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PRIMARY RESEARCH PAPER

Spatial and seasonal variations in benthic algal assemblages in streams in monsoonal Hong Kong

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Abstract Samples from stone surfaces were collected in pools within four unpolluted hillstreams (two shaded and two unshaded) in monsoonal Hong Kong (lat. 23°N) to elucidate the extent of spatial (within and among streams) and temporal (seasonal) variations in algal biomass and assemblage composition. Sampling continued for over 12 months, incorporating the dry season when streams were at baseflow, and the wet season when spates were frequent. We anticipated that algal biomass would be lower in shaded streams and during the wet season, with associated seasonal differences in assemblage composition or relative abundance of different growth forms (e.g. erect versus prostrate). Benthic chlorophyll *a* (a proxy for algal biomass) varied among streams from an annual mean of 11.0–22.3 mg m^{-2}. Dry-season standing stocks were 18% higher than during the wet season when spate-induced disturbance reduced algal standing stocks. Algal biomass varied significantly at the stream scale, but not at the pool scale, and was lower in unshaded streams, where standing stocks may have been limited by high densities of algivorous balitorid loaches (mainly *Pseudogastromyzon myersi*). An overriding effect of grazers on algal biomass could also have reduced variations resulting from spate-induced disturbance. Significant differences in assemblage composition among streams, which were dominated by diatoms and cyanobacteria (totally 82 taxa) were not systematically related to shading conditions. Seasonal variations in algal assemblages were statistically significant but rather minor, and did not involve major shifts in composition or growth form caused by spate-induced disturbance. The abundance of filamentous cyanobacteria in all the streams may have been due to 'gardening' by balitorid loaches that removed erect or stalked diatoms and favoured cyanobacteria that persist through basal regeneration of filaments. This explanation requires validation through manipulative experiments.

Keywords Periphyton · Cyanobacteria · Diatoms · Grazers · Spates · Balitoridae

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Introduction

Benthic algae in streams are influenced by a complex of interacting factors that vary spatially and temporally, including light regime, nutrients, current and substrate characteristics (e.g. Biggs & Thomsen, 1995; Burkholder, 1996; Hill, 1996; Stevenson, 1996; Roberts et al., 2004; Hillebrand, 2005). Physical disturbance during spates, leading to washout, abrasion and scouring of the substratum, can cause dramatic declines in benthic algal biomass (Power & Stewart, 1987; Grimm & Fisher, 1989; Stevenson, 1990; Bergey & Resh, 2006), and assemblage composition in spate-prone streams may be dominated by prostrate species (mainly diatoms) that are less vulnerable to abrasion and turbulent flow (Luttenton & Rada, 1986; Peterson & Stevenson, 1992; Bergey & Resh, 2006; Francoeur & Biggs, 2006).

Apart from abiotic influences, grazing by herbivores applies a pronounced top-down control on the benthic algae in streams under low- to moderate-intensity disturbance (Feminella & Hawkins, 1995; Hill et al., 1995; Hillebrand, 2005). Algal biomass is reduced or limited by the presence of herbivores but other effects are possible also; for example, grazing fishes can also cause a shift from dominance by diatoms to upright filamentous cyanobacteria (Power et al., 1988; Gelwick et al., 1997; Abe et al., 2006). Such changes could be attributed to grazer 'selectivity' or preference, but may simply reflect morphological constraints of the feeding apparatus that more readily allows ingestion of taxa with erect growth forms or other characteristics that make them susceptible to being eaten (Steinman, 1996).

While most research on benthic algal dynamics has concerned temperate streams (see examples cited above), the same array of abiotic and biotic factors appear to operate in the tropics (e.g. Power, 1984; Mosisch & Bunn, 1997; Flecker & Taylor, 2004; Davies et al., 2008) although their effects have been much less extensively documented. While few studies have been undertaken in tropical Asia (but see Bishop, 1973; Dudgeon, 1982; Rout & Gaur, 1994), spatial variations in standing stocks due to shading, current and nutrients have been demonstrated in correlative investigations and manipulative experiments (e.g. Dudgeon, 1988; Ghosh & Gaur, 1991, 1994; Dudgeon & Chan, 1992). Most studies of temporal dynamics (reviewed by Dudgeon, 2000) have shown a strong seasonal effect of spate-induced monsoonal flows with wet-season reductions in algal standing stocks. In spite of these seasonal declines, there is increasing evidence of algal importance in food webs in small tropical streams. The significance of autochthony for benthic macroinvertebrates has been well demonstrated in Hong Kong streams, even at sites receiving substantial inputs of terrestrial plant detritus (e.g. Salas & Dudgeon, 2003; Mantel et al., 2004; Lau et al., 2009). Similar results have been reported elsewhere in the tropics (e.g. Bunn et al., 1999; March & Pringle, 2003; Douglas et al., 2005; Brito et al., 2006). Nonetheless, a better understanding of the importance of algae for food webs and secondary production dynamics in tropical Asian streams could be achieved if their spatial and temporal dynamics were more clearly elucidated.

