



---

Eutrophication of Streams and Rivers: Dissolved Nutrient-Chlorophyll Relationships for Benthic Algae

Author(s): Barry J. F. Biggs

Source: *Journal of the North American Benthological Society*, Vol. 19, No. 1 (Mar., 2000), pp. 17-31

Published by: The North American Benthological Society

Stable URL: <http://www.jstor.org/stable/1468279>

Accessed: 14/03/2009 17:28

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=nabs>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



*The North American Benthological Society is collaborating with JSTOR to digitize, preserve and extend access to Journal of the North American Benthological Society.*

<http://www.jstor.org>

## Eutrophication of streams and rivers: dissolved nutrient-chlorophyll relationships for benthic algae

BARRY J. F. BIGGS<sup>1</sup>

*National Institute of Water and Atmospheric Research Ltd, P.O. Box 8602, Christchurch, New Zealand*

**Abstract.** Statistical models for predicting the effects on algal biomass of eutrophication are much better developed for lentic systems than for lotic systems, partly because of the dynamic physical nature of streams as controlled by flood regimes. I analyzed data from 30 sites in 25 runoff-fed streams and rivers to develop statistical models for mean monthly and maximum chlorophyll *a* as a function of soluble nutrient concentrations and days of accrual (reflecting the frequency of flood disturbance events). Variation in stream-water nutrients explained 12–22.6% of the variation in mean monthly chlorophyll *a* and 29.5–32.5% of the variation in maximum chlorophyll *a* among sites. Days of accrual explained 39.7% and 61.8 % of the variation in mean monthly and maximum chlorophyll *a*, respectively. Multiple regression models combining dissolved nutrient data and days of accrual explained 43.7–48.8% of the variation in mean monthly chlorophyll *a* and 72.1–74.1% of the variation in maximum chlorophyll *a* among sites. In streams with infrequent floods and long accrual periods (e.g., >100 d), a relatively small increase in dissolved nutrients greatly increased the frequency of high biomass events. However, as could be anticipated, this result did not occur in more flood-prone streams. A nomograph to predict oligo-, meso-, and eutrophic conditions as a function of nutrient concentrations and days of accrual is presented based on the regression models for maximum chlorophyll *a*. The models need further testing, but might be useful for predicting the effects of changes in nutrients on benthic algal biomass in other temperate streams and rivers. I suggest that variable nutrient criteria for the prevention of benthic algal proliferations could be set in streams in relation to regimes of local flood frequency and expected time available for biomass accrual. The present analysis suggests that managing nutrient supply could not only reduce the magnitude of maximum biomass, but also reduce the frequency and duration of benthic algal proliferations in streams.

**Key words:** stream ecology, eutrophication, enrichment, nutrients, nitrogen, phosphorus, flooding, disturbance, algae, periphyton, water resources management.

Eutrophication is a fundamental concern in the management of all water bodies and has been one of the focal points of contemporary research in lakes, leading to the development of several statistical models to predict the effects of nutrient loadings on phytoplankton biomass (e.g., see summaries by Welch 1992, Chapra 1997). There is now also considerable interest in the enrichment of streams and rivers (see discussion by Dodds and Welch 2000). For example, in 1992, the United States Department of Agriculture *National Water Quality Inventory* reported that enrichment and sedimentation were the most significant causes of water quality degradation in 44% of >1,000,000 km of streams and rivers surveyed in the US ([http://www.usda.gov/stream\\_restoration](http://www.usda.gov/stream_restoration)). Management problems caused by enrichment, and associated benthic algal proliferations, include aesthetic degradation (e.g., Wharfe et al. 1984, Biggs 1985, Biggs and Price 1987, Welch et al. 1988), loss of pol-

lution-sensitive invertebrate taxa through smothering of substrata by algae (e.g., Quinn and Hickey 1990), clogging of water intake structures (e.g., Biggs 1985), and degradation of water quality (particularly dissolved oxygen and pH) resulting in fish kills (e.g., Quinn and Gilliland 1989). Such effects have lead, in part, to a major new joint departmental initiative, the *Clean Water Action Plan*, to restore waterways in the US for sustainable use by future generations. However, a major impediment to restoration is still the lack of robust, numerical, nutrient-benthic algal biomass relationships that will enable nutrient criteria and associated restoration targets to be set.

In theory, dissolved nutrient concentrations (reflecting the sum of added nutrients, such as from waste discharges and recycled nutrients) should relate strongly to biomass if it were possible to obtain good estimates of supply rates. However, previous attempts to generate good explanatory power with dissolved nutrient-benthic algal biomass models has had varied suc-

<sup>1</sup> E-mail address: b.biggs@niwa.cri.nz

cess (Horner and Welch 1981, Jones et al. 1984, Aizaki and Sakamoto 1988, Biggs and Close 1989, Lohman et al. 1992, Biggs 1995, Dodds et al. 1997, Biggs et al. 1999, Chételat et al. 1999). The slow development of robust dissolved nutrient-benthic algal biomass models for lotic systems is probably a result of the great complexity of physical and biological interactions that determine biomass at any point in time (see summary by Biggs 1996). Clear trade-offs exist between processes responsible for biomass accrual and those responsible for biomass loss. Biomass accrual is a function of specific growth rates which, in turn, are a function of the rate of transfer of limiting nutrients into cells, light available for photosynthesis, and temperature. Biomass loss is a function of community age (senescence), periodic sloughing losses when the drag of sections of the developing mat exceeds the tensile or attachment strength of the mat, large losses because of temporally explicit disturbance events such as floods, and grazing losses by animals such as invertebrates and herbivorous fish during prolonged periods of hydrological stability (Biggs 1996). Unfortunately, the considerable investigation required to enable development and/or validation of a model of such interactions for a given stream or river is beyond the capacity of most water-resource management authorities. Indeed, such formulations are still the subject of much research (e.g., Horner et al. 1983, 1990, McIntire et al. 1996, Rutherford and Broekhuizen 1996).

However, mechanistic approaches may not be necessary to produce models of stream eutrophication for use at the broad scales at which management decisions for stream health are usually carried out. For example, most successful lake eutrophication models are statistical, and are based on a relatively small number of primary variables such as average nutrient loading and average residence time (Welch 1992, Chapra 1997). Biggs et al. (1998a, 1998b) have suggested that the number of variables that primarily control differences in mean monthly benthic algal biomass among unshaded, temperate streams reduces to growth, as a function of the limiting nutrient supply, and losses as a function of the frequency of flood disturbance (or, equivalently, the mean number of days of stable flow when biomass can accrue). Losses from grazing animals, particularly benthic invertebrates, may also be significant where both nu-

trient supply and flood frequency are moderate to low (e.g., Rosemond 1994, Biggs et al. 1998a, 1999). Indeed, Biggs (1988, 1995) and Biggs et al. (1999) have explained 78.8–88.6% of the variance in mean monthly chlorophyll *a*, or summer biomass, in various broad-scale studies of periphyton in New Zealand streams using combinations of nutrient variables and measures of flood disturbance frequency/days available for accrual.

The above studies suggest that it may be possible to develop simple, but useful, statistically based eutrophication models for streams and rivers (analogous to those developed for phytoplankton in lakes) if biomass losses from hydrological disturbance events, which dictate mean number of days available for biomass accrual ( $d_a$ ), are also included with a measure of nutrient supply ( $n$ ). This relationship is expressed as:

$$B^* = k_1 d_a + k_2 n + c \quad [1]$$

where  $B^*$  is the mean monthly biomass of benthic algae,  $d_a$  and  $n$  are as defined above,  $k_1$ , and  $k_2$  are coefficients, and  $c$  is a constant defined from the data.

