Benthic algal biomass and assemblage changes following environmental flow releases and unregulated tributary flows downstream of a major storage

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Abstract

The Severn River, Australia, is regulated by a large dam which reduces the magnitude of high flow events. Environmental flows (EFs) have been allocated to increase the magnitude of flows to improve ecological outcomes such as reducing filamentous algal biomass and re-setting succession to early stage communities. The effectiveness of EF releases from dams to alter benthic algae assemblages is poorly understood. Benthic algal biomass and assemblage structure were examined at two cobble dominated riffle sites downstream of the dam before and after two EFs. Both EFs had discharges of ~11.6 m^3s^{-1} (near bed flow velocity of ~0.9 m s^{-1}). Neither EF reduced benthic algal biomass (as chlorophyll *a*) but sometimes led to increases with some filamentous algae (*Stigeoclonium* and *Leptolyngbya*) increasing in density. An unregulated flow event from a tributary between the two sites increased discharge to 25.2 m^3s^{-1} (flow velocity of ~1.2 m s^{-1}) which decreased biomass and filamentous algal density. The similarity in flow velocities between scouring and non-scouring events suggests that thresholds may exist and/or suspended sediments carried from unregulated tributary flows may contribute to reduce filamentous algal biomass. As EFs are becoming more widespread, target velocities to reduce filamentous algae biomass are useful. EFs with flow velocities ~1.2 m s^{-1} may achieve this in river cobble dominated riffle sections dominated by filamentous algae. Lower flow velocities <0.9 m s^{-1} may result in no change or an increase in filamentous algae.

Introduction

It is widely accepted that flow regulation can have detrimental effects on the riverine environment, altering its biotic communities. Benthic communities are often subjected to altered flow patterns below dams as a result of water storage and controlled releases. The provision of stable flows in many regulated rivers has resulted in the loss of natural seasonality and variability, and the magnitude and frequency of high flow events are frequently diminished (Walker *et al.* 1995; Arthington and Pusey 2003). This can lead to aquatic communities downstream of dams being different from those of unregulated rivers (Bunn and Arthrington 2002).

Benthic algae are the dominant primary producers in most upland stream ecosystems (Biggs 1995; Biggs and Smith 2002) and are one of the main sources of energy for higher trophic levels (Minshall 1978; Thorp and Delong 2002). Disturbances such as floods are one of the most important regulators of spatial and temporal variability in benthic communities of rivers (Davis and Barmuta 1989; Tsai *et al.* 2014) and are a central structuring element for benthic algal assemblages (Duncan and Blinn 1989; Downes *et al.* 1998; Biggs and Smith 2002). Such phenomena, depending on magnitude, can temporarily reduce stream primary production (Tett *et al.* 1978; Uehlinger et al. 2003) and benthic algal abundance (Biggs and Close 1989; Grimm and Fisher 1989) and alter benthic algal assemblage composition (Peterson 1996; Biggs *et al.*1999). Flow velocity can reduce benthic algal biomass by scouring through friction and suspended sediment abrasion (Bourassa and Cattaneo 1998; Biggs and Gerbeaux 1992) or can increase biomass through increased nutrient mass transfer into the algal mat (Horner *et al.* 1990; Stevenson 1996). The flow velocities that lead to the change from biomass accrual to loss varies between rivers probably due to the nature and structure of attached algae (Biggs and Thomsen 1995; Biggs and Stokseth 1996), suspended solid concentrations (Horner *et al.* 1990; Francoeur and Biggs 2006) and other factors such as grazing (Mulholland et al. 1991; Wellnitz and Poff 2006). Interactions between disturbance timing and assemblage composition are also likely to influence resilience and the susceptibility to disturbance (Peterson and Stevenson 1992).

The impact of flow regulation by small dams on disturbance frequency and benthic communities may be relatively small (Downes et al. 2003). However, river regulation by large dams can result in a reduced number and magnitude of disturbance events, decreased flow velocities and increased levels of nutrients (Biggs *et al.* 1998; Ward and Stanford 1983). Dams reduce natural drying periods by maintaining relatively constant low or moderate flows for long time periods for irrigation or domestic water supply uses (McMahon and Finlayson 1995; 2003). These factors can alter benthic algal assemblages including increased biomass downstream of dams relative to unregulated rivers (Collier 2002; Uehlinger *et al.* 2003; Chester and Norris 2006). There is evidence that regulation can alter benthic algal assemblages from natural (Burns and Walker 2000; Ryder 2004; Cortez *et al.* 2012) with prolonged periods of low flow leading to late succession states often dominated by filamentous green algae (Burns and Walker 2000; Watts et al. 2009; Davie *et al.* 2012). These late stage benthic algal assemblages can be a less palatable food source for grazers and can have food web effects (Davey *et al.* 1987; Burns and Walker 2000; Chester and Norris 2006). The general public and river managers may also perceive nuisance algal growths as unsightly (Welch et al. 1988; Biggs 1996; Sturt et al. 2011).

