

Research Article

Invertebrate and microbial responses to inundation in an ephemeral river reach in New Zealand: effects of preceding dry periods

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Abstract. Inundation marks the shift from a terrestrial ecosystem to an aquatic ecosystem in ephemeral rivers. The forms and rates of responses by aquatic invertebrates and sediment microbes to inundation depend on desiccation resistance during preceding dry periods. We assessed invertebrate and microbial responses to inundation over a range of preceding dry periods in an ephemeral reach of the Selwyn River, New Zealand. Microbial response variables were dissolved oxygen consumption and non-specific esterase activity. Sampling sites along the reach had been continuously dry for 1–592 d prior to sample collection. The onset of flow simulated by an experimental inundation led to the appearance of aquatic invertebrates in all samples, but the assemblages

varied with the length of the preceding dry period. Taxon richness decreased linearly with dry period length while density decreased exponentially. These patterns indicate that a large number of individuals from desiccation-sensitive taxa were eliminated soon after flow ceased, and a low-density assemblage composed of a small number of desiccation-resistant taxa persisted during prolonged dry periods. As with invertebrate density, sediment respiration and non-specific esterase activity decreased with length of dry period, and were characterized by exponential decay functions. The results of the inundation experiments suggest that a temporal ecotone exists for about one week after the disappearance of flowing water, and before the terrestrial system stabilizes.

Key words. Alluvial river; ephemeral; ecotone; inundation; invertebrates; microbial activity; sediment respiration.

Introduction

Ecotones in river corridors are generally viewed as spatial phenomena: narrow transition zones between dissimilar environments, and interfaces that regulate material and energy transfer between adjacent eco-

systems (Naiman and Décamps, 1997). From this perspective, riparian zones are ecotones between terrestrial and lotic ecosystems, and hyporheic zones are ecotones between lotic and groundwater ecosystems. However, temporal ecotones also occur in river corridors; these are relatively short transitional periods between persistent, dissimilar states (Pinay et al., 1990). Inundation and drying in floodplain forests, ephemeral channels, and alluvial islands represent

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temporal ecotones between aquatic and terrestrial states (Mertes, 1997; Osterkamp, 1998; Jacobson et al., 2000a). The long-term states that are punctuated by inundation and drying may be predominately terrestrial or aquatic, depending on relative hydroperiod (the proportion of time that flowing water is present in a given period; Snodgrass et al., 2000). Relative hydroperiods decrease across floodplains with distance from the active channel, and with elevation on alluvial islands and bars (Junk et al., 1989; Tockner et al., 2000). In ephemeral rivers, which are permanently separated from underlying aquifers by unsaturated sediment (Sophocleous 2002), rapid infiltration through the channel causes relative hydroperiods to decrease with distance downstream of water sources (Jacobson et al., 2000a; Larned et al., in press). Ephemeral reaches with high relative hydroperiods (near water sources) are likely to be structurally and functionally similar to perennial rivers, and ephemeral river reaches with low relative hydroperiods (far from water sources) are likely to be similar to terrestrial ecosystems.

Inundation of previously dry river reaches can trigger ecological “hot moments” (McKnight et al., 1999; Stanley et al., 2004). Hot moments are relatively short periods during which biogeochemical reactions or biological processes begin or accelerate after long quiescent periods (McClain et al., 2003). Inundation can activate microbial and algal cells, deliver chemical substrates to reaction sites, and stimulate enzyme-controlled nutrient transformations and organic matter mineralisation (Romani and Sabater, 1997; Baldwin and Mitchell, 2000; Burns and Ryder 2001, Belnap et al., 2005). Hot moments include metazoan responses as well as microbial responses. Inundation of dry substrata can trigger hatching in desiccation-resistant eggs and cysts of aquatic invertebrates, and terminate diapause and aestivation (Brock et al., 2003; Tronstad et al., 2005). For terrestrial invertebrates that colonize ephemeral river channels during dry periods, inundation kills some organisms, and cues others to migrate or enter inundation-resistant stages (Tamm, 1984; Adis and Junk, 2002).

Several lines of evidence suggest that invertebrate and microbial responses to inundation will depend on the duration of the preceding dry phase. Drying initially causes rates of anaerobic microbial processes in sediments to decrease due to increased oxygen penetration (Baldwin and Mitchell, 2000). Prolonged dry periods result in high microbe mortality in surficial sediments due to dehydration and radiation (Qui and McComb, 1994; Castenholtz and Garcia-Pichel, 2000). Resistance or resilience in aquatic invertebrate assemblages is likely to decrease with increasing dry period duration (Boulton, 2003). Dry periods that are

longer than invertebrate generation times will reduce the efficacy of adaptive traits such as burrowing to deeper sediment layers and reproductive plasticity (Boulton, 2003). Other traits, including desiccation-resistant eggs, pupae and cysts, and use of atmospheric oxygen, allow some aquatic invertebrates to survive prolonged dry periods (Williams, 1996; Brock et al., 2003). Conversely, traits such as plastron respiration and water-resistant eggs allow some terrestrial invertebrates to resist inundation (Adis and Junk, 2002). Differences among aquatic and terrestrial species in resistance to desiccation and inundation are likely to cause shifts in community composition along hydroperiod gradients.

Longitudinal gradients in hydroperiods make ephemeral rivers useful systems for exploring ecological effects of drying and inundation. In this study, we examined effects of inundation on invertebrate assemblages and microbial activity along a 32-km reach of the Selwyn River, New Zealand. This reach comprised a gradient in relative hydroperiod from 0.11–1.00, where relative hydroperiod is the ratio of days of observed wetted channel to total days of observation. During the study, points along the gradient had been continuously dry for 1–592 d. We predicted that rates of invertebrate and microbial responses to inundation would decrease with duration of the preceding dry period. Further, we predicted that these responses would be non-linear due to critical dry period lengths beyond which biotic responses are sharply reduced. These critical dry periods correspond to temporal ecotones and are manifested as inflection points in dry period-biotic response relationships.