In this paper, I combine and reanalyze data from 3 different studies (Biggs 1995, Biggs et al. 1998a, 1999) on periphyton biomass dynamics in New Zealand streams and rivers to develop simple statistical models for benthic algal biomass, as proposed in equation 1. My goal is to provide robust tools to assist in the management of eutrophication of lotic systems. I also investigate extending the models to include maximum biomass during the year and the frequency of high-biomass events because algal proliferations and their frequency in streams, rather than mean biomass, can be of greatest interest to water managers.

## Methods

To reduce variance in the models, all data were obtained from similar hydro-physical types of streams and rivers, and were collected monthly using similar methods from natural stream substrata over at least 1y and using the same analytical protocols. Details of most methods are given in Biggs (1995), and Biggs et al. (1998a, 1999). In brief, all sites were in streams and rivers flowing from hill-country watersheds where snowmelt affected flow regimes for <3

mo/y, and lakes or large springs did not dominate flow regimes. None of the sites were affected by point-source pollution discharges or significant shading from riparian vegetation. The streams or rivers covered a broad range of enrichment regimes, reflecting differences in catchment land use and geology, and varied broadly in frequency of flood events, reflecting differences in local climate regimes. Discharge was monitored in all streams. I developed a dataset of 30 sites from 25 streams and rivers.

Sites were generally located in *runs* (moderate to swift flowing water with a smooth surface), except in the Kakanui and Kauru rivers where riffles were sampled because abnormally high densities of snails in the runs greatly constrained algal biomass accrual (Biggs and Lowe 1994, Biggs et al. 1998a). Each site was visited monthly for 13 to 19 mo and sampled for soluble nutrients and benthic algae. Water samples for nutrient analyses were collected in duplicate using sterile polyethylene containers, chilled to 1–4°C in the dark, and received in the laboratory within 24 h. Samples were filtered through pre-rinsed 0.45- $\mu\text{m}$  cellulose acetate filters, and the filtrate was frozen for later analysis of  $\text{NO}_2 - \text{N}$  +  $\text{NO}_3 - \text{N}$ ,  $\text{NH}_4 - \text{N}$ , and soluble reactive P (SRP).

Five (Kakanui and Kauru River sites) or 10 replicate samples (remaining sites) of benthic algae were collected every month from a known area of substrata (usually cobbles and large gravels) at equidistant points across a transect. These samples were then pooled for each transect on each monthly sampling and frozen for later analysis in the laboratory. Chlorophyll *a* concentration was determined by spectrophotometry following extraction in boiling 90% ethanol as described by Biggs (1995).

The relative abundance of taxa was determined on subsamples at the time of maximum biomass using the following method. After intensive examination at 400 and 640 $\times$  magnification on an inverted microscope, the dominant taxon was designated based on its contribution to the biovolume of the sample (i.e., an integration of frequency  $\times$  size) and given a rank of 8. Analysis of the sample continued for another 10–15 min and the total biovolume of all other taxa was then recorded relative to the dominant taxon on a linear scale up to 7. A whole subsample was scanned for each enumeration. Only chlorophyll-containing cells were enumerated.

More than 1 taxon could be assigned the same rank. Generally, 1 taxon, or at the most 3 taxa, made up >50% of community biovolume.

Soluble inorganic nitrogen (SIN) was determined as the sum of  $\text{NO}_2 - \text{N}$ ,  $\text{NO}_3 - \text{N}$ , and  $\text{NH}_4 - \text{N}$ . These forms of N, and SRP, were determined by autoanalyzer as described by Biggs and Close (1989). Mean monthly concentrations for these variables were calculated as arithmetic means. Mean monthly chlorophyll *a* concentrations were calculated as geometric means because the stream-specific data were rarely normally distributed.

Mean days of accrual was determined as the average time between flood events  $>3\times$  the median flow during the study period, which was calculated as  $[1/(\text{mean frequency of events per year } >3\times \text{ the median flow}) \times 365 \text{ d}]$ . Clausen and Biggs (1997, 1998) found highly significant negative correlations between mean monthly benthic chlorophyll *a* and the frequency of flood events  $>3\times$  median flow. The frequency of periods of high biomass in each stream was assessed as the number of monthly samplings each year where maximum chlorophyll *a* exceeded 60 and 200  $\text{mg}/\text{m}^2$ . These criteria have been suggested by Dodds et al. (1998) to discriminate oligotrophic from mesotrophic and mesotrophic from eutrophic streams, respectively.

## Results

### *Mean monthly chlorophyll a*

Mean monthly chlorophyll *a* ranged among systems from 0.73–81  $\text{mg}/\text{m}^2$  (Table 1). Among  $d_a$ , SRP, and SIN,  $d_a$  alone explained almost 40% of the variation in mean monthly chlorophyll *a* (Fig. 1, Table 2). Mean monthly SRP concentrations also explained a significant, but lower (22.6%) proportion of variation in mean monthly chlorophyll *a* (Fig. 2). Higher nutrient concentrations tended to occur in streams with longer periods of stable flow (i.e.,  $>20 \text{ d}$  accrual), and biomass in these systems was also higher for a given nutrient concentration than in streams with shorter periods of stable flow (and thus shorter accrual periods).

Together,  $d_a$  and SRP explained nearly 49% of the variance in mean monthly chlorophyll *a* (Table 2). From the regression equation, it can be shown that a gradient in mean chlorophyll *a* oc-

TABLE 1. Mean monthly soluble inorganic N (SIN) and soluble reactive P (SRP) concentrations, mean days of accrual ( $d_a$ ) mean and maximum monthly benthic chlorophyll *a* (chl. *a*) concentrations, and taxa dominating (Dom. taxa) the community at the time of maximum monthly chlorophyll *a* for 30 study sites. Dom. taxa: D = mucilaginous diatoms; D\* = filamentous diatoms; C = filamentous chrysophytes; R = red algae; Cy = Cyanobacteria; FGA = filamentous green algae. Mean monthly chlorophyll *a* concentrations are geometric mean values. Freq. >60 = frequency of biomass >60 mg/m<sup>2</sup> chlorophyll *a*; Freq. >200 = frequency of biomass >200 mg/m<sup>2</sup> chlorophyll *a*. Biggs (1995), and Biggs et al. (1998a, 1999), explain measures of variation in the mean nutrient and chlorophyll *a* data.

Stream-site	SIN (mg/ m <sup>3</sup> )	SRP (mg/m <sup>3</sup> )	$d_a$	Mean chl. <i>a</i> (mg/m <sup>2</sup> )	Max. chl. <i>a</i> (mg/m <sup>2</sup> )	Season of maxima	Dom. taxa	Freq. >60 (mo/y)	Freq. >200 (mo/y)
Bowers	17	2.7	16	3.8	65	fall	D	0	0
Camp	39	2.0	12	0.73	9.1	spring	D	0	0
Esk	82	7.7	183	55	769	fall	C	6.5	4.6
Granity	137	31.6	11	6.3	28	spring	R	0	0
Kyeburn	6.2	1.8	12	5.2	20	fall	Cy	0	0
Kakanui—Clifton	22	5.0	25	14	60	summer	D	0.6	0
Kakanui—Pringles	116	7	33	59	160	summer	R	7.1	0
Kauranga	55	1.8	17	17	163	fall	FGA	3.7	0
Kauru	35	6	22	18	160	winter	Cy	4.7	0
Maerewhenua	26	3.6	26	17	108	fall	D	2.8	0
Maraekakaho	78	21	73	281	1396	summer	C	11	8.3
Moawhango	80	4.1	45	26	402	fall	D	5.5	2.8
Motueka—1	35	3.8	17	2.2	48	winter	D	0	0
Motueka—2	28	3.0	17	2.4	48	winter	D	0	0
Motueka—3	170	3.7	17	2.9	173	fall	D	0.9	0
Motueka—4	162	5.7	22	7.0	351	fall	D	2.8	0.9
Motueka—5	113	4.2	22	9.5	126	fall	D	2.8	0
Pautahanui	232	29	33	23	163	fall	D	2.8	0
Rough	21	1.6	15	1.6	16	summer	D	0	0
Riwaka	172	5.7	19	109	566	fall	D	10.1	3.7
Sams	12	1.6	10	3.9	10	fall	Cy	0	0
Slaty	21	1.7	10	3.3	9.2	fall	FGA	0	0
Timber	24	1.7	17	1.3	15	spring	D	0	0
Turakina	224	25	24	14	317	winter	FGA	4.6	1.8
Tutaekuri	64	6.2	73	41	802	fall	FGA	6.5	2.8
Victoria	8.2	1.3	19	10	36	fall	Cy	0	0
West Kowai	38	1.8	42	3.7	53	fall	D	0	0
Woolshed	222	4.1	14	2.1	21	winter	Cy	0	0
Waimana	52	17	24	2.1	123	fall	D	0.9	0
Waiwakaiho	133	20	24	15	82	fall	D*	3.7	0

