Oecologia (1991) 85:343–348

Oecologia
© Springer-Verlag 1991

Mechanisms of algal patch depletion: importance of consumptive and non-consumptive losses in mayfly-diatom systems

Garry J. Scrimgeour[1], **Joseph M. Culp**[1,2], **Max L. Bothwell**[2], **Frederick J. Wrona**[1], **and Malcolm H. McKee**[1]

[1] Aquatic Ecology Group, Department of Biological Sciences, University of Calgary, Calgary, Alberta, T2N 1N4 Canada
[2] Environmental Sciences Division, National Hydrology Research Institute, 11 Innovation Blvd., Saskatoon, Saskatchewan S7N 3H5, Canada

Received April 20, 1990 / Accepted in revised form August 28, 1990

Summary. Laboratory experiments were performed to identify the mechanisms by which three mayfly grazers, *Baetis tricaudatus, Ephemerella aurivilli* and *Paraleptophlebia heteronea* deplete algae from substrates. Field observations indicated these mayflies foraged predominantly (> 70% of all individuals) within small (1–2 cm diameter), low biomass areas where algal biomass was significantly lower than the surrounding algal mat. We postulated four models of algal patch depletion based on the combined effects of a type II functional response consumptive model and four possible forms of non-consumptive loss. These models were tested in laboratory feeding trials by examining the relative importance of consumptive and non-consumptive removal of the diatom, *Navicula* sp., by the three common mayfly grazers. The trials were conducted in plexiglass streams that contained substrates with one of five biomass levels (0.11, 0.24, 0.43, 0.65, 0.92 mg/cm^2 dry weight) of the diatom food. After each 1 h feeding trial, consumption was measured, and the remaining algae scraped from the substrates so non-consumption and total patch depletion could be determined. Consumption by all three species followed a type II functional response; mayflies were capable of grazing diatom layers of extremely low biomass (0.11 mg/cm^2) and reached an asymptotic feeding rate when diatom biomass ranged from 0.24–0.43 mg/cm^2. Upper asymptotic feeding rates occurred at algal biomasses that were 20 times lower than algal biomass levels within foraging areas in the field and > 50 times the overall mean algal biomass on upper stone surfaces in the Bow River. When diatom biomass was low (0.11 mg/cm^2), the amount of algae ingested accounted for 27%-75% of total depletion of algal patches. Above this level, non-consumptive, foraging-related losses increased. Thus, depletion of diatom patches was non-linear and positively related with diatom biomass due to the disproportionate increase in non-consumptive losses combined with the type II functional response consumptive model (Case 4). This disproportionate increase in non-consumptive loss may result from (i) a passive process attributable to mechanical limitations of the feeding apparatus, (ii) an active selection process during foraging or (iii) instability of the diatom material resulting in disproportionately high foraging related dislodgement. Regardless of the mechanism, our experiments indicate the importance of considering algal patch depletion by mayfly grazers as a dual product of consumptive and non-consumptive foraging processes. Furthermore, the non-linear increase in nonconsumptive loss with increased algal biomass suggests this process may be a major mechanism of algal patch depletion by mayflies when algal biomass is high.

Key words: Herbivory – Functional response – *Baetis tricaudatus – Ephemerella aurivilli – Paraleptophlebia heteronea*

Grazing invertebrates can have strong community effects by altering species diversity, biomass, distribution and turnover rates of plants in aquatic and terrestrial ecosystems (Underwood and Jernakoff 1981; Lamberti and Resh 1983; McAuliffe 1984; Schowalter et al. 1986; Hill and Knight 1987). The ability of stream grazers, such as mayfly and caddisfly larvae, to reduce periphyton biomass and alter species composition to communities numerically dominated by diatoms is also well known (Lamberti and Resh 1983; Hart 1985; Lamberti et al. 1987; Steinman et al. 1987; McCormick and Stevenson 1989). For example, the mayfly nymph *Heptagenia criddlei* (Heptageniidae) reduced algal biomass by 80% after 10 days when mayfly density exceeded a threshold of 2800 m^2 (Colletti et al. 1987). At this density, *H. criddlei* also altered algal community structure from large (30 μm in length) upright diatom species which form the overstory assemblage, to smaller adnately attached species. Other mayfly larvae (e.g. *Ameletus*, Siphlonuridae) have also been shown to depress periphyton biomass to 1.83 g/m^2 at half ambient densities in stream enclosures (Hill and Knight 1987). Similarly, grazing by the larval caddisfly, *Helicopsyche*, resulted in low biomass organic

