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Empirical analysis of the removal rate of periphyton by grazers

Abstract To establish a general model for the removal rate of periphyton by grazers, we identified 27 publications in which removal rates could be estimated from grazer enclosure or exclosure experiments. When all the measurements obtained under different experimental conditions were extracted, these publications provided 107 data points. Multiple regression of these data showed that periphyton removal rate increased significantly with grazer body mass and food availability, and decreased with grazer crowding. Grazer body mass explained 65% of the variation, while crowding and food availability explained 7 and 6% respectively. Except for the significantly lower removal rate of amphibians, neither taxon of the grazer nor algal composition significantly affected removal rate. Experiments in the laboratory and in outdoor channels tended to give higher removal rates than experiments performed in streams or lakes. A comparison with previous allometric equations predicting the ingestion rate of other invertebrate guilds, and with experiments in which periphyton ingestion rate was measured as incorporation of labelled food, indicated that a large portion of periphyton is removed by the activity of the grazer rather than by direct ingestion. These results could be utilized to predict the impact of grazing on periphyton biomass.

Key words Grazing · Periphyton · Body size · Stream · lake

Introduction

Because of the importance of grazers in determining the distribution and abundance of periphyton in streams and lakes, periphyton grazing has been increasingly studied.

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For example, in a recent review of studies in experimental streams, Lamberti (1993) reported that grazing studies in the 1990s were at least 5 times more common than in the 1970s. The amount of experiments is now voluminous enough to warrant a summary of published data to establish an empirical model of periphyton grazing. In this study, we attempt such a generalization. Because our analyses are based on experimental enclosure or exclosure of grazers, we measure the net effect of grazing on periphyton biomass. We choose to define these measurements as "removal rates" to indicate that they comprise both algal ingestion and the loss of algae due to grazer activity (e.g. locomotion, case building). Ingestion rate models are already available for poikilotherms in general (Capriulo et. al. 1990), deposit feeders (Cammen 1980), and zooplankton (Peters and Downing 1984). These models could be used to estimate ingestion, but they could misrepresent the effect of grazing on periphyton since they do not account for algae dislodged by grazers.

Our analysis also serves to assess the extent of agreement among published studies and as a benchmark for future comparisons. Because the studies have been conducted under different experimental conditions, our model also suggests the importance of different variables on removal rate by grazers. However, the major goal of this analysis is to provide a simple tool to predict the impact of grazers on periphyton biomass.

Methods

Data were collected from a broadly based survey of the literature published from 1975 to date. No references were purposely omitted but some could have been overlooked. We examined articles where removal rate could be calculated by comparing the periphyton biomass in grazed and ungrazed plots. In such experiments, grazers were removed (exclosure experiments) or added (enclosure experiments) to an experimental plot, and periphyton biomass was subsequently compared to that in a reference untreated plot. We calculated periphyton removal rate per grazer per day R using the following equation:

$$R = \frac{\Delta U - \Delta G}{D \times N}$$

Table 1 Conversion factors utilized to transform grazer and periphyton biomasses expressed in other units to dry mass

Conversions	References
Grazers	
Dry mass (mg) = 0.25 wet mass (mg)	a
Dry mass (mg) = 1.18 ash-free dry mass (mg)	a
Periphyton	
Dry mass (mg) = 2.63 ash-free dry mass (mg)	b
Dry mass (mg) = 1.13 chlorophyll a (μg)	c

Conversions are the mean of data presented in:
a Cummins and Wuycheck 1971
b Bowen 1979; Capblancq and Cassan 1979; Eloranta 1982; Eloranta and Kunnas 1979; Gons 1982; Lakatos 1978; McIntire and Phinney 1965
c Hill and Knight 1987; Hill et. al. 1992; Hunter 1980; Lamberti et. al. 1987a, 1987b, 1992; Mulholland et. al. 1991

where U=periphyton biomass in the ungrazed plots, G=periphyton biomass in the grazed plots, D=days over which the change was measured, N=grazer density. In some studies, grazers were manipulated at the beginning of the algal colonization (type 1), while in others (type 2), established communities were manipulated. In type 1 experiments, we ignored both the initial lag phase in periphyton development and the saturation phase when sloughing increases, and therefore considered only the period of periphyton growth in the controls. We could not consider the initial lag phase because, during that phase, periphyton biomasses were too low to differentiate reliably between treatments and controls. In type 2 experiments, we also considered only the period when periphyton biomass was increasing in the controls to avoid confusion between the effects of substratum saturation and those of grazing. Is a few grazing studies, the ingestion of periphyton was measured a short-term uptake of labelled food. These measurements are not homologous to those derived from enclosure-exclosure experiments and therefore were not included in our statistical analysis of removal rates, but are used in subsequent comparisons.

