and site as an experimental block.

Feeding rate study

To assess the quantity of algae typically consumed by tetrigids at our study site, we conducted feeding rate trials in four 40-l plastic buckets set up on the cobble bar about 2 m from the water's edge. We placed two cobbles for shelter into each of the buckets and stocked five late nymph *P. aztecus*. *Cladophora* from the South Fork Eel River was dried at 65°C for 24 h, weighed to the nearest milligram, rehydrated and spun in a salad spinner 100 times to ensure a uniform moisture content. After supplying each of the buckets with 1.23 g (±0.13 g, weighed dry) algae, buckets were covered with fine netting. *Cladophora* was kept moist with a spray bottle. The trials ran for 2.5 days, at the end of which the algae were dried for 24 h and weighed to the nearest milligram. The difference in algal mass between the beginning and end of the trial, divided by 12.5 (five tetrigids feeding for 2.5 days) estimated average mass eaten per tetrigid per day for each bucket.

Stable isotope analysis

The trophic transfer of C in food webs results in minor changes of consumer stable C isotope ratios (δ^{13}C) (DeNiro and Epstein 1978; France 1996). When potential sources of food have distinct δ^{13}C, measurements of these may be used to distinguish the trophic importance of organic matter sources to food webs (Fry and Sherr 1984; Peterson and Fry 1987). Benthic algae in pools in the South Fork Eel River have high δ^{13}C relative to riffle algae and terrestrial plants because the limited supply of CO_2 results in reduced discrimination against ^{13}C (Finlay et al. 1999). We used the large difference between the δ^{13}C of pool algae and terrestrial plants to determine the contribution of these sources to tetrigids in the dominant riparian habitat on the river, cobble bars adjacent to shallow pools.

We analyzed δ^{13}C of potential food sources (i.e., epilithic pool algae and terrestrial plants) and tetrigids every 2–3 weeks from 13 June through 8 August 1999. Epilithic algae was scrubbed from 8.75 cm^2 surface of three cobbles using a toothbrush and squirt bottle. Three such composite samples were taken on each of the three rock bars on each sampling date. Leaves and stems were collected from all the terrestrial plants common at each of the three sites. Terrestrial plants were collected once during the summer and dried at 50°C. Each tetrigid sample included five tetrigids collected throughout the transect area of each study site. The tetrigids were kept alive for 24 h without food so they would clear their guts, and tetrigids that died in <24 h were not used. We also collected and analyzed gelastocorids and acridid grasshoppers in the same manner.

Dried epilithic algae, terrestrial plants and invertebrates were ground to a powder before stable C isotope analysis on a Europa 20-20 or a Finnigan MAT Delta Plus continuous flow isotope ratio mass spectrometer. We analyzed 3.5–4 mg of plant and alga samples, and 2 mg of insect samples. δ^{13}C are expressed relative to the international standard, Pee Dee belemnite. We analyzed approximately 20% of our samples in duplicate, and the average SD was <0.1‰ for δ^{13}C.

We used a two-source mixing model to determine the contribution of terrestrial plants and pool algae to the diet of tetrigids. The general form of the model was:

$$\begin{aligned}\delta^{13}\mathrm{C\ consumer} - F &= \left(\delta^{13}\mathrm{C\ pool\ algae} \times f\ \mathrm{pool\ algae}\right)\\ &\quad + \left[\delta^{13}\mathrm{C\ terrestrial\ plants}\right.\\ &\quad \left.\times\left(1 - f\ \mathrm{pool\ algae}\right)\right] \qquad (1)\end{aligned}$$

where F is trophic fractionation, and f pool algae is the fraction of diet from epilithic pool algae. We assumed a trophic fractionation for δ^{13}C of +0.4‰ between the tetrigids and their food source. This value is less than the +1‰ increase per trophic level often assumed for marine food webs (DeNiro and Epstein 1978), and was used because of the observation of lower trophic fractionation by freshwater consumers (France 1996; France and Peters 1997). We assumed for this model that tetrigids at our study sites did not feed on C4 plants or riffle algae. C4 plants, which have high δ^{13}C relative to C3 terrestrial plants (Peterson and Fry 1987), are very rare on the cobble bars used in this study. Riffle algae δ^{13}C are similar to those of terrestrial plants (Finlay et al. 1999), but the tetrigids probably did not have significant access to riffle algae. Tetrigids are rarely found along the river where the water velocity is