---

Offprint requests to: G. Scrimgeour

layers (0.3–1.4 μg/cm^2 chlorophyll *a*, bacteria 0.3–0.7 × 10^8 cell/cm^2) with a high turnover rate (Lamberti and Resh 1983). In fact, foraging by a stream herbivore *(Leucotrichia pictipes)* reduced algal biomass and altered species composition such that low biomass layers consisted predominantly of diatoms. In the absence of *L. pictipes* foraging, areas were rapidly overgrown by blue-green algae, apparently an unsuitable food source (Hart 1985).

Despite the large number of studies investigating the effects of grazers on lotic algal communities, the mechanisms by which grazers reduce the biomass of periphytic layers are unclear. Depletion of algal patches is likely related to losses of algal biomass through forager consumption (i.e. ingestion) and non-consumptive, foraging related disturbances (Lamberti and Resh 1983). Interestingly, non-consumptive foraging losses have been found to exceed ingestion for some stream-dwelling snails grazing on algae (Lamberti et al. 1989) and for terrestrial grazers (Hatto and Harper 1969, data presented in Harper 1977; Andrzejewska and Wojick 1970). Moreover, grazer-mediated disturbance of algae may be important for our understanding of trophic linkages because foraging-mediated export of algal material may be an important source of energy for downstream consumers (Lamberti et al. 1987; Power et al. 1988; Lamberti et al. 1989). However, the relative importance of consumptive and non-consumptive foraging losses in maintaining low biomass algal layers in streams is unknown.

This study examines the feeding of three mayfly grazers, *B. tricaudatus*, *P. heteronea*, *E. aurivilli* and related algal patch depletion. Field observations were performed to determine the microdistribution of each mayfly species on stone surfaces and their related foraging effects on periphytic algal communities. Additional laboratory experiments measured consumptive (i.e. the functional response), non-consumptive and total loss of biomass from monoculture patches of the diatom, *Navicula*. We compared these results to expectations from four general models which predict qualitative patterns in total algal biomass loss under a variety of non-consumptive loss mechanisms. From these comparisons we identify the relative importance of consumptive and non-consumptive losses by which these grazers deplete diatom mats.

Methods

Models of consumptive and non-consumptive foraging losses

Depletion of algal patches by grazers is determined by the combined effects of consumption (i.e. functional response) and non-consumptive foraging related losses. Consumptive loss most probably follows a type II functional response, since it is often appropriate for invertebrate grazers (Harper 1977; Downing 1981). This can be described by:

$$p(x) = ax/(1 + aT_h x)$$

where p is the predators functional response, x is prey density, a is the attack coefficient, and T_h is handling time (Holling 1959; Friedman 1980) (Fig. 1). Although the relationship between non-consumptive foraging losses (N_{cl}) and algal biomass may take a wide variety of qualitative and quantitative patterns, four general cases can be postulated. Case 1 represents the simplest situation where non-consumptive losses do not occur ($N_{cl} = 0$), resulting in the total measured algal biomass loss from a patch being equal to consumptive losses (i.e. the functional response). Case 2 represents the situation where non-consumptive losses are numerically constant with increasing algal biomass (i.e. density independent). This yields a total depletion that is qualitatively similar in pattern to the functional response, but differs quantitatively by the absolute amount of loss (Fig. 1a). Cases 3 and 4 predict the expected pattern of total loss when non-consumptive loss is density-dependent (Fig. 1b and c). Case 3 arises when non-consumptive loss is a constant proportion of algal biomass, while in Case 4 the non-consumptive loss is an increasing proportion of algal biomass.