Methods

Study site

The Selwyn River drains a 170 km² catchment in the eastern foothills of New Zealand’s Southern Alps (Fig. 1). The river mainstem flows for 35 km through the foothills, then for 60 km across and under the alluvial Canterbury Plains to coastal Lake Ellesmere. The alluvial portion of the Selwyn mainstem has two abutting sections: a 38-km losing section where surface water leaks through the channel to deep, poorly-confined aquifers, and a 22-km gaining section where the river receives groundwater from shallow aquifers and springs. The first 3 km of the losing reach are perennial, as surface flows from the foothills always exceed losses. The next 35 km is an ephemeral-losing reach; all surface flow is lost for at least part of each year. The ephemeral-losing reach ends at the upstream border of an intermittent-gaining reach, where river recharge from groundwater begins. After accu-

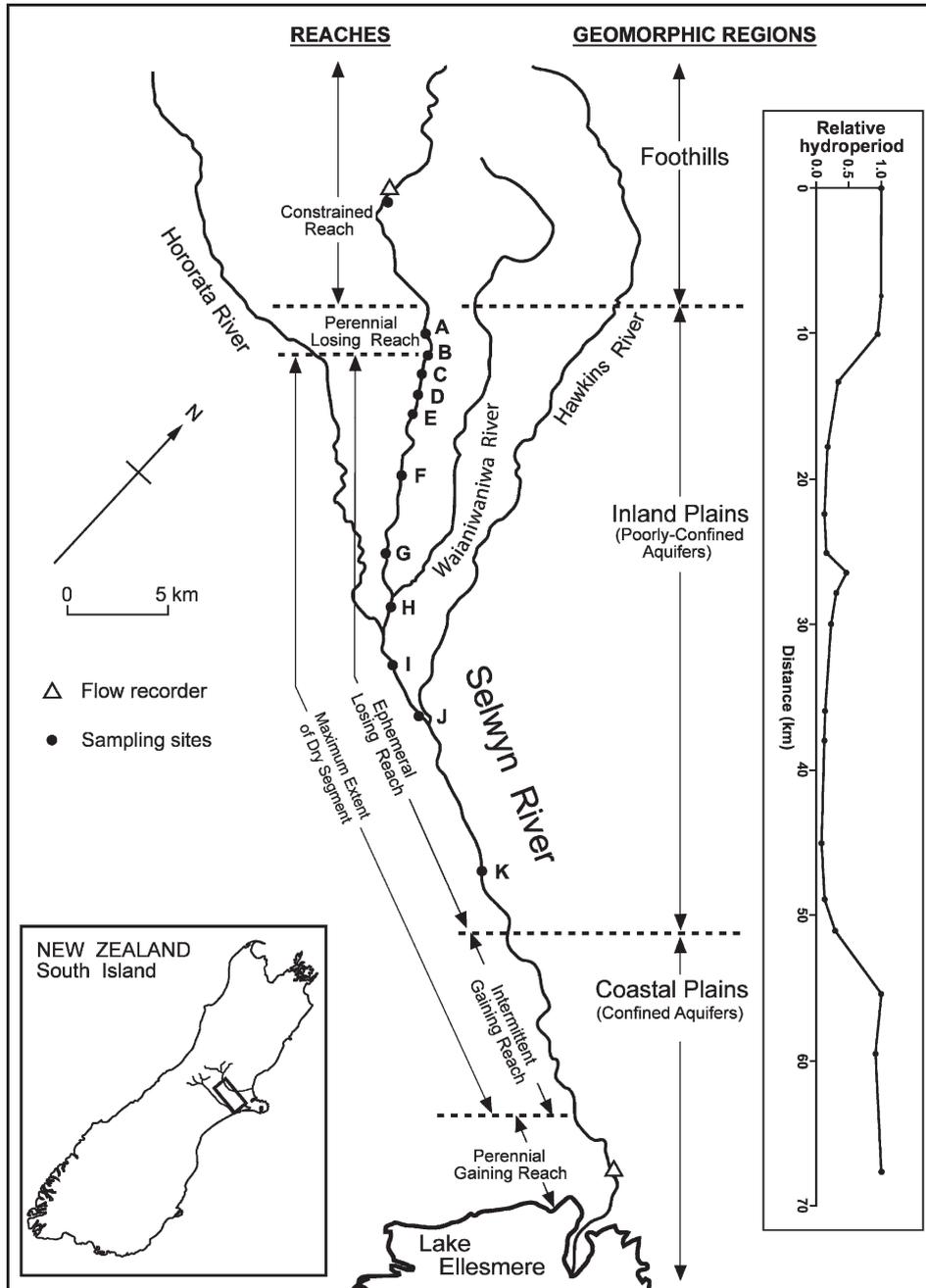


Figure 1. Selwyn River and major tributaries, SE New Zealand. Dotted lines indicate boundaries of major reaches and geomorphic regions. Letters along mainstem are sampling sites. Inset on right: gradient in relative hydroperiods along the Selwyn River. Distances on inset x-axis align horizontally with Selwyn River on adjacent map.

mulating groundwater for 8 km, the river becomes perennial, and the perennial-gaining reach extends for 15 km to Lake Ellesmere. Hydrological and geomorphological dynamics in the Selwyn River are described in detail in Larned et al. (in press).

In the ephemeral-losing reach, relative hydroperiod decreases with distance downstream, except at points where tributary inflows cause small-scale increases in relative hydroperiod (Fig. 1, inset). Rel-

ative hydroperiod in the ephemeral-losing reach ranges from 1.00 at the upstream border with the perennial-losing reach to 0.11 near the downstream border with the intermittent-gaining reach. As relative hydroperiod decreases, the average duration of dry periods increases. During years with near-average rainfall and groundwater recharge, dry periods in the ephemeral reach range from 1 d immediately downstream of the perennial-losing reach to ~ 45 d at the

downstream border with the gaining reach (Larned et al., in press). The austral winters of 2004 and 2005 were characterized by unusually low precipitation and groundwater recharge. Strongly reduced runoff from spring 2004 to winter 2006 extended the range of dry period lengths in the ephemeral reach from to 1–628 d. We used this extended dry-period gradient as a natural experiment to assess the responses of ephemeral river biota to inundation.

One site in the perennial-losing reach (Site A), and ten sites along the ephemeral reach (Sites B–K) were used for sample collections (Fig. 1). The dry period duration at each site at the time of sampling was estimated from the elapsed time since the last observed flow (Table 1). Site visits every 1–20 days during an ecological monitoring program allowed us to estimate dry period durations at each site with 0–18 d precision. When uncertainty about the date of last flow at a site was greater than one day, that date was estimated as the mid-point between the dates at which flow was last observed and the dry channel first observed. Ratios of uncertainty (in days) to elapsed time since the last observed flow ranged from 0–0.16. Two sites (B and C) near the border with the perennial reach were sampled after a dry period of 1 day. These sites were identified by marking the downstream edge of flowing water during periods of rapid recession (i.e., surface water receding upstream 5–10 m d⁻¹), and collecting samples near the marker 24 h later. At all sites, samples were collected from areas corresponding to runs in the main channel when flowing water was present.