Table 1 Results from repeated measures ANOVA on seasonal trends in tetrigid distribution. *Between subjects* pools months, while *within subjects* looks at the effect of month on distribution

Between subjects					
Source	SS	*df*	MS	*F*	*P*
Distance	1.45	1	1.45	26.08	0.001
Site	0.23	2	0.12	2.07	0.157
Error	0.95	17	0.06		
Within subjects					
Source	SS	*df*	MS	*F*	*P*
Month	0.41	2	0.21	9.36	0.003
Month×distance	0.44	2	0.22	9.92	0.002
Month×site	0.81	4	0.20	9.10	0.001
Error	0.75	34	0.02		

>10 cm/s (J. Bastow, personal observation), and all three study sites were adjacent to or just downstream of large pools (100–300 m long). We calculated SEs for *f* pool algae using the spreadsheet provided by Phillips and Gregg (2001).

Results

Transect surveys

We began the June survey at midnight at Wilderness Lodge and Merganser in order to establish diel activity patterns for tetrigids. Tetrigids were first observed between 0530 and 0600 hours and last observed at 2030 and 1900 hours at these two sites, respectively. We surveyed for at least 2 h after the last tetrigid was observed. Although tetrigid numbers dropped sharply after 2000 hours at Globus in June, we continued to observe tetrigids until 2300 hours, the last hour of the survey. We conducted subsequent surveys, in July and August, from 0800 until 2000 hours.

Despite considerable variation among sites in our transect surveys, there were striking seasonal and diurnal patterns in densities of active tetrigids. Tetrigid densities averaged from hourly counts made between 0800 and 2000 hours were fairly even across the first 6 m in June, whereas in July and August the average densities for the same portion of the day were much higher in the first meter (Fig. 1). Changes in the distribution of tetrigids across seasons were significant [repeated measures ANOVA (Winer et al. 1991), month×distance interaction, F=9.92, df=2, P<0.001, Table 1]. There were sharp drops in average densities after both the first meter and the fourth meter in July and August, and the aggregation in the first meter was more pronounced in August than July. Average densities were significantly higher in the first meter than those beyond 4 m in August (Tukey's P<0.05).

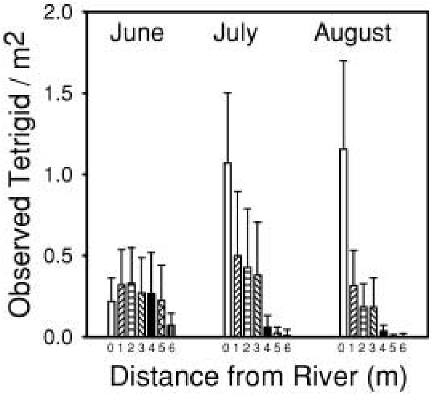

Fig. 1 Seasonal patterns in tetrigid distribution. Average (mean± 1 SE) observed tetrigid densities (individuals/m^2) between 0 and 7 m from the river's edge, calculated from 13 hourly counts at three sites (n=3) in mid June (*left*), mid July (*middle*) and mid August (*right*). Each transect was 1 m wide. The transects are labeled with the distance from the river at which they began