curred from low concentrations in streams with short accrual periods (i.e., frequent flood events) and low mean monthly nutrient concentrations to high chlorophyll *a* in streams with long accrual periods and high mean monthly nutrient concentrations (as predicted in fig. 1 of Biggs et al. 1998b).

#### Maximum chlorophyll *a*

Maximum recorded chlorophyll *a* ranged among systems from 9.1–396 mg/m<sup>2</sup> (Table 1).

The largest proportion of maxima occurred in fall (60%), followed by winter (17%), summer (13%), and spring (10%). These maxima generally coincided with the most prolonged periods of stable flow in the streams (Biggs 1995, Biggs et al. 1998a, 1999).

A quadratic function of  $d_a$  explained nearly 62% of the variation in maximum recorded chlorophyll *a* (Fig. 3, Table 3). Both mean monthly SIN and SRP concentrations explained significant variation in maximum chlorophyll *a* (Fig. 4, Table 3), but these  $r^2$ s were considerably lower than for  $d_a$ .

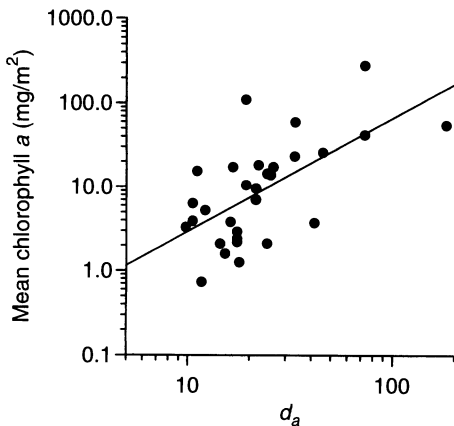


FIG. 1. Mean monthly benthic chlorophyll *a* concentration at 30 stream sites as a function of days of accrual ( $d_a$ ). The best-fit regression line is given. See Table 2 for regression statistics.

Multiple regression models combining  $d_a$  with mean monthly nutrient concentrations explained up to 74% of the variation in maximum chlorophyll *a* (Table 3). Season did not explain significant variance for these models (i.e.,  $p > 0.15$ ). A 3-dimensional response surface of maximum chlorophyll *a* as a function of  $d_a$  and SRP illustrated a gradient in maximum chlorophyll *a* from low concentrations in streams and rivers with few days of accrual and low mean monthly SRP concentrations to high chlorophyll *a* where there were long accrual periods (i.e., long periods of hydrological stability) and high mean monthly SRP concentrations (Fig. 5).

#### Frequency and duration of proliferations

Time available for benthic algal accrual and nutrient supply is also expected to influence the frequency and duration of benthic algal proliferations in streams. Indeed, the frequency and duration of proliferations over a given concentration may be as important in eutrophication management as attempting to control the specific level of biomass maxima. The average number of monthly sampling occasions where biomass exceeded 60 and 200 mg/m<sup>2</sup> chlorophyll *a* (denoting possible transitions from oligotrophy to mesotrophy, and mesotrophy to eutrophy; Dodds et al. 1998) was regressed against days of accrual and dissolved nutrient concentrations (SIN, SRP). The 4 regressions explained a moderate amount of variance in the frequency of

proliferations ( $r^2 = 0.308\text{--}0.465$ ), with  $d_a$  explaining the largest amount of variation ( $p < 0.001$ ) and nutrients having relatively low explanatory power ( $p = 0.045\text{--}0.337$ ). The SRP relationships are summarized in Fig. 6, from which it can be seen that the frequency with which biomass exceeded 200 mg/m<sup>2</sup> chlorophyll *a* increased from 1.5 mo/y to ~3 mo/y for an increase in mean monthly SRP from 5 to 15 mg/m<sup>3</sup> if  $d_a$  was <50 d. However, if  $d_a$  was >100 d, the frequency of proliferations >200 mg/m<sup>2</sup> chlorophyll *a* was predicted to increase from ~2.5 mo/y to >8 mo/y for the same 5 to 15 mg/m<sup>3</sup> increase in SRP. Thus, in the streams with stable flow regimes and long accrual periods, even relatively minor increases in SRP concentrations >5 mg/m<sup>3</sup> greatly increased the frequency of proliferations. Conversely, in the streams with short accrual periods, increased dissolved nutrients had much less of an effect on the frequency of proliferations because of regular flushing by floods.

#### Community composition

The highest biomass was formed by communities dominated by *Vaucheria* sp., a filamentous xanthophyte, and filamentous green algae (Figs 3, 4). Diatoms, filamentous Cyanobacteria/red algae, and filamentous green algae dominated communities at maximum biomass across the full gradients of SIN and SRP, although the 3

TABLE 2. Regression statistics for  $\log_{10}$  of mean monthly benthic algal biomass (mg/m<sup>2</sup> chlorophyll *a*) concentration as a function of mean days of accrual ( $d_a$ ) and mean monthly soluble nutrient concentrations. SIN = soluble inorganic N, SRP = soluble reactive P, mg/m<sup>3</sup> ( $n = 30$ ).

Effect	Value/ coefficient	SE	$p$ (2-tail)	$r^2$
1. Constant	-0.888	0.434	0.050	
Log <sub>10</sub> $d_a$	1.355	0.315	0.001	0.397
2. Constant	0.109	0.434	0.804	
Log <sub>10</sub> SIN	0.483	0.245	0.057	0.122
3. Constant	0.468	0.192	0.022	
Log <sub>10</sub> SRP	0.697	0.244	0.008	0.226
4. Constant	-1.229	0.494	0.019	
Log <sub>10</sub> $d_a$	1.245	0.320	0.001	
Log <sub>10</sub> SIN	0.284	0.206	0.179	0.437
5. Constant	-0.926	0.408	0.031	
Log <sub>10</sub> $d_a$	1.152	0.310	0.001	
Log <sub>10</sub> SRP	0.462	0.212	0.038	0.488

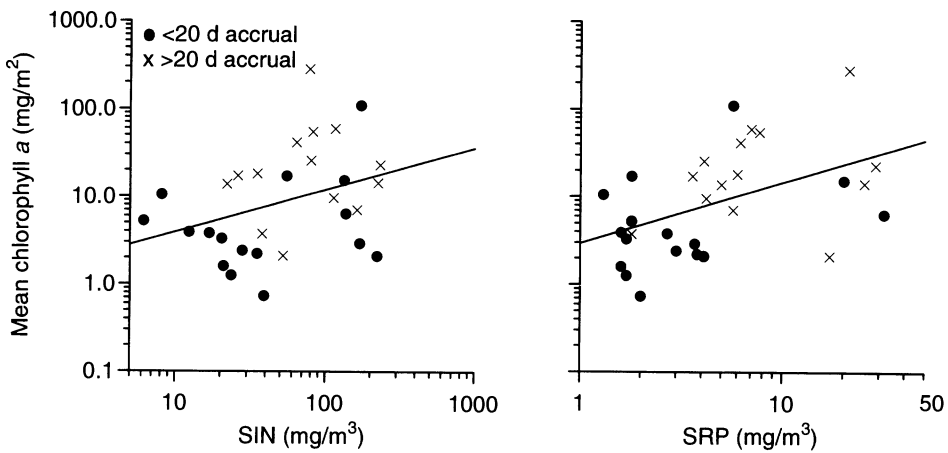


FIG. 2. Mean monthly benthic chlorophyll *a* concentrations for accrual periods of <20 d and >20 d at 30 stream sites as a function of mean monthly soluble inorganic N (SIN) and mean monthly soluble reactive P (SRP) concentration. Best-fit regression lines are given. See Table 2 for regression statistics.

