

GRAZER CONTROL OF STREAM ALGAE: MODELING TEMPERATURE AND FLOOD EFFECTS

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ABSTRACT: A computer model for epilithic algae and grazer biomass in streams is modified to better predict the effects of temperature and is calibrated for diatoms and mayflies. Mayflies are predicted to maintain low diatom biomass provided that (1) temperatures remain within their preferred range (10–20°C); and (2) mayfly populations are not adversely affected by floods. Algal blooms are predicted to occur in mayfly-dominated streams above 20°C—temperatures common in pasture streams over summer. We hypothesize that mobile bed streams are susceptible to blooms during summer low flows following floods because (1) they usually lack temperature tolerant snail grazers; and (2) mayfly recovery lags behind algal regrowth, and there is a short period when algae escape from “top-down” grazer control.

INTRODUCTION

Proliferations of periphytic algae (algal blooms) have been documented in a number of New Zealand rivers with stoney beds draining agricultural catchments (Biggs and Price 1987) and adversely affect ecosystem structure and function, river aesthetics, and some water uses. Most conspicuous are blooms of filamentous green algae, although proliferation of diatoms and blue-green algae are also of management concern. Algal blooms only occur sporadically, when the rates of accrual (autotrophic fixation plus colonization) exceed the rates of loss (sloughing, flow disturbance, and consumption by grazers).

Benthic macroinvertebrate grazers (principally aquatic insects) have a significant negative effect on algal biomass; for example, Welch et al. (1992) showed that 3,000 grazers m⁻² (1–3 g carbon m⁻²) were able to prevent “nuisance” blooms below nutrient point sources. However, grazers do not always exert strong “top-down” control on epilithic algae. Some important grazers in New Zealand streams are sensitive to high temperatures, notably mayflies (Quinn et al. 1994), and are poorly represented in streams once temperatures exceed 20°C (Quinn and Hickey 1990). M. R. Scarsbrook et al. (unpublished paper, 1999) postulated that high water temperatures during summer low flows release epilithic algae from top-down control by mayfly grazers thereby enabling them to bloom.

In the majority of streams, high flows periodically “reset” algal biomass through the loss processes of shear, abrasion, and bed disturbance. Floods not only reduce algal biomass but also scour macroinvertebrates. If recolonization by macroinvertebrates (e.g., from drift and/or refugia) is slow, then grazing pressure on epilithic algae may be low immediately following a flood, enabling rapid accrual of algal biomass (Mosisch and Bunn 1997).

During experimental work it is often difficult to separate the interactions between several abiotic and biotic factors that affect algal biomass, because stream ecosystems are inherently dynamic. Computer simulation models have the potential to help understand stream ecosystems, pose and test hypotheses, plan experimental work, and (eventually) predict the response

to changes in land use. This paper describes a dynamic, deterministic computer model developed as part of a multidisciplinary study of hill-country streams at Whatawhata, New Zealand (Quinn et al. 1997a) with the ultimate objective of designing stream restoration. We use the model to investigate two hypotheses. First, that algal blooms occur during summer low flows because high water temperatures adversely affect sensitive macroinvertebrate grazers. Second, that floods sporadically reduce grazer numbers thereby relieving algae from top-down grazer control.

REVIEW OF STREAM ECOSYSTEM MODELS

The ultimate objective of ecosystem modeling is to improve our ability to predict ecosystem response to management (e.g., land-use change or riparian restoration). We recognize that stream ecosystem models have not yet reached the point where quantitative predictions can be accepted with confidence. Nevertheless an ecosystem model, when used in conjunction with laboratory studies and field experiments, is a useful tool (McIntire and Colby 1978). By examining the sensitivity of model predictions to each coefficient it is possible to draw inferences about which stream processes are important.

There is extensive literature on computer models of phytoplankton-zooplankton interactions in lakes and estuaries [e.g., DiToro et al. (1971) and Canale (1976)] but few modeling studies of algal-grazer interactions in streams. A notable exception is the modeling work by McIntire (1973) and McIntire and Colby (1978) based on laboratory studies of epilithic algae and snail growth dynamics. The McIntire-Colby model predicts the biomass of a single epilithic algal functional group (a mixed diatom community) and of a single grazer functional group (the snail *Juga*) as affected by changes in light, temperature, velocity, nutrient, and detritus input. It shows that a combination of high winter silt loads, low light levels below the forest canopy, and grazing by snails is sufficient to explain the low algal biomass observed in forested Oregon streams.

Horner et al. (1983) developed a model in which the rate of change of algal biomass is

$$\frac{dP}{dt} = K_1 \mu L (k_t + k_i) (P_{\max} - P) - K_2 V^0 \quad (1)$$

where P = algal biomass (mg chl a m⁻²); t = time (days); $P_{\max}$ = maximum sustainable biomass; k_t and k_i = mass transfer coefficients in turbulent and laminar flow, respectively (cm s⁻¹); μ = phosphorus uptake rate (day⁻¹); f_l = light factor (dimensionless); V = water velocity (cm s⁻¹); and K_1 , K_2 , and θ = dimensionless constants that Horner calibrated using data from laboratory experiments and field observations. The first and second terms on the right-hand side of (1) quantify algal growth and scour loss rate, respectively. The Horner model

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does not explicitly include grazing, but it does require a priori specification of $B_{\max}$, which can make allowance for grazing losses if these are known. Eq. (1) is a "logistic model," which has the advantage over first-order growth models that, after a flood (when $P \sim 0$), the term $P_{\max} - P$ is nonzero, and it is not necessary to "restart" the model by prescribing the algal biomass. Uehlinger et al. (1996) modeled the effects of floods on algal biomass in the Necker River, Switzerland, by simulating the effects of light, temperature, density-dependent growth, and flow-induced detachment. They do not model grazing explicitly and predicted biomass is determined largely by density-dependent growth, continuous (slow) detachment during low flows, and catastrophic (high) loss during floods. The Uehlinger model requires specification of either the algal biomass, which survives floods, or the recolonization rate. Neither the Horner nor Uehlinger models simulates grazer-algal-flow interactions. D'Angelo et al. (1997) described a stream ecosystem model that predicts the spatial distribution of organic detritus, one algal group, four invertebrate groups, and one vertebrate group and successfully reproduces many reach-scale features of stream food web dynamics. The main focus of the D'Angelo model is medium-term (months-to-years) temporal and spatial dynamics in forested catchments, and it is not suitable for simulating short-term dynamics (e.g., algal blooms) in pasture catchments. Wootton et al. (1996) investigated the effects of flood disturbance on food web interactions in rivers using a multitrophic computer model that simulates epilithic algae, a predation-resistant but flood-susceptible caddisfly grazer, a predation-susceptible but flood-resistant grazer, and a predatory fish. Removing floods is shown to favor the predation-resistant caddisfly to the disadvantage of the predatory fish: a trend corroborated by field observations. The D'Angelo and Wootton papers illustrate the way ecosystem models can be used to conduct numerical experiments, test hypotheses, and hence help understand the response of complex stream ecosystems to management.