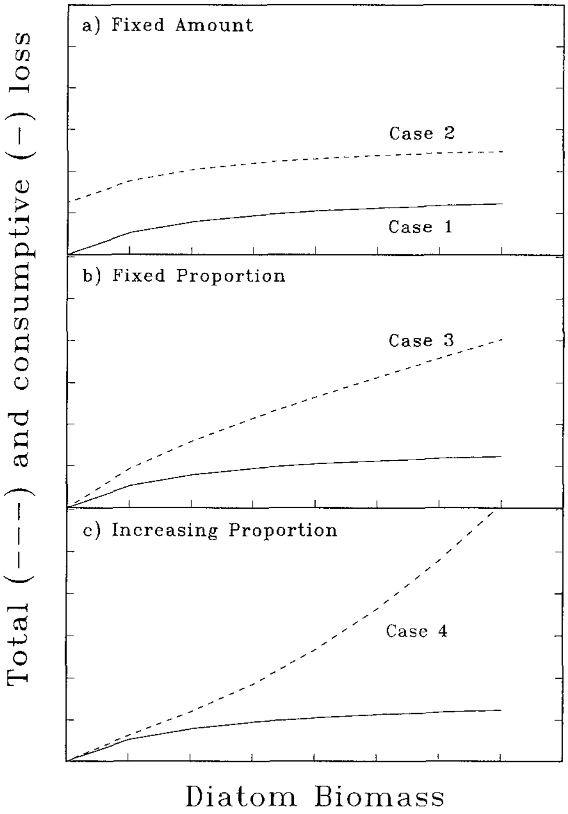

Fig. 1a–c. Predicted qualitative changes in total patch depletion based on combined effects of consumption (type II functional response) and four non-consumptive loss models. Non-consumptive loss (N_{cl}) models are: **a)** Case 1, where total patch depletion equals type II functional response; **a)** Case 2, constant loss, $N_{cl} = p(x) + \text{constant}$; **b)** Case 3, constant percentage of diatom biomass, $N_{cl} = f(x)$; **c)** Case 4, increasing proportion of diatom biomass, $N_{cl} = g(x)$

Study animals. Mayfly nymphs *Baetis tricaudatus* (Banks) (Baetidae), *Ephemerella aurivilli* Bengtsson (Ephemerellidae), and *Paraleptophlebia heteronea* (McDunnough) (Leptophlebiidae) are common insect herbivores that graze periphyton from stone surfaces in many streams of southern Alberta, Canada. In such streams these numerically dominant grazers can establish low biomass periphytic layers where they forage (Scrimgeour and Culp Unpubl. data). Although, similar observations have been made by Wiley and Kohler (1984), Hart (1985), and Lamberti et al. (1987), no study has attempted to quantify the mechanisms by which mayfly grazers deplete algal patches.

The field and laboratory systems

Field observations. Field observations of *Baetis*, *Paraleptophlebia*, *Ephemerella* on stone surfaces were made in two Alberta streams (Big Hill Springs Creek, 27 June; Bow River, 12 July) in summer 1989. Observations were made at one time period during the day (1200 h MDST, 6h after sunrise) and the night (0400 h MDST, 5 h after sunset) using transparent plexiglas boxes (50 × 50 × 10 cm) to facilitate viewing. By approaching the observation area from downstream and by avoiding casting shadows on the sample area, mayfly behaviour was not detectably altered by the observation process. To enable accurate observations between dusk and dawn, a low intensity red light was used to illuminate the substrate (Allan et al. 1986). On each sampling occasion, we counted the number of mayflies foraging on upper stone surfaces (i.e. tops and sides) of 4–7 large stones (16–64 cm^2) and noted whether mayflies were grazing within low biomass periphytic layers which were determined qualitatively by eye. At a later date (9 May 1990) quantitative differences in algal biomass on upper stone surfaces within foraging areas and in the surrounding thicker algal layer were documented in the Bow River. Between 0330–0500 MDST we randomly selected 15 stones (16–64 cm^2) from each of three riffles and recorded the position of foraging *Baetis, Ephemerella, Paraleptophlebia* on upper stone surfaces. The stones were collected and algae scraped from within foraging areas and from surrounding areas on upper stone surfaces with a stiff brush after the respective areas were delimited by a 1.0 cm^2 neoprene disk. Stone surface scrapings were dried to constant weight at 60° C and weighed to the nearest 0.01 mg on a Cahn electrobalance.

