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Primary Research Paper

Colonisation of introduced timber by algae and invertebrates, and its potential role in aquatic ecosystem restoration

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Abstract

As part of a habitat restoration experiment wood substrates (red gum) were introduced to two lowland streams of SE Australia in which habitat has been severely degraded by deposition of sand eroded from higher in the catchment. We monitored net primary production (NPP) and community respiration (CR), nutrient concentrations and the succession of algae and invertebrates (abundance and species richness), sampling at 2, 4, 8, 12, 16 and 20 weeks. Colonisation by algae was rapid, and there were distinct changes in the assemblages over the first 4 weeks. Thereafter, changes were much less marked. There were also differences in nutrient concentrations and some measures of algal abundance between the two creeks. As with the algae, invertebrates colonised these substrates extremely rapidly, peaking in abundance and richness in week 8. Invertebrate abundances closely tracked changes in the abundance of algae. By the end of the study both algal and invertebrate communities were in apparent decline, with sharp decreases in invertebrate and algal abundance and invertebrate species richness. Rates of GPP also declined toward the end of the experiment, and this coincided with the detachment of large mats of filamentous algae and the recession of flows over the summer months. However, in both streams the added timber quickly created habitat with high levels of primary production in an otherwise strongly heterotrophic stream system. These hotspots of autotrophic production were quickly colonised by high numbers of macroinvertebrates indicating timber addition may provide an effective means of augmenting habitat for algae and invertebrates in sanded streams.

Introduction

Fallen timber is a dominant component of many aquatic ecosystems, and influences a range of physical and biological processes such as scour and fill, material and solute retention, habitat creation and primary and secondary production (Sabater et al., 1998; Crook & Robertson, 1999; Drury & Kelso, 2000; Gurnell et al., 2002; Muotka et al., 2002). In some streams, such as sand bed streams, elements of large timber become particularly important in creating heterogeneity in the streambed via localised scour around the timber during high flows, and as localised hotspots for primary and secondary production (Hax & Golladay, 1998; Drury & Kelso, 2000). Large timber can be

particularly important in sand bed streams as it is often the only stable substrate available to algae and invertebrates.

While many streams are naturally sandy, throughout the world the substrate of a large number of streams has been converted to sand by human generated erosion and sedimentation (Cordone & Kelly, 1961; Rutherfurd, 1996; Wood & Armitage, 1997), often over extensive sections of their overall length – forming what are known as sand-slugs (sensu Nicholas et al., 1995). Severe sedimentation can smother existing stable substrates such as clay, cobbles and timber, and depletes the fauna of all but the interstitial taxa capable of persisting within the shifting sand (Cordone & Kelly, 1961; Chutter, 1969; Alexander & Hansen, 1986; Wood & Armitage, 1997). The dramatic loss of habitat caused by sand, coupled with the often large extent of sedimentation, creates a major restoration challenge (Shields et al., 1995, 2003; Bond & Lake, 2005), and there are few examples where ecological restoration of sand-bed streams has been attempted. The most widely advocated approach is to add timber to the channel to enhance hydraulic and structural diversity, and to create stable habitat patches. As yet there are no published studies on the invertebrate response to such habitat manipulations in sand slugged streams.

In trying to restore the fauna of sanded streams, fundamental questions are whether and how quickly introduced wood is able to provide suitable habitat for algae and invertebrates, and what factors are most relevant in shaping this process.

In the present study we examine the successional dynamics of algae and invertebrates colonising blocks of submerged river red gum *Eucalyptus camaldulensis* introduced into two lowland streams in south eastern Australia as part of a habitat restoration experiment (Bond & Lake, 2005). River red gum are the dominant riparian tree species in the study region (indeed throughout much of Australia), but riparian degradation and burial of existing instream timber by sand means that instream wood loadings and rates of recruitment are extremely low in the sanded sections of these creeks (O'Connor, 1992; Bond & Lake, 2003; Downes et al., in press).

Previous studies have shown that both algae and invertebrates may colonise submerged red gum rapidly (O'Connor, 1991; Scholz & Boon, 1993), but these colonisation dynamics have not previously been examined concurrently.

We examined rates of algae and invertebrate colonisation on fresh red gum introduced to the two streams, and concurrently monitored changes in net primary production (NPP) and community respiration (CR) as colonisation progressed. We hypothesised that colonisation by invertebrates would be delayed until biofilm development and algal production were sufficient to provide habitat, and/or an adequate food source, and hence anticipated some delay in colonisation by invertebrates.

Methods

Study area

The study was conducted in Creightons and Castle Creeks, two 2nd order lowland streams draining from the Strathbogie Ranges, a granite outcrop in the southern part of the Murray-Darling Basin in central Victoria, southeastern Australia. In the lowland sections the streams flow through an agricultural landscape dominated by sheep and cattle grazing, with some broad-acre cropping. The narrow riparian strip along each stream consists predominantly of mature river red gum (*Eucalyptus camaldulensis*), with very little natural regeneration. The understorey is dominated by introduced pasture grasses with some blackberry (*Rubus* spp.) (O'Connor & Lake, 1994).