METHODS

Computer Model

SAL1 (Stream ALgorithm 1) models a single function group of epilithic algae and a single group of invertebrate grazers. The algal group mimics diatoms growing attached to the streambed, which in New Zealand streams typically includes species such as *Cymbella kappii* and *Gomphonema herculeana* (Biggs 1990). The grazer group mimics mayflies, exemplified in New Zealand streams by *Deleatidium* spp., which are widely distributed, numerous, and known to consume epilithic algae (Rounick et al. 1982). In this paper other groups of epilithic algae (e.g., green and blue green algae), nonalgal carbon sources (e.g., heterotrophic biofilms and detritus), and other grazers (e.g., snails, caddisflies, and chironomids) are neglected. Macroinvertebrate and fish predators are not modeled explicitly although their effect is simulated by a first-order mayfly loss term. The study streams at Whatawhata are second- to fifth-order, typically 0.5–5 km long, and drain grazed and fertilized hill-country pasture. Quinn et al. (1997a,b) found high inorganic nutrient concentrations in these streams, and we assume that nutrients are always present in abundance. We are not concerned with spatial variations in the study streams and simulate a single homogeneous stream reach 3.6 km long. Algal and grazer biomass are expressed as carbon per unit area of the streambed (gC m^{-2}).

Algal Submodel

The rate of biomass accrual of epilithic algae is the difference between the rates of gain from carbon fixation and col-

onization and losses resulting from respiration, grazing (ingestion plus dislodgment), and scour

$$\frac{dP}{dt} = \text{Fix} + P_{\text{col}} - \text{Res} - \text{Gra} - \text{Scour} \quad (2)$$

where P = biomass of epilithic algae (gC m^{-2}); Fix = carbon fixation rate; P_{col} = algal colonization rate; Res = respiration rate; Gra = ingestion and dislodgment rate by grazers; and Scour = scour rate ($\text{gC m}^{-2} \text{ day}^{-1}$). Fixation rate is

$$\text{Fix} = p_{\max} f_1(I) f_2(T) f_3(P) \quad (3)$$

where $p_{\max}$ = maximum fixation rate ($\text{gC m}^{-2} \text{ day}^{-1}$); I = photosynthetically available radiation incident on the surface of the algal mat ($\mu\text{mol m}^{-2} \text{ s}^{-1}$); and T = temperature. The functions f_1 , f_2 , and f_3 are dimensionless, lie in the range of 0–1, and quantify the limiting effects of light, temperature, and biomass, respectively. Fixation rate follows a bilinear relationship with light

$$f_1(I) = \frac{I}{I_k}, \quad 0 < I < I_k; \quad f_1(I) = 1, \quad I > I_k \quad (4a,b)$$

where I_k = saturating radiation ($\mu\text{mol m}^{-2} \text{ s}^{-1}$). Assuming that radiation follows a half-sinusoid during daylight and averaging (4) over 24 h gives the daily mean fixation rate

$$\overline{f_1(I)} = \frac{\text{Day}}{12\pi} \left[\frac{I_{\max}}{I_k} - \sqrt{\left(\frac{I_{\max}}{I_k}\right)^2 - 1} + \frac{\pi}{2} - \sin^{-1}\left(\frac{I_k}{I_{\max}}\right) \right], \quad I_{\max} > I_k \quad (5a)$$

$$\overline{f_1(I)} = \frac{\text{Day}}{12\pi} \frac{I_{\max}}{I_k}, \quad I_{\max} < I_k \quad (5b)$$

where $I_{\max}$ = daily maximum radiation ($\mu\text{mol m}^{-2} \text{ s}^{-1}$); and Day = daylength (h). The maximum fixation rate is assumed to occur at the optimum temperature for epilithic algae T_{opt} and to decrease at higher and lower temperatures following an asymmetrical Gaussian distribution

$$f_2(T) = \exp\left(-\left(\frac{T - T_{\text{opt}}}{\Delta T_{\text{lower}}}\right)^2\right), \quad T_{\min} < T < T_{\text{opt}} \quad (6a)$$

$$f_2(T) = \exp\left(-\left(\frac{T - T_{\text{opt}}}{\Delta T_{\text{upper}}}\right)^2\right), \quad T_{\text{opt}} < T < T_{\max} \quad (6b)$$

Assuming that $f_2(T) = 5\%$ at both $T = T_{\min}$ and $T = T_{\max}$ gives

$$\Delta T_{\text{lower}} = \frac{T_{\text{opt}} - T_{\min}}{\sqrt{\ln 20}} \quad \text{and} \quad \Delta T_{\text{upper}} = \frac{T_{\max} - T_{\text{opt}}}{\sqrt{\ln 20}} \quad (6c)$$

When the algal mat is very thin (i.e., low biomass) all cells are illuminated and the fixation rate increases with increasing biomass. As the mat becomes thicker, however, the basal cells are shaded and do not photosynthesize so that the fixation rate per unit area approaches a maximum. Following McIntire (1973) we represent the population-level consequence phenomenologically by

$$f_3(P) = \left(\frac{P}{P_{\text{sat}} + P}\right) \quad (7)$$

where P_{sat} = density-dependence coefficient (gC m^{-2}), the algal biomass at which fixation is half the maximum rate. Whereas photosynthesis is confined to the illuminated surface layer, all cells in the algal mat respire, and it is appropriate to model respiration as a first-order process (McIntire and Phinney 1965)

$$\text{Res} = P_{\text{resp}} f_4(T) P \quad (8)$$

where P_{resp} = respiration rate (day^{-1}) measured at the reference temperature T_{ref} and

$$f_4(T) = Pk_{resp}^{T-T_{ref}} \quad (9)$$

with Pk_{resp} = temperature coefficient for algal respiration (dimensionless). Eq. (8) neglects photorespiration in the illuminated surface layer of the algal mat, and so the value of p_{max} in (3) is the maximum net fixation rate. During periods of low flow there is a small, continuous loss of algal cells by abrasion and scour (Uehlinger et al. 1996), which we simulate using an equation of the same form as (8). Effectively, the coefficient P_{resp} quantifies both respiration and low flow scour losses. It is difficult to predict the amount of algal biomass lost during, or present after, a flood. Scour loss rate depends not only on water velocity (Horner et al. 1983) but also the type of algae and the velocity regime under which they have developed (Biggs and Thomsen 1994), the mobility of the riverbed, and the scouring effect of suspended sediment (Rittmann 1989). In this study we simulate floods by periodic reductions in algal biomass, and after each flood we specify the surviving biomass and/or the rate of recolonization based on field observations.