Laboratory experiments. Late instar larvae of *Baetis*, (mean body length ± 1 SE = 5.4 ± 0.3 mm) *Ephemerella* (4.9 ± 0.3), and *Paraleptophlebia* (5.2 ± 0.4) were collected from the Bow River, a fifth order river in Calgary, Alberta, Canada (51 03 00 N, 114 03 00 W) during the period 22 May–4 June, 1989. Individuals were maintained for 2–4 weeks prior to experiments in holding tanks with still water in the laboratory at 11° C with a 16:8h day/night cycle. During this period, larvae were fed an ad-libitum supply of *Navicula* sp., a pennate diatom that is an important food source of all three mayfly species (Scrimgeour unpubl. data).

Feeding trials of mayflies on diatom patches were conducted in small (0.25 l, 50 cm^2), plexiglass streams (Walde and Davies 1984) to which filtered and oxygen saturated water was circulated (mean water velocity (±1 SE) = 7.6 (±0.2) cm/s; water temperature 11° C). Since all three species feed at night in the field, experiments were conducted in the dark between 0800–1600h MDST. Mayflies experienced a reversed day/night cycle for 48h (2 complete day/night cycles) prior to experiments. Food in each stream was present on the top surface of five plexiglass substrates (length, width and height = 2 × 1 × 1 cm). Algal mats were produced for the trials by inoculating plexiglass substrates with *Navicula* and algal biomass manipulated by varying the time period that substrates were maintained in culture. Diatoms were cultured in still water as pilot studies showed this method produced diatom layers of uniform biomass (mean CV = 12% across five biomass levels 0.11, 0.22, 0.43, 0.63, 0.92 mg/cm^2).

By culturing diatoms in still water, we assume that meal size and non-consumptive foraging related losses are not significantly affected by diatom culture method (i.e. still or flowing water). To test this hypothesis, we conducted an experiment where individual larvae were allowed to feed for a 1 h period on diatom mats cultured in either flowing (small plexiglass streams) or still water (Pyrex dishes). Experiments were conducted in small streams (0.25 l) containing five plexiglass substrates (2 × 2 × 1 cm) with upper surfaces covered with a diatom mat (diatom biomass = 0.42 mg/cm^2) and were replicated five times for all three mayfly species. The hypothesis that ingestion rates and non-consumptive losses were not significantly affected by diatom culture method (still, flowing) and mayfly species *(Baetis, Paraleptophlebia, Ephemerella)* was tested with a model 1, two-factor analysis of variance (ANOVA).

Larvae were acclimated to experimental conditions for 24 h prior to experiments and then starved for 24 h to clear foreguts. A pilot study showed that there was no significant difference in ingestion rates of starved (starvation period = 24 h) and fed (starvation period = 0 h) individuals at a diatom biomass of 0.42 mg/cm^2 for *Baetis* ($t = -0.17$, $P > 0.50$, $N = 5$), *Paraleptophlebia* ($t = -0.10$, $P > 0.50$, $N = 5$) and *Ephemerella* ($t = -0.69$, $P > 0.50$, $N = 5$). Each feeding trial consisted of allowing an individual to forage in a stream for a 1 h period. After this time, larvae were removed from streams and preserved in 10% formalin. Regurgitation of mayfly gut contents was not observed. Recently ingested material forms a distinct bolus in the foregut, and was removed under 12 × magnification. The remaining algae on grazed substrates was scraped using a scalpel. Total patch depletion equaled the difference between initial and final diatom biomass, and consumptive loss equalled the mass of larvae gut contents. Non-consumptive loss equaled the difference between total and consumptive losses. Experiments were replicated five times at each of the diatom biomass levels for all three mayfly species. Algae from all substrates in a given stream and ingested material were dried to constant weight at 60° C and weighed to the nearest 0.01 mg.