In their floodplain sections, where this study was conducted, Castle and Creightons Creek have both been affected by significant deposition of granitic sand, which was eroded from the upper catchments following extensive land clearing in the early 1900s (Davis & Finlayson, 2000). In Creightons Creek alone the volume of deposited sand is estimated at 240,000 m^3 (Davis & Finlayson, 2000). The deposited sand, which in places has caused aggradation of more than 2 m, filled in deep pools and buried fallen instream timber, so that the streams are now shallow with a flat sandy bed (Davis & Finlayson, 2000; Bartley & Rutherfurd, 2001). This sand is relatively unstable, with some bed movement even during baseflow periods (Davis & Finlayson, 2000). This combined with

low densities of large instream timber (Bond & Lake, 2003; Downes et al., in press) limits the availability of solid stable substrata for colonisation by algae and invertebrates.

In the study area, the now shallow channel coupled with the high interstitial volume of deposited sand greatly increases the likelihood that surface flows will be lost from these creeks during summer. Although generally similar in size (3–5 m wide and ~0.2–0.3 m deep), greater volumes of sand in Castle Creek cause it to stop flowing annually (typically from January to March), whereas Creightons Creek has ceased flowing in just two of the last 10 years.

Individual sites used in this study were a subset of those being monitored as part of a larger restoration experiment being conducted in the creeks, and included all of the 'high wood loading' treatment sites in this larger experiment. The three sites on each creek spanned a channel distance of approximately 15 km, and sites were all several kilometres apart form one another. At each site four large timber 'logs' (each $0.2\times0.2\times\sim5$ m [depending on stream width]) had been introduced into the stream approximately 8 m apart from one another in May 2001. The logs had been placed perpendicular to the flow with the general aim of creating localised scour pools and increasing channel heterogeneity at these sites. This added timber was cut red gum (*E. camaldulensis*) that had previously undergone little natural leaching (see Bond & Lake, 2005 for more details).

Sampling strategy

Small red gum wood blocks ($2\times2\times1$ cm^3) were used as individual sampling substrata, and were attached to a wooden baseplate using non-toxic silicon adhesive. Two plates, each with 42 wood sampling blocks attached, were placed in the stream at each site on the 15th of August 2001. The two plates were attached vertically to two logs selected randomly from the four at each site. Sampling extended from spring 2001 to early summer 2002 after which dropping water levels caused desiccation of the remaining blocks. Over this time blocks were collected after 2, 4, 8, 12, 16 and 20 weeks, with 10 blocks collected from each site on each day, except in week 20 when only 8 and 9 blocks remained at two sites (one on each creek) due to desiccation and accidental detachment. Five blocks were sampled from each plate at each time, but within each plate blocks were sampled at random.

Four of the blocks were collected *fresh* and placed in cold, dark conditions in order to be processed for chlorophyll-*a* and metabolism measures. Three blocks were used for assessing the algal community and preserved in 2% formaldehyde solution in the field. The three remaining blocks were preserved in 2% formaldehyde solution for invertebrate identification. Blocks were transferred directly to glass jars as they were dislodged from the plates, and the jars virtually encompassed the block before removal in order to prevent the loss of dislodged or escaping animals.

Physical and chemical measurements

Temperature, pH and conductivity of water were measured in the field using a Horiba U-10 water quality meter. Water samples were collected at every sampling site and sampling period, filtered through Acrodisc Dupor 0.2 μm pore size filters, and transferred to the laboratory in a cool dark box. Nutrients (phosphates, nitrate and ammonia) were analysed according to standard methods (APHA, 1998). Nitrate/nitrite (hereafter referred to as nitrate due to the dominance of this ion) was measured using the cadmium-reduction method, and filterable reactive phosphorous (FRP) was determined using molybdenum blue/ascorbic acid reduction. Ammonia (NH_3) was analysed using indophenol blue. The detection limit for each analysis was 1 μg/l.

Algal measurements

Chlorophyll-*a* from the blocks was extracted in 90% acetone. Blocks were left overnight at 4 °C in the dark and sonicated (for three subsequent periods of 3 min) to enhance pigment extraction (two consecutive sonications 2 min each in a Branson sonicating bath) (Sabater et al., 1998). Chlorophyll-*a* was calculated using the equation of Jeffrey & Humphrey (1975). The ratio between the optical densities (OD) at 430 and 665 nm were also calculated from the extracts to examine photosynthetic efficiency (Margalef, 1983).

Algae were detached from red gum blocks by sonication as described above, and collected into a glass vial. Sonication time was adjusted not to break the algal cells (Sabater et al., 1998), while assuring the complete detachment from the substrata. Total density (number of cells/cm^2) was determined with a Nikon inverted microscope using Utermöhl's technique (Utermöhl, 1931), at 400×. Algae (excluding diatoms) were identified to species level while counting. Diatoms were determined separately from the other algae and cyanobacteria present in the samples. Aliquots of all samples were acid-cleaned to remove organic matter and mounted in Naphrax (r.i 1.72). Identification and counting of diatoms was performed using a light microscope Olympus BH2 at 1000×. About 300 valves were counted on each slide and percentages of species present calculated. Identifications were based on Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b), Patrick & Reimer (1966) and Sonneman et al. (2000). Total count and diatom proportion data were combined to obtain a complete list of the algal species (diatoms and non-diatoms) for every sample.

Metabolism measurements

Metabolism (dissolved oxygen dynamics) was measured in the laboratory within 48 h of collection of blocks using Hansatech electrodes at 200 μmol m^{-2} s^{-1} under continuous stirring for 2 h at the stream water temperature (see Table 1).