The aims of this study were to investigate spatial and seasonal variations in algal biomass and assemblage composition in four Hong Kong streams representing a range of shading conditions, and to compare differences among seasons that might result from spate-induced disturbance caused by monsoonal rains during the wet season. Substantial densities of grazing balitorid loaches were present in all the streams (Yang & Dudgeon, 2009a). We also compared the taxonomic composition of benthic algal assemblages and the relative abundance of different growth forms (e.g. erect or upright versus prostrate or adherent) among streams and between seasons. We hypothesized that algal biomass would be higher in unshaded streams, and that assemblage composition in these streams would differ from that in shaded counterparts. In addition, we expected that spate-induced disturbance in the wet season would reduce biomass in all the streams, and that scouring or abrasion of erect or upright algae would cause increases in the relative abundance of prostrate or adherent forms.

Materials and methods

Study sites

Hong Kong Special Administrative Region is situated on the south eastern coast of China (lat. 22°09′–22°37′ N) within the Tropic of Cancer. It has a monsoonal climate, with distinct wet and dry seasons. Typhoons and intense rain events (>50 mm within 24 h) are frequent during the wet season (May–September) when 77% of the average annual precipitation occurs, and spates are frequent (Dudgeon & Corlett, 2004). Field sites were four-third-order, unpolluted hillstreams with different shading conditions, situated within or adjacent to country parks: Tai Po Kau Forest Stream (TPK, shaded), Mui Tze Lam Stream (MTL, shaded), Ng Tung Chai Stream (NTC, unshaded), Chuen Lung Stream (CL, unshaded). All streams had stony beds with oxygen-rich, slightly acidic and generally nutrient-poor waters of low conductivity (Table 1) reflecting the underlying igneous geology and highly weathered and leached soils (Dudgeon, 1992; Dudgeon & Corlett, 2004). Variations among streams in all characteristics apart from shading were minor (Table 1).

Three pools in each stream were selected so as to ensure that they were at least 20 m^2 during periods of baseflow (Table 1). Shading was estimated by a spherical densitometer (Model A, Robert E. Lemmon Forest Densitometers) to classify streams into unshaded and shaded categories. Measurements of physical habitat (pool size, etc.) and visual estimates of sediment composition followed Gordon et al. (1992). Physico-chemical parameters of stream water listed in Table 1 were monitored on each sampling date visit using YSI 85 and YSI 100 meters (Yellow Springs Instruments Co.). Benthic macroinvertebrate communities were diverse (for details, see Mantel et al., 2004; Li & Dudgeon, 2008) and algivorous balioridd loaches, mainly *Pseudogastromyzon myersi* Herre plus small numbers of *Liniparhomaloptera disparis* (Lin), were abundant (Table 1: see also Yang & Dudgeon, 2009a).

Algal biomass

During initial visits to each stream, three perimeter measurements (a, b and c) were made with a tape measure (to ±1 mm) on 40 stones, and their surface areas determined by measuring the weight of aluminum foil needed to wrap each one (see Graham et al., 1988). Linear regression was used to calculate the relationship between surface area and the sum of the products of each pair of perimeter measurements ($ab + ac + bc$) for stones in each stream, yielding r^2 values of 0.98 or above ($P < 0.001$). Accordingly, surface areas of stones sampled subsequently were calculated from perimeter measurements.

Stone-surface samples were collected approximately every 2 weeks in Tai Po Kau Forest Stream (TPK: August 2006–September 2007) and Ng Tung Chai Stream (NTC: August 2006–October 2007), and monthly in Mui Tze Lam Stream (MTL: October 2006–October 2007) and Chuen Lung Stream (CL: August 2006–September 2007) for the purposes of estimating benthic algal biomass. On each visit, samples were taken from five stones (8–18 cm in diameter) collected from each of three pools (total $n = 15$ per stream). Stones were gently washed in stream water to remove any attached animals, placed in separate plastic bags and transported to the laboratory within a dark cool-box. Each stone was brushed for 3 min (2 min with a wire brush and 1 min with a toothbrush) to remove periphyton and the resulting slurry adjusted to a known volume (100–200 ml) with deionized water. The suspension was well stirred and a 30 ml aliquot was passed through a glass-fiber filter (Advantec® GC50, 0.5 μm pores) for measurement of algal pigments (mainly chlorophyll *a*). Samples were deep-frozen briefly In order to rupture the algal cells, and phytopigments were extracted with acetone at room temperature in the dark (Axler & Owen, 1994; APHA, 1998; Thompson et al., 1999). Sample optical densities were measured with a spectrophotometer (Pharmacia LKB Novaspec II), and concentrations of chlorophyll *a* (normalized for stone surface area) were determined as a proxy for algal biomass. Measurements before and after acidification with 0.1 N hydrochloric acid were used to estimate and correct for phaeophytin *a*, and the physiological health of algal assemblages was assessed by the chlorophyll *a* to phaeophytin *a* ratio (Axler & Owen, 1994; APHA, 1998).