Grazer Submodel

The rate of change in grazer biomass is the difference between the rates of assimilation, colonization, basal respiration, activity respiration, predation, and export

$$\frac{dG}{dt} = \text{Ass} + G_{col} - \text{Res} - \text{Act} - \text{Pre} - \text{Exp} \quad (10)$$

where G = grazer biomass (gC m^{-2}); Ass = food assimilation rate; G_{col} = grazer colonization rate (drift and egg laying); Res = basal respiration rate; Act = activity costs; Pre = predation loss rate (including mortality); and Exp = export loss rate (including scour, drift, and emergence) ($\text{gC m}^{-2} \text{day}^{-1}$). The grazing rate depends on the maximum search rate s_{max} ($\text{m}^2 \text{g}^{-1} \text{day}^{-1}$) and the food handling time t_{hold} (day). The variable t_{hold} is the time required for grazers to digest prey, when they do not search for more food. The search rate per unit grazer biomass, given "accessible" algal prey biomass P^* and temperature T , is

$$s = \frac{s_{max} f_2(T)}{1 + s_{max} t_{hold} P^*} \quad (11)$$

where $f_2(T)$ has the same form as (6). When $T = T_{opt}$ and P^* is small, grazers search for food at s_{max} but at suboptimal temperatures and/or when food is present in excess the search rate decreases. Some algae are assumed inaccessible to grazers (e.g., they grow in strong current or in crevices) and

$$P^* = P - P_{refuge} \quad (12)$$

where P_{refuge} = algal biomass inaccessible to grazers (gC m^{-2}) (hereafter termed grazing refuge). The ingestion and assimilation rates are

$$I = sP^*G \quad (13)$$

$$\text{Ass} = \text{ass}I \quad (14)$$

where ass = fraction of ingested algal biomass assimilated into new grazer biomass (dimensionless). The amount of algal biomass dislodged by each grazer is proportional to its ingestion rate, and total removal by ingestion and dislodgment is

$$\text{Gra} = (1 + \text{dis})sP^*G \quad (15)$$

where dis = ratio of algae dislodged/ingested (typically ~ 100 – 300%). Basal respiration is calculated using (8) with coefficients relevant to grazers. Activity-related respiration is

$$\text{Act} = \text{act} s_{max} f_2(T)G \quad (16)$$

where act = amount of carbon expended by a grazer per unit area searched (gC m^{-2}). Predator-induced grazer mortality is proportional to grazer biomass

$$\text{Pre} = \text{pred} G \quad (17)$$

where pred = weight-specific predation loss rate (d^{-1}). As with algae we prescribed the grazer biomass and/or recolonization rate after each flood. Analytical solutions for the steady-state (equilibrium) biomass of grazers and algae are obtained by setting (1) and (10) to zero and solving simultaneously. Numerical solutions are obtained by solving (1) and (10) using fifth-order adaptive time step Runge-Kutta methods.

CALIBRATION

The algal and grazer submodels contain 12 and 15 coefficients, respectively, of which 8 (algal) and 12 (grazer) are estimated a priori from laboratory studies, field experiments, or the literature (Table 1). The remaining 4 (algal) and 3 (grazer) coefficients are estimated by matching observed and predicted biomass. Factors used to convert published data to units of carbon are $\text{C/AFDM} = 50\%$, $\text{C/DM} = 20\%$, $\text{C/O} = 38\%$, and $\text{chl a/AFDM} = 0.5$ – 1% (where C = carbon, O = oxygen, chl a = chlorophyll a, AFDM = ash-free dry mass, and DM = dry mass).

The algal loss rate P_{resp} (respiration + low flow scour) is estimated by matching predicted steady-state algal biomass with observed maximum algal biomass during blooms (Fig. 1). Grazing is neglected because high temperature, low dissolved oxygen, and/or high pH often suppress grazing activity during blooms (Welch et al. 1992). Maximum bloom biomass is typically 50 gC m^{-2} (Table 2), which is matched by $P_{resp} = 0.05 \text{ day}^{-1}$, a value which lies in the published range (Table 3). Diatoms are predicted to do best below 20°C , which is in general agreement with field and laboratory observations (Patrick 1974). Maximum algal biomass is sensitive to the maximum photosynthesis rate [here set to $p_{max} = 5 \text{ gC m}^{-2} \text{day}^{-1}$ based on published values (Table 3)] but is insensitive to variations of P_{sat} and I_k within the published range.

Grazing coefficients s_{max} , t_{hold} , and ass estimated from our measurements for *Deleatidium* sp. match published data for New Zealand and North American mayflies (Table 4). *Deleatidium* ingestion rate is highest between 15 and 20°C with a noticeable reduction at 25°C (Table 4), which is consistent with published lethal temperatures of 23 – 24°C (Quinn et al. 1994) and an optimum temperature of 20°C . We were unable to subdivide detritus production into consumptive (i.e., egestion) and nonconsumptive (i.e., dislodgment) losses and estimated t_{hold} assuming $\text{dis} = 0$. However, the feeding efficiency of mayflies ranges from 80% when food is scarce ($\text{dis} = 0.25$) to 5 – 20% when food is abundant ($\text{dis} = 4$ – 19) (Scrimgeour et al. 1991; Cattaneo and Mousseau 1995) and when running the model we assume $\text{dis} = 1$ (50% feeding efficiency). The predation loss rate is estimated a priori at $0.05 \text{ g g}^{-1} \text{d}^{-1}$ from measurements of fish biomass and productivity in pasture streams at Whatawhata (Hicks and McCaughan 1997) assuming a productivity/consumption ratio of 25% (Huyr 1996a).

Grazer activity cost act strongly affects steady-state grazer biomass (Fig. 2). Values in the range $\text{act} = 0.025$ – 0.075 gC m^{-2} give a predicted grazer biomass in the range of 1 – 2 gC m^{-2} that matches observations of total invertebrate biomass (Table 2). Steady-state algal biomass increases with increasing grazer activity cost (and hence decreasing grazer biomass) as would be expected (Fig. 2), but the predicted change in algal biomass is small.