Table 1. Physical and chemical variables measured for each stream averaged across the study period (14th August 2001–3rd January 2002)

	Mean ± SE (range)	
	Castle Creek	Creightons Creek
Water temperature (°C)	15 ± 1 (8–26)	15 ± 1 (9–24)
Conductivity (μS/cm) at 25 °C	326 ± 50 (136–515)	177 ± 7 (159–219)
pH	7.6 ± 0.1 (7.7–7.9)	8.0 ± 0.1 (7.7–8.2)
Dissolved oxygen (mg/l)	7.3 ± 0.4 (5.3–8.1)	8.1 ± 0.2 (7.8–8.7)
NO_x (μg N/l)	32 ± 4 (18–57)	229 ± 40 (11–488)
Ammonia (μg N/l)	19 ± 2 (8–47)	18 ± 2 (7–29)
FRP (μg P/l)	127 ± 46 (3–587)	11 ± 1 (6–16)

Two blocks at a time were incubated in the light (Net Primary Production [NPP]) and dark (Community Respiration [CR]) in a Perspex chamber with a flow through design. Rates of dissolved oxygen consumption or evolution were calculated from a linear regression of the data obtained for at least 45 min. A bank of quartz halogen lights supplied light in the photosynthetically active range, and temperature was controlled by placing the metabolism chamber in a controlled temperature water bath. Data from the dissolved oxygen measurements were transformed to rates of carbon assimilation and loss using a photosynthetic quotient of 1.2 and a respiratory quotient of 0.85 (Bott, 1996). Estimates of gross primary production (GPP) were obtained by summing NPP and CR.

Invertebrate measurements

Samples for invertebrate counts were passed through an 0.25 mm mesh and transferred to 75% ethanol. All macroinvertebrates, except Nematoda, were identified to species, morphospecies or genus, under a dissecting microscope (WILD, *Leica*, MZ8 [50×]) or a compound microscope (*Olympus* [600×]). Small naidids and some immature instars (6.4% of all animals) could only be classified to family or genus. They were treated as separate taxa in the analyses. Despite the small size of the blocks the relative abundances of species in these samples reflects those found on natural timber in these creeks (Downes et al., in press), and in much larger samples collected from the red gum sleepers (A. Glaister, unpublished data).

Statistical analysis

Metabolic changes and successional trends in the algal and invertebrate assemblages were examined through time using univariate and multivariate techniques. Univariate trends in abundance and species richness were assessed using repeated measures analysis of variance (ANOVA). Sites nested within each creek were treated as the sampling units of interest, with time and creek being treated as fixed terms in the model, and sites treated as random. Replicate blocks from each site at each time were used to provide average site level values, and thus did not contribute to the degrees

of freedom in the analyses. The factors 'Creek', 'Time' and the 'Creek×Time' interaction were thus tested over the 'Site (Creek)' term rather than the residual. Where the assumption of sphericity in the variance–covariance matrix was not met we adjusted *p*-values using the Huynh-Feldt (H-F) epsilon ε (Quinn & Keough, 2002), and in some cases transformations (log[*x*]) were required to meet distributional assumptions.

Multivariate trends were assessed using non-metric multidimensional scaling (NMDS) ordination and analysis of similarities (ANOSIM) was used to test specific hypotheses about temporal changes in the assemblages. Both NMDS and ANOSIM were performed on distance matrices based on the Bray–Curtis index (Bray & Curtis, 1957) applied to raw (untransformed and unstandardised) data, and were carried out using the software package PRIMER Ver. 5 (Plymouth Marine Laboratory, UK). We performed several different runs of NMDS. The first two focused separately on the algae and invertebrate assemblages and were based on centroids for each site at each time (i.e. averaging across replicate blocks), as a means of contrasting the spatial differences between the two creeks with the differences over time within each creek. The subsequent ordinations examined algae and invertebrate samples separately for each creek, but were based on the sample centroids for each time (i.e. averaging across both samples and sites) to illustrate temporal trends in the data. In each case 20 random starts were used in finding the best solution in ordination space. Hypothesis tests employed the one-way ANOSIM routine, and were based on 999 permutations of the data. Where ANOSIM detected significant differences between groups, the SIMPER routine in PRIMER was used to determine the relative contribution of each taxon to those differences. Following Clarke & Warwick (1994) we treated all taxa with a greater than 10% contribution to mean pairwise dissimilarity, and a dissimilarity Mean/SD ratio of less than 1 as being 'strong' contributors.

The correlation between temporal trends in the algal and invertebrate assemblages was assessed by Mantel test (Manly, 1986) using the Excel add-in POPTOOLS (Hood, 2005), with 999 permutations of the data used in estimating the significance of the test statistic *Z*.

