

Algal mats and insect emergence in rivers under Mediterranean climates: towards photogrammetric surveillance

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SUMMARY

1. In a nitrogen (N)-limited river subject to Mediterranean summer drought hydrology, the colour of macroalgal proliferations changed with successional and seasonal changes in epiphyte assemblages. New growth of the dominant macroalga, *Cladophora glomerata*, was green, as were proliferations of *Oedogonium*, *Mougeotia* and *Spirogyra*, which did not become heavily colonized with diatoms. Green *Cladophora* turned yellow as *Cladophora* filaments became colonized by diatoms that were not N fixers, and turned rust-coloured as later-successional epiphyte assemblages became dominated by dense *Epithemia turgida* and *E. sorex*, which both contain N-fixing cyanobacterial endosymbionts.

2. The rate and composition of insect emergence from floating algal mats differed among proliferations of different colour. The rates of emergence (individuals day⁻¹ 500 cm⁻²) of nematoceran flies were three to 25 times greater from yellow or rusty-coloured *Cladophora* mats than from green *Cladophora*, *Oedogonium* or *Mougeotia* mats that had lower epiphyte densities. Biomass emergence from *Cladophora* mats that were rusty in colour was eight to 10 times greater than from yellow *Cladophora* mats, because larger nematocerans dominated in rusty mats (Chironominae versus Ceratopogonidae in yellow mats).

3. Proliferations of *Epithemia*-infested *Cladophora* occur at and above drainage areas of about 100 km² (channel widths of 25–30 m) in this river network, coinciding with the drainage area threshold where a step increase in concentration of total dissolved N is observed during summer.

4. In rivers under Mediterranean climate regimes, algal succession during the prolonged low flow season is less subject to stochastic interruption by spates than in rivers under more continental climates. Under these summer drought conditions, photogrammetric detection of colour changes in algal proliferations may help us track reach or basin-scale change in their ecological functions.

Keywords: algae, epiphytic algae, insect emergence, nitrogen fixers, photogrammetric surveillance

Introduction

Attached algae often dominate primary production in flowing waters. Filamentous macroalgal proliferations build up, sometimes to nuisance levels, when high nutrient levels allow them to escape grazer control (Steinman, Mulholland & Hill, 1992; Borchardt, 1996; Biggs, Stevenson & Lowe, 1998). Filamentous algae can also proliferate in non-eutrophic rivers under Mediterranean hydrologic regimes, following winter floods that scour away grazers, providing a window of time for algal accrual early in the low flow season before grazer populations rebuild (Power, 1990; Power, Parker & Dietrich, 2008). While filamentous algae are typically nutritionally inferior and more mechanically resistant to grazing than microalgae (Feminella & Resh, 1991; Roll, Diehl & Cooper, 2005), this is not the case for many epiphytic algae that colonize macroalgal surfaces. Here we report results suggesting that functionally significant differences occur among epiphyte assemblages on algal proliferations, and that these can sometimes be detected and monitored by macroscopic colour analysis at scales useful in remote sensing.

Filamentous host taxa differ in architecture, surface area and cell wall texture and chemistry, which can all influence the quantity and quality of epiphytes. Epiphytes and hosts both differ in ability to fix nitrogen (N) (Williams & Burris, 1952), nutritional quality (e.g. C : N : P stoichiometry, essential fatty acid composition (Ahlgren *et al.*, 1990; Boyd, 1973; Brett & Muller-Navarra, 1997), secondary compounds including toxins (Carmichael, 1994), mechanical accessibility to grazers (Steinman, 1996); and assemblage effects on flow hydraulics (Dodds, 1991); and stream biogeochemical cycling, including biological oxygen demand (Biggs, 2000). Collectively, these functionally distinct traits influence the roles of algae in social-ecological systems (*sensu* Walker & Salt, 2006). For example, floating algal mats can greatly increase aquatic insect emergence, both by enhancing insect production and by providing partial refuge from aquatic predation (Power, 1990).

We studied seasonal changes in algal proliferations over a 7 km reach of the South Fork of the Eel River in Mendocino County, California, U.S.A., within the Angelo Coast Range Reserve (<http://angelo.berkeley.edu>) of northern coastal California, where influences of ecological and hydrologic factors on algae have

been investigated for 20 years. In this steep, incised basin, filamentous green algal proliferations become conspicuous in wider channels that receive ample sunlight. These conditions occur where drainage areas exceed 100 km², and bankfull channel widths are more than 25 m. These mainstem reaches have shallow gradients (<0.0005) so that floating algal mats accumulate in slack-water areas after filamentous macroalgal turfs detach from their substrata.

Under the region's Mediterranean climate, rainy winters are followed by biologically active summer low flow periods (Gasith & Resh, 1999). *Cladophora glomerata* (L.) (Kütz.), a filamentous green alga, dominates primary producer biomass during summer in productive, mainstem channels in the Eel drainage network. Each spring following winter scour, *Cladophora* initiates growth vegetatively from basal cells that survive winter flood scour on stable boulder and bedrock substrata. Larger blooms of *Cladophora* occur if spates during the preceding winter are large enough to mobilize much of the river bed, eliminating predator-resistant grazers such as the large armored caddisfly, *Dicosmoecus gilvipes* (Hagen) (Power, 1992; Power *et al.*, 2008). *Cladophora* biomass peaks in late spring or early summer, with attached turfs sometimes attaining lengths of 6–8 m. These turfs detach to form floating mats, and both mats and remnant turfs collapse to short (<3 cm high) filaments and loose detritus by late summer and early autumn, well before the onset of the autumn and winter rains, due to some combination of grazing and senescence from epiphyte overgrowth, self-shading, nutrient limitation or temperature stress. *Cladophora* becomes thickly overgrown with epiphytes in this and other (Burkholder & Wetzel, 1990; Dodds, 1991; Peterson & Grimm, 1992) systems, so that assemblage biomass can be dominated by epiphytes rather than the deeply buried host filaments. During late summer, *Cladophora* releases zoospores, and young filaments appear for the first time on winter-mobile pebble and small cobble substrata (Power, 1992). These secondary, smaller growths of *Cladophora* quickly become colonized by epiphytes and are grazed away before the onset of winter spates.

As *Cladophora* wanes, conspicuous proliferations of other filamentous green algae, predominantly *Oedogonium*, *Mougeotia* and *Spirogyra*, develop. These taxa, unlike *Cladophora*, acquire only sparse (*Oedogonium* and *Mougeotia*) or no (*Spirogyra*) epiphytes, because of chemical and textural differences in their cell walls.

Methods

Field monitoring and assessment

From 28 February, 2006 to 25 September, 2007, we recorded daily photos of a single pool using a Canon VB-C50i, Pan-Tilt-Zoom security camera (Canon Inc., Kanagawa, Japan). The camera is solar powered and attached to a wireless packet radio network. An automated script requests pictures of five preset locations at 08:00 hours PST and transfers them to a server at the field station and to the University of California-Berkeley campus. Resolution of the camera for still images is 640×480 pixels. From 30 April, 2006 to 5 September, 2006, we recorded hourly photos starting at 05:00 hours, ending at 21:00 hours at nine preset locations. These were used to help determine optimal hours of the day and season for taking pictures of the water.