We expressed algal and grazer biomass as dry mass. When necessary, data expressed in wet mass, ash-free dry mass, or chlorophyll were converted to dry mass. When the conversion was not supplied in the article, we used several conversion factors calculated from the literature (Table 1). When only the length of grazers was provided, we calculated their dry mass by applying published mass-length relationships (Eckblad 1971; Smock 1980; Meyer 1989). More rarely, only the species and the developmental stage of the grazer were mentioned in the articles. In those cases, an average weight was estimated from taxonomic descriptions in the literature. For snails, we always considered the dry mass free of shell.

Besides mass of periphyton and grazers, we extracted from each reference several variables that could affect the removal rate. We recorded the degree of grazer crowding (total biomass per unit of substratum), the available periphyton (the biomass in the ungrazed plot), and temperature (°C). When temperature was not provided in the article, we estimated it using an empirical model based on latitude (Straškraba 1980). We considered also the effect of a number of discrete qualitative variables by coding the data for grazer taxon, environment (lake, stream, laboratory), substratum (natural and artificial), experiment type (1 and 2), and algal composition [diatoms dominant (>70%); chlorophytes dominant (>70%); diatoms+chlorophytes].

We analysed the data by simple and multiple regression using the Statistix statistical package. The data were transformed to logarithms prior to analysis because this transformation linearizes body-size relationships. Residuals (observed minus predicted) of these regressions were assessed statistically for the effect of different grazer taxa, environments, substrata, and algal compositions with the Kruskal-Wallis non parametric analysis of variance, and visually, with box-and-whiskers plots (Tukey 1977).

Table 2 Experimental conditions under which removal rates were measured. For continuous variables we present the median and the range, while for categorical variables we present the number of data (number of studies in brackets) in each category. The references on which the calculations are based are: Cattaneo 1983; Cuker 1983; Dickman 1968; Doremus and Harman 1977; Eichenberger and Schlatter 1978; Feminella et. al. 1989; Gresens and Lowe 1994; Hart 1987; Hill and Knight 1987, 1988; Hill et al. 1992; Hunter 1980; Jacoby 1985, 1987; Kesler 1981b, Lamberti et. al. 1987a, 1987b, 1989, 1992; Mason and Bryant 1975; Mulholland et. al. 1991; Murphy 1984; Steinman 1991; Steinman et. al. 1987; Stewart 1987; Sumner and McIntire 1982; Tuchman and Stevenson 1991

Variable	Symbol	Unit	Median	Range
Grazer body mass	M	mg	14.75	0.04–2082
Grazer crowding	C	mg/m²	1349	20–18000
Food availability	P	mg/m²	47530	127–526000

Grazer taxa: Chironomids 8 (4); mayflies 9 (3); caddisflies 27 (6); snails 43 (15); amphipods 1 (1); amphibians 15 (2); fishes 4 (1)
Algal composition: Diatoms>70% 38 (13); chlorophytes>70% 14 (9); diatoms+chlorophytes 35 (6)
Environment: Stream 27 (9); lake 13 (5); outdoor channel 41 (6); laboratory 26 (7)
Substratum: Natural 36 (7); artificial 71 (20)
Method: Type I 43 (10); type II 64 (17)

Results and Discussion

Data

We found 27 publications in which removal rate could be calculated. Inclusion of different types of grazers, different grazer crowding, and periphyton availability resulted in a total of 107 data points from the 27 publications. The data were generated under widely different experimental conditions (Table 2). Snails and caddisflies were the grazers most often used, whereas less information was available for the smallest (chironomids and oligochaetes) and largest (amphibians and fishes) grazers. Studies were almost equally subdivided among the different environments, but experiments in outdoor channels and the laboratory yielded more data because these studies were more likely to examine several grazers and several levels of crowding and periphyton availability than experiments in natural environments. Algal assemblages were typically a mixture of chlorophytes and diatoms, but dominance by diatoms was more common than by chlorophytes.