Table 1. Estimated dry period duration and relative hydroperiod at sampling sites. Site letters correspond to Figure 1. Dry period duration: days since last observed wetted channel prior to invertebrate experiment sample collection (16 September 2005). Relative hydroperiod: ratio of observations of wetted channel:total observations from 8 October 2003 to 1 June 2006; $n = 51$ –55 observations per site.

Site	Dry period(d)	Relative hydroperiod
A	0	1
B	1	0.87
C	5	0.43
D	49	0.34
E	256	0.18
F	316	0.13
H	316	0.17
I	190	0.31
J	241	0.24
K	317	0.11

Invertebrate responses to inundation

Triplicate sediment samples were collected at 9 sites along the ephemeral reach (Fig. 1) in September 2005. Samples were collected by spade at random points

along the run at each site. At each point, 2.5 L of sediment was collected from 2 depths (0–10 cm and 10–20 cm). Depth stratification allowed us to determine whether depth-related differences in organic matter or moisture influenced responses to inundation. A 50-ml subsample from each sample was transferred to a plastic bag and sealed for determination of organic content and sediment moisture. The remaining material from each sample was placed in an 8-L container. The samples were transported to the laboratory within 1 hr and the 8-L containers were placed in an environmental chamber (12 h:12 h light:dark cycle, 15°C). Each container was inundated with 5 L of filtered, non-chlorinated tap water, shaken gently, and the surface water decanted through a 63- μ m mesh sieve. This initial elutriation step reduced the number of macroscopic invertebrates; the intent was to remove predators that might consume eggs, pupae and hatching larvae during the experiment. Invertebrates, eggs, and pupae retained on the sieve were preserved in 70% isopropyl alcohol. Tap water was then added to each container to replace the decanted water, and the containers were fitted with airstones for continuous aeration, and 1-mm mesh lids to retain emerging insects. An inundation period of 17 d was selected as a compromise between long periods that could result in sediment anoxia, and periods too brief for egg and cyst hatching.

After the 17-d inundation, sediments in each container were vigorously elutriated 5 times and each elutriate poured through a 63- μ m mesh sieve. Material retained on the sieve was preserved in 70% isopropyl alcohol and the sediment remaining in each bucket was used for grain-size analysis (see below). Each invertebrate sample was sub-sampled (25% by volume), and invertebrate adults, larvae, pupae, and eggs enumerated. Invertebrates were identified to the lowest taxonomic level possible, which varied with taxonomic group and developmental stage. Briefly, insects, molluscs, amphipods, and isopods were identified to family, genus or species, mites, nematodes, flatworms and tardigrades to phylum, and other taxa to class or family. Taxa were also classified as terrestrial or aquatic.

Sediment grain-size distribution, moisture and organic matter content

Following elutriation of invertebrates, sediment samples were air-dried then shaken through a series of nested sieves on a Endecotts EFL-2000 shaker (Winegardner, 1996). Sediments on each sieve were dried at 60°C to constant mass, and the percentage of total mass determined for six grain-size classes: <2, 2–4, 4–8, 8–16, 16–32, >32 mm. The 50-ml sediment samples from the invertebrate sampling sites were weighed

wet, dried at 60°C to constant mass, combusted for 4 h at 400°C, and reweighed. Moisture content was determined from differences in wet and dry mass, and organic content from differences in dry and combusted sediment mass.

Sediment respiration and microbial activity

Two experiments were carried out to distinguish the effects of dry period length and of dry periods followed by inundation on microbial enzyme activity and sediment respiration. In the first experiment, sediment samples collected in January 2006 were used to measure enzyme activity and respiration with minimal or no exposure to water. Samples were collected at Sites A–K (Fig. 1). Site B was sampled 1 d before and 1 d after drying. In the second experiment, the same measurements were made after sediment samples collected in May 2006 from Sites E–I were inundated for 17 d. The first and second experiments are referred to below as the ‘no-inundation’ and ‘inundation’ experiments, respectively. The inundation experiment encompassed a narrower range of dry periods (238–523 d) than the no-inundation experiment (0–486 d). Sites with dry periods between 1 and 230 d were no longer available at the time of the inundation experiment. None of the sites were rewetted between the January and May 2006 sampling dates.

For both experiments, three 700-ml depth-integrated (5–20 cm depth) sediment samples were collected at random points from runs in the main channel at each site. All samples were sieved (8 mm-mesh) in the field to remove very coarse material and reduce the effects of differences in sediment surface area at sites with dissimilar grain-size distributions (Jones et al., 1995). For the no-inundation experiment, enzyme activity and respiration measurements began within 2 h of sample collection. For the inundation experiment, the same measurements were made using sediments that had been held in aerated water for 17 d, as described above for the invertebrate experiment. To determine whether microbial contamination from tap water or air affected enzyme activity, controls were included in the inundation experiment. The controls consisted of sediment samples from three sites that were combusted for 4 h at 400°C to eliminate microbes and organic material prior to inundation.

Hydrolysis of fluorescein diacetate (FDA) by non-specific esterases was used as an assay for total enzyme activity (Schnürer and Rosswall, 1982). Esterase activity in sediment samples from the inundation and no-inundation experiments was measured using the procedures of Fontvieille et al. (1992), with some modifications. Three 1-g aliquots from each sediment sample were transferred to ashed glass vials with 3 ml

phosphate buffer (pH 7.6), and 0.1 ml FDA solution (FDA in 60% acetone, 2 g/L). Vials were incubated at 20°C in darkness for 60–90 min, and the reactions stopped by adding 3 ml HgCl₂ (400 mg L⁻¹) and freezing. The supernatant in each vial was filtered through a 0.45-µm acetate filter, and absorbance of the filtrate measured at 490 nm with a Shimadzu UV-2550 spectrophotometer, then converted to µmole fluorescein. The fluorescein detection limit using this technique is ~ 0.1 µM.

Respiration measurements in sediment samples from the inundation and no-inundation experiments followed the procedures of Jones et al. (1995) with modifications. Aliquots of ~ 350 ml sediment were transferred from the 700-ml samples to PVC tubes (28 mm inside diameter, 65 mm long), and the tubes were filled to the top with aerated tap water and closed with rubber caps fitted with air-release valves. Each tube was inverted 3 times to mix sediment and water, uncapped, and the dissolved oxygen concentration immediately measured with a TPS WP-82 meter and TPS ED500W sensor. The tubes were recapped, incubated for 4 h at 15°C, inverted 3 times, and dissolved oxygen was remeasured. Respiration rates were calculated as the differences between starting and ending dissolved oxygen concentrations. The contents of each tube were vigorously elutriated 3 times to separate particulate organic matter (POM) from coarse mineral sediment, and the elutriates from each tube were pooled and filtered (Whatman GF/F). The ash-free dry mass (AFDM) of POM on the filters and the biofilm AFDM on coarse sediments from the PVC tubes was determined from differences in dry and ashed sediment mass.