As the grazing refuge P_{refuge} increases, steady-state algal biomass increases (Fig. 3) as expected. For values in the range

TABLE 1. Summary of Model Coefficients

Coefficient (1)	Value (2)	Reference (3)
(a) Diatom		
Photosynthesis $p_{\max}$	5 gC m ⁻² day ⁻¹	Table 3
Light saturation I_k	230 μmol m ⁻² s ⁻¹	Biggs and Hickey (1994); Quinn et al. (1997b)
Minimum temperature $PT_{\min}$	5°C	Assumed
Optimum temperature PT_{opt}	20°C	Patrick (1974); Graham et al. (1982, 1985)
Maximum temperature $PT_{\max}$	30°C	Lester et al. (1988); Stevenson et al. (1996)
Density dependence P_{sat}	2.5 gC m ⁻²	McIntire (1973); Biggs and Hickey (1994)
Respiration rate P_{resp}	0.05 day ⁻¹	Calibration, Fig. 1
Reference temperature PT_{ref}	20°C	Optimum temperature
Temperature coefficient PK_{resp}	1.05	USEPA (1985)
Grazing refuge P_{refuge}	5 gC m ⁻²	Calibration, Fig. 3
Flood refuge P_{flood}	0.001–0.1 gC m ⁻²	Calibration, Fig. 7
Colonization P_{col}	0.001–0.1 gC m ⁻² day ⁻¹	Calibration, Fig. 5
(b) Mayfly		
Maximum search rate $s_{\max}$	3.2 m ² g ⁻¹ day ⁻¹	Table 4
Food handling time t_{hold}	1.4 day g g ⁻¹	Table 4
Assimilation ass	0.50	Table 4
Minimum temperature $GT_{\min}$	2°C	Assumed
Optimum temperature GT_{opt}	20°C	Quinn et al. (1994)
Maximum temperature $GT_{\max}$	23°C	Quinn et al. (1994)
Face-off time t_{face}	0 day g g ⁻¹	Assumed
Respiration rate G_{resp}	0.03 day ⁻¹	Roux (1979); McCullough et al. (1979); Vannote and Sweeney (1980)
Reference temperature GT_{ref}	20°C	Optimum temperature
Temperature coefficient GK_{resp}	1.05	USEPA (1985)
Activity coefficient act	0.05 gC m ⁻²	Calibration, Fig. 2
Predation rate P_{pred}	0.05 day ⁻¹	Hicks (1997); Hicks and McCaughan (1997)
Dislodgment factor dis	1	Scrimgeour et al. (1991); Cattaneo and Mousseau (1995)
Flood refuge G_{flood}	0.001–1 gC m ⁻²	Calibration, Fig. 7
Colonisation G_{col}	0.001–0.1 gC m ⁻² day ⁻¹	Calibration, Fig. 5

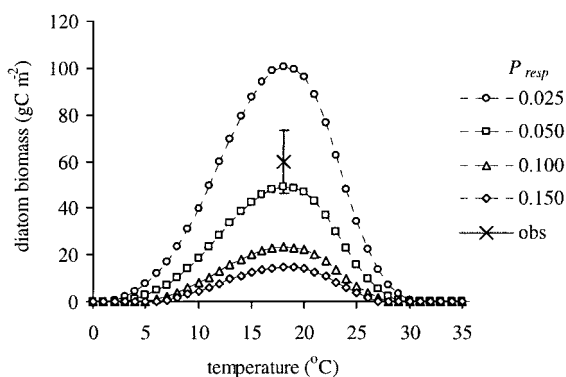


FIG. 1. Effects of Respiration Rate P_{resp} on Steady-State Diatom Biomass in Absence of Grazers. Observations (Mean $\pm$ Standard Error) Are from Table 2

$P_{\text{refuge}} = 0\text{--}5$ gC m⁻², grazer biomass also increases with increasing P_{refuge} . That is not intuitive and occurs because algal productivity (hence, grazer food supply) increases with algal biomass when the latter is low [see (7)]. Above $P_{\text{refuge}} = 5$ gC m⁻², however, algal biomass is high, algal productivity reaches a plateau, and the constant rate of food supply supports a constant grazer biomass. $P_{\text{refuge}} = 5$ gC m⁻² gives a grazer biomass of 1.5 gC m⁻², which matches observed total invertebrate biomass (Table 2).

Fig. 4 shows biomass predictions at constant flow in an unshaded pasture stream where temperature (20°C) is optimum for diatoms and mayflies. Results are plotted in the phase-plane omitting the first 400 days of each simulation. With increasing P_{refuge} the equilibrium algal and grazer biomass both increase, as is also apparent in Fig. 3. For $P_{\text{refuge}} < 0.5$ gC m⁻² biomass undergoes regular, cyclical variations (limit cycles). Biomass variations are out of phase and move counterclockwise around the trajectories. With increasing P_{refuge} the amplitude of the cycles decreases, and the period decreases from 70 days ($P_{\text{refuge}} = 0.001$) to 40 days ($P_{\text{refuge}} = 0.01$). For $P_{\text{refuge}} >$

TABLE 2. Algal Bloom and Macroinvertebrate Biomass in Streams

Reference (1)	Notes (2)	Value (gC m ⁻²) (3)
(a) Maximum algal biomass: New Zealand streams		
Biggs and Price (1987)	Three streams	93–146
Biggs (1990)	Five rivers	15–28
Welch et al. (1992)	Pokaiwhenua and Manawatu rivers	58–59
Biggs and Gerbeaux (1993)	Riwaka River	20–60
(b) Maximum algal biomass: North American streams		
McIntire and Phinney (1965)	Ungrazed laboratory channels	70.5
Fisher et al. (1982)	Desert Stream, Ariz.	80–145
Horner et al. (1983)	Literature review	25
Lamberti et al. (1989)	Unshaded laboratory channels	32
(c) Macroinvertebrate biomass: New Zealand streams		
Hopkins (1976)	Hinau and Horokiwi streams	1.3 $\pm$ 0.9 (mean $\pm$ SD)
Quinn and Hickey (1990)	100 Rivers study	1.2 (95 percentile), 0.8 (mean)
Scrimgeour (1991)	Ashley River, <i>Deleatidium</i>	0.5
Hurn (1996b)	Sutton Stream, primary consumers	0.8
Quinn et al. (1997a)	Streamside mesocosms	1
Quinn et al. (1997b)	Pasture streams	1–2

0.5 gC m⁻² there is a stable equilibrium point: biomass eventually becomes constant provided flow, temperature, and light do not change. The time taken to reach equilibrium depends on the initial condition but is typically 100 days. A sensitivity analysis was carried out (details omitted), which showed that the equilibrium point is stable when any of the following occurs: temperature is within 1–2°C of the upper or lower limit; grazing refuge exceeds 0.5 gC m⁻²; or algal colonization rate exceeds 1 gC m⁻² day⁻¹. For the expected range of model coefficients the equilibrium point is usually, but not always, stable.