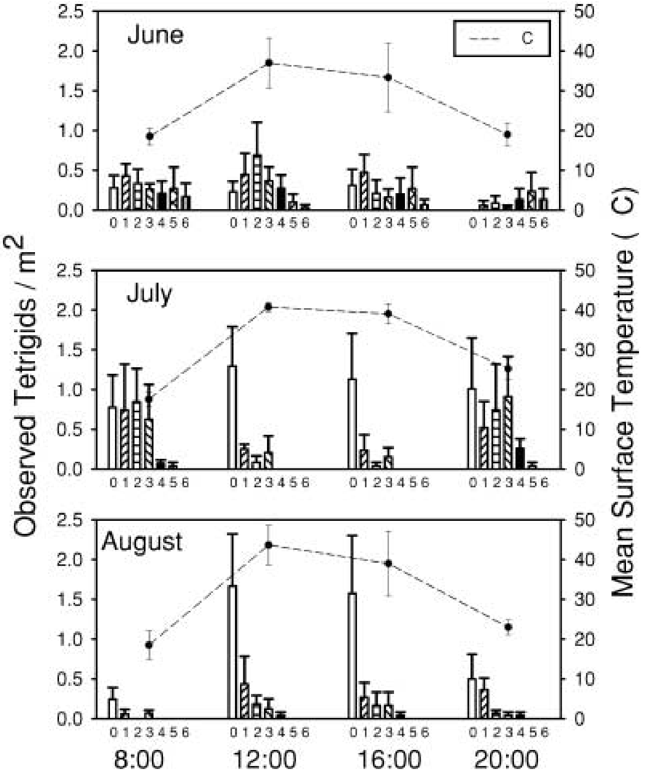

Fig. 2 Diurnal patterns in tetrigid distribution. Average (mean± 1 SE) observed tetrigid densities (individuals/m^2) between 0 and 7 m from the river's edge, calculated for 4 times during the day (0800, 1200, 1600 and 2000 hours) from three sites (n=3). Each transect was a meter wide. The transects are labeled with the distance from the river they began at. The diurnal patterns are shown separately for mid June (*top*), mid July (*middle*) and mid August (*bottom*)

This zonation did not occur in the June survey (Fig. 2), in which tetrigids were never aggregated within the first meter of the river. No transect had consistently higher tetrigid densities, and the only clear diurnal pattern was a decrease in tetrigid numbers by 2000 hours. This contrasts with the survey results from July and August (Fig. 2), where the average tetrigid densities were greatest in the first meter after 0800 hours in July and throughout the day in August. In July, tetrigids were abundant and fairly evenly distributed in the first 4 m in the morning and evening, and became aggregated in the first meter during the day. In August, the aggregation during the middle of the day was similar, but tetrigids were not abundant in the morning and evening.

Cobble bars were on average 4°C cooler between 0800 and 2000 hours (Fig. 2) in June than later in the summer, but the relative diel changes in temperature were similar. We observed the same diurnal temperature pattern throughout the summer, with midday (1200 and 1600 hours) temperatures 20°C higher than morning and evening (0800 and 2000 hours) temperatures.

Several non-tetrigid members of the invertebrate community showed similar patterns of near-river aggregation. Over 70% of the acridid grasshoppers were observed within 3 m of the river in July, and 96% of the gelastocorids observed within 1 m of the water in August (Table 2).

Resource manipulation

Resource additions altered the natural resource gradients and the distribution of tetrigids on cobble bars. Tetrigids showed a strong positive response to the water plus algae treatment (Fig. 3, Table 3). Post-hoc comparison of cell means (Zar 1996) revealed that only the water plus algae treatment differed significantly from the control ($P<0.001$, $P>0.9$ for comparisons between water alone or dry algae treatments and control). The response of tetrigids also varied between experimental sites (see Site in Post-manipulation response, Table 3), most likely because of higher densities of tetrigids at Merganser than Wilderness Lodge. The slow-drip buckets effectively increased the moisture content of the soil. Watered plots had, on average, twice as much water by percent mass as the unwatered substrate 2 m from the river (where the plots were located), but the difference was only marginally significant ($T=-1.75$, $df=4$, $P<0.08$, one-tailed *t*-test, arcsine square root-transformed data).