From 21 June, 2007 to 31 July, 2008, we sampled, photographed and microscopically examined large macro-algal proliferations and their epiphytes in a 7 km reach of the South Fork Eel River within the Angelo Coast Range Reserve, a protected research reserve maintained by the University of California Natural Reserve System ($39^{\circ}43'3.8''\text{N}$, $123^{\circ}39'7.8''\text{W}$). Algae were mapped by visual colour type and photographed along two cross-stream transects in each of five large pools. Photographs were taken with a digital camera (D40X; Nikon Corporation, Tokyo, Japan) mounted 5–6 m above the river surface on an extendable fibreglass rod. We created a single composition for each transect by mosaicking individual photos with photo-editing software (Photoshop CS3; Adobe Systems Incorporated, San Jose, CA, U.S.A.).

From 4–17 June to 11–21 July, 2008, we surveyed algae at 306 and 388 sites, respectively, distributed along reaches at 11 channel network positions in the South Fork Eel River catchment that ranged in drainage area from 0.54 to 169.2 km². Algae at each site were visually assessed along two to three cross-stream transects. Collections were made so that field assessment could be checked against quantitative microscopic assessment (400 \times magnification) in the laboratory, using Whipple grids (Canemco Inc., Quebec, Canada) with hits at 400 intersections counted per each of 10 fields to evaluate % cover for epilithic assemblages, and epiphyte counts along filaments from macroalgal proliferations, as described below.

Microscopic characterization of algae

Samples from algal proliferations in mainstem South Fork Eel sites were inspected under 400 \times in the laboratory for taxonomic characterization. Samples were counted within 24 h of collection, or after preservation in *c.* 3% formalin. For epiphyte counts, single filaments of host algae were stretched out on microscope slides, and all epiphytes across a 445 μ length (the maximum field diameter at 400 \times) were identified and enumerated. Ten filaments were counted to characterize a single sample. We optically dissected the host filament to count and identify epiphytes on both sides. Twenty widths of the host filament were measured with a reticle (ocular micrometer), permitting estimation of the number of epiphyte cells per host filament surface area, computed as a cylinder.

Nitrogen sampling

Sampling for analyses of concentration of total dissolved nitrogen (TDN) was conducted during summer baseflow conditions at multiple sites. Sites ranged from small headwater streams to sunny downstream reaches of the South Fork Eel River and its major tributary, Ten Mile Creek. This sampling design was used to examine changes in stream nutrient chemistry associated with increased algal productivity and N-fixer biomass in the primary study sites (described above) compared to the smaller tributary streams, which are less productive (Power, 1992; Finlay, 2003; McNeely, Finlay & Power, 2007). Water samples were filtered in the field with glass-fibre filters (Whatman GF/C; Fisher Scientific, Pittsburgh, PA, U.S.A.), refrigerated and shipped to the University of Minnesota within several days of collection. TDN was analysed on a Shimadzu total organic carbon/total nitrogen analyser (Series V Model cpn; Shimadzu Corporation, Kyoto, Japan) using high temperature combustion followed by analyses of N on a chemoluminescence detector (Shimadzu Corporation).

Emergence trapping

Emergence was measured from various types of algal mats from 5 to 20 July, 2007. Mats were placed for 24 h within PVC pipes (25.4 cm diameter) at four sites

along the river. Pipes stood vertically on the riverbed, so that 10–15 cm of pipe emerged above the water surface (Fig. S3). Pipe walls were drilled with four columns of 10 cm diameter holes spaced 6 cm apart by height and covered with 0.3 mm nylon mesh. These holes provided sufficient water or air exchange so that temperatures inside traps were similar to those outside. After mats were placed inside the PVC pipes, the surface of the pipe was covered with a clear vinyl plastic sheet with the downward side covered with Tanglefoot® (The Tanglefoot Company, Grand Rapids, MI, U.S.A.) colourless, odourless adhesive. These traps were more satisfactory than floating net traps we have used previously, because emergents did not drop back into the water to die undetected; spiders, Gerrids and other predators were not able to consume

emerged prey; and the spatial and algal sources of prey were quantitatively circumscribed.

Results

Epiphyte density and composition is partially predictable from macroscopic colour

Algal proliferations with different macroscopic colours and textures had different densities and compositions of epiphytes. New growth of *C. glomerata* was bright green (Fig. 1, lower left). Over time, *Cladophora* turfs and detached mats acquired a dun-yellow colour (Fig. 1, lower right) that indicated heavy overgrowth by diatoms, with *Cocconeis placentula* Ehr., *Cocconeis pediculus* Kütz., *Rhoicosphenia abbreviata* (Agardh)

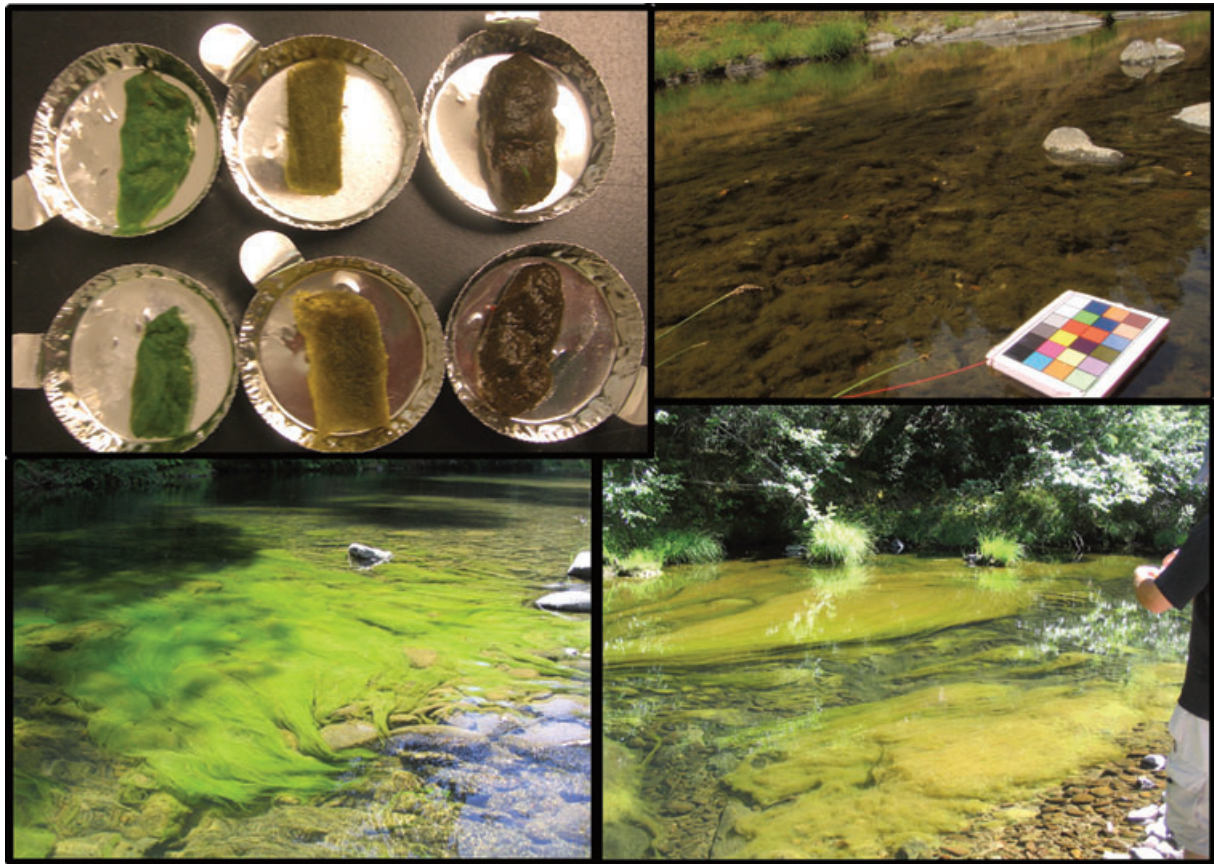


Fig. 1 Colour differences in algal samples (upper left) and field proliferations. Lower left: green *Cladophora* in tails of pools, before heavy epiphyte colonization (26 June, 2007); Lower right: *Cladophora* turns from green to yellow as it becomes more heavily colonized by *Cocconeis* and gomphonemoid diatoms, particularly in slack water along the river margin (foreground), where the host grows more slowly. Upper right: later successional *Cladophora* proliferations turn from yellow to rusty red due to thick layers of *Epithemia turgida* and *E. sorex*, epiphytic diatoms with nitrogen-fixing endosymbiotic cyanobacteria. In the foreground is the floating laminated grey and colour scale used to standardize digitized colour images of algae photographed under different environmental lighting.