Simultaneous measurements of algal and total macroinver-

TABLE 3. Carbon Fixation and Respiration Rates for Algae

$P_{\max}$ ($\text{gC m}^{-2} \text{ day}^{-1}$) (1)	P_{resp} (day^{-1}) (2)	Reference (3)
(a) Whatawhata		
1.3–1.7 1.2–3.2	0.10–0.22 0.15	Quinn et al. (1997a) Quinn et al. (1997b)
(b) Other studies		
2.5–3.5 1–2 5.9–7.7 0.4–4.8	0.02–0.5 0.017–0.020 0.018–0.023 0.02–0.05	Biggs and Hickey (1994) McIntire and Phinney (1965) Lamberti et al. (1989) Boston and Hill (1991) Graham et al. (1982, (1985)

tebrate biomass (excluding crayfish) in New Zealand streams were made during the so-called 100 Rivers study (Biggs 1990; Quinn and Hickey 1990). Fig. 4 shows a subset of these data from sites where nutrient concentrations were high (and hence unlikely to have limited algal growth) and flows did not exceed 20 times the median flow in the preceding 6 weeks (and hence floods are unlikely to have “reset” biomass). The model predicts an equilibrium mayfly biomass ($1\text{--}2 \text{ gC m}^{-2}$) which is slightly higher than the observations (mean of 0.4 , range of $0.1\text{--}1.19 \text{ gC m}^{-2}$). For $P_{\text{refuge}} = 5 \text{ gC m}^{-2}$ the equilibrium diatom biomass (5.5 gC m^{-2}) lies within the range of observations (mean of 6.6 , range of $0.6\text{--}25 \text{ gC m}^{-2}$).

Fig. 5 shows the effects of colonization rate on biomass trajectories. Algal and grazer colonization are assumed equal, and the initial biomasses are $P = 0.1$ and $G = 0.01 \text{ gC m}^{-2}$. The equilibrium points are all stable and, for the range of colonization rates shown, almost coincident. The predicted equilibrium algal biomass ($5.1\text{--}5.5 \text{ gC m}^{-2}$) falls within the range of the observations (mean of 6.6 , range of $0.6\text{--}25 \text{ gC m}^{-2}$). Increasing the colonization rates causes the equilibrium grazer biomass to increase but the algal biomass remains constant (details omitted). This behavior may not be intuitive but the explanation is that high algal colonization rate increases the food supply to grazers whose equilibrium biomass increases. For colonization rates of $0\text{--}0.1 \text{ gC m}^{-2} \text{ day}^{-1}$ predicted equilibrium grazer biomass ($1.5\text{--}2.0 \text{ gC m}^{-2}$) is comparable with the observed range ($0.1\text{--}1.9 \text{ gC m}^{-2}$). Peterson and Stevenson (1990) measured the rate at which diatoms colonized artificial substrates in Overalls Creek, Ky. (limestone bedrock with low algal standing crop) at $2,500 \text{ cells cm}^{-2} \text{ day}^{-1}$. Assuming cells are spherical and $20 \mu\text{m}$ in diameter this equates to a colonization rate of $1 \times 10^{-4} \text{ gC m}^{-2} \text{ day}^{-1}$

which lies at the low end of the range of $0\text{--}0.1 \text{ gC m}^{-2} \text{ day}^{-1}$ estimated from Fig. 5.

In Figs. 4 and 5 the predicted grazer biomass ($1.5\text{--}2.0 \text{ gC m}^{-2}$) is slightly higher than the 100 Rivers observations (mean of 0.4 , range of $0.1\text{--}1.9 \text{ gC m}^{-2}$) which suggests a calibration error. However, there are two reasons why observations and predictions may differ. First, the model predicts only grazer biomass whereas observations may include filter feeders, detritivores, and predators. Winterbourn et al. (1981) stated that New Zealand streams are dominated by browsers (i.e., the majority of invertebrates can exert grazing pressure on epilithic algae) and in gravel-bed rivers the mayfly *Deleatidium* sp. often comprises 90% of total invertebrate numbers (Scarsbrook and Townsend 1993). Thus it is not unreasonable to compare total observed macroinvertebrate biomass with predicted grazer biomass. Second, model predictions are at steady state, which is typically reached after 100 days of steady flow, temperature, and light. In the 100 Rivers study sampling was conducted during autumn low flows, and sites were excluded where flows had exceeded 20 times the median flow in the 6 weeks (42 days) preceding sampling. Nevertheless, biomass may not have reached equilibrium and may still have been recovering from previous floods or adjusting to altered temperature and light.

MODEL PREDICTIONS

Fig. 6 shows predicted steady-state diatom and mayfly biomass in an unshaded pasture stream. Flow, temperature, and daily maximum light are assumed constant. Below 20°C mayflies are predicted to exert heavy grazing pressure on diatoms. However, mayflies have a low thermal tolerance and do not survive above 21°C . If mayflies are the only grazers present, then diatoms are predicted to escape top-down control above 21°C and to bloom. Maximum predicted steady-state mayfly biomass is 1.5 gC m^{-2} , which is comparable with measurements of total grazer biomass.

We examined the effects of floods by resetting diatom and mayfly biomass to different levels (simulating floods of different severity) and predicting the subsequent recovery. No attempt was made to simulate the flow recession in detail: rather flow, temperature and light were assumed constant immediately after each flood. Fig. 7 shows predicted biomass trajectories in unshaded pasture streams. Temperature (20°C) is the optimum for mayflies and diatoms, and the colonization rates ($0.01 \text{ gC m}^{-2} \text{ day}^{-1}$) are the same for mayflies and diatoms. Diatom biomass increases rapidly immediately after each flood, because grazing pressure is low; however, mayfly

TABLE 4. Grazing Coefficients for Mayflies

Species (1)	Temperature (°C) (2)	Ingestion $S_{\max}^a$ ($\text{m}^2 \text{ gC}^{-1} \text{ day}^{-1}$) (3)	Food Handling ^a	Assimilation	Reference (6)
			t_{hold} (day g g^{-1}) (4)	ass (%) (5)	
(a) New Zealand mayflies					
<i>Deleatidium</i> sp.	8	2.00 ± 0.95	4.6 ± 7.6	42 ± 6	M. R. Scarsbrook et al. (unpublished paper, 1999)
	15	3.45 ± 1.80	2.6 ± 3.2	71 ± 22	
	20	3.20 ± 1.30	1.4 ± 1.2	39 ± 8	
	25	1.90 ± 0.60	5.3 ± 4.8	44 ± 11	
<i>Deleatidium</i> sp.				25–60	Huyrn (1996a)
(b) North American mayflies					
<i>Baetis tricaudatus</i>		1.2 ± 0.7	0.91 ± 0.53	—	Scrimgeour et al. (1991)
<i>Paraleptophlebia heteronea</i>	11	1.0 ± 0.7	1.74 ± 1.22	5–40	
<i>Ephemerella aurivilli</i>		7.3 ± 4.3	1.48 ± 0.81	—	
<i>Limnephilus</i> sp.	25	—	—	25–30	Roux (1979)
<i>Ephemerella</i> spp.	15–16	—	—	32–36	Vannote and Swenney (1980)
<i>Tricorythodes</i> sp.	18–20	—	—	33–57	McCullough et al. (1979)

^aMean $\pm$ standard error.