Feeding rates and stable isotope analysis

Experimentally enclosed tetrigid nymphs consumed approximately 3–5 times their own mass in *Cladophora* every day, 11.92±4.92 mg (±SE) dry mass. Nymphs of comparable size from the same site ranged in dry mass from 2.62 to 3.43 mg (8.76–12.36 mg wet mass).

A preliminary calculation suggests that this ingestion rate was ample for meeting tetrigid energetic demands. Assuming that tetrigid standard metabolic rate (SMR, in microWatts) scales with body mass (BM, wet mass in grams) as $SMR=906\ BM^{0.825}$ [from Lighton and Fielden (1995) for ants, beetles and spiders at 25°C], the energetic requirement of an 8.42-mg (wet mass) individual would be 17.60 µW. If algae ranges between 45–90% organic matter by dry weight (depending on the silt load and prevalence of diatoms), the amount ingested per individual per day would supply 145–290 µW (Winberg 1971), more than 8–16× the SMR. This wide margin suggests that even over a range of food qualities of algae, tetrigids ingest enough algae to meet their energetic needs for activity, growth and stress tolerance.

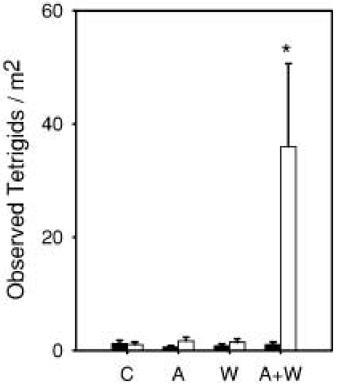

Fig. 3 Results of the resource manipulation experiment. Average (mean±1 SE) observed tetrigid densities (individuals/m^2) calculated from nine hourly counts in six replicates ($n=6$) of the four treatments [dry *Cladophora* (*A*), water (*W*), water and *Cladophora* (wet *Cladophora*, *A+W*), and unmanipulated control (*C*)]. The *black bars* represent the average observed densities before the addition of the resources, and the *white bars* represent the average observed densities after the addition. The *asterisk* indicates a significant difference ($P<0.001$) in post-manipulation densities

Table 2 Acridid grasshopper distribution in July and Gelastocorid distribution in August. Density refers to average (mean±1 SE) individuals/m2

Distance	Acrididae		Gelastocoridae	
	Density	% of total	Density	% of total
0–1 m	0.14±0.08	22.58	4.10±0.09	96.47
1–2 m	0.20±0.14	32.26	0.10±0.05	2.35
2–3 m	0.11±0.08	17.74	0.05±0.03	1.18
3–4 m	0.06±0.04	9.68	0	0
4–5 m	0.06±0.04	9.68	0	0
5–6 m	0.03±0.02	4.84		
6–7 m	0.02±0.02	3.23		

Table 3 2×2 ANOVA results from pre and post-manipulation experimental plots (with *Site* as a block)

Pre-manipulation					
Source	SS	*df*	MS	*F*	*P*
Water	0.000	1	0.000	0.006	0.937
Algae	0.002	1	0.002	0.215	0.648
Water×algae	0.007	1	0.007	0.861	0.365
Site	0.024	1	0.024	2.847	0.108
Error	0.162	19	0.009		
Post-manipulation					
Source	SS	*df*	MS	*F*	*P*
Water	1.77	1	1.77	13.05	0.002
Algae	1.88	1	1.88	13.9	0.001
Water×algae	1.57	1	1.57	11.56	0.003
Site	0.669	1	0.669	4.936	0.039
Error	2.576	19	0.136		

$\delta^{13}C$ of tetrigids were more similar to those of pool algae than those of terrestrial plants (Fig. 4). The mixing model suggested that *P. aztecus* derived all of their C