Results

Nutrient concentrations and water quality

Small but consistent differences were found between Castle and Creightons Creeks in several water quality parameters (conductivity, pH and dissolved oxygen). Together with temperature they underwent predictable and straightforward seasonal changes over the course of the study. Nutrient patterns were more complex. First, consistently high phosphorus (FRP) concentrations

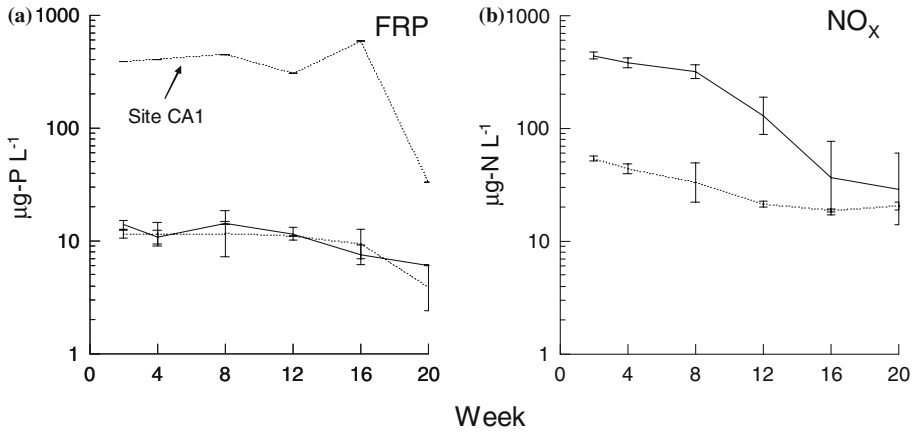

Figure 1. Temporal changes in the concentration (mean ± 1 SE) of (a) Phosphorus (FRP) and (b) Nitrates/Nitrites (NO_x) in Castle Creek (....) and Creightons Creek (—). Note that FRP is plotted separately for site 1 on Castle Creek (CA1), due to the apparent impact of sewage effluent on FRP concentration at that site. Error bars (here and subsequently) are based on site means.

were measured at the most downstream site on Castle Creek (CA1; plotted separately in Fig. 1a). We suspect these high concentrations were caused by groundwater seepage from a nearby sewage treatment plant. Otherwise, FRP concentrations were low, invariant through time and similar between streams (Fig. 1a). Ammonia concentrations were also generally low and consistent across sample sites/times (Table 1). In contrast, nitrate concentrations differed markedly between the two streams, initially being an order of magnitude higher in Creightons Creek, but declining rapidly over the course of the study to approach concentrations in Castle Creek by the end of the study (Fig. 1b).

Algal abundance and diversity

In both Castle and Creightons Creek blocks were rapidly colonised by diatom and non-diatom species, with high algal species richness by the second week of the experiment (Fig. 2a). Castle Creek samples typically contained more algal taxa (range: 15–38) than those from Creightons Creek (range: 17–28), but, overall, high inter-site variability and lack of sphericity in the dataset precluded detection of a significant difference between the two creeks (Table 2). In both creeks high algal species richness was achieved extremely quickly, with no significant trends in richness over time in either creek (Table 2).

Diatoms dominated the algal assemblages, accounting for between 49 and 98% of all algal cells. The most common taxa were the diatoms *Melosira varians*, *Achnanthidium minutissimum* and *Navicula rhynchocephala*, although the last was much less abundant in Creightons Creek. All three were also among the most rapid colonisers along with the cyanobacteria *Phormidium* sp. and the green alga *Klebsormidium* sp., which were also very quick to colonise in Creightons Creek.

Algal density (cells/cm^2) increased rapidly in both creeks as the blocks were colonised, but appeared to reach higher densities in Creightons Creek (Fig. 2b). Here too, however, departure from the assumption of sphericity resulted in a low H-F ε and therefore an extremely conservative (and non-significant) *F*-test (Table 2). Algal densities peaked in weeks 8–16 and were in decline at the final sampling date (week 20).

Rapid colonisation by algae was accompanied by rapid increases in chlorophyll concentration from week 2 to week 16, followed by a decline in week 20 in both streams (Fig. 2c). Chlorophyll concentrations were significantly higher in Creightons Creek than Castle Creek, which, combined with temporal differences, reflected distinct trajectories of algal abundance in each stream (the significant Creek×Time term in Table 2). From weeks 8 to 16, average chlorophyll concentration was 17.5 ± 3.3 μg/cm^2 in Castle Creek and 86.4 ± 8.5 μg/cm^2 in Creightons Creek. By the end of the experiment chlorophyll concentration had declined in both creeks, even though sampled substrates were still fully submerged. Chlorophyll concentrations and cell densities were highly variable among individual blocks (the error term in Table 2), but averaging across blocks, individual sites on each creek showed very similar trajectories, with sites accounting for little of the overall variation (Table 2). Most of the extracted pigment in the two creeks was chlorophyll-*a* (low contribution of carotenoids), as indicated by low values of the ratio OD_{430}/OD_{665} throughout the colonization experiment.

Metabolic measurements

In contrast to cell densities and chlorophyll concentrations, estimates of gross primary production (GPP; mg C m^{-2} day^{-1}) were similar in the two creeks (Table 2, Fig. 2d). Although GPP increased gradually in both creeks over the first 8–16 weeks (Table 2, Fig. 2d), these increases were much smaller than those observed for chlorophyll and cell densities. Community respiration also increased gradually over the course of the study (Fig. 2d), but again at a similar rate in each creek, and at all times was exceeded by GPP. Photosynthetic efficiency (measured as the ratio of GPP:Chl-*a*) rose steadily in Castle Creek, and was up to 6 times higher than in Creightons Creek by the end of the experiment (Fig. 2e).