Algal assemblage composition

Benthic algal samples were collected in all the four streams on three occasions 4 weeks apart in 2007 during the wet and dry seasons. Three stones were randomly selected from each pool, and brushed (as above) to remove periphyton. The resulting material from three stones was combined into one sample per pool, and hence there were three replicates for each stream on each sampling occasion (total $n = 72$; i.e. 36 per season × 2). Samples were fixed in Lugol's solution, and a 0.1 ml suspension of each was placed in a counting chamber and examined at 400× magnification with a compound microscope (Olympus® BX50F-3) equipped with an ocular grid. Algae were identified to major groups (Bacillariophyta, cyanobacteria, filamentous Chlorophyta, etc.) with further

Table 1 Environmental characteristics of the four study streams (TPK = Tai Po Kau, MTL = Mui Tze Lam, NTC = Ng Tung Chai, and CL = Chuen Lung)

	TPK	MTL	NTC	CL
Streams				
Universal Transverse Mercator (UTM) grid reference	50Q KK	50Q KK	50Q KK	50Q KK
	098 827	152 789	047 835	026 800
Altitude of study reach (m)	140	100	160	340
Riparian coverage (%)	75	92	30	10
	(50–90)	(90–95)	(5–45)	(5–15)
Water temperature (°C)	19.5	20.0	20.5	20.9
	(12.4–24.2)	(14.5–25.1)	(15.4–24.8)	(14.9–25.0)
Dissolved oxygen (mg l^{-1})	8.6	8.6	8.4	8.2
	(7.6–10.4)	(7.6–9.9)	(7.6–9.3)	(7.5–9.3)
pH	6.7	6.5	6.8	6.6
	(6.4–7.2)	(6.3–6.8)	(6.5–7.1)	(6.4–6.9)
Conductivity (μS)	25.7	23.8	29.2	22.7
	(6.0–34.5)	(17.3–32.4)	(9.9–40.2)	(15.6–30.6)
Pools				
Maximum depth (cm)				
Dry	48.9	35.3	60.6	60.0
	(29–65)	(25–53)	(43–75)	(39–76)
Wet	64.7	49.4	86.3	78.9
	(38–96)	(30–66)	(69–100)	(61–100)
Surface area (m^2)				
Dry	19.6	18.5	21.4	19.4
	(12.7–32.7)	(13.6–27.2)	(13.6–34.2)	(13.5–26.4)
Wet	24.5	25.7	26.6	24.6
	(14.5–33.0)	(16.7–38.9)	(16.1–41.4)	(21.5–28.9)
Benthic chlorophyll *a* (mg m^{-2})				
Dry	16.3	20.5	12.6	10.8
	(14.7–17.5)	(18.7–21.4)	(11.7–13.7)	(10.1–11.5)
Wet	12.6	20.0	8.3	10.2
	(9.4–16.2)	(16.4–24.3)	(6.3–9.6)	(10.0–10.5)
Substrate composition (% cover)				
Boulders (>256 mm)	30	35	20	40
Cobbles (64–256 mm)	20	35	45	30
Gravel (2–64 mm)	25	25	30	30
Sand (<2 mm)	25	5	5	0
Algivorous fish (indiv. m^{-2})				
Pseudogastromyzon myersi	6.0 ± 1.0	16.9 ± 3.0	23.2 ± 2.2	21.5 ± 2.2
Liniparhomaloptera disparis	0.6 ± 0.1	0	1.1 ± 0.3	1.8 ± 0.3

Except where noted, mean values are presented with ranges in parentheses. Data on pool size during the dry (November 2006–February 2007) and wet (May–September 2007) seasons are presented separately. Mean densities (± SE) of algivorous fish are from Yang & Dudgeon (2009a)

identification to genera in the case of diatoms and cyanobacteria. Algae were quantified using a 'point quadrat method' whereby algae that overlapped with intersections of the ocular grid were identified and tallied (Power et al., 1988; Gelwick & Matthews, 1992). At least 100 fields were counted, with 100 points (i.e. 10 × 10 grid intersections) examined per field. Assemblage composition was expressed as the proportion of intersection points touched by each taxon (i.e. percentage composition). Although this technique does not measure algal biovolume directly, it includes an estimation of relative algal size since a large algal cell can overlap more than one grid intersection. Diatoms in samples collected from each stream during the dry season were identified to species level to provide a more detailed assessment of taxonomic composition. However, because species level identification of diatoms was laborious, comparisons of seasonal and spatial variations in assemblage composition were based on identifications to the level of genus. This approach is supported by the observation that genus-level data for diatoms correlate well with species-level patterns (Heino & Soininen, 2007).

Data analyses

Three-way nested ANOVA followed by Student–Newman–Keuls (SNK) tests were conducted to test for spatial (among streams and among pools) and seasonal (dry versus wet) differences in algal biomass (estimated by chlorophyll *a* concentration) and phaeophytin *a* to chlorophyll *a* ratios. In all ANOVAs, data from TPK and NTC, which were sampled twice each month, were combined to yield monthly mean values that could be compared with data from monthly sampling at MTL and CL. In order to further facilitate inter-stream comparisons and avoid transitional weather periods, only monthly mean data from November 2006 to February 2007 (dry season) and from May to September 2007 (wet season) were included in the ANOVAs.