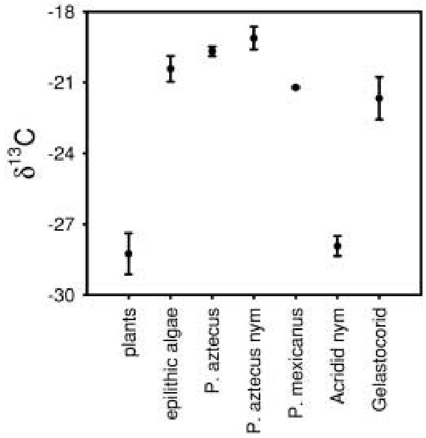

Fig. 4 Average (mean±1 SE) $\delta^{13}C$ values (‰) for terrestrial plants (n=22), epilithic algae (n=15), acridid nymphs (n=3), gelastocorids (n=3), *Paratettix aztecus* adults (n=5), *P. aztecus* nymphs (n=4) and *P. mexicanus* adults (n=2) from three sites throughout the summer. Each insect sample represents five pooled individuals from the same site on the same date

Table 4 Estimated percent of assimilated C from pool algae (±1 SE) for two species of Tetrigidae, a riparian Acrididae, and a Gelastocoridae using a two-source mixing model. The mixing model assumed insects ate only pool algae and terrestrial plants. Estimates are given for two different assumed values of $\delta^{13}C$ trophic fractionations

Taxa	+0.4‰ Fractionation	+1‰ Fractionation
Paratettix aztecus adult	106.02±5.69	98.87±5.33
P. aztecus nymph	112.98±7.26	105.82±6.94
P. mexicanus	87.66±4.53	80.50±4.27
Acrididae	7.56±6.08	0.41±6.43
Gelastocoridae	86.39±9.75	79.24±9.64

from pool algae (Table 4). The assumption of +0.4‰ trophic fractionation of ^{13}C had only a slight effect on this result; when we assumed a trophic fractionation of +1‰ for ^{13}C, the portion of C that *P. aztecus* adults received from pool algae dropped to 99%. *P. mexicanus* appeared to have a slightly more terrestrial diet, with 88% of its assimilated C acquired from pool algae. Gelastocorids at our study site had a similarly aquatic diet, while the riparian acridid grasshoppers had a largely terrestrial diet (Table 4). *P. aztecus* $\delta^{13}C$ values ranged from –18.25 to –20.27 (with a mean of –19.43±0.23). This variation was unrelated to either site or date. *P. mexicanus* $\delta^{13}C$ values varied little over the summer.

Discussion

The study of energy exchange between aquatic and terrestrial habitats has a rich tradition in stream ecology (Hynes 1970; Cummins et al. 1973; Fisher and Likens 1973; Vannote et al. 1980; Goulding 1980; Winemiller 1990). Studies of trophic exchanges in watersheds have typically focused on forest inputs of detritus and terrestrial insects to streams (e.g., Mason and MacDonald 1982; Jackson and Fisher 1986; Gray 1989, 1993; Nakano et al. 1999). Forest resources appear to fuel the production of aquatic invertebrates (Wallace et al. 1997, 1999) and fish (Goulding 1980; Nakano et al 1999) in small, shaded streams, where such inputs are large relative to local primary production (*but see* Mayer and Likens 1987; Finlay 2001).