Data analysis

Changes in invertebrate assemblages along the dry-period gradient were examined using correspondence analysis (CA) with ADE4-R software (Thioulouse et al., 1997). Eggs, pupae and terrestrial taxa were omitted, and aquatic invertebrate densities were log₁₀(x+1)-transformed prior to CA. Relationships between dry period duration and invertebrate density and richness were examined by linear and non-linear regression, using the curve fitting tool in Sigma Plot 10.0 (Systat Software, Inc.). All regressions were tested for normality of residuals with Kolmogorov-Smirnov tests (Bradley 1968).

Relationships between sediment respiration rates and FDA hydrolysis rates and dry period duration in the inundation and no-inundation experiments were examined by regression. Because sediment respiration rates were more closely related to POM than to biofilm AFDM on coarse grains, respiration rates were normalized using POM, and are reported as mg

Table 2. Invertebrate taxa in initial elutriations and in experimental containers after 17 days of inundation. Depths (0–10 cm and 10–20 cm) are sediment depths below river channel surface. Categories: A = aquatic, T = terrestrial. Asterisks: taxon present.

Taxon	Category	Initial		Inundation	
		0–10 cm	10–20 cm	0–10 cm	10–20 cm
Arachnida					
Acarina	A	*	*	*	*
Araneida	T	*	*		
Chilopoda	T	*	*		
Collembola	T	*	*	*	*
Cladocera	A			*	*
Copepoda					
Cyclopoida	A			*	*
Harpacticoida	A			*	*
Copepodites	A			*	*
Ostracoda	A	*		*	*
Coleoptera					
Elmidae (larvae)	A			*	
Staphylinidae (adults)	T	*	*		*
Unidentified	T	*			
Ephemeroptera					
Leptophlebiidae	A	*	*	*	
<i>Deleatidium</i> spp.	A			*	
Diptera					
Chironomidae (adults)	A	*	*		
<i>Ephydrella</i> sp.	A			*	*
<i>Eriopterini</i> sp.	A			*	*
Orthocladiinae	A			*	*
Hemiptera					
Aphidae	T	*	*		
Hymenoptera					
Formicidae	T	*			
Megaloptera					
<i>Archichauliodes diversus</i>	A			*	
Trichoptera					
<i>Olinga</i> sp.	A	*	*	*	
<i>Oxyethira</i> sp.	A			*	*
<i>Pycnocentroides</i> sp.	A				*
Cnidaria					
<i>Hydra</i> sp.	A				*
Nematoda	A			*	*
Oligochaeta					
<i>Eiseniella</i> sp.	A			*	*
Enchytraeidae	A			*	
Naididae	A			*	*
Tubificidae	A			*	*
Unidentified	A	*	*	*	*
Protura	T	*	*		
Tardigrada	A			*	*
Eggs		*	*	*	*
Pupae		*	*		

O_2 g AFDM_{POM}⁻¹h⁻¹. FDA hydrolysis rates were normalized using sediment dry mass, and are reported as $\mu\text{mole FDA g DM}^{-1}\text{h}^{-1}$.

Results

Invertebrate response to inundation

A total of 25 aquatic and 8 terrestrial invertebrate taxa were recovered in 54 sediment samples from the ephemeral reach of the Selwyn River (Table 2). Half of the invertebrate taxa in the initial elutriation were terrestrial; the most abundant of these were Collem-

bola, aphids, and ants. Collembola and Staphylinidae (Coleoptera; rove beetles) were the only terrestrial taxa that survived as adults or hatched during the 17 d inundation. Aquatic taxa dominated the inundated samples (Table 2); the most abundant of these were copepods, oligochaetes and nematodes. Invertebrate eggs were recovered in 10% of the initial elutriation samples (average abundance: 0.8 egg per sample, range: 0–12), and in 69% of the post-inundation samples (average abundance: 11.3 eggs per sample, range: 0–100). These results suggest that relatively few eggs were inadvertently elutriated at the start of the experiment.