Regression was used to test for a relationship between algal mean biomass and rainfall in each month for each stream, and rainfall during the preceding month. Biomass data for three pools in each stream in each month were averaged to derive monthly mean algal biomass; rainfall data (mm), used as a proxy for discharge, were from the Hong Kong Observatory (Hong Kong Observatory, 2006, 2007). All parametric statistical tests were undertaken with SPSS (Version 15.0), and data were $\log_{10}$-transformed whenever such transformation improved the homogeneity of variance.

Ordination by non-metric multidimensional scaling (NMDS) based on Bray–Curtis similarities was used to examine the effects of stream and season on the algal assemblage composition. The ordination used data on the mean proportion of each algal taxon in the three pools in each stream on each sampling occasion, and values were arcsine-transformed prior to analysis. Two-way crossed analysis of similarities (ANOSIM) was conducted to compare the assemblage structure between seasons (dry versus wet) and among streams followed, where necessary, by the similarity percentages procedure test (SIMPER) to determine the contributions made by individual taxa to average dissimilarity. All ordinations and subsequent multivariate analyses were performed using PRIMER 6 (Version 6.1.5; Clarke & Warwick, 2001).

Results

Biomass and condition of algae

Benthic algal biomass, as estimated by chlorophyll *a*, varied spatially and temporally, and exhibited particularly marked fluctuations during the wet season (Fig. 1). Three-way nested ANOVA revealed that algal biomass was higher in the dry season (Table 2), especially in TPK and NTC. Despite significant seasonal changes in algal biomass, standing stocks were unrelated to monthly rainfall in TPK, MTL and CL ($F_{1,10} \leq 2.197$, $P > 0.169$), but the anticipated negative relationship was apparent in NTC ($F_{1,10} = 8.120$, $P = 0.017$, $r^2 = 0.393$). The same outcome was obtained when the analysis was repeated using rainfall during the previous month as the independent variable (i.e. at NTC only: $F_{1,10} = 5.263$, $P = 0.045$, $r^2 = 0.345$).

There were significant spatial differences in algal standing stocks at the stream level (Table 2) but these followed the opposite trend to that expected from shading conditions: MTL had the highest mean algal biomass, followed by TPK, while unshaded NTC and CL supported similar, relatively low, standing stocks (Table 2). There was no small pool-scale effect on algal biomass, nor was there any significant interaction between stream and season (Table 2).

Annual chlorophyll *a* to phaeophytin *a* ratios among streams were similar (Fig. 1), and there were no significant inter-stream differences (Table 2). However, the ratio was significantly higher during