There is recognition among water managers of the importance of natural flow regimes in maintaining river integrity below dams (Robinson and Uehlinger 2003). Environmental flows that mimic natural flow variations to improve ecological health (Patten *et al.* 2001; Robinson and Uehlinger 2003; Richter and Thomas 2007) have been suggested as a mechanism to reduce excessive benthic algal growths in regulated rivers although little is known about their ability to achieve such biological objectives (Flinders and Hart 2009). Experimental floods in the Swiss Alps below a major dam temporarily reduced periphyton biomass, although the biomass again increased in subsequent years after the floods (Uehlinger et al. 2003). Low-level managed flows in the Mitta Mitta River, Australia were used to reduce biofilm biomass and reset taxonomic composition to early stage communities (from filamentous green and blue-green algae to diatoms) with flow release (Watts et al. 2006). Few studies in Australian systems have examined the effects of flow velocity from floods or managed pulses on benthic algae scouring (Watts et al. 2009).

The Severn River in Australia flows west from the Great Dividing Range and is regulated by Pindari Dam in the upper cobble dominated area of the river. Nitrogen concentrations and to a lesser extent phosphorus and silica concentrations are elevated below the dam relative to nearby unregulated rivers (Davie 2013). Large filamentous algal growths dominate the Severn River for extended periods of the year. Although a common state naturally under low flow conditions, these filamentous growths likely occur for longer periods under regulation due to reduced high flow event number and magnitude. Nearby unregulated rivers show different benthic algal assemblage structure (Davie 2013). River managers consider this unsightly and there is an interest in shifting the benthic algal communities towards those of unregulated rivers with more frequent disturbances, leading to early stage algal assemblages.
Environmental flow releases from Pindari Dam termed ‘stimulus flows’ have been allocated to reduce downstream benthic algal biomass and change assemblage structure to reduce filamentous green algae in favour of an early succession assemblage that more resembles local unregulated rivers. It is recognised that other factors from dam releases such as higher

nutrient concentrations may make this goal more difficult or impossible, although a trajectory towards this may be sufficient. Research into the effectiveness of environmental flows may allow the refinement of the flow targets (change in delivery pattern or magnitude) to improve benthic algal management (Robinson and Uehlinger 2003). The hypotheses for this study were that: 1. Benthic algal biomass would be reduced after environmental flow releases from Pindari Dam, and 2. Assemblage structure would change away from filamentous algae after environmental flows. As a greater magnitude flow event from an unregulated tributary occurred at the lower site during our study we hypothesised that 3. This flow event would be more effective at reducing benthic algae biomass than the environmental flows.

Materials and Methods

Study Area

The Severn River is a regulated river in inland northern New South Wales, Australia (Fig. 1). It is a fourth order stream, 235 km long and a tributary of the Macintyre River within the Murray-Darling Basin. It flows northwest from its headwaters near Glen Innes before it is regulated at Pindari Dam (30 km east of Ashford) and 85 km from the Macintyre River Junction. Pindari Dam is 85 m high with a maximum storage capacity of 312 x 10^6 m^3 and a multi-level off-take that is usually set at the depth of the thermocline to reduce the downstream transport of problematic phytoplankton blooms. An unregulated tributary, Frazers Creek, drains approximately 820km^2 between the Severn and Macintyre Rivers and joins the Severn River upstream of the town of Ashford. Land surrounding the sample sites is grazed, with approximately 60% of land cleared of remnant vegetation. Mean river depth and width at bankfull at Glenora Bridge (GB) and Ashford Bridge (AB) are 4.51 m and 94.19, and 3.18 and 86.5 m, respectively.

Unlike many streams in the Murray-Darling Basin that had higher winter flows prior to regulation, the Severn River prior to regulation had higher summer flows (October through February; NSW DWE 2009), with low flows in late winter. Consequently, regulation has not severely altered the general timing of flows as most irrigation water is released during summer, though flow variability and mean peak magnitude are much less than natural.

Experimental Procedure

This study was conducted from September to December 2008. Benthic algae samples were collected from riffle reaches in the Severn River at two sites below Pindari Dam (Fig. 1). The top site, GB, was located approximately 10 km downstream of the dam and is narrower than the downstream site, a further 15 km downstream. AB is immediately downstream of the confluence with Frazers Creek, the first major tributary below the dam. At GB, samples were taken before and after two environmental flow events (30/9/08 and 14/10/08, 28/10/08 and 18/11/08, 25/11/08, 2/12/08). At Ashford Bridge, samples were taken as for Glenora Bridge. However, after the second environmental flow release samples were taken before and after three different unregulated flow pulses (25/11/08, 2/12/08, 18/12/08).