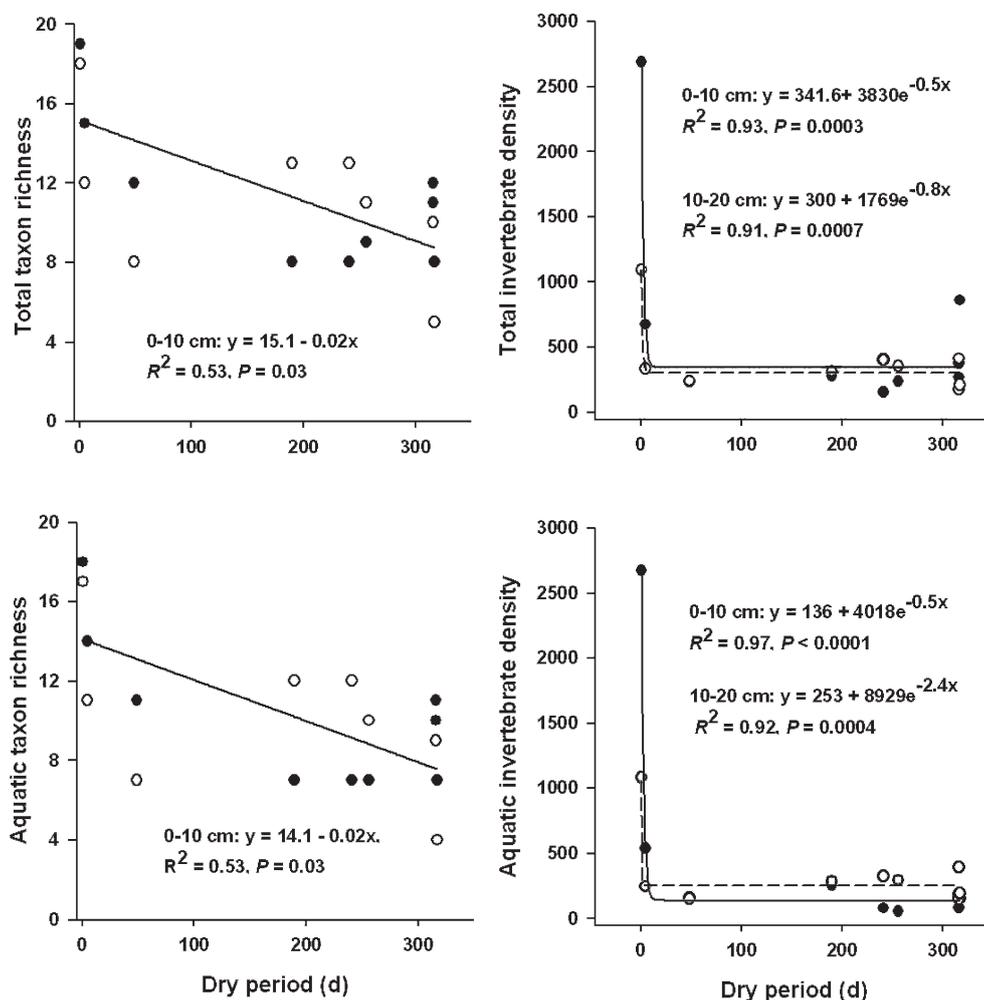


Figure 2. Total and aquatic taxon richness and invertebrate density from the inundation experiment. Points are averages of three samples from each site and depth. Solid circles: surface sediments (0–10 cm). Open circles: subsurface sediments (10–20 cm). Lines and equations are for significant regressions. Solid lines: regressions for surface sediments. Dashed lines: regressions for subsurface sediments.

After 17 d of inundation, an average of 10.2 (range: 4–18) aquatic invertebrate taxa and 1.1 (range: 1–3) terrestrial taxa were present in the sediment samples. Total taxon richness and aquatic taxon richness in surface sediments (0–10 cm depth) decreased linearly with increasing dry period (Fig. 2). Over the 317-d dry-period gradient, mean aquatic taxon richness following inundation decreased by 65%. No statistically significant relationships between taxon richness and dry period were detected in subsurface sediments (10–20 cm depth), and there were too few terrestrial taxa from either depth to analyze.

Average invertebrate densities were 162 (range: 10–1275) aquatic invertebrates and 44 (range: 0–232) terrestrial invertebrates per 2.5 L sediment sample. In contrast to the linear decrease in taxon richness, invertebrate densities decreased rapidly, then levelled off with increasing dry period length (Fig. 2). After a 5-d dry period, total invertebrate densities and aquatic

invertebrate densities in the inundated samples had declined to 20–25% of the densities in samples from the 1-d dry period. Negative exponential decay models accounted for much of the variation in the invertebrate density data from surface and subsurface sediments (Fig. 2). The good fit of exponential decay models indicates that invertebrates inhabiting dry river sediments comprised two major groups, a large group that is highly sensitive to drying and a much smaller group that is resistant to drying.

The CA indicated that invertebrate assemblages in the inundated samples varied with the preceding dry period and with sediment depth. Approximately 45% of the variance in the inundation experiment data was explained by the first 2 factors of the CA, F1 and F2 (F1: 25.7%, F2: 19.8%). Larval *Deleatidium* sp. (mayfly), *Olinga* sp. and *Oxyethira* sp. (caddisflies), *Archichauliodes diversus* (dobsonfly), and Elmidae (beetles), and microcrustaceans were the most influential taxa on

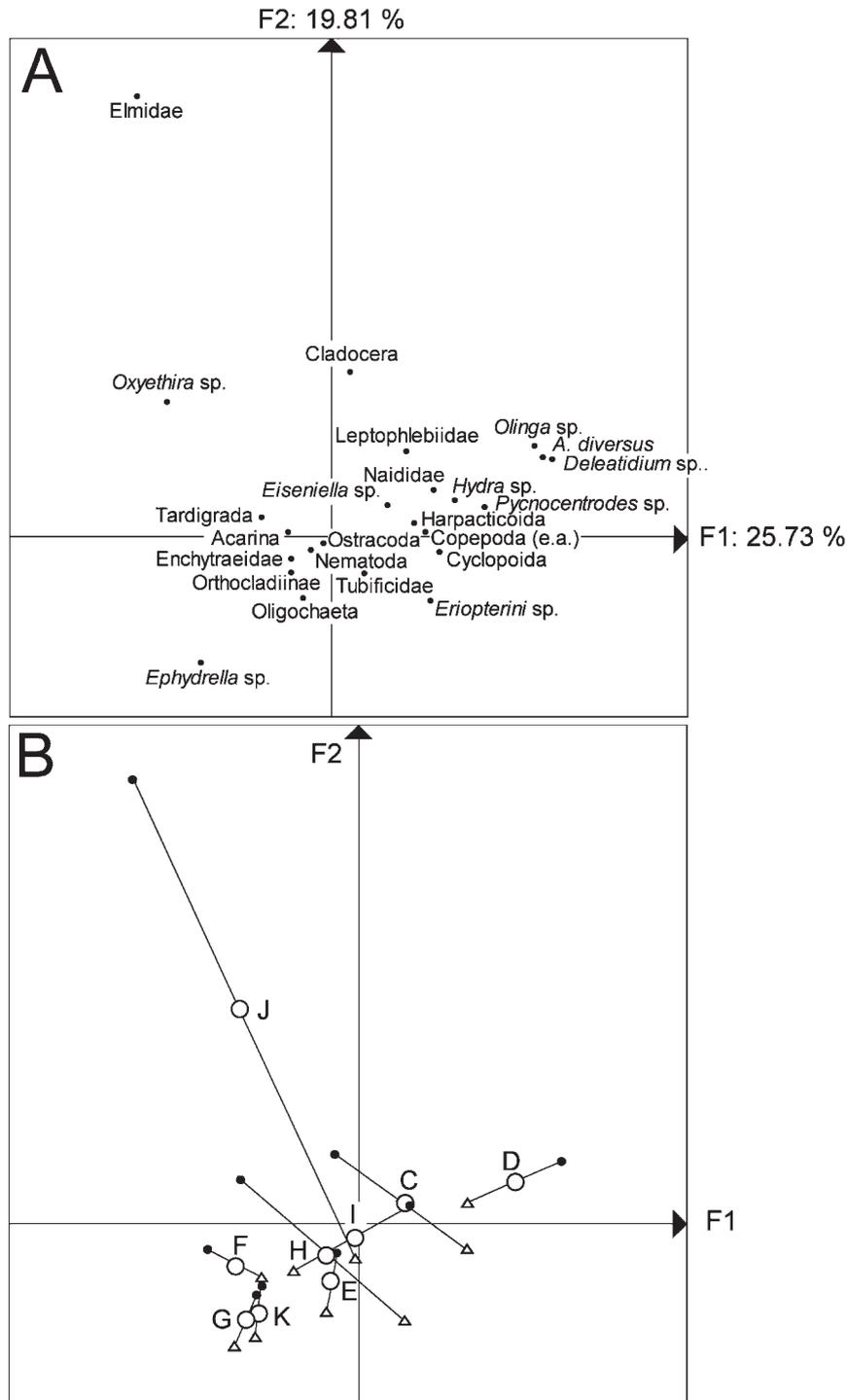


Figure 3. Correspondence analysis ordinations for invertebrates in inundation experiment. A) Ordination of taxa. B) Ordination of sites. Open circles: centroid for each site. Closed circles: surface sediment (0–10 cm depth). Triangles: subsurface sediment (10–20 cm depth). See Figure 1 for site locations.