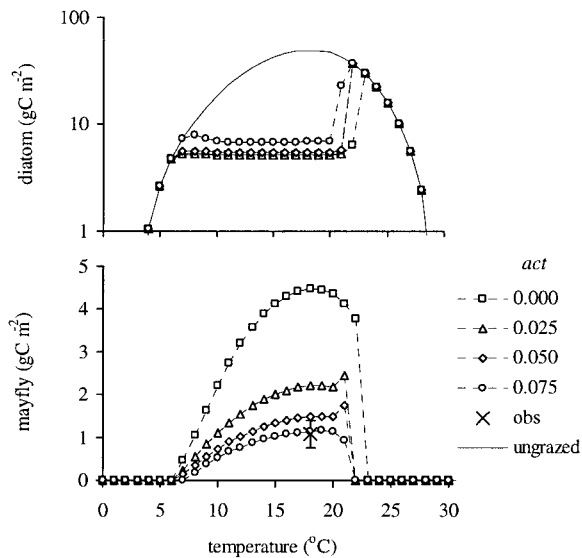


FIG. 2. Effects of Grazer Activity Costs act on Steady-State Mayfly and Diatom Biomass

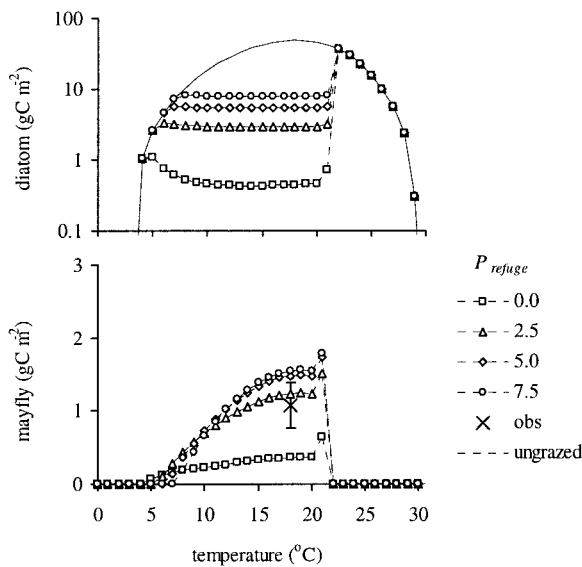


FIG. 3. Effects of Grazing Refuge P_{refuge} on Steady-State Diatom and Mayfly Biomass

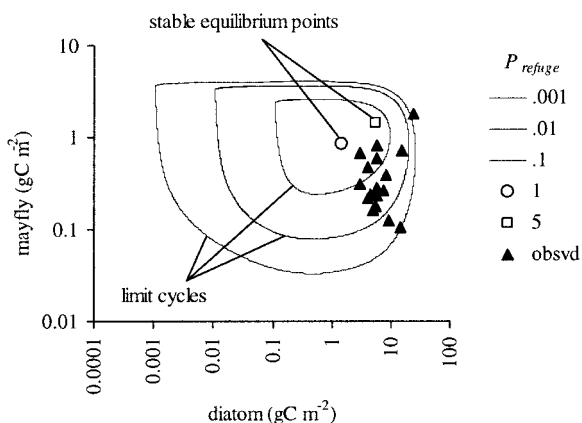


FIG. 4. Effects of Grazing Refuge P_{refuge} on Trajectories of Diatom and Mayfly Biomass. Observations Are from 100 Rivers Study (Biggs 1990; Quinn and Hickey 1990)

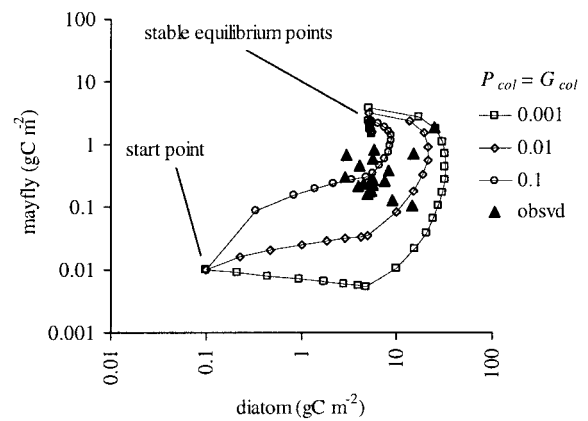


FIG. 5. Effects of Colonization Rate on Predicted Biomass. First Seven Points on Each Trajectory Are 1 Day Apart, Thereafter They Are 2 Days Apart

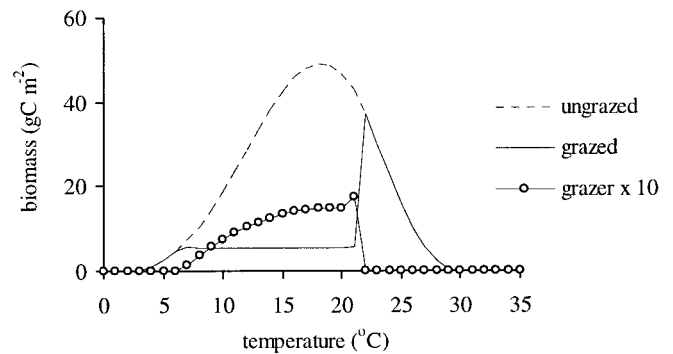


FIG. 6. Predicted Steady-State Biomass for Diatoms and Mayflies in Pasture Stream. Note Grazer Biomass Has Been Scaled by 10