Invertebrate abundance and species richness

Invertebrate communities were dominated by naidid worms and chironomids, and abundances increased rapidly with significant changes in total abundance and taxon richness through time

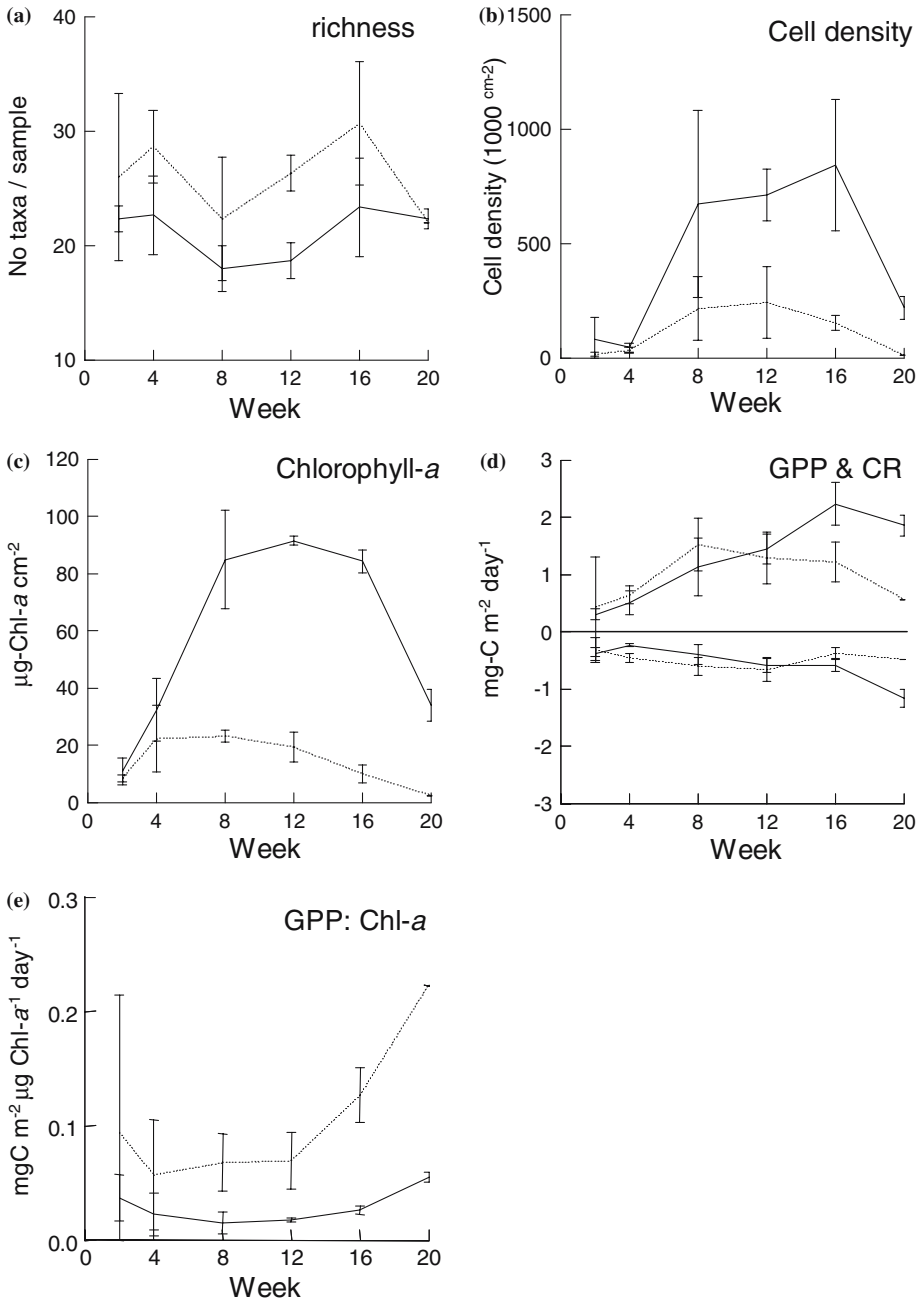

Figure 2. Temporal changes in algal abundance and diversity (mean ± 1 SE) in Castle Creek (....) and Creightons Creek (—) as indicated by changes in (a) taxon richness, (b) cell density, (c) chlorophyll-*a*, (d) GPP (top) and CR (bottom), and (e) photosynthetic efficiency (GPP:Chl-*a*).

(Table 3). In Creightons Creek there was a more than 10-fold increase in abundance between week 2 (11.1 ± 3.6 mean ± SE animals/block) and week 8 (154.1 ± 57.6), when abundance peaked. Differences between the two creeks were also significant (Table 3), with Castle Creek attaining a maximum density of just 25.6 ± 13.5 animals per block in week 16 (Fig. 3a). In both creeks taxon richness increased

Table 2. Summary of analysis of variance examining differences in (a) algal taxon richness (b) algal cell densities, (c) chlorophyll concentrations and (d) gross primary production (GPP) through time and between creeks