F1 (Fig. 3A). The distribution of sites along F1 corresponded to the dry period gradient (Fig. 3B). Site scores for surface and subsurface sediment samples were negatively correlated with dry period length (linear correlation coefficient $r = -0.73$, $P = 0.026$, n

$= 9$ for surface samples; $r = -0.85$, $P = 0.004$, $n = 9$ for subsurface samples). Site scores for surface samples were positively correlated with sediment moisture content ($r = 0.69$, $P = 0.040$, $n = 9$), but site scores for subsurface samples were not ($P = 0.534$, $n = 9$).

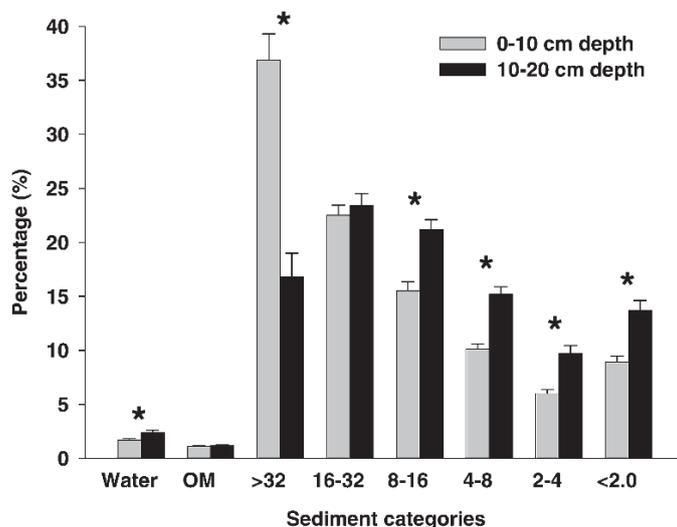


Figure 4. Moisture, organic matter content, and sediment grain-size classes (mm) in surface and subsurface sediments collected in September 2005. Data from 8 sites along the dry-period gradient have been pooled. Column values are means + 1 SE. Asterisks indicate significant between-depth differences ($P < 0.001$).

Elmidae and the larval dipteran *Ephydrella* sp. were the most influential taxa on F2 (Fig 3A). For each sampling site, surface sediments had higher F2 scores than subsurface sediments, indicating a consistent shift in invertebrate assemblages between depths (Fig. 3B). Elmidae, *A. diversus*, *Deleatidium* sp., *Olinga* sp., and Leptophlebiidae (mayfly) larvae occurred exclusively in surface sediments, while oligochaete worms were abundant in subsurface sediments but rare in surface sediments (mean abundance: 14.2 per surface sample, 1.9 per subsurface sample). F2 scores were not significantly correlated with dry period length or moisture content.

Sediment grain-size distribution, moisture and organic matter content

Surface sediments were dominated by the coarsest grain size class measured (> 32 mm), and had significantly less fine material than subsurface sediments (Fig. 4). At most sites, the channel surface was covered by an armored layer of cobbles, and surface accumulations of fine sediments were rare. Sediment moisture content was significantly lower in surface samples compared to subsurface samples (Fig. 4), but this difference was strongly influenced by one site with a 1-d dry period. There were no detectable relationships between sediment moisture or organic matter and dry period length, and no detectable difference in organic matter content between the two sediment depths (Fig. 4). Sediment moisture content and organic matter content were positively correlated ($r = 0.37$; $P = 0.010$, $n = 54$), which may reflect higher moisture retention by organic matter compared with sand and gravel.

Microbial activity and sediment metabolism

Esterase activity in the no-inundation experiment was negatively related to dry period length. A negative exponential decay model provided a good fit to the dataset (Fig. 5A), indicating a rapid decline in activity between dry periods of 1–7 d. After a 417-d dry period, esterase activity had decreased to 0.01–0.02 $\mu\text{mole FDA g DM}^{-1} \text{h}^{-1}$. These low esterase activity rates corresponded to fluorescein concentrations of 28 to 40 nM, above the 10 nM detection limit.

After 17 d of inundation, esterase activity in sediments that had been dry for 256–523 d was comparable to that in non-inundated sediments from a similar dry-period range (Fig. 5A). Esterase activity in the inundated sediments decreased with increasing dry period length, but the rate of decrease was $< 0.5\% \text{ day}^{-1}$. Linear and exponential decay models fit the inundated sediment data comparably (Fig. 6A). Esterase activity in control samples was $< 0.002 \mu\text{mole FDA g DM}^{-1} \text{h}^{-1}$, and fluorescein concentrations were below the detection limit, indicating that there was little microbial contamination from air or tap water during the experiment.

Respiration rates of sediments in the no-inundation experiment declined rapidly with dry period from 0–7 d, levelled off, then appeared to increase (Fig. 5B). We had no basis for eliminating the last points from consideration, so they were included in the regression. A negative exponential decay model provided a good fit to the no-inundation dataset (Fig. 5B). Respiration rates in saturated sediments from the perennial reach (mean ± 1 standard deviation: $0.76 \pm 0.29 \text{ mg O}_2 \text{ g AFDM}_{\text{POM}}^{-1} \text{h}^{-1}$, $n = 3$) were higher than in sediments from all ephemeral