streams with the lowest SIN concentrations were all dominated by filamentous Cyanobacteria/red algae. Although *Vaucheria* was confined to the streams that were least disturbed by floods (i.e., high  $d_a$ ), the other taxonomic groups dominated communities across the full gradient of  $d_a$  (Fig. 3). Thus, these coarse taxonomic groups did not display strong habitat partitioning as a function of nutrient resources or successional time.

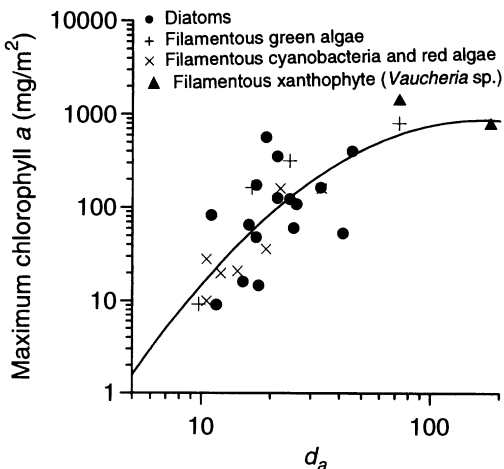


FIG. 3. Maximum monthly benthic chlorophyll *a* concentration at 30 stream sites as a function of days of accrual ( $d_a$ ). The best-fit regression line is given. Symbols denote dominant taxa. See Table 3 for regression statistics.

## Discussion

There is a great need to advance understanding of nutrient effects on lotic algal biomass and to develop new tools to better control eutrophication of streams and rivers. Knowledge in this area has lagged far behind that of lake eutrophication. I have presented statistical models that explain moderate to high amounts of variation in benthic algal biomass based on a mechanistic understanding of the processes of benthic algal accrual in streams. These models should advance our endeavors to manage the eutrophication of temperate lotic systems. A similar approach may also work for streams in non-temperate regions. A critical advancement offered by this study is the explicit incorporation of time available for the accrual of benthic algal biomass. Also, I have demonstrated that the frequency of high-biomass events increases greatly as nutrients increase in streams where average accrual periods exceed ~50 d.

### *Days of accrual vs nutrient effects on algal biomass*

Days available for biomass accrual explained more variation in both mean monthly and maximum chlorophyll *a* than nutrient concentrations. This result suggests that variability in flow regime is more important than nutrients in determining the potential for algal proliferations in streams. Biggs and Close (1989) also concluded that flow regimes were at least as important

TABLE 3. Regression statistics for  $\log_{10}$  of maximum monthly benthic algal biomass ( $\text{mg}/\text{m}^2$  chlorophyll *a*) concentration as a function of mean days of accrual ( $d_a$ ) and mean monthly soluble nutrient concentrations. SIN = soluble inorganic N, SRP = soluble reactive P,  $\text{mg}/\text{m}^2$  ( $n = 30$ ).

Effect	Value/ coefficient	SE	<i>p</i> (2-tail)	<i>r</i> <sup>2</sup>
1. Constant	-2.886	1.449	0.057	
$\log_{10} d_a$	5.223	1.937	0.012	
$(\log_{10} d_a)^2$	-1.170	0.624	0.072	0.618
2. Constant	0.711	0.317	0.031	
$\log_{10}$ SIN	0.688	0.168	0.001	0.325
3. Constant	1.400	0.184	0.001	
$\log_{10}$ SRP	0.797	0.233	0.002	0.295
4. Constant	-2.946	1.217	0.023	
$\log_{10} d_a$	4.285	1.649	0.015	
$(\log_{10} d_a)^2$	-0.929	0.529	0.091	
$\log_{10}$ SIN	0.504	0.144	0.002	0.741
5. Constant	-2.714	1.264	0.040	
$\log_{10} d_a$	4.716	1.696	0.010	
$(\log_{10} d_a)^2$	-1.076	0.545	0.059	
$\log_{10}$ SRP	0.494	0.160	0.005	0.721

as nutrients in generating differences in mean and maximum algal biomass among streams. Nutrients will be most important in influencing accrual of algal biomass in streams with relatively benign hydrological conditions or where extended periods of low flow occur in certain seasons (e.g., Mediterranean type climates).

Nutrient inputs are likely to be easier to con-

trol than frequency of flood disturbances for stream ecosystem management. However, downstream of reservoirs it might be possible to develop flushing flow regimes to reduce the duration of time available for proliferations to develop. The resistance of communities varies with age, biomass, taxonomic structure, and community physiognomy (Biggs and Close 1989, Peterson and Stevenson 1992, Biggs and Thomsen 1995), and it is likely that bed shear stress will need to be increased >3-fold during flushing flows to achieve significant washout of epilithic algal accumulations (Biggs and Thomsen 1995).

The variable  $d_a$  was calculated as an annual mean for each stream. I did not attempt to determine  $d_a$  based on when samples were collected in relation to the previous flood event, as has been done in several previous studies (e.g., Biggs 1988, Grimm and Fisher 1989, Peterson and Grimm 1992, Biggs et al. 1999). There were several reasons for this decision. First, it is difficult to know how much biomass has been removed by each flood event; the amount of residual biomass strongly influences rates of regeneration (Peterson et al. 1994, Francoeur et al. 1998). The extent of bed movement can indicate the degree of sloughing (Francoeur et al. 1998, Biggs et al. 1999), but such information was only available for some of the sites used here. Second, recolonization time is strongly influenced by propagule availability and taxonomic structure

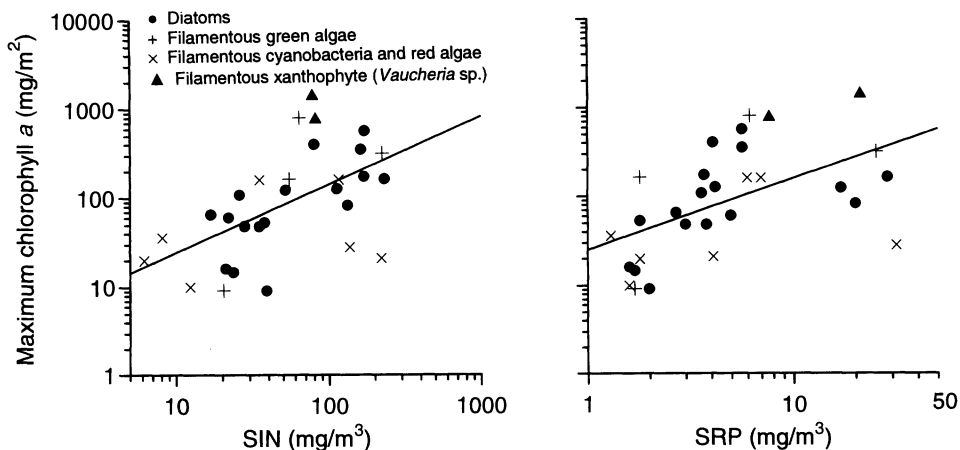


FIG. 4. Maximum benthic chlorophyll *a* concentration at 30 stream sites as a function of mean monthly soluble inorganic N (SIN) and mean monthly soluble reactive P (SRP) concentration. Best-fit regression lines are given. See Table 3 for regression statistics.