Statistical analysis and curve fitting. Non-linear curve fitting (Williams and Juliano 1985; Trexler et al. 1988) using the Quasi-Newton method on SYSTAT (Wilkinson 1988) was used to discriminate among functional response models I, II, III and to calculate model parameters: a (attack coefficients), b (handling times) and their respective 95% confidence intervals.

The hypothesis that meal size was not significantly affected by diatom biomass, mayfly species or the interaction of these factors was tested with a model 1 two-factor ANOVA. For all analyses, data were transformed by $\log_{10}$ transformation to remedy inequality of variances as indicated by examination of residuals. The hypotheses that: (1) total patch depletion and (2) feeding efficiency [(biomass of ingested material/total patch depletion) × 100] was significantly affected by diatom biomass and mayfly species was tested with analysis of covariance (ANCOVA). For all analyses an alpha < 0.05 was used.

Results

Field observations

Individual foraging mayflies were often (> 70%, n = 150 observations) found grazing within circular (range 1–2 cm diameter) low biomass periphytic layers which were interspersed among thicker algal layers. In particular, *Ephemerella* and *Baetis* in the Bow River, and *Baetis* in Big Hill Springs Creek grazed within low biomass periphytic layers on upper stone surfaces. Numbers of mayflies foraging on upper stone surfaces were significantly higher (Paired *t*-test: $t = 4.2$, $df = 15$, $P < 0.001$) during the night ($\bar{x} = 188.8\ m^2$) than the day ($\bar{x} = 51.0\ m^2$) in the Bow River in July 1989 and in Big Hill Springs Creek in September 1989 (night: $\bar{x} = 428\ m^2$, day $\bar{x} = 332\ m^2$, $t = 3.03$, $df = 7$, $P < 0.02$). Mean algal biomass within foraging areas in the Bow River ($\bar{x} = 4.94\ mg/cm^2$ DW) was significantly lower ($t = 2.74$, $P < 0.01$) than overall algal biomass (13.55 mg/cm^2) on upper stone surfaces.

Consumptive and non-consumptive loss

Meal size and total patch depletion were not significantly affected by diatom culture method ($F = 1.94$, $F = 1.63$,

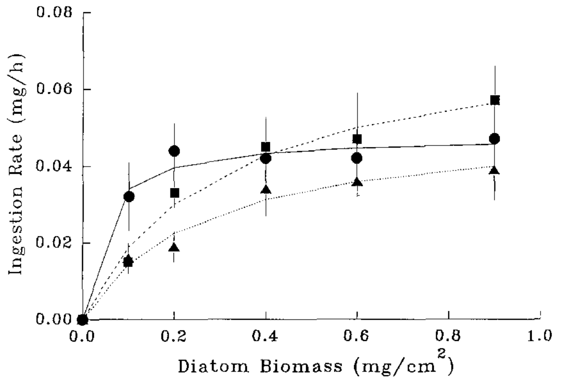

Fig. 2. Functional response curves (ingestion rate $\bar{x} \pm 1SE$) of ingestion rates for the mayflies *Baetis* (■), *Ephemerella* (●), and *Paraleptophlebia* (▲) when grazing on patches of the diatom prey, *Navicula*

Table 1. Attack coefficients (mg/h) (a) and handling times (mg/h) (T_h) ($\pm$95% CI) of *Baetis, Paraleptophlebia* and *Ephemerella* grazing diatoms in laboratory streams determined from a type II functional response model, $p(x) = ax/(1 + aT_hx)$

Species	a	T_h
Baetis	0.18 ± 0.07	11.7 ± 4.0
Paraleptophlebia	0.18 ± 0.06	18.9 ± 6.0
Ephemerella	1.03 ± 0.32	20.9 ± 7.0

$P < 0.001$) or the interaction of mayfly species and culture method ($F = 1.48$, $F = 1.49$, $P > 0.05$) at a diatom biomass of 0.42 mg/cm^2, although these were significantly affected by mayfly species (ANOVA: meal size $F = 23.53$, total patch depletion $F = 18.69$, $P < 0.001$).