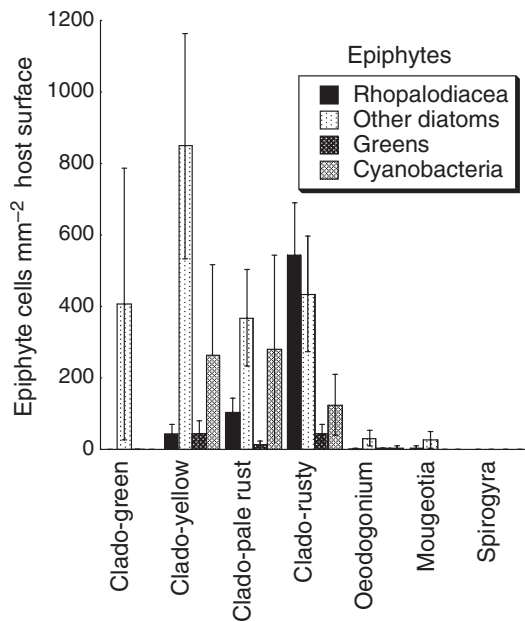


Fig. 2 Average density (with 2 SE) of functional groups of epiphytes on different macroalgal hosts. 'Clado-' refers to *Cladophora*; 'green', 'yellow' and 'rusty' are colours of proliferations that may indicate distinct ecological functions, as described in the text; 'pale rust' is transitional between yellow and rusty stages.

Lange-Bertalot, *Achnantheidium minutissimum* (Kütz.) Czarnecki and *Gomphonema* spp. dominating epiphyte assemblages (Fig. 2, Table 1). Later, *Cladophora* turfs acquired a distinctly more reddish-brown ('rusty') colour (Fig. 1, upper right); these were dominated by the diatoms *Epithemia turgida* (Ehrenb.) Kütz. and *E. sorex* Kütz. (Table 1, Fig. 2). These two diatoms, and another less common Rhopalodiaceae, *Rhopalodia gibba* (Ehr.) O. Muller, contain N-fixing cyanobacterial endosymbionts. Despite large variability, differences in epiphyte composition among the six macroalgal host types were significant (one-way ANOVA: $F = 9.9$, $P < 0.0001$, d.f. = 6), and driven by extremely high loads of Rhopalodiaceae on rust-coloured *Cladophora* (from a Tukey HSD *a posteriori* test). These differences in cell counts would be more pronounced with evaluation of biovolume, as *E. turgida* cells were much larger than most other diatoms that we encountered.

Cladophora proliferations at different river positions (Fig. 1) and tracked through time at single sites (Fig. S1) showed colour transitions from green to yellow to rusty, suggesting that there were succes-

sional or seasonal influences, or both, on the diatom taxa dominating *Cladophora* epiphyte assemblages. The colour of assemblages was distinct enough to be detected in photographs taken 5–6 m above the river surface (Fig. S2), indicating that these transitions and the spatial location and extent of *Cladophora* proliferations could be monitored photogrammetrically with automated cameras installed above the stream at permanent locations or mounted in low-flying miniature helicopters, balloons or blimps. Different successional stages co-occurred at sites where environmental gradients such as cross-channel variation in stream flow altered growth rates of the *Cladophora* host. For example, proliferations of green *Cladophora* were maintained where mid-channel velocities provided favourable flow conditions (nutrient fluxes) for the host macroalga, while yellow or rusty proliferations (mid- or late-successional, respectively) developed earlier in slack water along river margins. Figure 1 (lower right) shows the mid-successional state, colonized by non-rhopalodiacean diatoms (primarily *Cocconeis*, *Achnantheidium* and *Rhoicospheonia*). A later stage of rusty *Cladophora* (colonized primarily by non-rhopalodiacean diatoms but with incipient colonization by *Epithemia*) occurs along the slower-flowing river margins where *Cladophora* growth may have been reduced by lower nutrient flux.

As *Cladophora* biomass declined and decomposed due to grazing and senescence, other filamentous green macroalgae proliferated and remained bright green over the weeks they were observed, as they acquired few (*Oedogonium*, *Mougeotia*) or no (*Spirogyra*) epiphytes.

Potential contributions to N loading in the river ecosystem

A sharp increase in TDN occurred at a drainage area threshold of 100 km² in the South Fork Eel River (Fig. 3), where the winter-active channel becomes *c.* 25–30 m wide and the river bed sunlit enough to support large proliferations of filamentous green algae and associated epiphytic *Epithemia* (Figs 4 & 5). The increase in TDN from June to July (Fig. 3) coincides with the increased proportional cover of *Epithemia*-laden rusty *Cladophora* over this period (Fig. 5). Declining specific UV absorbance of the dissolved organic carbon in these river water samples

Table 1 Numbers of epiphytic cells mm⁻² surface area on different macroalgal hosts. Sample sizes shown in parentheses, nitrogen-fixing diatoms in the family Rhopalodiaceae are shown in bold