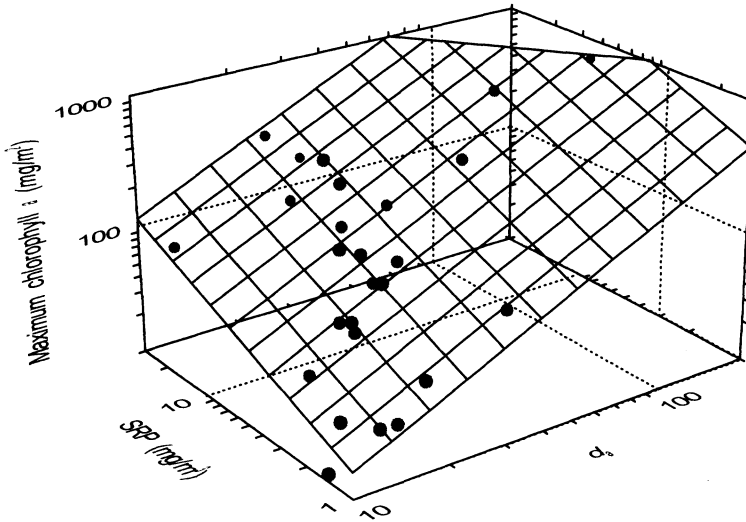


FIG. 5. Linear response surface of maximum chlorophyll *a* concentration as a function of soluble reactive P (SRP) concentration, and days of accrual ( $d_a$ ). See Table 3 for multiple regression statistics.

of the pool of immigrants (Peterson 1996); these data were also not available for the streams.

#### *Effects of season*

Variations in the seasonal distribution of stable flows and associated accrual periods might be expected to introduce variability into the regression models for maximum biomass because seasonal variations in light levels and temperature can strongly influence growth rates (De-Nicola 1996, Hill 1996). Indeed, higher growth rates did occur during summer in a subset of the streams (Francoeur et al. 1999). However, season did not explain significant additional variance when included as an independent variable in the models.

#### *Community composition effects*

No consistent change in Division of the taxon dominating algal communities at the time of maximum biomass was observed as enrichment increased. This result was unexpected and conflicts with a number of other previous studies (e.g., Biggs and Price 1987, Biggs et al. 1998b, Chételat et al. 1999). Also, adding a variable for the Division of the dominant taxon in the multiple regressions explained little further variance in maximum chlorophyll *a*. I expected unenriched streams to support communities of low

biomass dominated by filamentous Cyanobacteria/red algae, changing progressively with enrichment to mucilage-forming diatoms, filamentous xanthophytes, and finally high-biomass filamentous green algae (Biggs et al. 1998b). The results demonstrated that successional patterns associated with enrichment are difficult to predict. In particular, diatoms were dominant taxa across the full range of nutrient concentrations, indicating that they may not necessarily be displaced by larger, more competitive taxa such as filamentous green algae in enriched streams at times of maximum biomass (e.g., Biggs et al. 1998b). Indeed, Chételat et al. (1999) found that the proportion of the mat composed by diatoms also increased across a nutrient gradient as mat biomass increased in some Canadian streams.

#### *Forms of nutrients for stream eutrophication models*

Benthic algal biomass in streams has now been correlated with dissolved, total, and in-mat nutrient concentrations (e.g., Biggs and Close 1989, Lohman et al. 1992, Biggs 1995, Biggs et al. 1998b, 1999, Dodds et al. 1998, Chételat et al. 1999). The traditional approach in lakes has been to use total nutrients for statistical models of biomass because of the rapid uptake and storage of nutrients such as P by phytoplankton and because of the partial remineralization of these nutrients as phytoplankton sink to the bottom

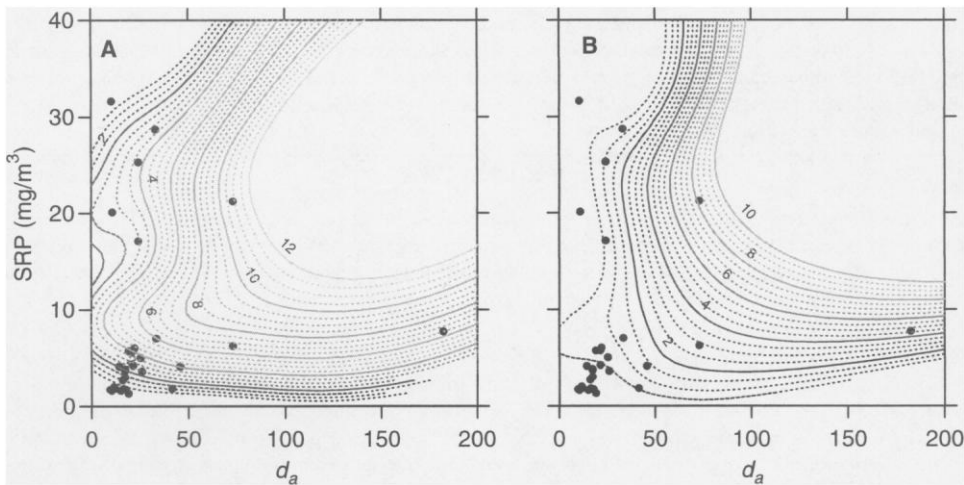


FIG. 6. Contour plots of frequency (mo/y) of benthic algal biomass exceeding 60 mg/m<sup>2</sup> (A) and 200 mg/m<sup>2</sup> chlorophyll *a* (B) as a function of days of accrual ( $d_a$ ) and mean monthly soluble reactive P (SRP) concentration.

and decay (Welch 1992, Dodds 1993, Chapra 1997). To determine which approaches/models would be best for managing eutrophication of streams, we 1st need to consider the technical advantages and limitations of the different approaches (Table 4), and then the relative variation in benthic algal biomass that the different models explain (Table 5).

Clearly, there is a range of benefits and disadvantages for each nutrient variable (Table 4), and it may be some time before the best approach is unequivocally defined. A fundamental requirement of the total nutrient approach is that sloughed benthic algae are deposited downstream, most likely in low-velocity areas such as pools, where they decay and nutrients remineralize. This assumption needs testing over a range of river environments and in streams of different channel slopes. Although deposition might occur quite easily for diatoms, which tend to be negatively buoyant (e.g., some diatoms emigrate into the water column and settle downstream as part of recolonization processes; Peterson 1996), extensive field observation of New Zealand streams suggests that such deposition is much less common for filamentous green algae and cyanobacterial mats, which tend to be neutrally buoyant. However, in shallow, low-gradient streams where low velocities occur, sloughed filamentous mats can become entangled on projections such as snags or stones (e.g., see fig. 9e of Biggs 1996). These entangled

mats may then become important sites for remineralization during extended periods of low flow. Such entanglement of mats is infrequently observed in moderate to high-gradient streams.

The use of nutrient concentrations of mats as a measure of enrichment (e.g., Biggs 1995, Biggs et al. 1998a) is appealing because of the potentially close relationship between mat nutrients and algal growth kinetics (e.g., Auer and Canale 1982). However, there are difficulties in relating mat nutrients back to nutrient supply regimes, there is the potential for large bias caused by non-photosynthetic sediments trapped in the mats, and analyses are expensive.