Loss of diatoms from control streams (i.e. mayflies absent) due to dislodgement by the current was <2% diatom biomass for all diatom biomass levels. All mayfly species displayed a type II functional response, that is, a decelerating curve to a positive asymptote. This model accounted for more of the variation in foraging rate *Baetis* ($r^2 = 0.96$), *Paraleptophlebia* ($r^2 = 0.97$), and *Ephemerella* ($r^2 = 0.96$) than a type I or type III model for all species ($r^2 < 0.56$). Upper asymptotic feeding rates were reached when diatom biomass ranged from 0.24 to 0.43 mg/cm^2 (Fig. 2). Meal sizes were significantly affected by the interaction of diatom biomass and mayfly species ($F = 4.76$; $P < 0.001$). This significant interaction is likely related to the high attack coefficient of *Ephemerella* which resulted in a rapid increase in grazing rate to an upper asymptote at a diatom biomass of 0.24 mg cm^2 (Table 1). In contrast, attack coefficients for *Baetis* and *Paraleptophlebia* were five times lower and grazing rates increased more slowly to upper asymptotes at a diatom biomass of 0.43 mg/cm^2. Handling times (T_h) ranged from 11.64–20.85 mg/h but did not differ significantly among species as indicated by overlap of 95% confidence intervals (Table 1). Mean prey depletion was <31% of the total diatom biomass and predator satiation did not occur since recently ingested material filled <10% of the foregut region.

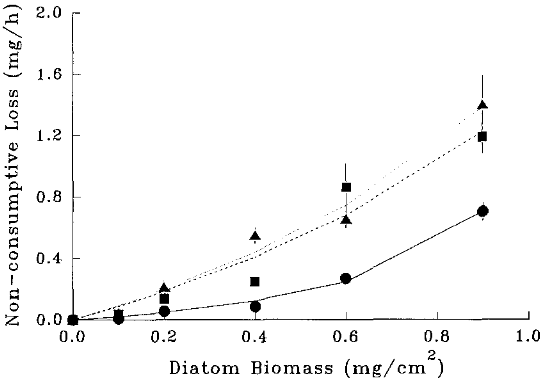

Fig. 3. Linear regressions of non-consumptive foraging related losses (N_{cl}) ($\bar{x} \pm 1SE$) by *Baetis* (■), *Paraleptophlebia* (▲), and *Ephemerella* (●) and diatom biomass (B). *Baetis* log $N_{cl} = -1.47 + 1.80(B)$ ($r^2 = 0.82$, $P < 0.01$), *Paraleptophlebia* log $N_{cl} = -1.14 + 1.49(B)$ ($r^2 = 0.86$, $P < 0.001$), *Ephemerella* log $N_{cl} = -1.91 + 1.61(B)$ ($r^2 = 0.88$, $P < 0.001$). Statistical analyses were performed on the linearized, transformed data

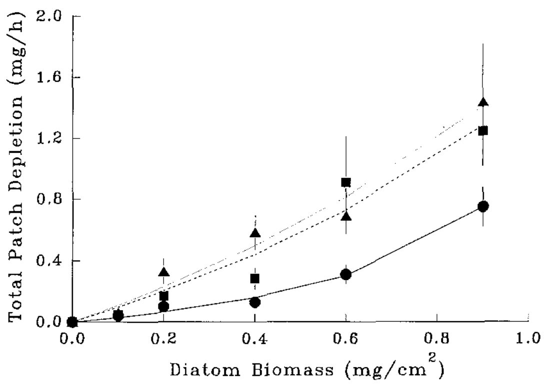

Fig. 4. Linear regressions of mean ($\pm$1SE) total patch depletion of diatom patches (D) by *Baetis* (■), *Paraleptophlebia* (▲) and *Ephemerella* (●) and diatom biomass (B). *Baetis* log $D = -0.19 + 1.55(B)$ ($r^2 = 0.86$, $P < 0.001$), *Paraleptophlebia* log $D = -1.06 + 1.40(B)$ ($r^2 = 0.75$, $P < 0.001$), *Ephemerella* log $D = -1.39 + 1.03(B)$ ($r^2 = 0.78$, $P < 0.001$). Statistical analyses were performed on linearized, transformed data