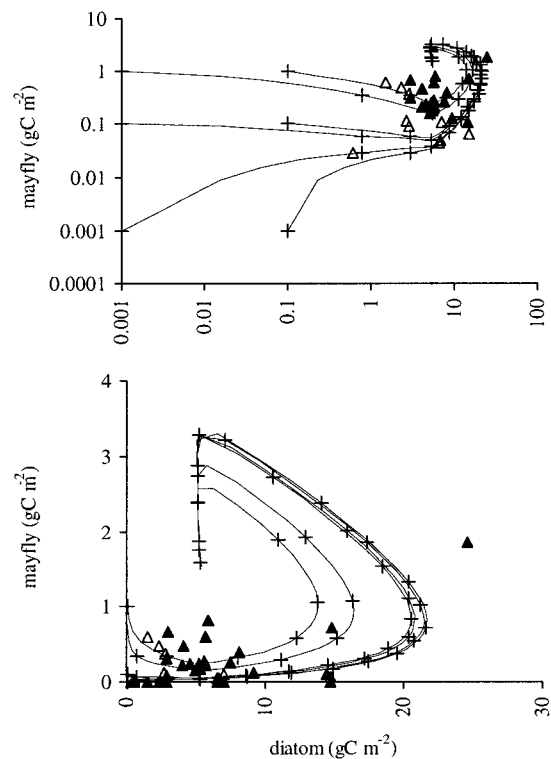


FIG. 7. Predicted Mayfly and Diatom Biomass Trajectories following Flood Resets. Time is Marked Every 10 Days (+). Observations Are from 100 Rivers Study at Eutrophic Sites Where Flows Did (Δ) or Did not ($\blacktriangle$) Exceed 20 Times Median in 6 Weeks Prior to Sampling

biomass increases subsequently and grazing pressure is re-exerted on the diatoms. In Fig. 7 the model trajectories encompass the majority of the 100 Rivers observations. An important feature of Fig. 7 is that in each case there is a postflood algal bloom before equilibrium becomes established. For some combinations of model coefficients the model predicts limit cycles, and postflood blooms are also predicted when the equilibrium point is unstable (details omitted). There are only two situations when a postflood bloom is not predicted: first, when biomass remains close to the equilibrium values; and second, when the postflood biomass lies above the equilibrium point (or limit cycle). The former only occurs if the flood is too small to disturb the stream, and the latter occurs in the unlikely event that the flood increases grazer and/or algal biomass. Francoeur et al. (1998) reported that a flood (10 times the annual median flow) reduced algal biomass on cobbles and gravels by 91% but on more stable boulders and microform bed clusters by only 51–62%. The average algal biomass surviving the flood ($0.2\text{--}0.4\text{ gC m}^{-2}$) is comparable with the initial value of 0.1 gC m^{-2} in Fig. 7. Postflood grazer biomass has not been measured in the study streams, and we assumed values in the range of $0.001\text{--}0.1\text{ gC m}^{-2}$. The postflood bloom is predicted to occur 20–30 days after the flood, but it takes 50–80 days to reach equilibrium. Mosisch and Bunn (1997) observed postflood blooms after 60 days in tropical rain forest streams. The difference in the timing of the postflood bloom between the observations in rain forest streams (60 days) and our model predictions in pasture streams (20–30 days) may reflect differences in shade. Mosisch and Bunn (1997) did not monitor invertebrate populations and were unable to determine whether the epilithon decline observed after 60 days was attributable to grazing or nonconsumptive (e.g., sloughing) loss.

DISCUSSION

The following is concluded from the modeling study:

1. Provided that temperature remains within their preferred range, mayflies maintain steady-state diatom biomass at low levels.
2. Above their thermal tolerance mayflies die out, and at steady-state there is a diatom bloom.
3. Diatom and mayfly biomass can undergo cyclical variations even when flow, temperature, and light are constant, during which diatoms bloom periodically.
4. Floods reduce diatom and mayfly biomass, and under most circumstances, there is a postflood diatom bloom.

The computer model makes a number of simplifying assumptions, which may affect these conclusions. Conclusions 1 and 2 are based on steady-state model predictions, but it is questionable whether a true steady-state is ever achieved in nature. It takes 50–80 days for predicted biomass to reach equilibrium after a perturbation (Fig. 7). Flows sometimes remain constant for this length of time at Whatawhata during the summer, and in spring-fed streams elsewhere, but in many rivers, floods occur frequently and steady-state predictions are of limited applicability. Even when flow is steady, temperature and light vary from day-to-day although model predictions (details omitted) indicate that such variations have a relatively small effect on biomass.

Experimental studies [e.g., Lamberti et al. (1989) and Stevenson et al. (1996)] show that grazers can reduce algal biomass, but in most experiments, grazer biomass is selected by the investigator and remains constant. In this study the computer model allows grazer and algal biomass to vary until a balance is achieved, without imposing any such constraints. Predicted mayfly biomass is comparable with observations of total macroinvertebrate biomass in New Zealand streams,

which provides some measure of verification of model calibration and support for Conclusion 1.

Predicted mayfly biomass is sensitive to the predation loss rate, but although there is some uncertainty in our estimate of predation loss at Whatawhata, we do not believe this is high enough to invalidate Conclusion 1. Before the model can be applied in other streams, however, it will be necessary to estimate grazer predation loss either from productivity estimates of secondary consumers (as in this study) or by extending the model to include additional functional groups. The model assumes a single functional group of algae, but pasture streams usually contain a mixture of algae, some of which may be more temperature tolerant and/or less palatable to grazers than others. Neither the relative growth rates of different algae nor the food preferences of different grazers are well quantified in New Zealand streams, which precludes multispecies modeling. Although the model may be oversimplistic in this respect, we do not believe this invalidates the main conclusions of the study.

The model assumes that epilithic algae and grazers occupy the same habitat. In streams, however, epilithic algae are most abundant on the upper rock surfaces where light and velocity are high, whereas grazers are most commonly found underneath rocks where the risks of drift and predation by fish are lowest (Scrimgeour and Culp 1994). If the habitats of epilithic algae and grazers only partially overlap, it is conceivable that “clumps” of high algal biomass may develop in areas avoided by grazers and Conclusion 1 may not hold everywhere in the stream.

A weakness of the model is that it omits detritus and microheterotrophs from the food web. Many New Zealand macroinvertebrates (including *Deleatidium* sp.) are generalist feeders that consume not only epilithic algae but also detritus and/or heterotrophic biofilms (Winterbourn et al. 1981; Rounick et al. 1982). The extent to which generalist feeders exploit algae opportunistically when algae is abundant while “subsisting” upon organic detritus during periods of algal famine is unknown. It is not obvious whether alternative carbon sources are likely to increase or decrease grazing pressure on algae, and hence how they affect Conclusion 1. If alternative carbon sources help maintain high grazer numbers when algal biomass is low they may eliminate the “limit cycles” shown in Fig. 4 and affect Conclusion 3. Currently there is insufficient information about detritus inputs and biofilm growth rates in the study streams, or food preferences by grazers, to address this question using the model.