Regression analysis

Multiple regression analysis of the data shows that removal rate (R; mg dry mass per day per grazer) is correlated positively with grazer body mass (M; mg dry mass) and food availability (P; periphyton biomass; mg/m²),and negatively with crowding (C; total grazer biomass; mg/m²). The equation

$$\log R = 0.179 + 0.99 \log M - 0.71 \log C + 0.46 \log P \qquad (1)$$

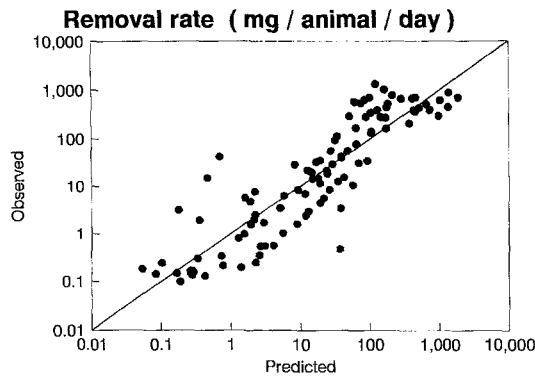n=104; r^2=0.78; F=125; P<0.0001

Fig. 1 Relationship between the removal rates of periphyton by grazers predicted by Eq. 1 and those observed. The *line* represents a 1:1 relationship
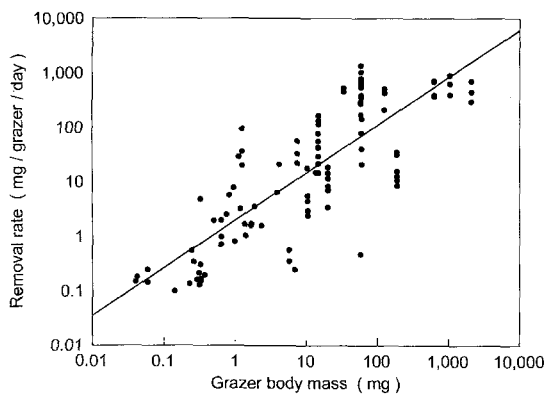

Fig. 2 Relationship between the removal rate of periphyton and the grazer body mass (Eq. 2)

Fig. 3 Removal rate of periphyton predicted by Eq. 1 for different grazer sizes. The *top panel* shows the effect of different levels of crowding when the periphyton availability is fixed at the median level of 47530 mg/m². The effect of periphyton availability is instead presented in the *lower panel* where Eq. 1 is solved keeping grazer crowding fixed at the median value of 1349 mg/m²

explains 78% of the variation observed in removal rate (Fig. 1).

The median residual shows that observed values differ from the predicted values by a factor of 2.2, but in the worst cases the difference could exceed an order of magnitude (Fig. 1).

Grazer body mass is the most important correlate of removal rate. A simple regression using only grazer body mass explains 65% of the variation in removal rate (Fig. 2):

$$\log R = 0.293 + 0.87 \log M \qquad (2)$$

$n=107$; $r^2=0.65$; $F=203$; $P<0.0001$

Grazer crowding and food availability explain respectively 7% and 6% of the remaining variation in removal rate. Their effects are illustrated graphically (Fig. 3) by solving Eq. 1 for fixed grazer body masses when either of food availability or grazer crowding is kept constant at its median value. A tenfold increase in crowding decreases removal rate approximately 5 times. A decrease in grazing efficiency with increasing density has been noticed in previous studies (Doremus and Harman 1977; Lamberti et. al. 1987a). At high grazer densities, there is competition for a limited food source and increased ag-
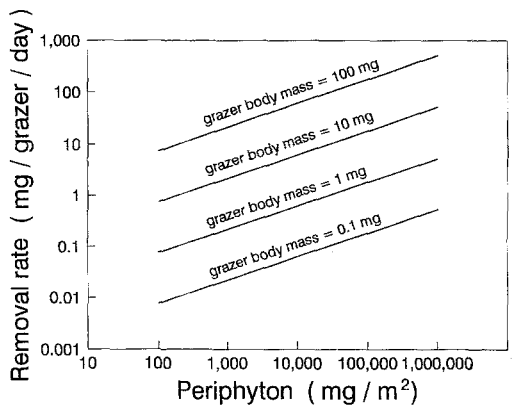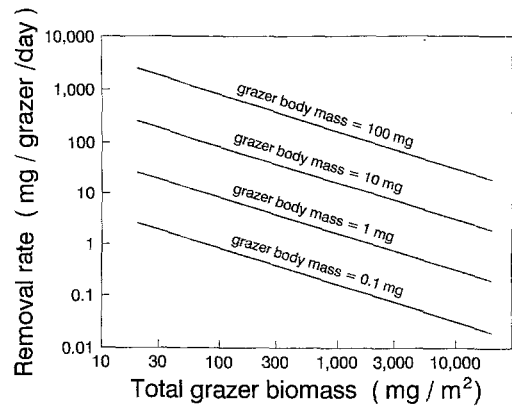
gressive behaviour (Lamberti et. al. 1987a). A negative effect of crowding has also been observed in the filtering and feeding rates of zooplankton (Peters and Downing 1984).