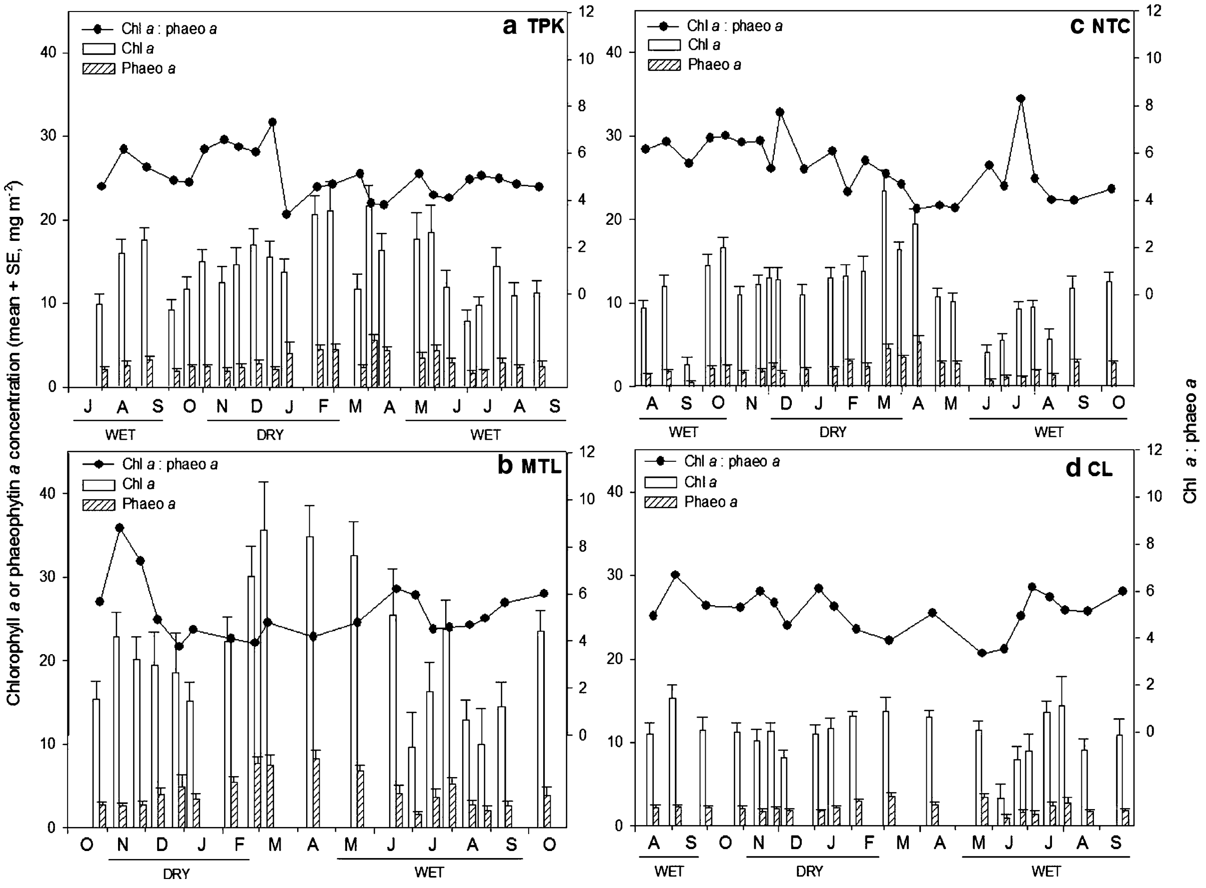

Fig. 1 Concentrations (mean + SE, mg m^{-2}) of chlorophyll *a* and phaeophytin *a* and mean chlorophyll *a* to phaeophytin *a* ratios in Tai Po Kau (TPK, **a**), Mui Tze Lam (MTL, **b**), Ng Tung Chai (NTC, **c**) and Chuen Lung (CL, **d**) from August (or October) 2006 to September (or October) 2007. Durations of the dry and wet seasons are indicated by *horizontal lines*

the dry season and, gain, was most apparent at TPK and, especially, NTC (Table 2); a dry-season peak ratio (of 8.3) was conspicuous at MTL (Fig. 1). There was no pool-scale effect on chlorophyll *a* to phaeophytin *a* ratio, nor was there any interaction between stream and season (Table 2).

Algal assemblage composition

In all, 82 benthic algal taxa were recorded from the study streams (Appendix 1—See Electronic supplementary material); most were diatoms (67 species; 12 genera). Richness in each stream was similar: 47 and 49 taxa in shaded MTL and TPK, and 46 and 52 taxa in unshaded NTC and CL, respectively. Diatoms dominated in terms of abundance in all the streams, consisting mainly of *Gomphonema* (12 species); *Cocconeis* (3 species) and *Achnanthes* (14 species); *Navicula* (18 species) was the most abundant of the nine other diatom genera (Table 3). Cyanobacteria (9 genera) ranked second, represented mostly by filamentous forms (*Homoeothrix*, *Oscillatoria* and *Calothrix*) and unicellular *Chamaesiphon* (Table 3). Filamentous Chlorophyta (4 genera) and all other taxa combined (mainly the unicellular chlorophyte *Characium* and the rhodophyte *Audouinella*) were minor assemblage components (together making up <3% of the total).

Two-way crossed ANOSIM revealed significant inter-stream differences in assemblage composition (Global $R = 0.815$, $P = 0.001$; for all pairwise tests: $R \geq 0.667$, $P = 0.01$) as reflected in the rather clear separation of samples from each stream in the ordination diagram (Fig. 2). It was notable that the composition of samples from the two shaded streams (TPK and MTL) was more similar than samples from

Table 2 Algal biomass (as chlorophyll *a*, mg m^{-2}) and chlorophyll *a* to phaeophytin *a* (chl *a*: phaeo *a*) ratios of periphyton in four Hong Kong streams (abbreviations as in Table 1) from October 2006–September 2007

	Algal biomass (mg m^{-2})			Chlorophyll *a*: phaeophytin *a*		
	Annual	Dry season	Wet season	Annual	Dry season	Wet season
Streams						
TPK	14.1 ± 1.0	16.3 ± 1.6	12.6 ± 1.4	5.0 ± 0.2	5.7 ± 0.4	4.7 ± 0.2
MTL	22.3 ± 2.5	20.5 ± 2.3	19.9 ± 3.9	5.2 ± 0.3	5.3 ± 1.0	5.3 ± 0.3
NTC	12.4 ± 1.5	20.5 ± 2.3	12.4 ± 1.5	5.3 ± 0.3	6.0 ± 0.4	4.8 ± 0.5
CL	11.0 ± 0.6	10.8 ± 1.0	10.2 ± 1.2	5.0 ± 0.3	5.1 ± 0.4	5.1 ± 0.6
Three-way nested ANOVA						
Season	$F_{1,92} = 13.81, P < 0.001$			$F_{1,92} = 6.85, P = 0.010$		
Stream	$F_{3,8} = 17.14, P = 0.001$			$F_{3,8} = 0.15, P = 0.929$		
Pool (stream)	$F_{8,92} = 1.32, P = 0.246$			$F_{8,92} = 1.61, P = 0.134$		
Stream × season	$F_{3,92} = 1.86, P = 0.142$			$F_{3,92} = 2.26, P = 0.087$		
SNK tests for streams	NTC = CL < TPK < MTL			No test		