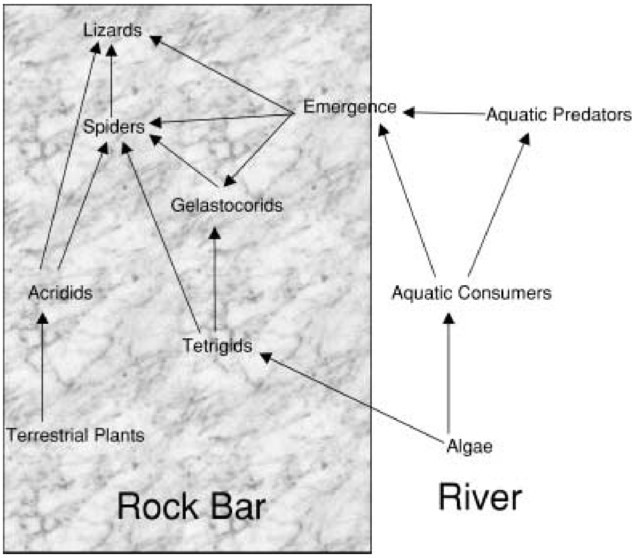

Fig. 5 A simplified diagram of the river and riparian food web

Recent empirical studies from rivers in a wide variety of biomes have demonstrated that energy flow in the reverse direction can also influence the abundance and diversity of terrestrial consumers, and food web dynamics in riparian systems (Jackson and Fisher 1986; Power and Rainey 2000; Sabo 2000; Nakano and Murakami 2001). This is especially true for larger, more open streams in which primary production by algae is much higher than in shaded tributaries. While many of these recent studies suggest that aquatic insects provide the dominant mechanism by which aquatic primary production enters terrestrial food webs, this study demonstrates that riverine algae may also enter these food webs via direct consumption by shoreline, terrestrial scavengers, some of which specialize on detrital algae. Tetrigid grasshoppers receive between 88–100% of their C from riverine sources. This energy is conveyed up to higher levels of the terrestrial food web by predation by vertebrates and invertebrates. For example, stable isotope signatures of gelastocorids reflect a diet consisting of at least 86% aquatic C. This signature most likely reflects consumption of adult forms of aquatic herbivores (such as Ephydridae) and terrestrial scavengers of aquatic production (such as Tetrigidae) (Fig. 5).

Riparian grasshopers: specialists on aquatic resources

The addition of wet *Cladophora* to experimental plots increased tetrigid densities 30-fold, while the addition of water and dry *Cladophora* did not significantly increase grasshopper density over control plots. Pygmy grasshoppers are one of many terrestrial consumers that numerically track natural or experimentally manipulated spatial variation in river-derived resources at the South Fork Eel River. Densities of ground spiders (Lycosidae) declined by an order of magnitude when wetted algal mats were removed from shoreline plots, and recruited as heavily to similar plots where algae mats were added (Parker and Power, unpublished data). These spiders attack midges (Chironomidae and Ceratopogonidae) emerging from the wetted portions of mats and shore flies (Ephydridae) which aggregate on the mats as adults. The abundance of lizards (*Sceloporus occidentalis*, Iguanidae) was 1.8–2.5× higher in 90-m^2 cobble bar plots with ambient aquatic insect flux, than in plots where aquatic fluxes were experimentally reduced by 60% (Sabo 2000). Thus, consumers of various trophic ranks are capable of tracking variation in aquatic resource inputs in near-shore habitats. Both spiders and lizards are generalist predators that consume a variety of aquatic and terrestrial invertebrate prey. By contrast, isotope analysis of Tetrigidae from our study site revealed that riparian pygmy grasshoppers are specialists, feeding almost exclusively on algae during the summer.

Seasonality and the response of tetrigids to resources

After winter rains and seasonal high flows, the river recedes rapidly during the spring, leaving behind a film of mud and algal detritus on the newly exposed cobble bars. The algae in this film appear to be the primary food source for the tetrigids in June, as *Cladophora* mats do not begin washing ashore until July. The tetrigids are evenly distributed over the first 6 m from the water's edge in June (Fig. 1), which may be the result of feeding on an evenly distributed food source, being less limited by dessication than later in the summer, or both.

Cladophora mats begin washing ashore in July, providing a concentrated algal food source at the water's edge. The tetrigids aggregate on *Cladophora* mats as soon as they become available. Tetrigids aggregate at the river even where such mats are not present, however, suggesting that microalgae also begin washing ashore at this point in the season.