Algal type	Epiphyte	Host type															
		Cladophora-green (5)		Cladophora-low (4)		Cladophora-yellow (4)		Cladophora-pale rusty (4)		Cladophora-dark rusty (5)		Oedogonium (5)		Mougeotia (2)		Spirogyra (5)	
		average	SE	average	SE	average	SE	average	SE	average	SE	average	SE	average	SE	average	SE
Diatom	<i>Achnanidium</i>	2	(2)	352	(315)	87	(42)	55	(30)	3	(3)	0	(4)	0	(1)	0	(1)
	<i>Cocconeis pediculus</i> live	364	(364)	151	(64)	75	(25)	70	(51)	17	(16)	0	(1)	0	(1)	0	(1)
	<i>Cocconeis pediculus</i> dead	11	(10)	183	(93)	44	(21)	130	(50)	2	(1)	1	(1)	0	(1)	0	(1)
	<i>Cocconeis placentula</i> live	10	(9)	43	(17)	5	(3)	4	(4)	2	(2)	0	(2)	0	(2)	0	(2)
	<i>Cocconeis placentula</i> dead	14	(7)	46	(17)	8	(7)	12	(12)	2	(2)	0	(2)	0	(2)	0	(2)
	<i>Diatoma</i>	2	(1)	0		0		1	(1)	0	(1)	0	(1)	0	(1)	0	(1)
	<i>Epithemia turgida</i>	0		40	(24)	83	(34)	415	(100)	1	(1)	4	(4)	0	(1)	0	(1)
	<i>Epithemia sores</i>	0		2	(2)	19	(13)	112	(39)	0	(1)	1	(1)	0	(1)	0	(1)
	<i>Fragilaria</i>	0		0		88	(88)	1	(1)	0	(1)	0	(1)	0	(1)	0	(1)
	<i>Gomphonema</i> spp.	1	(1)	23	(17)	22	(19)	117	(41)	2	(1)	0	(1)	0	(1)	0	(1)
	<i>Navicula</i> sp.	1	(1)	1	(1)	0	(1)	1	(1)	0	(1)	0	(1)	0	(1)	0	(1)
	<i>Nitzschia</i> spp.	0		3	(1)	1	(1)	3	(1)	1	(1)	0	(1)	0	(1)	0	(1)
	<i>Rhoicosphenia</i>	2	(2)	47	(26)	37	(13)	36	(17)	1	(1)	0	(1)	0	(1)	0	(1)
	<i>Rhopalodia</i>	0		2	(1)	0	(1)	18	(15)	0	(1)	0	(1)	0	(1)	0	(1)
	<i>Synedra</i>	0		0		0		4	(4)	1	(1)	25	(23)	0	(23)	0	(23)
	<i>Ankistrodesmus</i>	0		1	(1)	0	(1)	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
	<i>Apiocystis</i>	0		11	(7)	2	(2)	2	(2)	1	(1)	0	(1)	0	(1)	0	(1)
<i>Characium</i>	0		5	(3)	4	(4)	2	(1)	0	(0)	0	(0)	0	(0)	0	(0)	
<i>Closterium</i>	0		0		0		0	(0)	0	(0)	0	(0)	0	(0)	0	(0)	
<i>Gongrosira</i>	0		27	(27)	0		20	(12)	0	(0)	0	(0)	0	(0)	0	(0)	
<i>Mougeotia</i>	0		1	(1)	2	(2)	1	(1)	0	(1)	0	(1)	0	(1)	0	(1)	
<i>Oedogonium</i>	0		1	(1)	4	(3)	19	(14)	1	(1)	0	(1)	0	(1)	0	(1)	
Cyanobacteria	<i>Calothrix</i>	0		3	(2)	20	(12)	15	(13)	1	(1)	0	(1)	0	(1)	0	(1)
	<i>Chamaesiphon</i>	0		253	(249)	251	(250)	15	(12)	3	(3)	0	(3)	0	(3)	0	(3)
	<i>Nostoc</i>	0		6	(6)	0		72	(72)	0	(0)	0	(0)	0	(0)	0	(0)
	<i>Heteroleibleinia</i>	0		1	(1)	8	(8)	22	(22)	1	(1)	0	(1)	0	(1)	0	(1)
totals	Rhopalodiaceae diatoms	0		44	(27)	102	(40)	545	(146)	1	(1)	5	(4)	0	(4)	0	(4)
	non-Rhopalodiaceae chlorophytes	407	(381)	849	(315)	367	(135)	435	(163)	31	(21)	26	(23)	0	(23)	0	(23)
	cyanobacteria	1	(0)	45	(35)	12	(11)	45	(26)	2	(1)	0	(1)	0	(1)	0	(1)
		0		263	(254)	279	(263)	124	(85)	5	(4)	0	(4)	0	(4)	0	(4)

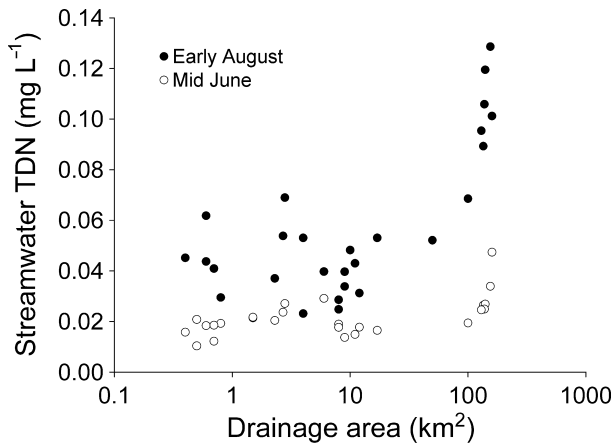


Fig. 3 Downstream changes in total dissolved nitrogen in river water in the upper South Fork Eel River network, in mid-June and early August 2006.

(J. Finlay, unpubl. data) suggested that the downstream spike in TDN, which was mostly dissolved organic N, was at least partially associated with aquatic autotrophs. Human contributions to the downstream increase in TDN in this drainage network are probably not significant, because the nearest town (Branscomb, CA) is well upstream from the study site, and human population density decreases downstream in our study area within this catchment.

Preliminary direct *in situ* measurements have shown high rates of N fixation by *Epithemia*-covered *Cladophora* blooms ranging from 0.3 to 1.7 $\mu\text{g N g}^{-1}$ (dry wt) h^{-1} , up to five times higher than rates measured in green and more than double those recorded for yellow *Cladophora* proliferations incubated under the same field conditions (J. Welter, A. Bratt and M. Moenkedick, unpubl. data).

Emergence

Rusty *Cladophora* mats and *Cladophora* mats infested and woven by midges (Fig. 7) were hotspots of aquatic insect biomass emergence, while large numbers of insects emerged from these and also from yellow-coloured *Cladophora* mats colonized by non-N fixing diatoms (Fig. 7). The rates of emergence by numbers (individuals $\text{day}^{-1} 500 \text{ cm}^{-2}$) of nematocerans were three to 25 times greater from heavily colonized (yellow, woven or rusty-coloured *Cladophora* mats) than from green *Cladophora*, *Oedogonium* or *Mougeotia* mats with low epiphyte densities. Biomass emergence from *Cladophora* mats that were rusty in colour was eight to 10 times greater than mass emergence from yellow *Cladophora* mats, due to larger body sizes of *Pseudochironomus* and other dominant chironomids in rusty or woven *Cladophora* (Fig. 7, Fig. S4). Emergence from yellow *Cladophora* was dominated by very small ($\leq 1 \text{ mm}$) ceratopogonid midges whose light adult colour, interestingly, matched the background colour of the mats from which they emerged (Fig. S4e).

Discussion

Environmental, taxonomic and successional influences on colour of algal proliferations

To ascertain whether macroscopic colour is a reliable guide to functional attributes of algal proliferations, we must understand why algal mats change colour in particular contexts. Colour in algal assemblages depends in part on the dominant taxa, and in part on changes over time in their physiological states, ecological succession and the environment.

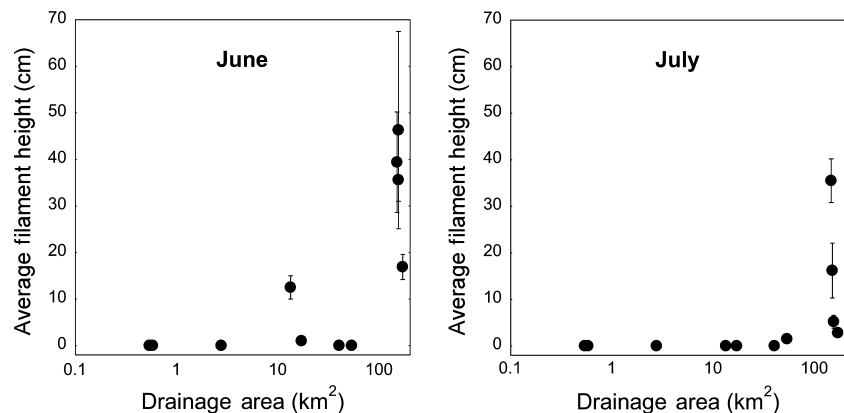


Fig. 4 Average height of algae (with 1 SE) surveyed along cross-stream transects at 11 drainage network positions in June and July 2008. Field estimates of attached algal height are positively correlated with biomass (Power *et al.*, 2008, which also give details of this survey method).