Data presented are mean ± SE for annual biomass, and biomass during the dry and wet seasons. Three-way nested ANOVA of seasonal and spatial differences (among streams and among pools within streams) in these parameters, and consequential SNK tests, are also shown

the unshaded pair of streams (CL and NTC) situated on opposite sides of the diagram. NTC appeared to differ considerably from the other streams, and SIMPER confirmed that average dissimilarity (AD) between NTC and the other streams was relatively high (AD = 27–35% versus 17–22% for any pairing between TPK, MTL and CL). The distinctiveness of NTC samples was due to high relative abundance of *Homoeothrix* (up to 46% in the dry season) and relative scarcity of *Gomphonema* (<18% versus >30% at the other streams: Table 3); in addition, the filamentous cyanobacteria *Calothrix,* which was present elsewhere, was not found at NTC. The prostrate diatom *Cocconeis* was the least abundant in CL while adherent *Achnanthes* was more plentiful in NTC and TPK than CL or MTL (Table 3). *Chamaesiphon* was the most abundant in MTL and scarce in CL and, together with *Calothrix*, contributed to the separation between this pair of streams (AD = 22.3%). Differences between TPK and MTL (AD = 19.9%) likewise reflected the relative abundance of *Calothrix* (especially in TPK) and, during the wet season, the quantities of *Achnanthes* and *Homoeothrix* (Table 3). TPK and CL (AD = 17.4%) differed mainly with respect to the high relative abundance of *Gomphonema* and scarcity of *Cocconeis* at CL.

There was no clear separation of dry- and wet-season assemblages on the NMDS ordination diagram (Fig. 3), but two-way crossed ANOSIM indicated a significant seasonal effect on algal composition (Global $R = 0.611$, $P = 0.001$). SIMPER revealed that the four top-ranked taxa contributing to the AD of 18.4% between seasons were *Homoeothrix* (16.4% contribution), *Gomphonema* (13.1%), filamentous chlorophytes (11.2%) and *Cocconeis* (10.6%). However, with the exception of *Homoeothrix* (21.9 ± 3.1% in the dry season versus 14.5 ± 2.6% in the wet season), seasonal differences in the relative abundance of these taxa averaged across streams were negligible (1.3–2.2%: Table 3).

Discussion

Among the many spatial and temporal factors that can affect algal biomass and composition, we anticipated that rainfall (i.e. spate-induced disturbance) would drive seasonal variations, and our investigation was designed to test this. In addition, we assumed that shading conditions and grazing fishes would influence on spatial variation among the unpolluted hillstreams we investigated since they were otherwise similar with respects to habitat morphology, substrate and water chemistry. Differences in substrate composition, flow and water depth at small spatial scales (pools within streams) may have been influential also, but none of the analyses showed any significant variation in benthic algae at the pool scale.

Table 3 Percentage cover (mean ± SE) of algal taxa in four Hong Kong streams during the dry and wet seasons (stream abbreviations as in Table 1)

	TPK	MTL	NTC	CL
Dry season				
Cyanobacteria				
Filamentous				
Homoeothrix	18.5 ± 3.1	10.9 ± 4.3	46.0 ± 2.7	12.2 ± 3.3
Oscillatoria	3.7 ± 1.2	0.4 ± 0.1	1.8 ± 0.8	2.2 ± 0.2
Calothrix	4.1 ± 1.5	0.8 ± 0.6	0	8.9 ± 0.5
Other genera	0.6 ± 0.3	1.4 ± 0.2	2.4 ± 0.1	0
Unicellular				
Chamaesiphon	3.3 ± 0.8	4.3 ± 1.8	1.6 ± 0.2	0.4 ± 0.0
Other genera	0.1 ± 0.1	0.7 ± 0.3	0.8 ± 0.4	0
Chlorophyta				
Filamentous	0.7 ± 0.4	0.7 ± 0.4	0.8 ± 0.4	3.8 ± 3.0
Bacillariophyta				
Achnanthes	18.0 ± 1.7	19.3 ± 7.6	27.9 ± 4.6	12.9 ± 1.7
Cocconeis	10.4 ± 0.8	16.7 ± 1.3	11.7 ± 2.2	9.8 ± 2.0
Gomphonema	35.7 ± 3.2	41.2 ± 5.7	3.8 ± 0.9	47.0 ± 2.2
Other genera	4.7 ± 1.9	3.6 ± 1.1	3.2 ± 0.3	2.8 ± 0.8
Wet season				
Cyanobacteria				
Filamentous				
Homoeothrix	6.0 ± 1.6	13.9 ± 4.2	25.5 ± 6.7	12.4 ± 5.0
Oscillatoria	4.2 ± 0.9	3.1 ± 0.5	1.7 ± 1.2	3.5 ± 0.6
Calothrix	4.8 ± 1.1	0.2 ± 0.2	0	9.2 ± 1.5
Other genera	2.0 ± 0.2	0.2 ± 0.1	0.3 ± 0.3	0.1 ± 0.1
Unicellular				
Chamaesiphon	1.8 ± 0.5	8.0 ± 3.4	1.3 ± 0.5	0.4 ± 0.3
Other genera	1.4 ± 0.5	0.2 ± 0.1	0.4 ± 0.1	0.1 ± 0.1
Chlorophyta				
Filamentous	5.0 ± 1.1	4.0 ± 1.1	0.3 ± 0.2	3.8 ± 0.4
Bacillariophyta				
Achnanthes	23.4 ± 0.5	9.1 ± 1.3	24.6 ± 4.2	17.2 ± 4.5
Cocconeis	13.5 ± 4.6	11.1 ± 2.6	14.2 ± 6.4	4.3 ± 1.9
Gomphonema	31.0 ± 4.6	44.6 ± 9.5	17.4 ± 3.2	43.4 ± 3.3
Other genera	6.9 ± 1.1	5.7 ± 1.2	14.3 ± 3.2	5.6 ± 1.3