The variance explained by models based on dissolved, particulate, and mat nutrient concentrations varies widely (Table 5). Models of dissolved and mat nutrient concentrations (with and without disturbance frequency or  $d_a$ ) explain the most variance in chlorophyll *a*. The dissolved nutrient-biomass models for maximum biomass developed in the present study (Table 3) might be the most useful tools for managing eutrophication of temperate gravel/cobble-bed streams because: 1) they are based on data collected over a complete year (i.e., all seasons), from an extensive number of sites, using uniform methods, and 2) the data set covers the full range of nutrient regimes likely to be found in streams. These models also yield the flexibility to incorporate the influence of region-

TABLE 4. Summary of general technical and practical advantages and disadvantages of using different nutrient forms in benthic algal biomass-nutrient regression models in streams and rivers. Soluble nutrients = soluble reactive P and soluble inorganic N in the stream waters; Total nutrients = total P and total N in the stream waters; Mat nutrients = total P and total N in the benthic algal mat normalized to ash-free dry mass; CV = coefficient of variation.

---



---

### Soluble nutrients

*Advantages.*—A relatively direct measure of the bioavailable form of nutrients and therefore mechanistically sound. Point source effluent effects can be assessed directly. Temporal variability moderate–low relative to other nutrients (e.g., CV ~20–110% for soluble reactive P; Biggs and Close 1989, Biggs 1995). Analyses are relatively quick and cheap. Extensive data are already available.

*Disadvantages.*—Single measurements in time are a poor indicator of nutrient supply regime because of effects of dynamic biotic uptake and remineralization (e.g., Jones et al. 1984, Dodds 1993, Biggs 1995). The contribution of subsurface springs/seeps is difficult to account for. About a year of monthly measurements is best to obtain a reliable estimate of mean supply concentrations (fewer samples may be possible where flow regimes are relatively stable). Nutrients bound to organic matter *might* become available if the organic matter is deposited in quiescent areas, and therefore the projected dissolved nutrient supply could underestimate the actual supply. Low levels of detection are required for analysis.

### Total nutrients

*Advantages.*—Incorporates all forms of the nutrients (dissolved and those bound to both organic and inorganic particulates), and thus yields a measure of the overall, potential, nutrient supply. Nutrients from subsurface inflows and groundwater are broadly incorporated in the measure. Extensive data are available on land use-total nutrient effects. Total nutrients are widely used variable in lake eutrophication management so this variable might be useful for comparing lentic vs lotic enrichment processes (e.g., Dodds et al. 1998). River data would also be useful to quantify nutrient inputs to lakes and estuaries.

*Disadvantages.*—Correlated with chlorophyll in water column (Jones et al. 1984). Thus, a proportion of particulate nutrients in streams is probably derived from suspended benthic algae, creating potential for circular reasoning in its application. Therefore the approach requires the following assumptions: that particulates and algae will eventually settle in quiescent areas; a proportion of the nutrients in these deposited particulates and algae will become available to the benthic algae; and the proportion of bioavailable nutrients will be similar among streams, and overtime, regardless of differences in the type of particulates (e.g., organic vs inorganic). Analyses require a digestion step, which makes processing more expensive. Frequent monitoring is required to get good estimates of mean concentrations (e.g., weekly for a year) because of moderate–high temporal variability (e.g., CV ~30–500% for total P; Biggs and Close 1989).

### Mat nutrients

*Advantages.*—A direct measure of nutrient status of the algae and can be related to specific growth M rates through mechanistic models such as the Droop model (e.g., Auer and Canale 1982). Integrates the history of nutrient supply, including mineralized nutrients from deposited organics and subsurface supply from seeps and groundwater.

*Disadvantages.*—It is difficult to relate back to supply concentrations of dissolved or total nutrients (therefore, difficult to use as a basis for managing nutrient loadings). The results are likely to be biased to varying degrees by the amount and type of non-algal particulates deposited in the mat. The influence of particulates will increase as the algal biomass:particulates mass ratio decreases. Analysis requires a digestion step and a measurement of organic biomass, which increases costs. Moderate temporal variability, so moderate–high sampling frequency is required (CV of mat %P commonly ~90–200%; Biggs 1995).

---

al variations in flow regimes when managing enrichment effects.

#### *Application of the models for managing stream or river eutrophication*

Biomass levels >150–200 mg/m<sup>2</sup> chlorophyll *a* are very conspicuous in streams, are probably

unnaturally high, and can compromise the use of rivers for contact recreation and productive sports fisheries (e.g., Horner et al. 1983, Welch et al. 1988, 1989, Biggs 1996, Dodds et al. 1998, Biggs 2000). Based on frequency distributions of chlorophyll *a* from a large number of temperate streams and rivers around the world, Dodds et

TABLE 5. Summary of published studies with regression analyses of benthic algal biomass as a function of different forms of nutrients on natural substrata in gravel/cobble-bed streams. SRP = soluble reactive P; SIN = soluble inorganic N; TIN = total inorganic N; TN = total N; TP = total P.

Study	Chlorophyll measure	Nutrients	Total $r^2$	Comment
Aizaki and Sakamoto (1988)	Mean	SRP	0.81	Mean for 10–13 sites over summer
		TIN	0.83	
		TP	0.66	
		TN	0.76	
Biggs and Close (1989)	Mean	SRP	0.53	Mean of samples collected monthly for 15 mo at 9 sites
		TP	0.55	
	Max.	SRP	0.25	Maximum biomass of 25 accrual cycles vs mean SRP during each cycle (in 9 rivers)
Lohman et al. (1992)	Mean	TP	0.47, 0.60	Mean summer values at 22 sites in 12 rivers measured in 2 separate years
		TN	0.58, 0.60	
Biggs (1995), Biggs et al. (1998b)	Mean	Mat TN	0.87	Mean of samples collected monthly for 13 mo at 15 sites; multiple regression with frequency of high-velocity perturbations being the other variable
Dodds et al. (1997)	Mean	SRP	0.089	Data from a range of studies using natural and artificial substrates
		TP	0.14	
		SIN	0.35	
		TN	0	
	Max.	SRP	0.071	
Biggs et al. (1999)	Mean	TP	0.078	Mean of samples collected monthly for 13 mo at 12 sites; multiple regression with frequency of bed movement and frequency of high-velocity perturbations being the other variables
		SIN	0.30	
		SRP	0.88	
Chételat et al. (1999)	Summer	TP	0.56	33 sites in 13 streams sampled once in summer
		TN	0.50	

al. (1998) have suggested that the boundary between mesotrophic and eutrophic streams and rivers be set at 200 mg/m<sup>2</sup> chlorophyll *a* for maximum biomass. My statistical models show that to prevent maximum biomass from exceeding 200 mg/m<sup>2</sup> chlorophyll *a* in streams with accrual periods of >50 d, mean monthly dissolved nutrient concentrations must be quite low (e.g., ~20 mg/m<sup>3</sup> SIN and ~2 mg/m<sup>3</sup> SRP). Previous experimental studies that have assessed maximum benthic algal biomass over a gradient of limiting nutrient supply support these predictions. For example, in outdoor trough experiments, Bothwell (1989) found that concentrations of 2–4 mg/m<sup>3</sup> SRP could result in maximum biomass of diatoms exceeding 200

mg/m<sup>2</sup> chlorophyll *a* after 40 d of accrual. Similarly, studies in laboratory troughs have shown algal biomass to exceed this level at >3 mg/m<sup>3</sup> SRP (at 0.6 m/s water velocity) after 17 d (Horner et al. 1990), and after 21 d at ~5 mg/m<sup>3</sup> SRP (Walton 1990 as cited in Welch 1992).

The predictive ability of my dissolved nutrient-biomass models now needs to be tested, but several constraints should be considered. First, the models were derived for unshaded streams and therefore do not account for temporal or spatial variability in light. Davies-Colley and Quinn (1998) determined that, in channels <4.5–5.5 m wide, riparian shading could significantly reduce benthic algal biomass compared with unshaded streams. Second, the relation-

ships were derived for streams with coarse gravel and cobble substrata. These models will generally overestimate benthic algal biomass in streams with extensive areas of sand and silt (unless water velocities are very low, e.g.,  $<0.1$  m/s). Third, the utility of a flow threshold of  $>3\times$  median discharge to define a disturbance and commencement of biomass accrual needs to be more widely assessed. For example, the effects on benthic algae of floods meeting the  $>3\times$  median discharge criterion may vary depending on the degree of bed armoring and associated sediment movement (Clausen and Biggs 1998, Biggs et al. 1999).