Stream Flow Gauging

Stream flow was measured at four gauges operated by the NSW Office of Water, including a release gauge from Pindari Dam, a gauge downstream from Pindari Dam at Ducca Marri (approximately 2 km upstream of GB) and a gauging station at Ashford (immediately downstream of the AB site). An additional gauge measured flow in Frazers Creek. Flow was converted to mean velocity at each study site by relating discharge to near-bed velocity ($P < 0.0001$; $r^2 = 0.92$), measured approximately 0.05 m above cobbles with a pygmy flow meter (CMC 200, Hydrological Services, Australia).

Nutrients and Water Quality

Duplicate water samples were collected on each sampling occasion for nutrients. Samples were filtered through 0.45 µm syringe filters on-site and immediately frozen for later analysis for soluble reactive phosphorus (SRP), oxidised nitrogen (NO_X-N) and soluble silica (Si), following standard methods (APHA 1995). Single samples were taken for turbidity measurement using a calibrated Hach Turbidimeter, Model 2100A. Temperature was measured *in situ* using calibrated Wissenschaftlich-Technische Workstatten (WTW) Oxi 330/SET meter.

Benthic Algal Samples

On each sampling occasion, an area approximately 10 m wide × 30 m long within the riffle was sampled. Cobbles were randomly selected from this zone. On each sampling occasion a pooled sample of six cobbles was replicated four times for benthic algae samples. Cobbles were excluded if less than 65 mm in diameter or too large to lift single-handedly (approximately greater than 200 mm). Cobble size was determined by measuring the *b* axis of 100 random cobbles at each site. The *b* axis is the second largest axis of any particular cobble, with *a* longest and *c* shortest. Mean cobble sizes at GB and AB were 60.21 and 80.93 mm respectively. The surface area of each cobble was calculated using the aluminium foil technique described in Lowe et al. (1996).

Benthic algae on cobbles were sampled by scrubbing using a stiff nylon brush and rinsing with filtered river water to wash dislodged algae into a bucket. This technique removed more than 95% of cells present (Davie *et al*. 2012). Both the brush and bucket were rinsed thoroughly with water between samples to avoid cross contamination. The slurry for each cobble was transferred to a labelled 500 mL jar and stored on ice in the dark until processing (within 12 hours).

In the laboratory, benthic algal samples were made up to a total volume of 500 mL by adding filtered water and blended for 1 minute to homogenise the sample. From this sample, sub-samples for chlorophyll *a* determination (5 mL) and algal identification and enumeration (50 mL) were removed. Sub-samples for chlorophyll *a* were filtered onto GF/C filters then frozen. Chlorophyll *a* was determined by standard methods (APHA 1995) using the grinding technique and acetone as the solvent. Measurements were corrected for phaeophytin. Due to instrument error during processing, seven of the eight chlorophyll *a* samples collected before any flow events began (30 September 2008) were lost. In an attempt to overcome this, chlorophyll *a* concentrations were estimated from a linear regression of all chlorophyll *a* on total cell density ($r^2 = 0.74$) performed for each sample.

Algal samples for identification and enumeration were preserved and stained by adding approximately 2 mL of Lugol's Iodine. A 1 mL aliquot of the preserved sample was placed in a Sedgwick-Rafter counting chamber and cells were counted under a compound microscope with brightfield illumination at 200× magnification. Counts were performed until a minimum of 200 cells counted of the dominant taxa were enumerated or until the entire 1 mL was counted to provide a precision of ±15% (Hötzel and Croome 1999). Total algal cells per cobbles were determined and then concentration per m^2 was determined by normalising for cobble surface area exposed to water (c.f. Biggs and Hickey 1994). Benthic algae were identified to genus level using the keys of Gell *et al.* (1999) and Sonneman *et al.* (2000).

Statistical Analyses

Differences in benthic algal assemblages between sites and after different flow events were tested using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). Significant relationships between the main factors, site and time and their interaction were tested using 999 permutations and a P level of less than 0.01 considered significant. Benthic algal assemblages were further analysed by single-factor PERMANOVA according to flow type with a minimum 997 permutations and P level of 0.01. The flow types of pre-flow (samples taken before the environmental release), dam release (first samples taken after the environmental flow) and unregulated flow (samples taken after the unregulated tributary flow) were used. Data were combined from the two sites to make these groupings (except for the unregulated tributary flow group which only included Ashford Bridge). To account for large differences in benthic algal density, data was log *x*+1 transformed prior to analysis. Bray-Curtis distance was used to form similarity matrices for the benthic algal data. The PERMANOVA model assumed independence of data through time and we checked homogeneity of variance among treatments using PERMDISP (Anderson *et al.* 2008). Where unequal variances were found we reduced the chances of a Type I error by rejecting the null hypotheses at an alpha level of 0.01. The data was further analysed by using a two factor ANOSIM for site and time or one-way ANOSIM for flow type with a P value of less than 0.01 considered significant (Clarke 1993; Clarke and Warwick 2001). Taxa contributing to significant differences between flow types were examined using similarity percentage analysis (SIMPER; Clarke 1993; Clarke and Warwick 2001). Multi-dimensional scaling (nMDS) plots were generated for benthic algal data separately to display similarities among sites, times and flow types. The software package PERMANOVA+ for PRIMERv6 was used for all analyses (Clarke and Gorley 2006; Anderson et al 2008).