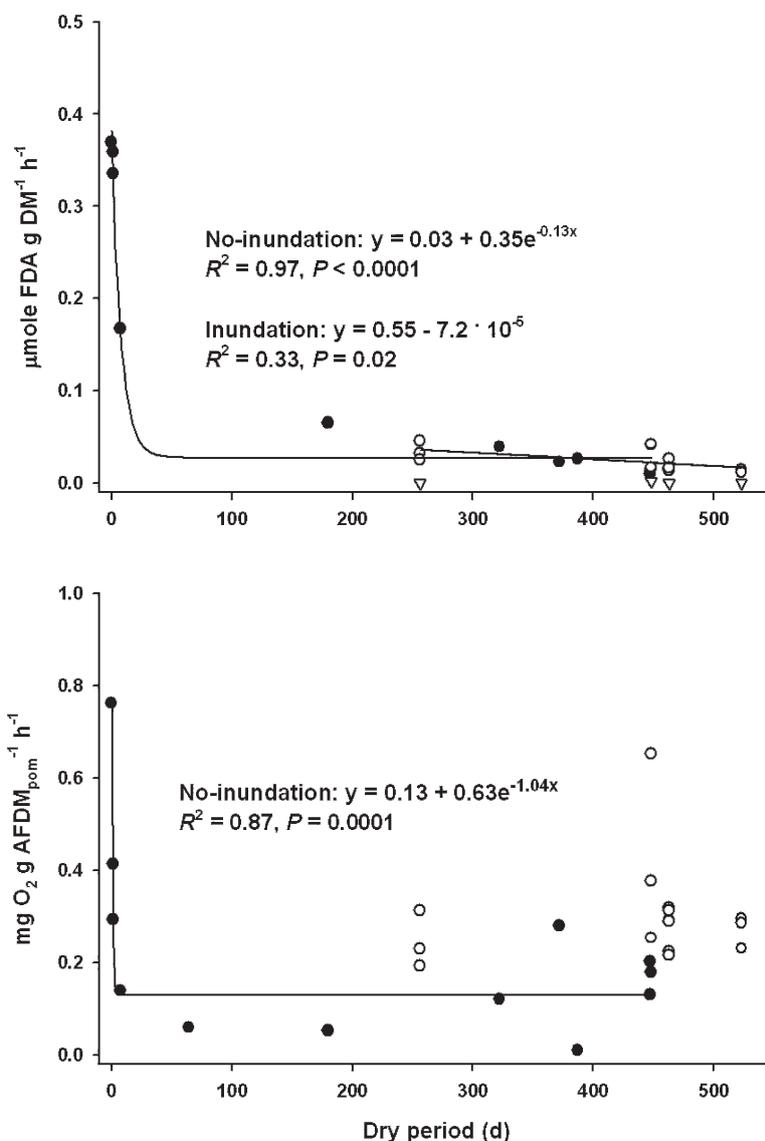


Figure 5. Regressions relating esterase activity (top panel) and sediment respiration (bottom panel) to dry period length in the Selwyn River. Closed symbols: no-inundation experiment. Open symbols: inundation experiment. Open triangles: inundation experiment controls. Points are average values from 2–3 subsamples. Lines and equations are for significant regressions. Solid lines: no-inundation experiment. Dashed lines: inundation experiment.

sites (mean \pm 1 standard deviation: 0.17 ± 0.09 mg O₂ g AFDM_{POM}⁻¹ h⁻¹, $n = 33$).

After 17 d of inundation, there was no detectable relationship between sediment respiration rate and dry period, although rates tended to be higher for inundated sediments than for non-inundated sediments (Fig. 5B). Esterase activity and sediment respiration rates were significantly correlated in samples from the no-inundation experiments (linear correlation coefficient $r = 0.70$, $P = 0.012$, $n = 36$), but not in the inundation experiment ($P = 0.23$, $n = 15$).

Discussion

Effects of dry periods in ephemeral river reaches

Perhaps as a result of the unclear provenance of ephemeral rivers, ecological processes in these environments have rarely been studied by aquatic or terrestrial scientists. Even less attention has been given to ecosystem and community level responses to variable hydroperiods within ephemeral rivers. Dry reaches in ephemeral rivers to be described as “biologically inactive” (Stanley et al., 1997), but this is inaccurate. Energy flow, nutrient cycling, trophic interactions, and biological succession continue in dry reaches, albeit dominated by different taxa and

biogeochemical pathways than in saturated sediments (e.g., Boulton, 1991; Jacobson et al., 2000b). Moreover, some invertebrates that are common in flowing water can persist for long periods in dry river sediments, and recolonize the benthos soon after the onset of flow (Brock et al., 2003; Tronstadt et al., 2005). The onset of flow that was simulated by our inundation experiment led to the appearance of aquatic invertebrate taxa in all samples. There was no possibility of aerial colonization or drift, so these invertebrates consisted of desiccation-resistant taxa, and a smaller number of desiccation-sensitive taxa that survived short dry periods.

The close fit of the negative exponential decay model to invertebrate densities over the dry period gradient was unexpected. The implication of this model is that a constant proportion of individuals die or emigrate over time after sediments dry. Populations affected by density-dependent mortality and dispersal are often characterized by negative exponential decay (e.g., Herzig, 1995). Aquatic invertebrates in drying river sediments may experience density-dependent mortality or emergence, but the specific mechanisms are as yet unclear. Density-dependent emergence was observed for the common mayfly *Deleatidium* sp. under falling water conditions in the Selwyn River (C. Robinson, unpubl. data). It is possible that crowding or predation in saturated interstitial spaces during the initial phases of drying results in density-dependent emergence or mortality in ephemeral reaches.

In contrast to the abrupt changes in invertebrate density, taxon richness decreased approximately linearly over the dry period gradient. Together, these two patterns indicate that a large number of individuals from a small number of desiccation-sensitive taxa disappears soon after a river reach dries, and a low-diversity assemblage of resistant taxa persists during prolonged long dry periods. The desiccation-sensitive group from the Selwyn River was represented by *Deleatidium* sp., *Olinga* sp., and *Archichauliodes diversus*. The presence of these taxa after short (1–5 d) dry periods indicates that they have some means of avoiding desiccation. *Deleatidium* sp., *Olinga* sp., and *Archichauliodes diversus* are highly mobile and occur in both benthic and hyporheic zones in New Zealand rivers (Scarsbrook and Halliday, 2002). These taxa appear to respond to surface drying by burrowing towards saturated subsurface zones. The desiccation-resistant assemblage that appeared in inundated sediments after long dry periods (>200 d) was dominated by copepods, ostracods, and nematodes, with lower densities of a small number of insect taxa. Desiccation-resistant stages are well-known in copepods and ostracods (Dahms, 1995), and the presence of copepodites in inundated samples after long dry periods

indicated hatching from desiccation-resistant eggs. Aquatic nematodes may survive extended dry periods in a state of anhydrobiosis (complete dehydration) (Ricci and Pagani, 1997). Other aquatic taxa may survive dry periods as active larvae. For example, chironomid dipterans from the subfamilies Orthocladiinae and Chironominae are frequently classed as desiccation-tolerant, active larvae (e.g., Tronstad et al., 2005), and Orthocladiinae were common in our samples after dry periods > 200 d. However, some chironomids in ephemeral environments undergo anhydrobiosis (Kikawada et al., 2005), and it is not clear whether assumptions about active larvae are accurate.