The amount of periphyton available has instead a positive effect on grazing: removal rate is tripled with a tenfold increase in periphyton biomass. This result is not surprising, for herbivores would normally consume more when food limitation is reduced. In addition, grazer movements through a thick and more easily detachable community could result in increased algal export. Apparently the effects of grazing are less pronounced in a biomass-poor environment.

Temperature is not significantly correlated with removal rate. Because temperature is important in all physiological processes, this lack of significance is somewhat surprising. Perhaps the effects of temperature are too small to be detected in our model where the residual variation is rather large. The range in temperature in our study (9–26°C) is also somewhat limited compared to the potential natural ranges. In any case, the temperature effect is smaller than those of crowding and periphyton availability.

Because the inclusion of several points from the same study could bias our results, we also analysed the data

choosing only one entry for each taxon under study in each source. When we had to choose among several possible entries in a given paper, we used the one where grazer crowding and periphyton availability were the closest to the natural ones; when the natural conditions were not stated, we choose intermediate conditions. These data confirm the importance of grazer mass in explaining the variation in removal rate. The regression on size is:

$$\log R = 0.215 + 0.89 \log M \tag{3}$$

$n=40$; $F=94$; $r^2=0.70$; $P<0.0001$

This equation is similar in slope, intercept, and coefficient of determination to Eq. 2 obtained with the entire data set, suggesting that the inclusion of several data from single papers has not biased our results.

Effect of other variables

To test the effect of other experimental conditions on removal rate we compared the residual variation around Eq. 1 among different grazer taxa, environments, substrata, and algal assemblages. Visual inspection of box-and-wiskers plots (Fig. 4) suggests that removal rate is similar among all grazer taxa, except amphibians which tend to have significantly lower rates. This visual suggestion is confirmed by a Kruskall-Wallis non-parametric analysis of variance. There is a significant difference among grazers when all taxa are considered ($P=0.01$), but this disappears when amphibians are excluded ($P=0.57$). The lower rates observed for amphibians may result because some tadpoles feed by filtering as well as scraping, whereas our estimates reflect only grazing. Since these rates are based on only two studies, further testing is necessary. A more robust comparison can be made between caddisflies and snails where more studies are available (Table 2). Surprisingly, there is no significant difference between these two grazers despite large morphological and behavioral differences. In an experiment utilizing both caddisflies (*Dicosmoecus*) and snails (*Juga*), Steinman et. al. (1987) calculated higher rates for caddisflies, probably reflecting their higher motility. This trend is not confirmed in our more general comparison.

Removal rates calculated in experiments in lakes and streams tend to be lower than those measured in experimental systems, such as laboratory or outdoor channels (Fig. 4; Kruskall-Wallis $P=0.02$). In the natural environment, alternative food resources may reduce grazing pressure and/or grazers could be less active because of the presence of predators even if they are not directly accessible to predation. Cyr and Pace (1993) report a similar difference between observed ingestion rate in zooplankton in the field and rate predicted from laboratory studies.

We also note a slight tendency for removal rates to be higher on natural than artificial substrata ($P=0.05$). No
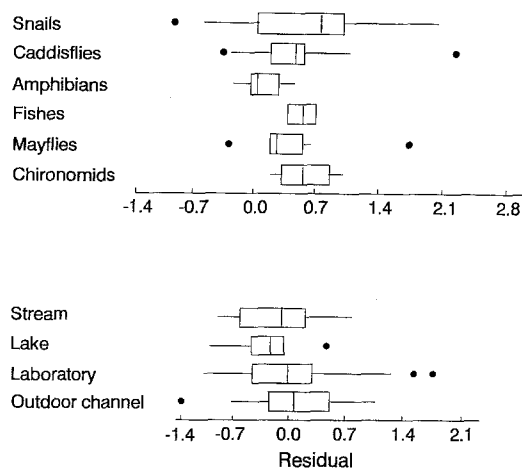

Fig. 4 Box-and-whisker plots of the residuals of Eq. 1 observed for different taxa (*top panel*) and different environment (*lower panel*). The median value is marked by the *central line*; 25- and 75-percentile values form the *ends of the box*; *whiskers* delimit the range of the observations except for extreme values, defined as those that lie beyond 1.5 × the box length. These extremes are represented by *points* (Tukey 1977)

significant differences (Kruskall-Wallis non-parametric analysis of variance) are found among removal rates in communities with different algal composition ($P=0.21$). However, the classes of community structure that we could establish in our general analysis are very broad, so we cannot exclude the possibility that finer differences in algal taxonomy affect grazing rate. The measurements of removal rate are similar ($P=0.64$) whether the grazers are introduced at the beginning of the colonization (type 1) or in established algal assemblages (type 2), at least when the initial lag phase is not considered.