Results

Hydrology of the Severn River during the study

In the months preceding the study, two flow releases from Pindari Dam of a similar magnitude to those used as stimulus flows in the Severn River occurred in August and September 2008. Conversely, rainfall driven flow events similar to those observed in the study had not occurred in Frazers Creek for more than one year (August 2007). The first two flow events at both sites were the result of planned environmental flow releases from Pindari Dam (Fig. 2). The first starting 3 October 2008 lasted for 12 days and had a total volume of 7.54 x 10^6 m^3. The hydrograph showed a gradual rise to approximately 5.79 m^3 s^{-1} for four days, before rising to a maximum discharge of approximately 11.50 m^3 s^{-1} for a further three days before flows declined. The second event (starting 4 November 2008) lasted 12 days with a total release volume of 8.25 x 10^6 m^3. This event had steeper rising and falling limbs and a peak discharge of 12.53 m^3s^{-1} for one day (Fig. 2). Discharge from Frazers Creek into the Severn River during these flows was negligible (Fig. 2). Approximately one week later, several unregulated flow events from Frazers Creek increased discharge at the Ashford site only. The first started on the 20 November 2008, lasted for seven days with a rapid rise to 25.23 m^3 s^{-1} in just two days before discharge reduced (Fig. 2). A second unregulated flow event followed lasted for seven days with a peak discharge of 12.09 m^3 s^{-1} followed by another discharge peak of 39.87 m^3 s^{-1}.

Water Quality in Relation to Flow Events

At GB, NO_X was highest immediately after the first flow event and remained low for the remainder of the study. SRP decreased following flow events and rose during low-flow periods (Fig. 3). Soluble silica declined steadily until flow two and rose during the remaining samplings, whereas turbidity was low throughout the study (Fig. 3). At AB, both NO_X and

SRP declined immediately after the first flow event but increased with the unregulated tributary flow events (Fig. 3). Soluble silica remained stable throughout the study. Turbidity levels were low (<5 FTU) until the unregulated tributary flow when they increased to above 15 FTU. Water temperature in the river was consistently lower at GB than at AB, where it increased after unregulated tributary flow events (Fig. 3).

Chlorophyll a *Response to Flows*

At GB, chlorophyll *a* density significantly increased after the first dam release ($p<0.05$) and again after the second (not significantly), but then declined (Fig. 4). Chlorophyll *a* also increased at AB after each dam release though only significantly for the first flow release. Near-bed flow velocity at both sites during these flow events was approximately 0.8 m s^{-1} to 0.9 m s^{-1}. Following the first unregulated tributary flow event, chlorophyll *a* density dropped by approximately half and reduced further with subsequent flow events. Near-bed flow velocities were above 1.2 m s^{-1} for the first unregulated tributary flow peak, above 1.0 m s^{-1} for the second and was above 1.8 m s^{-1} for the third large flow peak. A significant negative relationship was found between flow (5 day antecedent) and chlorophyll *a* for the AB site ($P <0.05$, $r^2 = 0.66$) as well as the combined AB and GB sites ($P <0.01$, $r^2 = 0.44$).

Benthic Algal Assemblage Changes

PERMANOVA of site and time showed significant effects for both time (Pseudo-F = 5.51; Perm = 996; $P <0.001$), site (Pseudo-F = 7.12; Perm = 998; $P <0.001$) and their interaction (Pseudo-F = 3.38; Perm = 999; $P <0.001$) without significant homogeneity of dispersion (PERMDISP $P = 0.04$). All pairwise comparisons of time were significantly different (Perm = 967; $P <0.001$) to each other except between samples from the time period after the unregulated flows (Perm = 35; $P > 0.208$). Figure 5a shows an nMDS plot of the two sites through time. The samples from both sites group together for sampling periods before EFs 1, 3 being towards the bottom of the figure and periods after EFs (2 and 4) towards the top with time period 3 less similar to the others. The sampling periods 5, 6 and 7 are most different for the Ashford Bridge site plotting to the right of the figure, which received the unregulated flow event. At Glenora Bridge during the time period 5 and 6 showed little separation from the earlier time periods. ANOSIM showed a strong statistical difference between times (R >0.66; *P* <0.001) while there was no significant difference between sites (R = 0.22; *P* =0.05).