	SS	df	MS	F	ε	p
(a) *Taxon richness*						
Creek	183.356	1	183.356	18.407	0.33	0.076
Time	178.336	5	35.667	1.244		0.330
Creek×Time	35.336	5	7.067	0.246		0.936
Site (Creek)	39.844	4	9.961	0.347		0.842
Error	516.156	18	28.675			
(b) *Cell density*						
Creek	2.906	1	2.906	10.985	0.41	0.089
Time	8.120	5	1.624	7.139		0.001
Creek×Time	0.738	5	0.148	0.649		0.666
Site (Creek)	1.058	4	0.265	1.163		0.360
Error	4.095	18	0.227			
(c) *Chlorophyll-a*						
Creek	2.591	1	2.591	81.656	0.27	0.042
Time	2.149	5	0.43	10.670		<0.001
Creek×Time	0.957	5	0.191	4.750		0.007
Site (Creek)	0.127	4	0.032	0.788		0.549
Error	0.685	17	0.04			
(d) *GPP*						
Creek	0.619	1	0.619	3.286	0.44	0.185
Time	7.989	5	1.598	5.095		0.004
Creek×Time	2.509	5	0.502	1.600		0.211
Site (Creek)	0.754	4	0.188	0.601		0.667
Error	5.644	18	0.314			

over time, but peaked between weeks 12 and 16 (Fig. 3b). Abundant taxa (e.g. *Nais* sp., *Chaetogaster* sp., *Cricotopus* sp. and *Cladotanytarsus* sp.) generally followed similar trends to overall abundance, peaking in weeks 8–12. In week 20 there were marked declines in the abundance and diversity of invertebrates (including common taxa), which again mirrored the declines in algal abundance.

Taxa classified as collector-gatherers dominated the community, along with a small number of scrapers and xylophagous taxa. Most taxa were small bodied (<2 mm), the major exception being trichopterans (5–10 mm), which, although relatively rare, could, as late instars, account for much of the faunal biomass on the small blocks. The presence of trichopteran retreats, chironomid and worm tubes, pupae in cases, and egg masses indicated the importance of the wood blocks as attachment sites.

Changes in assemblage composition

ANOSIM revealed clear differences in the composition of both algal and invertebrate assemblages in Castle and Creightons creeks ($R=0.421$, $p=0.001$ and $R=0.456$, $p=0.01$; Fig. 4a, b). Within each creek, there were also significant changes in the invertebrate assemblages over time ($R=0.504$, $p=0.01$ and $R=0.496$, $p=0.001$ in Castle and Creightons Ck, respectively; Fig. 4d), whereas algal assemblages underwent significant temporal change in composition only in Creightons Creek ($R=0.375$, $p=0.03$; Castle Creek $R=0.177$, $p=0.13$; Fig. 4c). Subsequent analyses using SIMPER indicated that four species (*Melosira varians, Achnanthidium minutissimum, Navicula rhynchocephala* and *Oscillatoria* sp.) accounted for 48% of the overall average dissimilarity (67.6%) in algal assemblages between

Table 3. Summary of analysis of variance examining differences in (a) invertebrate abundance and (b) invertebrate species richness over time and between creeks

	SS	df	MS	F	ε	p
(a) *Invertebrate abundance*						
Creek	2.673	1	2.673	47.222	0.45	0.025
Time	2.884	5	0.577	7.393		0.001
Creek×Time	0.648	5	0.13	1.662		0.195
Site (Creek)	0.226	4	0.057	0.726		0.586
Error	1.404	18	0.078			
(b) *Invertebrate species richness*						
Creek	201.214	1	201.214	19.757	0.56	0.038
Time	374.322	5	74.864	12.209		<0.001
Creek×Time	79.969	5	15.994	2.608		0.061
Site (Creek)	40.738	4	10.185	1.661		0.203
Error	110.373	18	6.132			

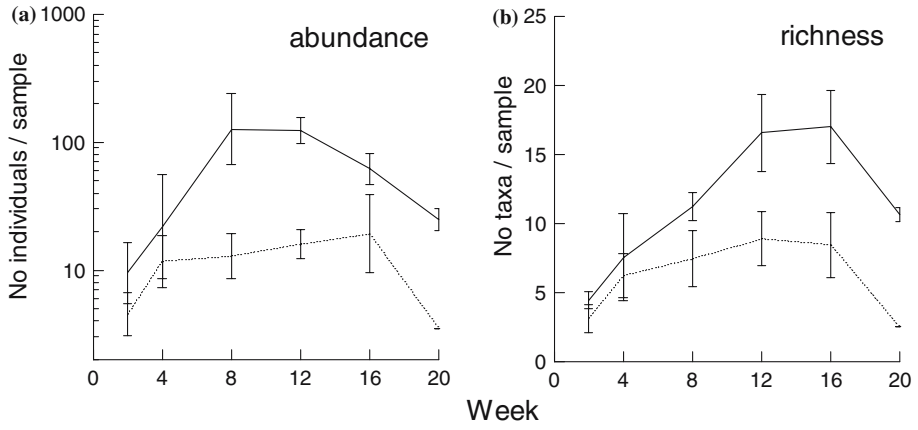

Figure 3. Temporal changes (mean ± 1 SE) in (a) abundance and (b) species richness of invertebrates in Castle Creek (....) and Creightons Creek (—).

creeks. Invertebrates showed a similar trend, with the four most common taxa (*Nais* sp., *Cricotopus* sp., *Chaetogaster* sp. and *Cladotanytarsus* sp.), accounting for 54% of the overall dissimilarity between creeks (83.0%). These differences were generally associated with a greater abundance of these taxa in Creightons Creek.

Averaging across replicate samples from each site, total animal abundance was strongly correlated with chlorophyll concentration ($r = 0.84$, $p < 0.001$) and algal cell densities ($r = 0.77$, $p = 0.003$). Invertebrate species richness was also strongly correlated with measures of algal abundance (chl-*a*; $r = 0.82$, $p < 0.001$ and cell densities; $r = 0.76$, $p < 0.001$), possibly due to the correlation between animal abundance and species richness ($r = 0.65$, $p < 0.001$).