My models left a significant amount of variance in benthic chlorophyll *a* levels unexplained. This result is expected because several other determinants of algal biomass accrual (e.g., local water velocities, differences in bed sediment size among sites, and the exact timing of biomass maxima) were not accounted for. In particular, losses incurred by grazing benthic invertebrates were not explicitly included in the models. The sites generally had mixed grazer communities with mayflies and caddisflies dominating unenriched streams, and snails, chironomids, and oligochaetes dominating the more enriched systems (Biggs 2000, B. J. F. Biggs, unpublished data). Such communities can exert significant grazing pressure on benthic algal communities during hydrologically benign periods (see review by Steinman 1996 and fig. 6 of Biggs et al. 1999).

For eutrophication management of lotic systems, it is 1st necessary to set critical biomass targets for the system in question and then use the statistical models presented in Table 3 to calculate nutrient criteria to prevent the target biomass from being exceeded. The local hydrological regime or average time available for biomass accrual must also be taken into account. Initial biomass targets might be set in 2 ways. First, it might be sufficient to adopt biomass criteria for general trophic state that have been developed from frequency distributions of chlorophyll *a* over a large number of temperate streams (see Dodds et al. 1998). These oligotrophic, mesotrophic, and eutrophic criteria assume high, medium, and low levels of protection, respectively, for uses such as aesthetic appreciation, water quality, and biodiversity of stream ecosystems. Second, if specific uses for a waterway have been identified (e.g., trout fishing) it might be

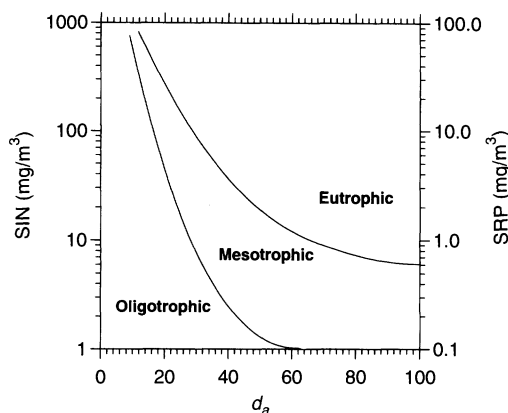


FIG. 7. Nomograph of mean monthly soluble nutrient concentrations that are predicted to result in maximum benthic algal biomass indicative of oligotrophic, mesotrophic, and eutrophic conditions for varying days of accrual ( $d_a$ ) in gravel/cobble-bed streams. The oligotrophic-mesotrophic boundary was set at  $60 \text{ mg/m}^2$  chlorophyll *a* and the mesotrophic-eutrophic boundary was set at  $200 \text{ mg/m}^2$  chlorophyll *a* (after Dodds et al. 1998). These boundaries also equate to maximum biomass criteria adopted for the protection of benthic biodiversity (oligo- to mesotrophic), aesthetics, and trout fishery values (meso- to eutrophic) in New Zealand streams (Biggs 2000). The lines delineating the trophic boundaries were calculated using soluble inorganic N (SIN) equation 4 in Table 3. However, they also approximate P-limited communities by reference to the right-hand scale, which has been set at  $0.1\times$  the SIN scale, because the mean ratio of biomass from the SIN and soluble reactive P (SRP) models was 10.8.

necessary to develop a *dose-response* relationship between benthic algal biomass (the dose) and the use (the response) that is to be protected. Biggs (2000) took this approach in setting % cover of green filamentous algae and diatom biomass criteria for benthic biodiversity (based on % *cleanwater* benthic invertebrate taxa), aesthetic uses, and trout fishing in New Zealand streams.

Figure 7 illustrates the biomass criteria delimiting oligotrophic, mesotrophic, and eutrophic streams (after Dodds et al. 1998) as joint functions of nutrients and  $d_a$  using equation 4 in Table 3. It is possible to read average concentrations of dissolved nutrients that should result in maximum chlorophyll *a* biomass below a nominal limit (e.g.,  $200 \text{ mg/m}^2$  chlorophyll *a* to prevent eutrophy) for any expected accrual period. Nomographs for any other maximum biomass

limits could be generated using the models in Table 3. The use of these models might enable a sliding scale of nutrient criteria to be adopted in relation to differences in hydrological regimes of streams among different regions. Such an approach avoids the application of broad-scale criteria that may have little meaning in some systems, or that may not protect other systems. Indeed, setting nutrient criteria in relation to the natural disturbance regime for a site, or that recognizes seasonal differences in flow regimes, would give greater regional flexibility in how eutrophication of lotic systems is managed through better use of the natural cleansing capacity of waterways. The flood disturbance measure of frequency per year of high flow events  $>3\times$  the median flow (Clausen and Biggs 1997, 1998), as used here, could provide a basis for classifying streams regionally and then developing local or regional nutrient targets.

It may not be possible to attain dissolved nutrient levels low enough to prevent benthic algae from exceeding specific target values. For example, agricultural development may be deemed essential to the maintenance of local human communities. However, any mitigation measures that reduce nutrient supply rates, such as might occur following planting of riparian buffer strips, might be valuable because my analysis has shown that the frequency (and therefore overall duration) of proliferations decreases greatly in hydrologically stable streams as nutrient levels are reduced. Indeed, for maintenance of aesthetics and higher trophic levels in streams, the duration of benthic algal proliferations over a critical level may be as important, or more so, than the specific levels that maximum biomass might reach.

Many governmental agencies monitor discharge and dissolved inorganic nutrients. Yet use of such data to help manage eutrophication of stream ecosystems has been very limited. The models presented here may provide a valuable tool to enable discharge and dissolved nutrient data to be used more extensively for making management decisions. Moreover, the data sets currently held by many government agencies may be useful in testing my models or constructing similar models that are more specific to an ecoregion. The result could be increased explanatory power and improved ability to manage stream eutrophication at the local scale.

### Acknowledgements

I am grateful for discussions with Jan Stevenson, Walter Dodds, and Gene Welch. I thank Vladimir Nikora, Ian Hawes, and Clive Howard-Williams for useful suggestions on the initial manuscript, and Chris Peterson, Kirk Lohman, Walter Dodds, and an anonymous reviewer for comments and suggestions that improved the final version. I am also grateful for financial support from the 'Environmental Hydrology and Habitat Hydraulics' programme (Contract No. CO1813) administered by the New Zealand Foundation for Research, Science and Technology and to the New Zealand Ministry for the Environment. The paper was completed with logistical support from Rex Lowe and the University of Michigan Biological Station.