PERMANOVA analysis by the single-factor of flow type was supported as the PERMANOVA analysis between sites and flow types for the pre-flow and dam release groupings showed no interaction (Pseudo-F = 1.1; Perm = 999; *P* = 0.32) with significant homogeneity of dispersion (PERMDISP *P* = 0.68). The benthic algal assemblage structure differed significantly among the three flow types (Pseudo-F = 11.7; Perm = 999; *P* <0.001). The multivariate PERMANOVA pairwise comparisons showed strong significant differences (*P* = 0.001) among the benthic algae communities of the three flow types (Table 1). There was no homogeneity of dispersion for benthic algal samples between flow types (PERMDISP; F = 6.8, *P* <0.05).

An nMDS plot of the benthic algal assemblages for flow types clearly separated the three groups, with the unregulated flow being most different (Fig. 5b). ANOSIM supported these observations with a strong statistical difference between the unregulated flow assemblages and the other assemblages (R >0.65; *P* <0.001), while this was less strong between the pre-flow and dam-release communities (R = 0.32; *P* <0.001).

SIMPER analysis indicated that eight benthic algal genera were associated with over 50% of the dissimilarity between the pre-flow and dam release assemblages. Of these *Stigeoclonium, Leptolyngbya, Heteroleibleinia*, *Synedra*, *Oscillatoria* and *Navicula* increased after the dam releases while *Gomphonema and Fragilaria* decreased (Table 2). Differences between the dam release and unregulated flow assemblages were associated with reductions in density and only seven genera were associated with over 50% of the dissimilarity between assemblages. These were reductions in *Stigeoclonium, Leptolyngbya, Synedra, Fragilaria, Navicula, Heteroleibleinia and Oscillatoria.* All algae recorded after the unregulated flow decreased in density compared to the dam release assemblage.

Fig. 6 shows changes in cell density as bubble plots overlaid on the Figure 5a nMDS for some of the key genera influenced by the flow changes including *Stigeoclonium, Leptolyngbya, Synedra* and *Fragilaria*. *Stigeoclonium* and *Leptolyngbya* are shown to be at very low biomass before the dam releases, increase after the dam releases, and then reduce in biomass after the unregulated flow. *Synedra* and *Fragilaria* do not change in biomass greatly after the dam release but are both reduced in biomass after the unregulated flow events.

Fig. 7 shows the changes in percent composition of the main algal groupings for the different flow types. Diatoms dominated the pre-flow assemblage with smaller and similar contributions by cyanobacteria and filamentous green algae. After the dam release both filamentous algae and cyanobacteria increased their contribution and diatoms decreased. After the unregulated flow release, diatoms increased their contribution relative to the dam release. Filamentous algae were reduced in their percent contribution after the unregulated flow relative to both the pre-flow and dam releases communities.

Discussion

Environmental flow releases from Pindari Dam of approximately 11.6 $m^3 s^{-1}$ (near bed flow velocity of approximately ~0.9 m s^{-1}) led to an increase in chlorophyll *a* biomass at both sites although this was not always significant. Most benthic algal genera increased in cell density and assemblage composition changed significantly. These results suggest that the environmental flows delivered were not sufficient to reduce benthic algal biomass. The releases are likely to have been sub-scouring, with discharge and velocity not sufficient to scour benthic algae (Humphrey and Stevenson 1992). Sub-scouring can increase benthic algal growth (Stevenson 1984; Grim and Fisher 1989; Stevenson 1990; Tsai *et al.* 2014) as any losses of benthic algae due to scour is counter-balanced by enhanced growth with increased nutrient diffusion, nutrient uptake and photosynthesis (Horner *et al.* 1990; Stevenson 1996). In sub-tropical streams, Tsai et al. (2014) found that although storm induced high flow events reduced algal biomass, slower flow rates stimulated algal growth. In a study looking at the effectiveness of environmental flows, low level managed flow releases in the Mitta Mitta River, Australia of 3.5-10.4 $m^3 s^{-1}$ were not effective at scouring benthic algae but instead led to an increase in some filamentous taxa (Watts et al. 2006).

Generally, nutrient levels in-stream did not increase greatly because of the dam releases, although NOx did increase after the first release at the site immediately below the dam. It is possible that higher flows raised biomass by increasing rates of nutrient mass transfer into the algal mats without concurrent sloughing, as well as reducing the boundary layer around benthic algal cells (Raven 1992; Biggs *et al.* 1998). This effect may be more likely to benefit algae in relatively nutrient-poor systems (Horner *et al.* 1990; Raven 1992) and nutrient levels were not high in the river during the study. The role of grazing in reducing benthic algal biomass during the study is considered small as the density of macroinvertebrates was low and usually less than 0.3 individuals cm^{-2} with scrapers representing less than 40% of the proportion of macroinvertebrates (Davie 2013). Although variation was witnessed in the chlorophyll *a* values at both sites with values generally fluctuating between 15 and 30 mg m^{-2} due to environmental factors, after the higher tributary flow events levels were reduced to less than 10 mg m^{-2} after the first event, and the down to less than 5 mg m^{-2} after the next two events.