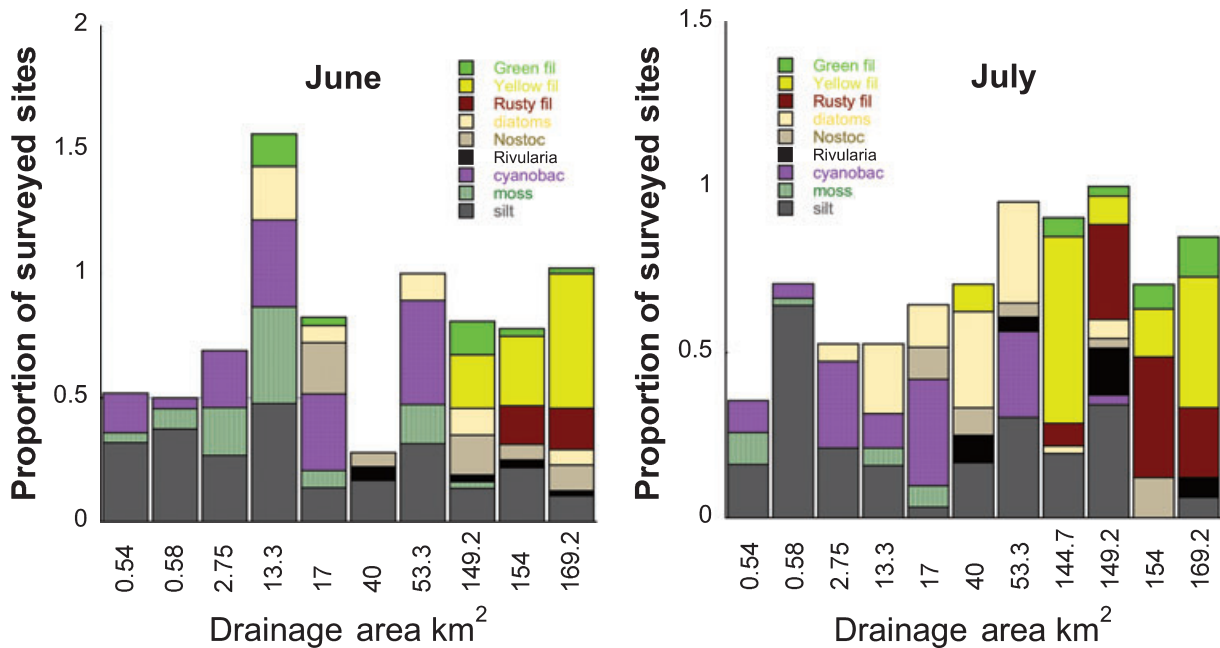


Fig. 5 Proportion of surveyed sites with different visually assessed algal cover at the 11 drainage network positions in June and July 2008. Visual assessments of functional types of cover were checked with microscopic examination at 400 \times of samples collected from these sites at each sampling period (see text).

Filamentous chlorophyta tend to be bright green during vigorous growth phases when cell contents are full and plastids abundant. Intensity of green colour is not always positively correlated with algal growth rate; however, when growing at sub-optimal light levels, filamentous green algae develop darker, more intense green colour because of cells' compensatory higher production of chlorophyll (Hill, Ryon & Schilling, 1995).

Heavy growths of epiphytic diatoms change the colour of their assemblages in two ways – by adding their own carotene and xanthophyll pigments that generally confer a golden, brown (Pace, 1941) or orange-brown (Margulies, 1970) colour, and by reducing the viability of filamentous green hosts so that host cells lose content and become pale or bleached. In addition, the physiognomy of the epiphytic diatom assemblage plays a role in algal mat colour. *Cocconeis* is relatively thin in the peralver axis with flattened plastids. In addition *Cocconeis* usually forms a monolayer on *Cladophora* in the Eel River. Both of these attributes result in the pale yellow colour of *Cladophora* bearing an epiphyte assemblage dominated by *Cocconeis*. Assemblages with an abundance of stalked diatoms also appear pale, as diatoms are spread out from the *Cladophora*. Our observations during June,

July and August 2006–08 in the South Fork Eel suggested that assemblages dominated by the diatoms *Cocconeis*, *Gomphonema*, *Achnantheidium* and *Rhoicosphenia* were pale green, yellow-green or yellow.

In contrast to *Cocconeis* and stalked diatoms, *Epithemia* spp. are thicker in the peralver axis and tend to colonize on top of one another (Marks & Power, 2001; Fig. 8). Multilayered *Epithemia*-dominated assemblages were distinctively darker (reddish brown) than assemblages dominated by non-Rhopalodiaceae in our system.

Under light-limited conditions, however, assemblages dominated by *Cocconeis* can also appear rusty. During October, when the sun path is low and light reaching certain canyon-bound reaches of the Eel is attenuated, an assemblage designated as rust-coloured in the field was dominated by *Cocconeis*, not *Epithemia* (M. Power, pers. obs.). *Cocconeis* can also dominate epiphyte cover of rusty coloured proliferations collected from shaded understories of thick floating algal mats during the summer (P. Furey, pers. obs.). This colour is probably due to increase in cellular content of accessory pigments in *Cocconeis* under light limitation. Several studies have shown that algal pigments respond to light and other environmental factors (Margulies, 1970; Round,

1973). In contrast Millie *et al.* (1997) found that a carotenoid, gyroxanthin diester and its absorbance signature were reliable indicators of *Gymnodinium breve* Davis, a dinoflagellate causing red tides in Florida, throughout the range of physiological states characterizing bloom inception through senescence.

Succession within epiphytic assemblages in the South Fork Eel and similar systems is intertwined with seasonal changes in N availability and temperature that affect relative growth rates of hosts and epiphytes. As N fixers (Floener & Bothe, 1980), Rhopalodiaceae often dominate periphyton in low N environments (Fairchild & Lowe, 1984; Bahls & Weber, 1988; Mulholland *et al.*, 1991; Peterson & Grimm, 1992). Nitrogen becomes more limiting relative to photosynthetic demand in the South Fork Eel over the course of the summer, as producer biomass accrues and river flow and groundwater inputs ebb, giving *Epithemia* spp. a growth advantage over non-fixing epiphytes. In late summer incubations in the South Fork Eel, epiphyte assemblages on *Cladophora* filaments incubated in ambient, N-poor ($7 \mu\text{g L}^{-1}$) Eel River water were dominated by *Epithemia* spp., while epiphytes in chambers experimentally enriched with N ($300 \mu\text{g L}^{-1}$) were dominated by non-N-fixing diatoms *A. minutissimum* and *Nitzschia palea* (Marks & Power, 2001). Similarly, *E. sorex* dominated unenriched, but not $\text{NO}_3\text{-N}$ enriched experimental substrata in an Arizona desert stream (Peterson & Grimm, 1992).