### Literature Cited

- AIZAKI, M., AND K. SAKAMOTO. 1988. Relationships between water quality and periphyton biomass in several streams in Japan. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 23:1511–1518.
- AUER, M. T., AND R. P. CANALE. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron. 3. The dependence of growth rates on internal phosphorus pool size. *Journal of Great Lakes Research* 8:93–99.
- BIGGS, B. J. F. 1985. Algae: a blooming nuisance in rivers. *Soil and Water* 21:27–31.
- BIGGS, B. J. F. 1988. Algal proliferations in New Zealand's shallow stony foothills-fed rivers: toward a predictive model. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 23:1405–1411.
- BIGGS, B. J. F. 1995. The contribution of disturbance, catchment geology and landuse to the habitat template of periphyton in stream ecosystems. *Freshwater Biology* 33:419–438.
- BIGGS, B. J. F. 1996. Patterns in benthic algae of streams. Pages 31–56 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, California.
- BIGGS, B. J. F. 2000. New Zealand periphyton guidelines: detecting, monitoring and managing of enrichment of streams: background and guidelines. Ministry for the Environment, Wellington, New Zealand. (Available from: Publications Section, Ministry for the Environment, P.O. Box 10362, Wellington, New Zealand.)
- BIGGS, B. J. F., AND M. E. CLOSE. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative

- effects of flows and nutrients. *Freshwater Biology* 22:209–231.
- BIGGS, B. J. F., C. KILROY, AND R. L. LOWE. 1998a. Periphyton development in three valley segments of a New Zealand grassland river: test of a habitat matrix conceptual model within a catchment. *Archiv für Hydrobiologie* 143:147–177.
- BIGGS, B. J. F., AND R. L. LOWE. 1994. Responses of two trophic levels to patch enrichment along a New Zealand stream continuum. *New Zealand Journal of Marine and Freshwater Research* 28:119–134.
- BIGGS, B. J. F., AND G. M. PRICE. 1987. A survey of filamentous algal proliferations in New Zealand rivers. *New Zealand Journal of Marine Freshwater Research* 21:175–191.
- BIGGS, B. J. F., R. A. SMITH, AND M. J. DUNCAN. 1999. Velocity and sediment disturbance of periphyton in headwater streams: biomass and metabolism. *Journal of the North American Benthological Society* 18:222–241.
- BIGGS, B. J. F., R. J. STEVENSON, AND R. L. LOWE. 1998b. A habitat matrix conceptual model for stream periphyton. *Archiv für Hydrobiologie* 143:25–56.
- BIGGS, B. J. F., AND H. A. THOMSEN. 1995. Disturbance of stream periphyton by perturbations in shear stress: time to structural failure and differences in community resistance. *Journal of Phycology* 31:233–241.
- BOTHWELL, M. L. 1989. Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1293–1301.
- CHAPRA, S. C. 1997. *Surface water-quality modeling*. McGraw-Hill, New York.
- CHÉTELAT, J., F. R. PICK, A. MORIN, AND P. B. HAMILTON. 1999. Periphyton biomass and community composition in rivers of different nutrient status. *Canadian Journal of Fisheries and Aquatic Sciences* 56:560–569.
- CLAUSEN, B., AND B. J. F. BIGGS. 1997. Relationships between benthic biota and hydrological indices in New Zealand streams. *Freshwater Biology* 38:327–342.
- CLAUSEN, B., AND B. J. F. BIGGS. 1998. Streamflow variability indices for riverine environmental studies. Pages 357–364 in H. Wheatler and C. Kirby (editors). *Hydrology in a changing environment*. John Wiley and Sons, Chichester, UK.
- DAVIES-COLLEY, R. J., AND J. M. QUINN. 1998. Stream lighting in five regions of North Island, New Zealand: control by channel size and riparian vegetation. *New Zealand Journal of Marine and Freshwater Research* 32:591–606.
- DENICOLA, D. M. 1996. Periphyton responses to temperature at different ecological levels. Pages 149–181 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, California.
- DODDS, W. K. 1993. What controls levels of dissolved phosphate and ammonium in surface waters? *Aquatic Sciences* 55:132–142.
- DODDS, W. K., J. R. JONES, AND E. B. WELCH. 1998. Suggested classification of stream trophic state: distributions of temperate stream types by chlorophyll, total nitrogen, and phosphorus. *Water Research* 32:1455–1462.
- DODDS, W. K., V. H. SMITH, AND B. ZANDER. 1997. Developing nutrient targets to control benthic chlorophyll levels in streams: a case study of the Clark Fork River. *Water Research* 31:1738–1750.
- DODDS, W. K., AND E. B. WELCH. 2000. Establishing nutrient criteria in streams. *Journal of the North American Benthological Society* 19:186–196.
- FRANCOEUR, S. N., B. J. F. BIGGS, AND R. L. LOWE. 1998. Microform bed clusters as refugia for periphyton in a flood-prone headwater stream. *New Zealand Journal of Marine and Freshwater Research* 32:363–374.
- FRANCOEUR, S. N., B. J. F. BIGGS, AND R. L. LOWE. 1999. Nutrient limitation of algal biomass accrual in streams: seasonal patterns and comparison of methods. *Journal of the North American Benthological Society* 18:242–260.
- GRIMM, N. B., AND S. G. FISHER. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8:292–307.
- HILL, W. R. 1996. Effects of light. Pages 121–148 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, California.
- HORNER, R. R., AND E. B. WELCH. 1981. Stream periphyton development in relation to current velocity and nutrients. *Canadian Journal of Fisheries and Aquatic Sciences* 38:449–457.
- HORNER, R. R., E. B. WELCH, M. R. SEELEY, AND J. M. JACOBY. 1990. Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. *Freshwater Biology* 24:215–232.
- HORNER, R. R., E. B. WELCH, AND R. B. VEENSTRA. 1983. Development of nuisance periphytic algae in laboratory streams in relation to enrichment and velocity. Pages 121–134 in R. G. Wetzel (editor). *Periphyton of freshwater ecosystems*. Junk, The Hague, The Netherlands.
- JONES, J. R., M. M. SMART, AND J. N. BURROUGHS. 1984. Factors related to algal biomass in Missouri Ozark streams. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 22:1867–1875.
- LOHMAN, K., J. R. JONES, AND B. D. PERKINS. 1992. Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark

- streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1198–1205.
- MCINTIRE, C. D., S. V. GREGORY, A. D. STEINMAN, AND G. A. LAMBERTI. 1996. Modeling benthic algal communities: an example from stream ecology. Pages 669–704 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, California.
- PETERSON, C. G. 1996. Response of benthic algal communities to natural physical disturbance. Pages 375–402 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, California.
- PETERSON, C. G., AND N. B. GRIMM. 1992. Temporal variation in enrichment effects during periphyton succession in a nitrogen-limited desert stream ecosystem. *Journal of the North American Benthological Society* 11:20–36.
- PETERSON, C. G., AND R. J. STEVENSON. 1992. Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology* 73:1445–1461.
- PETERSON, C. G., A. C. WEIBEL, N. B. GRIMM, AND S. G. FISHER. 1994. Mechanisms of benthic algal recovery following spates: comparison of simulated and natural events. *Oecologia* 98:280–290.
- QUINN, J. M., AND B. W. GILLILAND. 1989. The Manawatu River cleanup—has it worked? *Transactions of the Institution of Professional Engineers, New Zealand* 16:22–26.
- QUINN, J. M., AND C. W. HICKEY. 1990. Magnitude of effects of substrate particle size, recent flooding and catchment development on benthic invertebrate communities in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 24:411–427.
- ROSEMOND, A. D. 1994. Multiple factors limit seasonal variation in periphyton in a forest stream. *Journal of the North American Benthological Society* 13:333–344.
- RUTHERFORD, J. C., AND N. BROEKHUIZEN. 1996. Streams of numbers. *Water and Atmosphere* 4:25–28.
- STEINMAN, A. D. 1996. Effects of grazers on freshwater benthic algae. Pages 341–373 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, California.
- WELCH, E. B. 1992. *Ecological effects of wastewater: applied limnology and pollutant effects*. Chapman and Hall, London, UK.
- WELCH, E. B., R. R. HORNER, AND C. R. PATMONT. 1989. Prediction of nuisance periphytic biomass: a management approach. *Water Research* 23:401–405.
- WELCH, E. B., J. M. JACOBY, R. R. HORNER, AND M. R. SEELEY. 1988. Nuisance biomass levels of periphyton algae in streams. *Hydrobiologia* 157:161–168.
- WHARFE, J. R., K. S. TAYLOR, AND H. A. C. MONTGOMERY. 1984. The growth of *Cladophora glomerata* in a river receiving sewage effluent. *Water Research* 18:971–979.

Received: 15 April 1999

Accepted: 7 December 1999