In this study, the unregulated tributary flow was approximately 25.2 m^3 s^{-1} (near-bed flow velocity of ~1.2 m s^{-1}). This led to a decrease in chlorophyll *a* biomass and a change in taxonomic composition. SIMPER analysis indicated that all algal genera decreased in density after the unregulated flow with mean density for *Stigeoclonium*, *Synedra*, *Navicula*, *Heteroleibleinia* and *Oscillatoria* the most reduced. *Synedra* has been suggested as an indicator of river regulation (Growns and Growns 2001) and this is supported by its occurrence before, and its reduction after the unregulated flow event. The overall proportion of cyanobacteria increased following the dam and unregulated flows. Cyanobacteria can be resistant to removal by high flow events (Blenkinsopp and Lock 1994). Watts et al. (2006) found that benthic cyanobacterial taxa could tolerate higher velocities than filamentous green algae taxa following flows of ~ 10.4 m^3 s^{-1} (approximately 1.0 m s^{-1}) and suggested when they are non-toxic are an important part of the benthic food web. Burns and Walker (2000) also found that two grazing decapods consumed a large proportion of filamentous cyanobacteria as part of their biofilm diet in a floodplain river.

The literature from studies examining the velocities required to reduce benthic algal biomass varies considerably (Table 3). How benthic algae respond to river flow can be influenced by growth form with the possibility of detachment greater in semi-erect and filamentous growth forms (Raven 1992). Biggs and Stokseth (1996) also suggest that the assemblage growth form determines the response to variations in velocity with filamentous green algal assemblages reduced at lower velocities than other growth forms. Differing effects on loss can also depend on the initial assemblage composition with filamentous algal assemblages to be least resistant, and non-filamentous diatom assemblages to be most resistant to shear stress (Biggs and Thomsen (1995). Disturbance frequency and pre-conditioning to particular flow velocities may also influence the susceptibility to flow events of different velocities (Peterson and Stevenson 1992). The studies shown in Table 3 suggest that there is considerable variability in the velocities required to reduce algal biomass and the effectiveness of biomass removal differs. Jowett and Biggs (1997) found moderate reduction in benthic algal biomass at velocities between 0.6 and 0.9 m s^{-1} and others have also found biomass was reduced within or above this range (Horner *et al.* 1990; Bourassa and Cattaneo 1998; Ryder et al. 2006; Watts *et al.* 2006).

The variability in responses of benthic algae to flow are clearly demonstrated within the Mitta Mitta River, Australia. Moderate flows over several years were sufficient to reduce algal biomass at a velocity of 1.0 m s^{-1} (Watts et al. 2006) while in the same river, after an excessive build-up of filamentous algae, much higher flows (velocities of greater than 1.2 m s^{-1}) were not sufficient to scour and instead led to a large increase in chlorophyll *a* compared to before the flow event (Watts *et al.* 2008). Similarly, in manipulative field experiments in an upland gravel bed stream, 133 day old algal communities were not significantly reduced by artificial scouring while younger 49 day old communities were scoured (Peterson *et al.* 1994).

In streamside mesocosm experiments using tile substrates, Flinders and Hart (2009) found chlorophyll *a* was reduced at velocities above 1.5 m s^{-1}. Higher velocities such as 2.4 m s^{-1}

resulted in greater chlorophyll a reduction. These velocities are considerably higher than we found in this in this study. Flumes may underestimate scouring potential as they can carry reduced sediment load, and this sediment may be important in the physical abrasion of benthic algae (Grimm and Fischer 1989). The movement of fine sediment and debris may increase rates of benthic algae removal in streams through shading and abrasion (Acs and Kiss 1993; Francoeur and Biggs 2006). Loss rates with sediment can be approximately double of those without sediment (Horner *et al.* 1990).

The turbidity data from our study showed a small but distinct rise from below 7 FTU to over 25 FTU with the unregulated flow event. Samples were not taken in the peak of the flow, but it is likely that turbidity (and suspended solids load) would have been greater during these periods. Turbidity from the dam releases was below 5 FTU, probably because finer sediments are lost from below dams as a result of impoundment (Kingsford 2000). Low concentrations of suspended material in dam releases may necessitate release of more water from Pindari Dam for benthic algal scouring than if concentrations were higher.