As anticipated, there was significant seasonal variation in algal biomass. Standing stocks in the four streams were, on average, 18% higher in the dry season. Chlorophyll *a* to phaeophytin *a* ratios were also higher during the dry season, with the relatively low wet-season ratios indicating that there were more damaged cells or higher algal mortality in situ due to scouring or abrasion (Power & Stewart, 1987; Francoeur & Biggs, 2006). The temporal trend in algae was in accordance with the general wet-season-low and dry-season-high pattern that prevails in monsoonal Asia (Bishop, 1973; Dudgeon, 1982, 1999, 2000) and in many other parts of the seasonal tropics (e.g. Mosisch & Bunn, 1997; Davies et al., 2008). Spates can also reduce algal standing stocks to low levels in temperate streams, although the timing of the disturbance may be less predictable than in monsoonal latitudes (e.g. Power & Stewart, 1987;

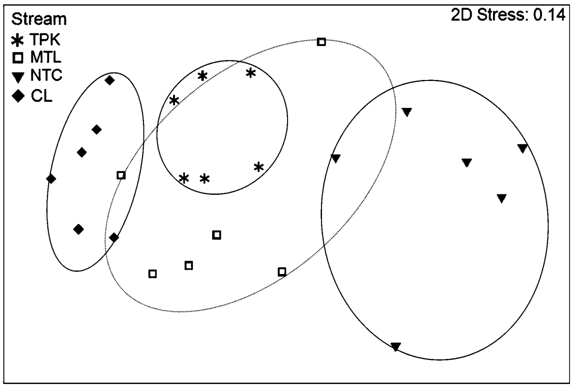

Fig. 2 NMDS ordination diagram of benthic algal assemblages in four Hong Kong streams (*abbreviations* as in Fig. 1). The *ovals* represent significant differences in assemblage structure confirmed by ANOSIM

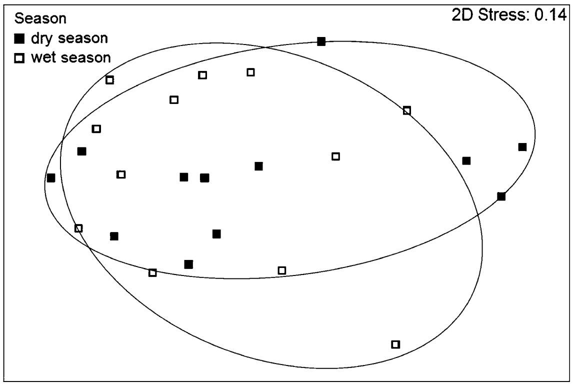

Fig. 3 NMDS ordination diagram of benthic algal assemblages in four Hong Kong streams on three occasions during each of the dry and wet seasons. The *ovals* represent significant differences in assemblage structure confirmed by ANOSIM

Grimm & Fisher, 1989; Stevenson, 1990; Biggs & Thomsen, 1995). Intense rainfall events (>50 mm within a day) causing spates occurred several times during the 2007 wet season in Hong Kong (Hong Kong Observatory, 2007), and an expected negative relationship between monthly algal biomass and rainfall was found in NTC, but not in the other three streams. A likely explanation is that the intensity of spates, rather than the total rainfall per month, determines the degree of scouring and biomass reduction since some critical flow threshold would need to be exceeded before bed movement is initiated and disturbance becomes severe (Stevenson, 1990; Biggs, 1996).

Seasonal differences in algal biomass were significant and consistent across streams, but the dry-season increase was not substantial. An overriding ‘top-down’ effect of grazers on algal biomass could reduce the temporal variability resulting from spate-induced disturbance by limiting algal densities, and prevent a ‘bottom-up’ response to higher light availability in unshaded streams. Elsewhere, grazers can limit algal standing stocks in conditions that are otherwise favourable to production, and thus regulate biomass at levels lower than limits imposed by physical factors (Rosemond 1994; Hillebrand, 2005), or even alter the susceptibility of algal assemblages to spate-induced disturbance (Pringle & Hamazaki, 1997). In general, algae with erect or upright growth forms are vulnerable to scour, abrasion or sloughing (Peterson & Stevenson, 1992; Biggs & Thomsen, 1995) whereas prostrate taxa that adhere tightly to the substratum are relatively resistant (Luttenton & Rada, 1986; Bergey & Resh, 2006; Francoeur & Biggs, 2006). We did not observe a seasonal shift from assemblages dominated by upright taxa in the dry season to adherent taxa during the wet season, and variations in assemblage composition were due to minor changes in the relative abundance of species common throughout the study. Filamentous *Homoeothrix* showed the largest seasonal change in abundance, from 22% in the dry season to 15% in the wet season averaged across the 4 study streams. *Homoeothrix* can withstand high grazing pressure through basal regeneration (Power et al., 1988; Abe et al., 2001) allowing it to persist during the dry season, but the basal cells may be damaged by scouring and abrasion during spates. *Gomphonema* was less abundant during the wet season, as might be expected from its upright growth form, but small wet-season decreases in adnate *Achnanthes* and prostrate *Cocconeis* were also evident.