The results of the invertebrate and microbial activity experiments suggest that a temporal ecotone exists, which corresponds to a shift from aquatic to terrestrial conditions. Invertebrate densities in inundated sediments, and sediment respiration and esterase activity rates in non-inundated sediments decreased by 55–80% during 7 d of channel drying, then remained nearly constant over dry periods of 1–13 months. Temporal ecotones have been defined as short transition periods between long periods of stable abiotic or biotic conditions (Pinay et al., 1990). In the present study, the temporal ecotone was the short period corresponding to the shift in invertebrate density and microbial activity from those characteristic of flowing waters to those characteristic of dry riverbeds. The presence of spatial or temporal ecotones in river corridors increases habitat heterogeneity, which can increase biodiversity at the landscape level (Ward and Tockner, 2001). In addition, longitudinal gradients of dry and inundated periods in ephemeral rivers like the Selwyn increase successional diversity (i.e., mosaics of dry and saturated riverbed patches at various stages of terrestrial and aquatic succession) (Ward et al., 2002).

FDA hydrolysis rates reported for saturated streambed sediments range from 0.002–70 $\mu\text{mole FDA g DM}^{-1}\text{h}^{-1}$, and vary with sediment organic matter, dissolved nutrient and oxygen concentrations, and sediment depth (Marmonier et al. 1995, Mermillod-Blondin et al., 2000; Claret et al., 2001). Although this range encompasses the rates measured in our inundation and no-inundation experiments, it is too broad to make direct comparisons. In our no-inundation experiment, FDA hydrolysis rates were nearly constant in sediments that had dried for < 7 d (0.32–0.37 $\mu\text{mole FDA g DM}^{-1}\text{h}^{-1}$), then decreased by an order of magnitude after longer dry periods. In a related situation, esterase activity was predicted to vary directly with sediment moisture in a drying sandbed stream in Australia (Claret and Boulton, 2003). The predicted relationship was not observed, and the

authors suggested that a threshold sediment moisture level exists, below which enzyme activity decreases sharply. Our results lend some support to this threshold concept: esterase activity decreases sharply over a narrow range of dry periods, but the temporal resolution of our sediment moisture measurements was too coarse to identify the moisture threshold.

Sediment respiration rates reported for saturated stream sediments range from 0.03–31 mg O₂ g AFDM_{POM}⁻¹ h⁻¹, and vary with temperature, dissolved nutrient concentrations, organic matter content and microbial biomass (Jones et al., 1995; Hill et al., 2000; Uehlinger et al., 2003). The range of sediment respiration rates in our no-inundation experiments (0.05–0.8 mg O₂ g AFDM_{POM}⁻¹ h⁻¹) is in the low end of the range for saturated sediments, and may reflect lower microbial biomass and sediment organic matter, and the scarcity of dissolved nutrients in ephemeral river sediments. Dissolved nutrients are intermittently available to microbes in dried river sediments during rainfall (Belnap et al., 2005), but long-term availability is far greater in flowing water. In our inundation experiment, water temperature was held constant, organic matter content remained low, and respiration rates were within the range observed for the dry (no-inundation) sediments. These observations suggest that 17 d of inundation did not substantially affect microbial biomass or sediment organic matter. In the absence of multifactorial experiments in which nutrients, organic matter, sediment moisture and temperature are varied, the relative importance of drying on river microbial activity remains unclear.

Comparisons with surface soils and vadose zones

In comparison with river sediments, effects of drying on respiration and enzyme activity are well known for soils. Positive relationships between soil respiration and enzyme activity rates, and soil moisture content have been reported for many soils subjected to desiccation (e.g., Orchard and Cook, 1983; Schjønning et al., 2003). In a study of drying effects on agricultural soils, Orchard and Cook (1983) reported that respiration rates decreased exponentially for 2–5 d, then levelled off; a pattern very similar to the exponential decay observed in the current study (Fig. 6B). These curves may reflect the net effect of rapid lysis of desiccation-sensitive microbes and continued respiration in microbes that are either desiccation-resistant or physically protected by clay and organic matter aggregates.

FDA hydrolysis rates in soils are typically orders of magnitude greater than for coarse river sediments (Taylor et al., 2002). High levels of microbial biomass, organic content and soluble nutrients, and low pH in natural soils may preclude direct comparisons with

river sediments that are lower in microbial biomass, organic matter, and nutrients, and are circum-neutral (Ellis et al., 1998). However, the characteristic exponential decay relationships noted above may be general responses of sediment microbial processes to prolonged drying.

Studies of microbial processes in the unsaturated sediments between soils or river channels and the regional water table (i.e., vadose zones) may be more comparable to ephemeral river sediments than surface soils or saturated stream sediments. Vadose zones in semi-arid and arid environments lack saturated flow for periods that are comparable to dry periods in ephemeral rivers (Stephens, 1996), and support microbial assemblages that are more desiccation-tolerant than surface soil assemblages (Kieft et al., 1993; Holden and Fierer, 2005). We are unaware of vadose-zone respiration measurements made using techniques comparable to ours, but did locate published FDA hydrolysis rates for four vadose environments (Vinther et al., 2001; Legout et al. 2005). Organic matter levels (0.2–2.6%) and FDA hydrolysis rates (0.02–0.07 μmole FDA g DM⁻¹ h⁻¹) in the four vadose zones closely matched the values from Selwyn River sediments that had dried for > 7 d (organic matter: 0.4–1.8%, FDA hydrolysis: 0.01–0.07 μmole FDA g DM⁻¹ h⁻¹).

Vadose and ephemeral river ecosystems share several ecological characteristics. Biogeochemical processes in ephemeral alluvial rivers and coarse-grained vadose systems are generally water- and organic carbon-limited (e.g., Kieft et al., 1993, Jacobson et al., 2000b). Inundation in ephemeral rivers and saturating recharge in vadose systems lead to ecological “hot moments” (Belnap et al., 2005; Holden and Fierer, 2005). Both systems can shift from a predominance of anaerobic microbial processes to aerobic processes during drying phases (Baldwin and Mitchell, 2000; Holden and Fierer, 2005). We suggest that consideration of relatively well-studied vadose ecosystems can provide insight into poorly-understood ephemeral river ecosystems.

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