Impact on secondary production and emergence

Epiphytic diatoms often increase the nutritional value of algal proliferations for primary consumers, as they are digestible and high in lipid content, including polyunsaturated fatty acids that are nutritionally limiting to invertebrates and vertebrates (Boyd, 1973; Ahlgren *et al.*, 1990; Park *et al.*, 2002). N-fixing Rhopalodiaceae may also lower C : N ratios, a potentially major contribution to secondary production in N-limited river ecosystems like the South Fork Eel (Dodds, 1991; Power, 1991). Alternatively, however, nitrogenous compounds elaborated by cyanobacteria may be indigestible or toxic (Carmichael, 1994). The edibility of *Epithemia* for a common nematoceran midge (*Pseudochironomus richardsoni* Malloch) was indicated by high midge densities in rusty *Cladophora* proliferations, the abundance of empty *Epithemia*

frustrules in midge guts, and the restoration of green colour in *Cladophora* near midge tufts (Fig. 6, see also Power, 1991).

In addition to providing food, algal proliferations, particularly floating mats, also offer favourable oviposition sites for adult female aquatic insects. For their progeny, floating mats provide sun-warmed thermal incubators and partial refuges from fish and other aquatic predators. Floating algal mats (and mats of other vegetation) act as valves in aquatic ecosystems, increasing both the production of certain aquatic insects and the proportion of this production that is routed out of rivers into catchments (Power, 1990). While emergence by numbers was similar between yellow (*Cocconeis*-, *Achnantheidium*-dominated) mats and rusty (*Epithemia*-dominated) mats, biomass emergence from rusty mats was much greater, because chironomid midges emerging from rusty mats were larger than ceratopogonid midges emerging from yellow mats (Fig. 7, Fig. S4). Interestingly, dark chironomid adults were more cryptic on their dark rusty mats while pale yellow ceratopogonid adults were more cryptic on the yellow mats where they dominated emergence (Fig. S4). Body size of emergence affects trophic transfers to terrestrial or aerial insectivores. Larger chironomids are more profitable and detectable prey for insectivores like bats, which abound over the South Fork Eel and other California rivers, while ceratopogonids may be more subject to predation by small predators, like riparian spiders.

Nitrogen cycling

Nitrogen is generally the limiting macro-nutrient in western temperate river ecosystems (Grimm, 1987; Hill & Knight, 1988; Dodds, 1991; Power, 1991; Peterson & Grimm, 1992). While proliferating filamentous macroalgae and most epiphytes take up dissolved N from the water column, algal proliferations colonized by N-fixing epiphytic taxa such as Rhopalodiaceae or certain cyanobacteria (e.g. *Rivularia* or *Nostoc*) may become sources of N to ecosystems, particularly as they decompose or are consumed by grazers. Densities of *Epithemia* on *Cladophora* are high (Figs 2 & 8). In addition, proliferations of *Cladophora* in the Eel and elsewhere present enormous ecological surface area. Taft & Kishler (1973) showed that proliferations of *Cladophora* in Lake Erie increased

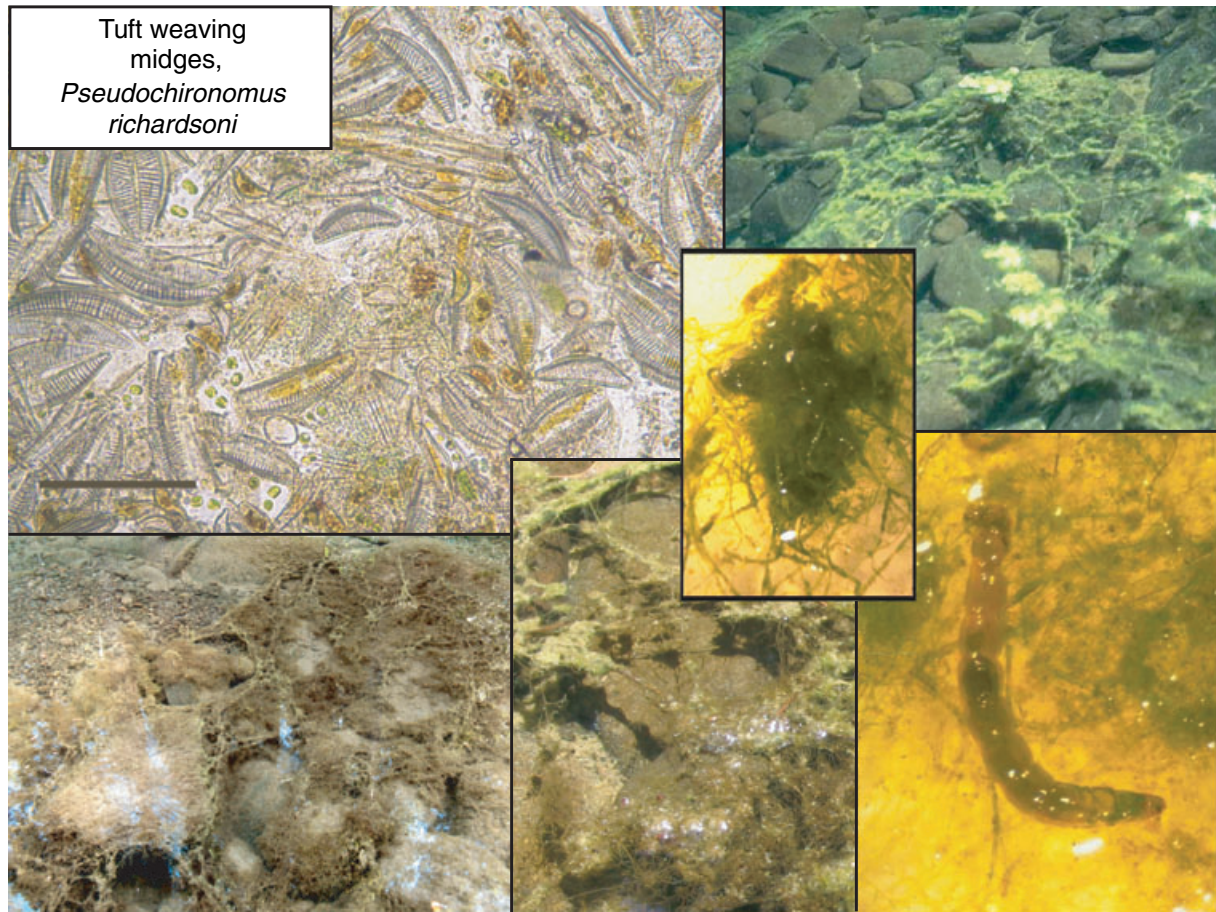


Fig. 6 Centre: tuft (c. 1 cm long) woven in *Cladophora* by the tuft-weaving nematoceran midge, *Pseudochironomus richardsoni* (lower right). Retreats appear greener than the background due to midge grazing and removal of *Epithemia*. Infestations of rusty coloured, *Epithemia*-covered *Cladophora* turfs by the midge (lower left, upper right) take on a ropy, knotted architecture. Grazing of *Epithemia* from *Cladophora* filaments in and adjacent to the midges' woven retreats removes the rusty epiphyte assemblage and restores green colour to the *Cladophora* turf (upper right). The guts of this common and functionally important grazer (Power, 1990) are often filled with empty *Epithemia* frustules, easily recognizable from their distinctive half-moon shape and up-curved raphes (upper left, scale bar = 100 μ m).

the functional surface area of the littoral zone by 2000; our computations suggest that this multiplier could be as high as 200 000 for 6–8 m long, branched *Cladophora* turfs in the Eel River. Together, these observations suggest that when *Cladophora* proliferations are smothered with *Epithemia*, N loading could potentially be prodigious. In the South Fork Eel River, a sharp increase in TDN occurs at the drainage area threshold at which algal proliferations become large and floating algal mats are retained (Fig. 3). Preliminary measurements (J. Welter *et al.*, unpubl. data) have found the highest rates so far from *Epithemia*-covered *Cladophora*. More data are needed, however, to evaluate contributions to river N loading from other N fixers (e.g. riparian white alder, *Alnus rhom-*

bifolia) and free living benthic cyanobacteria (*Nostoc parmeloides* and *Rivularia* sp.), which also are more abundant along sunlit reaches where drainage areas exceed 100 km². Differences among peak seasonality activities of these various fixers may help us distinguish their relative contributions to dissolved N in this drainage network.