Algal scavengers as an alternate source of riverine energy for generalist insectivores

Three factors suggest that the specialization of tetrigids on algae represents an important energy flux from the river to the terrestrial food web. First, the densities of tetrigids in mid summer are high for riparian insects (>30 individuals/m^2 on algal mats). Second, exported algal detritus is an abundant food source for these consumers, especially in July. Finally tetrigids rely almost exclusively on aquatic primary production, and consume up to their body weight in damp algae per day. Unlike riverine fluxes of aquatic insects to riparian habitats (Gray 1989, 1993; Jackson and Fisher 1986; Sabo 2000; Power et al., in press; Henschel, in press), this flux occurs at the base of the food web, suggesting that rivers may provide resources for terrestrial consumers via a variety of trophic pathways

There are a large number of predators that could benefit from the riverine energy entrained by terrestrial scavengers, such as tetrigids, ants and smaller ground beetles (Carabidae). These scavengers may be of special importance in that they make aquatic primary production available to small cursorial predators. The winged adults of truly aquatic insects (Odonata, Trichoptera, and Ephemeroptera) spend more of their time in the air than tetrigids, which are generally sedentary, only leaping when disturbed. In addition, adult Odonata, Plecoptera and Trichoptera are often too large to be caught by riparian arthropod predators, such as ground spiders, toad bugs (Gelastocoridae), tiger beetles (Cicindelidae), and ground beetles (Carabidae). The distribution of small riparian insects which feed on beached algae may help explain patterns in the distribution of small predatory riparian arthropods.

It is important to understand the role of terrestrial algivores play in riparian food webs because alterations to hydrologic regimes can dramatically affect the availability of their food (e.g., Power 1992). The film of algal detritus on which tetrigids feed in the early summer is made available by winter flooding followed by summer drought. Artificially regulated rivers without natural seasonal fluctuations in discharge will not expose substrate previously overgrown by algae in the seasonally predictable regime to which Mediterranean species have adapted. Additionally, the accrual of large amounts of *Cladophora* depends on the natural winter flood-summer drought flow regime found in northern Californian rivers (Power 1992). Although a small standing crop of *Cladophora* may grow in regulated streams lacking natural fluctuations in discharge, little is exported to shorelines to become available to tetrigids, ants, ground beetles and other riparian scavengers. If terrestrial scavengers make aquatic C available to riparian predators and detritivores that cannot make use of the adult aquatic insects, we would expect changes in the availability of beached algae to impact multiple trophic levels of the riparian food web. Landuse or water management higher in the drainage network may have pervasive effects on downstream riparian communities as a result of links between rivers and watersheds at a variety of trophic levels.

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References

Bhalerao AM, Paranjape SY (1986) Studies on the bioecology of a grouse locust *Euscelimena harpago* Serv. (Orthoptera: Tetrigidae). Geobios (Jhodpur) 13:145–150

Borror DJ, Triplehorn CA, Johnson NF (1989) An introduction to the study of insects, Sixth edn. Saunders College, Harcourt Brace Jovanovich, pp 213

Cummins KW, Petersen RC, Howard FO, Wuycheck JC, Holt VI (1973) The utilization of leaf litter by stream detritivores. Ecology 54:336–345

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506

Finlay JC (2001) Stable carbon isotope ratios of river biota: implications for energy flow in lotic food webs. Ecology 82:1052–1064

Finlay JC, Power ME, Cabana G (1999) Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. Limnol Oceanogr 44:1198–1203

Fisher SG, Likens GE (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol Monogr 43:421–439

France RL (1996) Absence or masking of metabolic fractionations of ^{13}C in a freshwater benthic food web. Freshwater Biol 36:1–6

France RL, Peters RH (1997) Ecosystem differences in the trophic environment of ^{13}C in aquatic food webs. Can J Fish Aquat Sci 54:1255–1258

Fry B, Sherr EB (1984) δ^{13}C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib Mar Sci 27:13–47

Goulding M (1980) The Fishes and the forest. University of California Press, Berkeley, Calif.