While we observed significant inter-stream differences in algal biomass, they did not match shading conditions and, surprisingly, standing stocks were lower at unshaded NTC and CL than at shaded TPK or (especially) MTL. Algal biomass tends to increase in response to reductions in shading (e.g. Hill, 1996; Roberts et al., 2004; Fuller et al., 2008), but the consequences of enhanced light availability can be modified by grazing pressure, especially where grazers are numerous enough to consume any increases in productivity (e.g. Power, 1984; Rosemond, 1994; Hill et al., 1995; Hillebrand, 2005). Populations of algivorous *Pseudogastromyzon myersi* and *Liniparhomaloptera disparis* in shaded TPK were little more than a quarter those in CL or NTC; densities in shaded MTL were also lower than at the unshaded streams (Table 2; see also Yang & Dudgeon, 2009a). We suspect that inter-stream differences in algal standing stocks mirror the controlling influence of fish grazing on algal production, with more productive unshaded streams able to sustain higher fish densities that, in turn, deplete algal standing stocks (see also Power, 1984). However, we cannot rule out the possibility that benthic chlorophyll *a* concentrations (as used in this study) may be an inadequate proxy for algal biomass due to the tendency of shade-adapted algae to have higher chlorophyll *a* to carbon ratios (Hill, 1996), thereby confounding comparison of algal biomass among streams with different degrees of shading.

Variations in algal assemblage composition among streams were not related to shading conditions and mainly involved changes in relative abundance of common taxa, although the complete absence of *Calothrix* from NTC was notable. *Gomphonema*, which was generally abundant, was least numerous in NTC, and its erect, stalked growth form makes it vulnerable to grazers (Wellnitz et al., 1996; Wellnitz & Rader, 2003). Since *Gomphonema* is a major food of *Pseudogastromyzon myersi* (Yang & Dudgeon, 2009b), high fish densities at NTC might account for its scarcity. Fishes, by removing *Gomphonema*, may have facilitated the growth of competitors such as the short, filamentous cyanobacteria *Homoeothrix* which was conspicuously abundant at NTC. Fish grazing in temperate streams can change diverse algal assemblages made up mainly of diatoms into layers of cyanobacteria dominated by *Calothrix* or *Homoeothrix* (Gelwick et al., 1997; Power et al., 1988; Abe et al., 2001, 2006). Similar shifts have been attributed to the activities of benthivorous fishes in the Neotropics (Power, 1990; Flecker, 1996; Pringle & Hamazaki, 1997; Flecker & Taylor, 2004).

The properties of adherent algae impart both resistance to scouring and reduce susceptibility to grazers (Peterson & Stevenson, 1992), and thus confound attempts to assess the relative contributions of spate-induced disturbance and grazing to differences in assemblage structure. Information on seasonal changes in grazing intensity might help to resolve this matter, but gut content analyses indicate that *Pseudogastromyzon myersi* feeds intensively throughout the year (Yang & Dudgeon, 2009b). Other influences may also be at work: the greater abundance of unicellular *Chamaesiphon* in TPK and MTL could, for example, reflect shade adaptation by this prostrate cyanobacterium (Hill, 1996), although inter-stream differences in the relative abundance of *Achnanthes*, which was more common in unshaded NTC and shaded TPK than in CL or MTL, must be due to other causes. The dominance or scarcity of each algal taxon in each stream will be due to a combination of factors, including changes in the relative densities of co-occurring species, and stream-specific patterns of abundance may also result from individual requirements or tolerances of species that were treated herein at the generic level.

The spatial and temporal dynamics of benthic algal assemblages are outcomes of a complex series of interactions between biotic and abiotic factors, including seasonal ‘pulse’ disturbance by spates and more consistent ‘press’ disturbance of grazing. Grazing can limit the extent of seasonal variation in benthic algal biomass, and change assemblage composition with consequences for benthic primary production (e.g. Power et al., 1988; Kupferberg, 1997; Abe et al., 2007). Under nitrogen-limited conditions, ‘gardening’ by fishes may even lead to a shift towards dominance of nitrogen-fixing cyanobacteria and increased productivity (Power et al., 1988). Since algivorous *Pseudogastromyzon myersi* is present at high densities in Hong Kong streams, its feeding may affect algal biomass and composition thus contributing to some of the patterns described in this study. Exploration of such possibilities will require manipulative experiments.

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