Conclusion 2 is that at high temperature mayflies die out thereby enabling diatoms to bloom. Mayflies are poorly represented in streams whose summer temperature exceeds 20°C (Quinn and Hickey 1990) and Rutherford et al. (1997) showed that temperatures commonly exceed 20°C in pasture streams during the summer. Thus Conclusion 2 may be valid in streams where mayflies are the only significant grazers. However, warm pasture streams at Whatawhata support large numbers of other grazers: notably snails, caddisflies, and chironomids (Quinn et al. 1997b). Snails tolerate high temperatures [up to 32°C (Quinn et al. 1994)] and M. R. Scarsbrook et al. (unpublished paper, 1999) show they have the potential to control epilithic algae up to temperatures of 30°C . There are currently insufficient data on ingestion, assimilation, and predation loss rates to include snails, caddisflies, and chironomids in the model. Consequently, Conclusion 2 needs to be qualified with the proviso that algae are likely to bloom when temperatures exceed 20°C only in streams where temperature tolerant grazers are unable to replace mayflies. Mobile bed streams (e.g., those with cobble and gravel beds that experience frequent floods) contain few snails because they cannot withstand bed movement and are slower to recolonize after floods than in-

sects with a free-flying adult stage [e.g., Scrimgeour and Winterbourn (1989); Scarsbrook and Townsend (1993)]. Mayflies are often the dominant grazers in such streams (Scrimgeour 1991).

It is not clear whether Conclusion 3 is valid generally. The model predicts limit cycles for certain combinations of model coefficients but stable equilibrium points for others. It is possible that changes in model structure (such as the addition of additional trophic levels or alternative carbon sources) will change the dynamics of the model equations. In this study we have not considered the effects of cyclical variations of flow, temperature, and light that arise from quasi-periodic weather patterns and seasonal changes. Such external "forcing" can give rise to very complex dynamic behavior in predator-prey equations that are of interest to mathematical ecologists. In most streams, however, the dominant forcing is floods and there is rarely sufficient time for limit cycles (or more complex patterns) to become established.

Conclusion 4 is that floods are followed by an algal bloom. It is easy to understand why an algal bloom occurs when the flood reduces grazer biomass because this releases algae from top-down grazer control. The model also predicts a bloom when the flood reduces only algal biomass, because immediately after the flood grazers are short of food and starve. This latter conclusion may be invalid if alternative food sources (e.g., detritus or microheterotrophs) sustain grazers just after the flood. It may also be invalid if grazers respond to low food availability by reducing their searching activity: currently in the model grazer search rate is highest when food is scarce. The severity of the postflood bloom depends on the biomass that survives the flood and the recolonization rates, but we do not have reliable estimates of these parameters in the study streams at Whatawhata. Pasture streams receive high loads of fine sediment that accumulate in the streambed (Quinn et al. 1997a), and we can hypothesize that grazers have few hyporheic zone refugia. If so, then we would expect fewer grazers to survive floods in pasture streams and for this to lead to larger postflood algal blooms than in gravel-bed streams; however, it is desirable to investigate this hypothesis experimentally.

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APPENDIX II. NOTATION

The following symbols are used in this paper:

- Act = grazer activity costs ($\text{gC m}^{-2} \text{ day}^{-1}$);
 act = carbon expended by grazer per unit area searched (gC m^{-2});
 Ass = grazer food assimilation rate ($\text{gC m}^{-2} \text{ day}^{-1}$);
 ass = fraction of ingested algal biomass assimilated into new grazer biomass (dimensionless);
 Day = daylength (h);

- dis = ratio of nonconsumptive to consumptive losses for epilithic algae (dimensionless);
 Exp = export loss rate for grazers (including scour, drift, and emergence) ($\text{gC m}^{-2} \text{ day}^{-1}$);
 Fix = carbon fixation rate by epilithic algae ($\text{gC m}^{-2} \text{ day}^{-1}$);
 f_1, f_2, f_3 = limiting effects of nonoptimal light, temperature, and biomass ($0 < f < 1$) (dimensionless);
 f_4 = effects of temperature on respiration rate (algae or grazers) (dimensionless);
 G = grazer biomass (gC m^{-2});
 G_{col} = grazer colonization rate by drift and egg laying ($\text{gC m}^{-2} \text{ day}^{-1}$);
 Gra = removal rate of epilithic algae by grazers (ingestion plus dislodgment) ($\text{gC m}^{-2} \text{ day}^{-1}$);
 I = radiation (photosynthetically available radiation) incident on surface of algal mat ($\mu\text{mol m}^{-2} \text{ s}^{-1}$);
 I_k = saturating radiation ($\mu\text{mol m}^{-2} \text{ s}^{-1}$);
 I_{max} = daily maximum radiation ($\mu\text{mol m}^{-2} \text{ s}^{-1}$);
 K_1, K_2 = dimensionless constants;
 k_t, k_l = mass transfer coefficients in turbulent and laminar flow, respectively (cm s^{-1});
 P = biomass of epilithic algae (gC m^{-2});
 P_{col} = algal colonization rate ($\text{gC m}^{-2} \text{ day}^{-1}$);
 P_{max} = maximum sustainable algal biomass (gC m^{-2});
 p_{max} = maximum fixation rate by epilithic algae ($\text{gC m}^{-2} \text{ day}^{-1}$);
 Pre = loss rate of grazers by predation and mortality ($\text{gC m}^{-2} \text{ day}^{-1}$);
 $pred$ = weight-specific, grazer loss by predation and mortality (day^{-1});
 P_{refuge} = algal biomass inaccessible to grazers (gC m^{-2});
 P_{resp} = algal respiration rate measured at the reference temperature T_{ref} (day^{-1});
 Pk_{resp} = temperature coefficient for algal respiration (dimensionless);
 P_{sat} = density-dependence coefficient for algal fixation (gC m^{-2});
 Res = respiration rate ($\text{gC m}^{-2} \text{ day}^{-1}$);
 $Scour$ = algal loss rate by scour ($\text{gC m}^{-2} \text{ day}^{-1}$);
 s_{max} = maximum search rate by grazers ($\text{m}^{-2} \text{ g}^{-1} \text{ day}^{-1}$);
 T = water temperature ($^{\circ}\text{C}$);
 t_{hold} = food handling time (day gC gC^{-1});
 $T_{min}, T_{opt}, T_{max}$ = minimum, optimum and maximum temperature for photosynthesis, grazing, or predation ($^{\circ}\text{C}$);
 T_{ref} = reference temperature for respiration (algae or grazers) ($^{\circ}\text{C}$);
 V = water velocity (cm s^{-1});
 θ = dimensionless constant; and
 μ = phosphorus uptake rate (day^{-1}).