Residual analysis of Eq. 3 based on the reduced data set is less powerful, because of the smaller number of cases, but identifies the same trends.

Comparison with other empirical models

We compared our predictions of periphyton removal rate of grazers to other allometric equations predicting the ingestion rate of poikilotherms in general (Capriulo et. al. 1990), deposit feeders (Cammen 1980), and zooplakton (Peters and Downing 1984). We also compared our removal rate with experiments in which ingestion of periphyton by grazers was measured by isotope uptake (Fig. 5). For these comparisons we used Eq. 3 based on natural levels of grazer crowding and periphyton availability. The ingestion model closer to our predictions of removal rate is that for deposit feeders. The intercepts of the two equations are very close, but, while the slope of the deposit feeder relation (0.74) is very similar to the usual allometric slope of 0.75, the removal rate increases more sharply with size (slope 0.89). Zooplankton ingestion is much lower than all the other relationships. The equation predicting the ingestion rate for poikilotherms in general is parallel to our model of removal rate but there is about
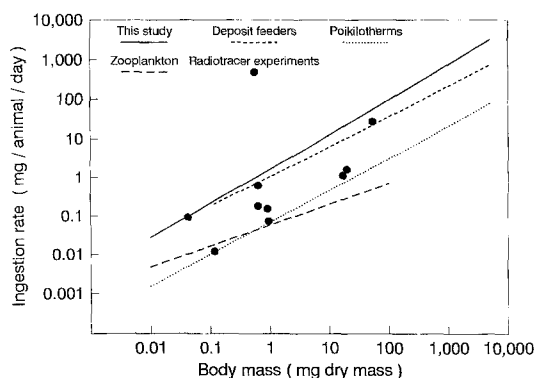
Fig. 5 Comparison between our model (Eq. 3) of removal rate by grazers as function of grazer size and the allometric equations that predict ingestion rate for deposit feeders (Cammen 1980), zooplankton (Peters and Downing 1984), and poikilotherms in general (Capriulo et. al. 1990). The *points* indicate the ingestion rates of periphyton grazers measured by incorporation of labelled food. From: Calow and Fletcher 1972; Kairesalo and Koskimies 1987; Kesler 1981a; Lamberti et. al. 1989; Malone and Nelson 1970; McCullough et. al. 1979; Rounick and Winterbourn 1983; Trama 1972

an order of magnitude difference in the intercept. Measurements of grazer ingestion rate obtained in radiotracer experiments fall between the lines for our model and that for poikilotherms. The equation fitting these grazer ingestion values (I; mg/grazer/day)

$$\log I = -0.566 + 0.83 \log M$$
$$n=8; \ r^2=0.68; \ F=16; \ P=0.004$$

indicates that, on average, grazing rates are 6 times lower than removal rate. This discrepancy could be in part related to the methodological differences between radiotracer experiments and enclosure-exclosure experiments. In zooplankton, radiotracer experiments yield lower filtering and feeding rates (Peters and Downing 1984). Probably this difference arises from the fact that removal rate of periphyton by grazers includes the effect of physical damage due to locomotion, case building and other activities. This "export rate" in grazing experiments has been measured only rarely (Castenholz 1961; Eichenberger and Schlatter 1978; Sumner and McIntire 1982; Lamberti et. al. 1987b) but these studies suggest a large effect of mechanical disturbance on the removal rate of periphyton. Grazers are very messy consumers, almost as wasteful as the average North American who discards 10 times the energy that he or she consumes (Antoine Morin, University of Ottawa, personal communication). However, this waste contributes to algal seston and to the detrital food chain and is probably very important for the economy of the stream (Lamberti et. al. 1987b).

Applications and limitations

Despite the heterogeneity of the literature on which this study is based, and the use of several conversion factors,

there is broad consistency in the results. The general equations that we have calculated likely provide less biased predictions than any single datum in the literature. Because these equations account for periphyton removal by both direct ingestion and detachment, they should provide a more realistic prediction of grazer impact than models based solely on ingestion rate. Those models would instead be more appropriate for estimating energy flow to grazers.

Our analysis points to the importance of experimental conditions on removal rate. Removal rate of individual grazers will be highest when the grazer population is sparse but in a rich environment. Because of these environmental effects, grazing experiments should involve realistic densities of grazers and periphyton. One strong limitations of all grazing experiments is that interspecific effects of facilitation or competition between grazers are not measured. Due to the logistic limitations of the experiments, grazers are all of the same size and taxon. When several grazer types are examined in one study, they are usually in separate channels or plots. The consequence of this artificiality on the measurements of removal rate remains to be explored.

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