Non-consumptive, foraging-related losses for all three mayfly species were non-linear and positively related with diatom biomass (Fig. 3). There were also significant differences in regression slopes among species (ANCOVA for coincidental slopes $F_{(2,87)} = 39.62$, $P < 0.025$), with slopes for *Paraleptophlebia* and *Baetis* being higher than for *Ephemerella.*

Total patch depletion and feeding efficiency

Depletion of diatom patches by *Baetis, Ephemerella* and *Paraleptophlebia* was non-linear and positively related with diatom biomass (Fig. 4). This is due to the disproportionate increase in non-consumptive losses combined with the type II functional response consumptive model (i.e. Case 4). Depletion rates differed significantly among mayfly species; *Paraleptophlebia* larvae reduced algal patches at a significantly greater rate than *Baetis* or

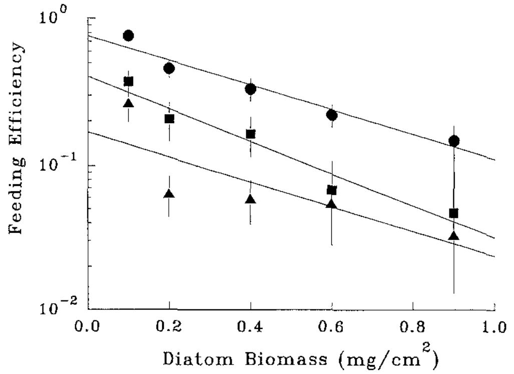

Fig. 5. Linear regressions of mean (± 1SE) (FE) feeding efficiency. [FE = (mean meal/total patch depletion)] × 100 for *Baetis* (■), *Paraleptophlebia* (▲), and *Ephemerella* (●) and diatom biomass (B). *Baetis* log FE = − 1.304–1.658(B) ($r^2 = 0.86$, $P < 0.001$), *Paraleptophlebia* log FE = − 0.753–0.898(B) ($r^2 = 0.76$, $P < 0.001$), *Ephemerella* log FE = − 0.096–0.85(B) ($r^2 = 0.87$), $P < 0.001$). Statistical analyses were performed on linearized, transformed data

Ephemerella (ANCOVA for coincidental regressions slopes: $F_{(2.87)} = 412.14$, $P < 0.001$) (Fig. 4).

Feeding efficiency was negatively related with diatom biomass such that grazing was most efficient in low biomass diatom layers for all species (Fig. 5). Nevertheless, there were highly significant differences in regression intercepts (ANCOVA: $F_{(2.87)} = 41.80$, $P < 0.001$) among mayfly species. Thus, *Ephemerella* was the most efficient grazer with values ranging from 75% at low diatom biomass (0.11 mg/cm^2) to only 11% at high biomass (0.92 mg/cm^2), while efficiency for *Baetis* and *Paraleptophlebia* was between 36.9–26.6% (low biomass) and 4.7–1.5% (high biomass). Since there were no significant differences in regression slopes (ANCOVA: $F_{(2.87)} = 1.10$, $P > 0.05$), these relative differences in feeding efficiency among species were consistent across all diatom biomass levels (Fig. 5).

Discussion

Grazer-mediated depletion of diatom patches was strongly affected by diatom biomass and grazer species. At low biomass levels (0.11 mg/cm^2), consumption was the primary mechanism by which *Ephemerella* depleted diatom patches of low biomass but, for *Paraleptophlebia* and *Baetis*, this accounted for less than 40% of total patch depletion. Above this diatom biomass level, feeding efficiency declined and more than 55% of total depletion by all mayfly species was due to non-consumptive, foraging related losses. Indeed, at the highest diatom biomass level (0.92 mg/cm^2), consumption accounted for only a small proportion of algal depletion (3.3–14.8%). Non-consumptive loss rates were higher for *Paraleptophlebia* and *Baetis* than for *Ephemerella* across all diatom biomass levels. These differences among mayfly species are unlikely due to mechanical constraints of packing algal food particles into the foregut because the food bolus filled < 10% of the foregut region. Rather, species-specific differences in depletion rates appear to reflect differences in the ability of mandibulate mouthparts to collect and process algal material.