While there were similar *patterns* of difference in the algal and invertebrate assemblages (i.e. differences between creeks, and over time in Creightons Creek), a Mantel test revealed only a weak correlation between pairwise dissimilarities in the two datasets ($r = 0.244$, $p < 0.001$), and thus, to a large degree, the faunal and algal assemblages changed independently from one another over time (see Fig. 4c, d).

Discussion

Most research examining the effectiveness of timber reintroduction as a restorative measure has focused on changes induced by wood at the reach scale, such as the response of fish (e.g. Riley &

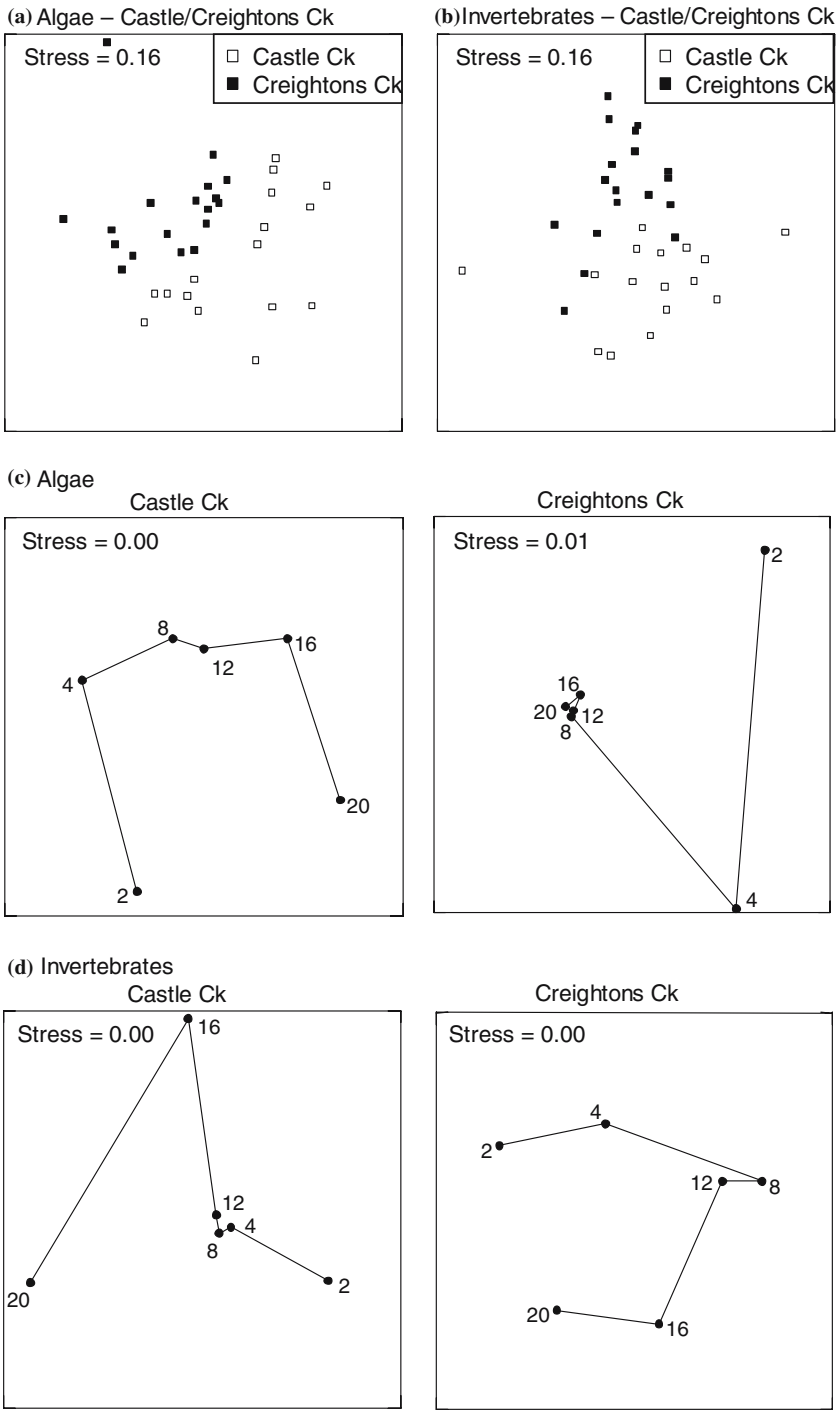

Figure 4. Ordination plots from NMDS showing spatial differences in the (a) algal and (b) invertebrate assemblages between Castle and Creightons Creeks, and temporal trends over time in each creek for (c) algae and (d) invertebrates. Note points represent site averages in (a) and (b) and site/time averages in (c) and (d).