The loss of benthic algae in a given assemblage is not generally a linear function of velocity (Biggs and Close 1989). This makes it more difficult to predict the levels of flow required for benthic algal reductions, which will depend on the type of assemblage present at the time of the flow releases. Flinders and Hart (2009) also suggest that velocity does not have a linear relationship with benthic algal biomass, but rather that velocity thresholds may exist after which reductions occur. A reason for the threshold velocities and other rapid reductions in biomass above certain velocities may be that in low-velocity and low-nutrient streams the over storey mat of algae limits the supply of nutrients to the understorey (Stevenson and Glover 1993). In addition, light limitation of the understorey due to extreme attenuation of light through the mat may lead to senescence of the underlying layers. This may result in large losses in biomass above certain velocities. Large-scale biomass removal can be a function of change from the normal conditions that the algae have adapted to through the strength of their attachment (Horner and Welch 1981). The relative strength of the attachment is a function of the velocity prevailing during colonisation and growth (Horner *et al.* 1990).

Whether a velocity threshold exists in the Severn River is not clear, but the results from our study can be used to suggest suitable discharge targets for the Severn River downstream of Pindari Dam. Flows of 23 $m^3 s^{-1}$ with a near bed flow velocity of >1.2 $m s^{-1}$ may be sufficient to reduce benthic filamentous algal biomass and change assemblage composition based on the tributary flow. It is likely the greater suspended solids concentration from the unregulated tributary was important for scouring (Acs and Kiss 1993; Francoeur and Biggs 2006). Flow releases of ~0.9 $m s^{-1}$ from the dam did not scour the algae, while one of the unregulated flows of a similar velocity did reduce chlorophyll *a*, and from a lower starting concentration of biomass (Fig. 4). Further, the close levels between sub-scouring flows from the dam releases (up to 0.9 $m s^{-1}$) and the scouring tributary flows (1.2 $m s^{-1}$) suggests that sediment load may have an important role in scouring benthic algae.

Developing ecologically effective environmental flow regimes is a challenge for river managers globally (Dyer and Thoms 2006). However, in many regulated rivers sufficient water is rarely available to ensure environmental flow releases are fully effective (Dyer and Thoms 2006), and managers are under pressure to allocate only the minimum amount of water for environmental needs (Chester and Norris 2006). The allocations of water for the environmental flows from Pindari Dam were a total of 7.54×10^6 m^3 and 8.25×10^6 m^3 for the two flow events, respectively. With the same water allocation, releases could be delivered from the dam at a faster rate to generate a velocity similar to the tributary event with flow peaking at 23 $m^3 s^{-1}$ for at least one day. It is desirable to simulate a natural high flow event as possible (Matthaei *et al.* 1996) and this would also lead to a flow hydrograph that more resembled the unregulated flow event, than the more stepped hydrographs delivered with environmental flows (Fig. 2).

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Table 1. Results from PERMANOVA pairwise test analyses for differences between flow types, including *t* values, significance levels and number of unique permutations.

Comparison of flow type	t	*P* (perm)	Unique perms
Pre-flow vs Dam release	2.3628	0.001	997
Pre-flow vs Unreg	3.2845	0.001	999
Dam release vs Unreg	4.6717	0.001	998

Table 2. SIMPER analysis of benthic algal genera contributing to differences (Bray-Curtis distance) between assemblages after different flow events.

Pre-flow and dam release

Genus	Mean abund for pre-flow	Mean abund for dam release	Consistency Ratio	Contribution (%)
Stigeoclonium	0.27	2.96	1.63	10.64
Leptolyngbya	1.41	3.59	1.48	9.84
Heteroleibleinia	0	1.53	1.09	5.82
Synedra	1.26	1.97	1.58	5.62
Gomphonema	1.55	1.14	1.32	4.91
Oscillatoria	0.82	1.36	1.17	4.80
Fragilaria	2.27	2	1.41	4.64
Navicula	1.23	1.83	1.28	4.41

Dam release and unregulated flow

Genus	Mean abund for dam release	Mean abund for unreg flow	Consistency Ratio	Contribution (%)
Stigeoclonium	2.96	0.3	1.8	10.85
Leptolyngbya	3.59	1.5	2.82	9.32
Synedra	1.97	0.19	1.83	7.54
Fragilaria	2	0.67	1.79	6.14
Navicula	1.83	0.36	1.72	6.03
Heteroleibleinia	1.53	0.14	1.18	5.93
Oscillatoria	1.36	0.06	1.23	5.48

Pre-flow and unregulated flow

Genus	Mean abund for pre-flow	Mean abund for unreg flow	Consistency Ratio	Contribution (%)
Fragilaria	2.39	0.67	1.65	8.49
Synedra	1.35	0.19	1.03	7.35
Gomphonema	1.5	0.11	2.58	7.19
Leptolyngbya	1.27	1.5	1.60	6.93
Rhoicosphenia	1.61	0.89	1.59	5.52
Amphora	0.99	0	3.76	5.06
Navicula	1.15	0.36	1.66	4.24
Actinastrum	0.96	0.33	1.69	4.20
Scenedesmus	0.68	0.16	1.15	4.16

Table 3. Summary table of the velocities required to remove benthic algae from substrates in some recent studies.