Gray LJ (1989) Emergence production and export of aquatic insects from a tallgrass prairie stream. Southwest Nat 34:313–318

Gray LJ (1993) Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. Am Midl Nat 129:288–300

Henschel JR (in press) Subsidized predation along river shores affects terrestrial herbivore and plant success. In: Polis GA, Power ME, Huxel GR (eds) Food webs in landscapes. Chapman and Hall, New York

Hering D, Platcher H (1997) Riparian ground beetles (Coleoptera, Carabidae) preying on aquatic invertebrates: a feeding strategy in alpine floodplains. Oecologia 111:261–270

Hynes HBN (1970) The Ecology of running waters. University of Toronto Press, Toronto

Jackson JK, Fisher SG (1986) Secondary production, emergence and export of aquatic insects of a Sonoran stream. Ecology 67:629–638

Lighton JRB, Fielden LJ (1995) Mass scaling of standard metabolism in ticks: a valid case of low metabolic rates in sit-and-wait strategists. Physiol Zool 68:43–62

Mason CF, MacDonald SM (1982) The input of terrestrial invertebrates from tree canopies to a stream. Freshwater Biol 12:305–311

Mayer MS, Likens GE (1987) The importance of algae in a shaded headwater stream as food for an abundant caddisfly (Trichoptera). J N Am Benthol Soc 6:262–269

Milne LJ, Milne M (1980) The National Audubon Society field guide to North American insects and spiders. Random House, New York, pp 416–417

Nakano S, Murakami M (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proc Natl Acad Sci USA 98:166–170

Nakano S, Miyasaka H, Kuhara N (1999) Terrestrial-aquatic linkages: iparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435–2441

Paranjape SY, Bhalerao AM (1985) Bioecological observations on a pygmy locust, *Potua sabulosa* Hancock (Tetrigidae; Orthoptera). Psyche 92:331–336

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. Oecologia 127:171–179

Polis GA, Hurd SD (1995) Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. Proc Natl Acad Sci USA 92:4382–4386

Polis GA, Hurd SD (1996) Linking marine and terrestrial foodwebs: allochthonous inputs from the ocean supports high secondary productivity on small island and coastal land communities. Am Nat 147:396–423

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316

Power ME (1990) Benthic turfs vs. floating mats of algae in river food webs. Oikos 58:67–79

Power ME (1992) Hydrologic and trophic controls of seasonal algal blooms in northern California rivers. Arch Hydrobiol 125:385–410

Power ME, Rainey WE (2000) Food webs and resource sheds: towards spatially delimiting trophic interactions. In: Hutchings MJ, John EA, Stewart AJA (eds) Ecological consequences of environmental heterogeneity. Blackwell Science, Oxford, pp 291–314

Power ME, Rainey WE, Parker MS, Sabo JL, Smyth A, Khandwala S, Finlay JC, McNeely FC, Marsee K, Anderson C (in press) River to watershed subsidies in an old-growth conifer forest. In: Polis GA, Power ME, Huxel GR (eds) Food webs in landscapes. Chapman and Hall, New York

Rehn JAG, Grant HJ Jr (1961) Orthoptera of North America. Monographs of the Academy of Natural Sciences, Philadelphia, Pa.

Rose MD, Polis GA (1998) The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79:998–1007

Sabo JL (2000) River-watershed exchange: the effects of rivers on the population and community dynamics of lizards (Sceloporus occidentalis). PhD dissertation. University of California, Berkeley, Calif.

Summerhayes VS, Elton CS (1923) Contributions to the ecology of Spitsbergen and Bear Island. J Ecol 11:214–286

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. Can J Fish Aquat Sci 37:130–137

Wallace JB, Eggert SL, Meyer JL, Webster JR (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104

Wallace JB, Eggert SL, Meyer JL, Webster JR (1999) Effects of resource limitation on a detrital-based ecosystem. Ecol Monogr 69:409–442

Winberg GG (1971) Symbols, units and conversion factors in studies of fresh water productivity. Academic Press, London

Winer BJ, Brown DR, Michels KM (1991) Statistical principles in experimental design, third edn. McGraw-Hill, New York

Winemiller KO (1990) Spatial and temporal variation in tropical fish trophic networks. Ecol Monogr 60:331–367

Zar JH (1996) Biostatistical analysis, third edn. Prentice-Hall, Upper Saddle River, N.J.