Fausch, 1995; Zika & Peter, 2002) or changes in organic matter retention (Lemly & Hilderbrand, 2000; Muotka & Laasonen, 2002; Negishi & Richardson, 2003), rather than processes or changes occurring directly on the added timber. In lowland streams, and in particular those degraded by sand slugs, submerged timber can contribute a significant proportion of the total surface area available for colonisation by algae and invertebrates (Wallace & Benke, 1984; O'Connor, 1992; Scholz & Boon, 1993), in which case the direct colonisation of added timber may be important in restoring communities at the reach scale. Even where wood covers little of the total channel area, these habitats can contribute significantly to total primary and/or secondary production (Wallace & Benke, 1984; Benke et al., 1985; O'Connor, 1992) or harbour a suite of taxa distinct from those associated with other habitats (O'Connor, 1991; Johnson et al., 2003). This may be particularly true in sand bed streams where the constant movement of sediments limits primary production resulting in highly heterotrohphic communities (Uehlinger et al., 2002).

In the present study we showed that colonisation by algae and invertebrates can be extremely rapid even on hardwood timber added to a stream. Thus, as well as creating habitat for fish at a macro-scale (Bond & Lake, 2005), added timber is rapidly utilised as habitat at the micro-scale. Furthermore, in these streams many of the species found colonising wood are comparatively rare in samples taken from the benthos (Downes et al., in press), supporting our notion that timber provides a distinct resource patch for invertebrates, and perhaps also algae, in these streams.

Stable sites for colonisation by invertebrates and algae are extremely limited at these sites for much of the year due to the combined effects of an unstable shifting sand bed, and a paucity of large timber (O'Connor & Lake, 1994; Bond & Lake, 2003). Allocthonous detritus is common by comparison, although again is depleted by a lack of riparian vegetation and low instream retention. As a result, these streams are strongly heterotrophic, with only low levels of primary production at the reach scale (Atkinson et al., submitted), a pattern also observed by Uehlinger et al. (2002) in the Hassayampa River, a sandy desert stream in the United States. However, in spite of limited overall primary production in Creightons and Castle Creeks, isotopic analyses (Stuart Bunn, unpublished data) suggest that algae are an important source of carbon for secondary and tertiary consumers in these streams. While at certain times of the year flows can drop to levels where patches of the sand bed stabilize allowing the development of algal mats (O'Connor, 1993), these patches are comparatively rare and are rapidly destroyed by higher flows, including those associated with summer storms (O'Connor & Lake, 1994). In contrast, timber substrates remain stable over a wide range of flows. We propose therefore that despite the paucity of timber substrates in these streams, the greater stability of these substrates makes them critical as sites for primary and secondary production.

The dynamics of flow also impart a major impact on the biota of these creeks (O'Connor & Lake, 1994). In the sanded sections of the stream flows recede each summer leaving few refugia for the biota (Bond & Lake, 2004) causing significant mortality as described for some sandy desert streams (Fisher & Grimm, 1990; Stanley et al., 1997). Floods also are an important form of stochastic disturbance influencing both algal and invertebrate assemblages (O'Connor & Lake, 1994). However, the stable flow regime and high nutrient concentrations during this study are typical of late spring in these streams (Vanderkruk, 2004) and provided ideal conditions for high rates of primary production. The observed declines in nutrient levels toward the end of the study are thought to occur as a result of denitrification in localised anoxic downwelling zones of the sandy streambed (Vanderkruk, 2004). High rates of subsurface denitrification probably occur year round in Castle Creek, but only in summer in Creightons Creek due to the greater winter discharge, and hence lower effective subsurface flow, in the later creek.

Invertebrate colonisation closely tracked increases in algal biomass within and between the two creeks, and occurred with little delay. Although rapid colonisation of red gum by macroinvertebrates was observed by O'Connor (1991), this was on previously submerged and subsequently defaunated timber. It has been suggested that conditioning of timber, particularly hardwoods, is required before invertebrates will colonise (Phillips & Kilambi, 1994; Magoulick,

1998), but our results suggest otherwise, at least in situations where algae rapidly develop. It is probable that the wood and colonising algae provided a mixture of resource requirements for invertebrates. Few of the abundant taxa on blocks are considered herbivores, and many were probably feeding on organic detritus trapped amongst the filamentous algae. The additional habitat structure is also likely to be important in providing either shelter from predators, or an abundance of prey (Downes et al., 2000). There are also likely to be much longer-term changes in the makeup of the fauna as wood begins to decay, such as the appearance of specialist gougers (e.g. elmid beetles; Hax & Golladay, 1993), which were largely absent from our samples, but are abundant in samples taken from naturally recruited and heavily decayed timber in these creeks.

Based on the results of our study we conclude that the addition of timber to these sites and rapid colonisation could help create localised hot spots of primary and secondary production, which are otherwise low due to the lack of stable substrates in these streams (Atkinson et al., submitted). In the context of restoration this may have important implications for the structure and function of these ecosystems, particularly if algae and invertebrate consumers influence higher trophic levels such as fish and other predators. Many of the colonising taxa are also comparatively rare in these streams due to the paucity of stable substrates, although despite this, colonisation was extremely rapid, perhaps in part due to the larger logs to which plates were attached providing a proximate source of colonists.

At present the influence that micro-scale patterns of colonisation have on processes at the whole stream level, such as metabolism and higher-level trophic interactions, remain unknown. Monitoring to assess macro-scale, or site-level changes in benthic and wood-dwelling invertebrate fauna, as well as changes in rates of whole-stream metabolism is presently underway. This continued research will answer the question of whether the patch-level patterns of colonisation documented here are reflected in changes in biotic patterns and processes occurring at the site-scale, and thus whether timber addition is an effective means of restoring ecosystem processes in sanded streams.

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