Author (Year)	**Measure**	**Velocity (m s^{-1})**	**Change**	**Taxa / growth form**	**Location**
This study (2014).	Chlorophyll *a*	~ 0.9	No or slight increase in biomass, some filamentous taxa increasing	Diatoms, filamentous green algae and cyanobacteria	Eastern Australia
	Taxonomic composition	~ 1.2	Decrease in biomass and filamentous green algae		
Biggs et al. (1998).	Chlorophyll *a*	0.18-0.2	Increase in stalked and short filamentous diatoms	Mucilaginous diatom communities	Four rivers and large artificial stream in the South Island of New Zealand
	AFDM	> 0.2	Decrease in stalked and short filamentous diatoms	Stalked/short filamentous diatom communities	
	Taxonomic composition	< 0.2	Increase in filamentous greens	Long filamentous green algal communities	
		> 0.2	Decrease in filamentous greens		
Biggs and Gerbeaux (1992).	Chlorophyll *a*	0.2 - 0.58	Decrease	Stalked and adnate diatoms, *Ulothrix*, *Stigeoclonium*	New Zealand
Biggs and Stokseth (1996).	Abundance (AFDM)	< 0.3	Increase	Diatoms and filamentous green algae	One river in New Zealand and one river in Norway
		> 0.7	Decrease		
Bourassa and Cattaneo (1998).	Chlorophyll *a*	0.03 - 0.95	Decrease		12 streams in Canada
Flinders and Hart (2009).	Chlorophyll *a*	> 0.2	Decrease *Melosira varians* and *Pleurosia laevis*		Streamside mesocosms, USA
	AFDM		Increase in *Cladophora glomerata*		
	% organic matter (OM)	> 1.5	Decrease in chlorophyll *a* and AFDM Increase in % OM		
Horner et al. (1990).	Chlorophyll *a*	> 0.6	Decrease	*Phormidium*, pennate diatoms, *Mougeotia*, *Fragilaria*, *Synedra*	Mesocosm, USA
		< 0.6	Increase		
Jowett and Biggs (1997).	Biomass	0.60 - 0.9	Moderate decrease in chlorophyll *a*	Mainly diatoms	Two New Zealand rivers
		<0.3	Chlorophyll *a* increased		
Ryder et al. (2006).	Dry mass	0.3, 0.55 1.0	Decrease in all measures	Diatom dominated with some filamentous green algae	Timber block in a lab flume in south eastern Australia
	AFDM		All filamentous algae removed with velocity > 0.55 m s^{-1}		
	Chlorophyll *a*				
	Taxonomic composition				
Watts et al. (2006).	Biomass	1.0	Filamentous green algae decreased Cyanobacteria increased	Filamentous green algae and cyanobacteria	Southern Australia
Townsend and Padovan (2005).	Biomass	0.025 - 0.055	Increase	Spirogyra	Northern Australia

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Fig. 1. Location of the Severn River, Pindari Dam, Frazers Creek and the sampling sites Glenora Bridge and Ashford Bridge used in this experiment.

Fig. 2. Discharge in the Severn River from Pindari Dam and at Ashford, and Frazers Creek. Arrows represent sampling periods at both sites, whilst the last arrow was only sampled at Ashford Bridge.

Fig. 3. Mean nutrient concentrations (n=2) for oxidised nitrogen (NO_X), soluble reactive phosphorus (SRP) and soluble silica (Si) as well as single readings for turbidity (FTU) and water temperature in the Severn River at Glenora Bridge (left) and Ashford Bridge (right).

Fig. 4. Chlorophyll *a* concentrations (●) and discharge (solid line) in the Severn River at GB (top) and AB (bottom).

Fig. 5. nMDS plot of benthic algal assemblage changes on individual cobbles as related to a) site and timing of sampling (1 is first sampling period, 2 the second etc. as relates to Fig 4. and b) different flow types. Pre-flow (■) is before the environmental flow release, dam release (▼) is after the environmental flow release from Pindari Dam and Unreg flow (◆) is the assemblage after the natural unregulated flows.

Fig. 6. nMDS ordination of some key changes in genera which changed in cell density for the different time periods and sites. a) *Stigeoclonium*, b) *Leptolyngbya* c) *Synedra* and d) *Fragilaria* show samples for each flow type as corresponding to the nMDS in Fig. 5a. Each circle represents the biomass of the different benthic algae with greater biomass indicated by a larger circle.

Fig. 7. Changes in percent abundance of dominant algal groups for the groupings of pre-flow, dam release and unregulated flow.