Towards photogrammetric monitoring of algal proliferations for ecological forecasting

Given the potential complexity of controls on the colour of functionally distinct epiphytic diatom taxa, the association of colour with ecological function of algal proliferations may be more reliable in distinctly

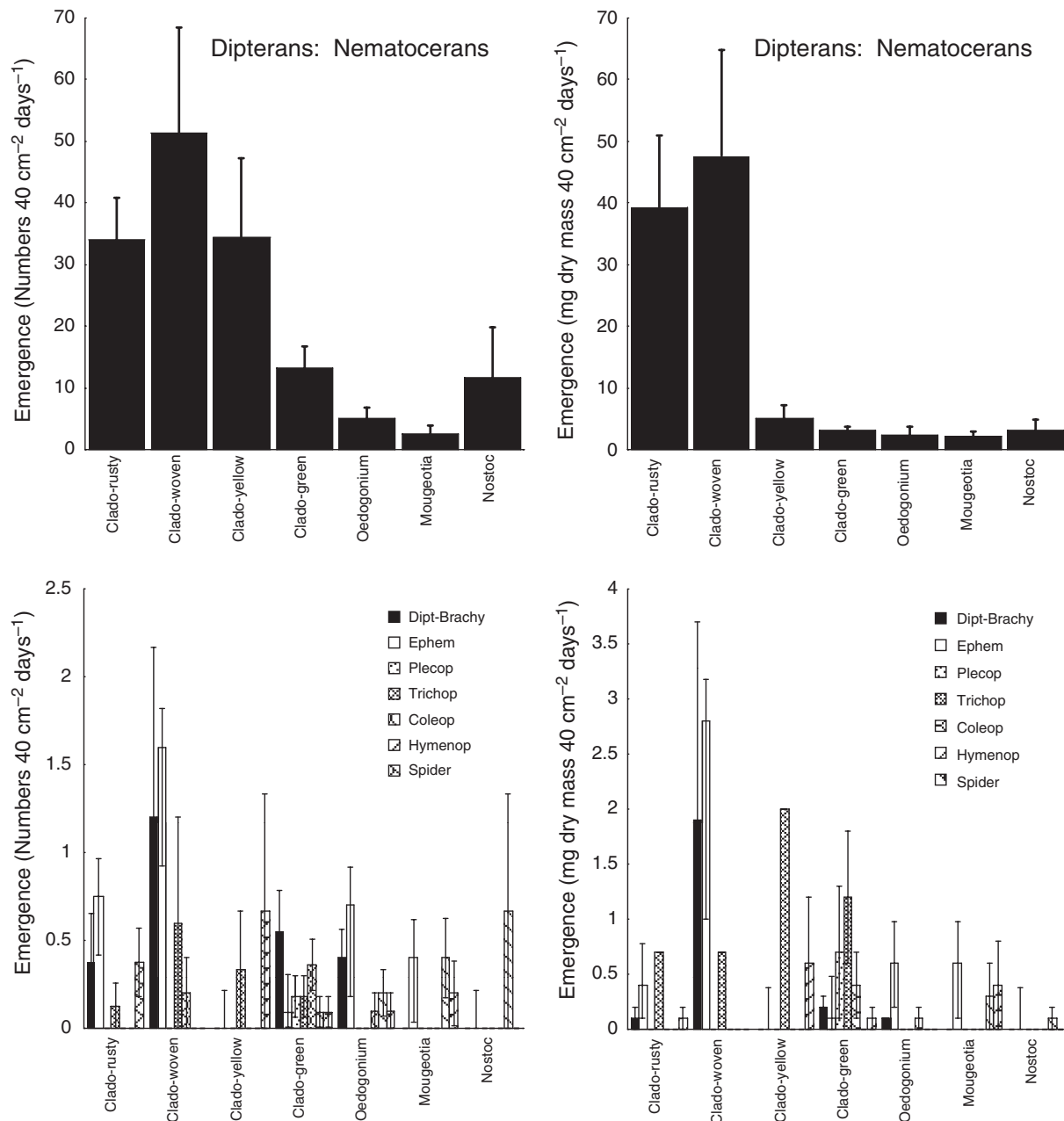


Fig. 7 Numbers and biomass emergence (means with 1 SE above histogram bars) of nematoceran flies and other insect orders from algal proliferations of different colours.

seasonal regimes (e.g. under Mediterranean, or possibly snow-melt driven hydrographs). Under Mediterranean hydrologic regimes, succession can proceed for months over the low-flow period, free of disruption by spates, which can occur during any month of the year under continental climate regimes. Therefore, in Mediterranean systems and possibly seasonal snow-melt rivers, time since disturbance that resets

river biotic succession is more likely to correspond to predictable seasonal changes in environmental conditions such as nutrient availability, flow and temperature. In these cases, post-disturbance algal succession, taxonomic dominance and associated macroscopic colour changes may be more highly correlated than under hydrologic regimes in which disturbance is more irregularly timed.

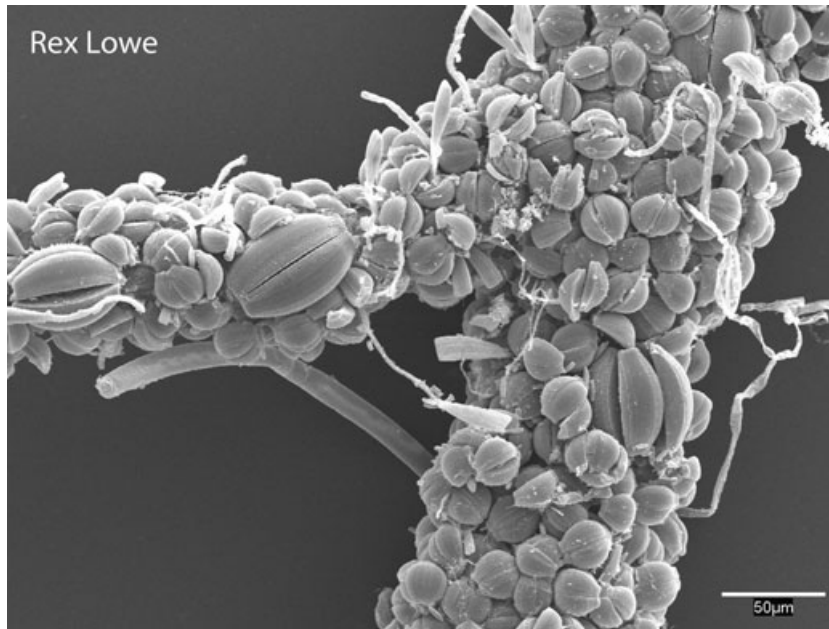


Fig. 8 Scanning electron micrograph of *Cladophora glomerata* sampled in July 2006 from the South Fork Eel River showing multiple layers of *Epithemia sorex* (smaller cells) and *E. turgida* covering the filamentous *Cladophora* host (photo by Rex Lowe, scale bar = 50 µm).

Ecologists are increasingly called upon to assess status and trends in ecosystems, and forecast their likely responses to altered land use, climate and biota. To respond, we must expand our repertoire of rapid assessment tools, including ways to relate patterns detected by automated or remote sensing technology to ecological function and consequences on the ground. In rivers and other freshwater and nearshore marine ecosystems, we need rapid but functionally meaningful ways to assess consequences of algal proliferations over large spatial scales (Biggs, 2000; Holt *et al.*, 2003; Stevenson & Smol, 2003; Stumpf *et al.*, 2003). Algae have been used in environmental assessment as indices of environmental conditions, and are also of interest because of their own potentially strong beneficial or adverse effects on ecosystems (Biggs & Price, 1987; Lowe & Pan, 1996; Stevenson & Smol, 2003). The ambitious National Water Quality Assessment initiative has generated a rich data set on periphyton community structure across rivers in the U.S.A. The approach has employed many microscopists generating algal species data for multivariate analyses used to assess and monitor stream biological integrity (Stevenson & Smol, 2003). Because algal proliferations are spatially heterogeneous and extremely dynamic, changing dramatically over days or weeks, however, algal variability over drainage basin, whole lake or regional shoreline scales of societal concern not be characterized with traditional focused,

labour-intensive field transect or point sampling methods.

In rivers under Mediterranean climate regimes characterized by predictable, prolonged periods of stable low flow, photogrammetrics, ‘the science of extracting quantitative and qualitative data from multiple sequential recorded images... (Shields, Forsman & Stancil, 1994)’ may help meet this challenge. Photogrammetric surveillance from stationary automated cameras mounted over rivers, or from low-flying devices (e.g. miniature remote controlled helicopters, blimps or weather balloons) can potentially map ecological rates (e.g. N fixation, aquatic insect emergence) onto visually distinct algal patches. We are improving on our preliminary work by standardizing colour assessment with hand-held grey and colour scales for calibrating field photographs (Fig. 1 upper right), and by expanded sampling of emergence, N fixation and other algal-mediated processes to scale up from local results to reach or basin-wide budgets. In addition to algal colour changes, mat texture, habitat, seasonal and successional context, and other macroscopically observable properties or phenomena could be useful for assessing environmental conditions supporting proliferations, or the ecological impacts of the algae.

Consumer resource dynamics (e.g. Lotka-Volterra cycles) obscure biomass correlations of consumers and resources. For example, Pomeroy & Butler (2005)

found that while infrared colour was a good indicator of chlorophyll concentration on the surface of intertidal mudflats, it did not predict abundances of the benthic invertebrates that presumably consume these intertidal algae. Primary consumers can alternatively track resources and be positively correlated with them, or deplete resources and be negatively correlated. Filamentous algal proliferations are more long-lasting than single-celled epipelagic diatoms relative to their invertebrate consumers, but infestation densities and emergence rates from these mats will also change over time. Initially, frequent repeat surveillance and considerable on-the-ground experimental natural history will be needed to develop useful interpretations and estimate ecosystem model parameters from photogrammetry of algal proliferations. After dynamics and feedbacks are better understood, however, automated fixed or aerial mobile cameras could make it feasible to monitor a drainage network extensively and frequently enough to estimate effects of algal proliferations on carbon or N cycling, or on population dynamics of aquatic invertebrates or vertebrates.

We feel that the effort is warranted, given the growing importance of algal proliferations under global change. For example, greenhouse warming will likely increase the geographic range and activity and abundance of mosquitoes and other aquatic insects that vector disease. In many freshwater habitats, mosquitoes are associated with mats of algae or other floating vegetation (Hess & Hall, 1943; Orr & Resh, 1987, 1991; Rejmankova *et al.*, 2004; Greenway, 2005). Will changes in river hydrologic regimes (flow patterns) increase or decrease mat extent and duration through the summer low flow season? Photogrammetry is already being used to monitor offshore blooms of harmful marine phytoplankton (Holt *et al.*, 2003; Stumpf *et al.*, 2003). Remote sensing and automated monitoring technologies relevant to inland fresh waters are increasingly available (Power *et al.*, 2005). These observations and interpretations would support predictive modelling of the distributions of matter or organisms in basins, as well as upstream-downstream fluxes and the exchange between the channel, catchment and atmosphere. These advances would deepen our understanding of inland algal blooms and their ecological consequences, at the basin-wide scales we will need to comprehend and manage change over the coming decades.

Acknowledgments

We thank the National Science Foundation (DEB – 0543363), the NSF National Center for Earth Surface Dynamics and the California Center for Biodiversity (University of California, Berkeley) for support, the CRISES at Angelo research group, particularly Steve Thomas, Anika Bratt and Maria Moenkedick for nitrogen fixation measurements, Jim Bishop for advice about color photogrammetry and the University of California Natural Reserve System and Peter Steel and his family for providing the Angelo Coast Range Reserve as a protected research reserve.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Colour changes of the *Cladophora* turf at one site monitored over time in 2006 with a robotic camera. The red arrow points to the small proliferation growing from a bedrock ledge on the upper part of the photograph. The maximal elongation of the

attached turf occurred on 26 June; yellow floating mats appeared on 16 July, 2006 and turned rusty by 20 July, deepening in rusty colour by 6 August.

Figure S2. Low aerial photographs with a pole mounted-camera (right) of algal proliferations at four sites on 27 June, 2007. (a) GirlyMon Pool. Flow is from top to bottom, at the lower left of the photo, the green patch is an *Oedogonium* – *Mougeotia* proliferation; the rust coloured turf along the right hand third of the photo is *Epithemia*-covered *Cladophora*; (b) downstream tail of McKinley Pool and head of Jane's Riffle in upper right of photograph, above sedge tussock. Flow is from bottom to top of photograph. The proliferation of green *Cladophora* here is lightly colonized primarily by *Cocconeis*; (c) Upper Skunk Pool; flow is from bottom to top of picture. From river left, the dry cobble bar borders pale rusty *Cladophora* (colonized primarily by *Cocconeis*, *Achnantheidium* and *Rhoicosphenia* but with incipient colonization by *Epithemia* spp., the centre patch is yellow green *Cladophora* heavily colonized by non-epithemiacean diatoms (primarily *Cocconeis*, *Achnantheidium* and *Rhoicosphenia*). On river right, pale rusty *Cladophora* colonized primarily by these non-Rhopalodiacean diatoms but with incipient colonization by *Epithemia* spp. Epiphyte succession may be more advanced on *Cladophora* along slower-flowing river margins where host growth is reduced in low flow. Shadows preclude colour analysis along the right-hand margin of the photograph.

Figure S3. Emergence traps used in South Fork Eel River. Traps are 25.4 cm diameter PVC pipes with 4 columns of 6 cm diameter holes cut along the sides and covered with 0.3 mm mesh. Clear PVC sheets with 'Stickem Special' odourless glue cover the tops of traps to capture emerging insects.

Figure S4. Emergence sampled over 24 h from (a) *Oedogonium*, (b) green *Cladophora*, (c) rusty *Cladophora*, (d) yellow *Cladophora* and (e) a field photograph showing white adult ceratopogonid midges recently emerged from a yellow *Cladophora* mat (white vial cap is 14 mm in diameter).

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(Manuscript accepted 17 December 2008)