The mayfly larvae, *Baetis, Ephemerella* and *Paraleptophlebia,* displayed a type II functional response as is often observed in herbivore-plant interactions (Hatto and Harper 1969; Downing 1981). This decelerating function results because time spent handling food (i.e. pursuing, subduing, consuming, and cleaning mouthparts) increases with food density and, ultimately, limits ingestion rate (Holling 1959). For grazing mayflies such as *Baetis, Paraleptophlebia* and *Ephemerella,* handling time may limit food intake because time spent brushing diatoms from the substrate and processing these cells may take an increasingly larger proportion of foraging time. Additionally, the response for all three mayfly species indicates their ability to graze diatom layers of extremely low biomass (0.11 mg/cm^2), and feeding rates of all species reached an upper asymptote when diatom biomass was low (i.e. 0.24–0.43 mg/cm^2). In fact, these asymptotic feeding rates occur at algal levels that are 20–56 times lower than algal biomass values measured on upper stones surfaces in the Bow River. This dramatic difference between the biomasses that will produce asymptotic feeding rates and the ambient algal biomass levels in the Bow River and elsewhere (Winterbourn et al. 1985; Morikawa 1988) suggests mayflies may often experience superabundant food conditions on upper stone surfaces. Furthermore, mayfly nymphs of *Baetis, Ephemerella* and *Paraleptophlebia* in the Bow River and *Baetis* in Big Hill Springs Creek foraged predominantly within low biomass areas on upper stone surfaces and not within the higher biomass mats. Because algal biomass within grazed areas is well above the level at which feeding rates reached an asymptote in the laboratory, restricting foraging to these areas of lower algal biomass likely would not have resulted in reduced ingestion rates. The presence of mayflies within low biomass areas on upper stone surfaces may be due to foraging-mediated depletion of the higher biomass mats or preference for low biomass areas which may occur in the absence of grazers and are subsequently grazed. Field observations in Big Hill Springs Creek and in the Bow River suggest that low biomass areas are a direct result of foraging-related activities since small, circular, low biomass areas have not been found on stones in the absence of mayflies.

Depletion of diatom mats by the mayflies was positively related with diatom biomass and reflected the combined effects of a type II functional response consumptive model and a non-linear increase in non-consumptive, foraging-related losses as predicted by Case 4 (Fig. 1c). Two hypotheses may explain this disproportionate increase in non-consumptive loss. First, non-consumptive loss may be a passive process resulting from mechanical limitations of the labial and maxillary palps to brush and process large amounts of algal material. Thus, above a threshold diatom biomass, mayflies may be unable to process the large biomass of diatoms swept from substrates. Additionally, high biomasses may result in increased instability of the diatom matrix (Stockner and Shortreed 1978; Bothwell 1989). In this instance, foraging activity would result in disproportionately higher dislodgement of cells with increased diatom biomass levels. Alternatively, increases in non-consumptive losses may result from an active selection process, where algal cells or groups of algal cells are consumed selectively to maximize energy intake. This mechanism has been proposed in a multi-species algal assemblage where grazing caddisflies *(Leucotrichia pictipes)* (Hydroptilidae) actively remove low quality blue-green algae from within their foraging patch (Hart 1985). Presently, we are unable to distinguish between the active and passive hypotheses.

To predict the impact of herbivores on plant communities it is clear that foraging related losses need to be considered as a dual product of consumptive and non-consumptive foraging processes. In fact, the non-linear increases in non-consumptive losses with increased algal biomass suggests this process likely exceeds the importance of consumptive losses as a process of algal patch depletion by mayflies in streams.

Acknowledgements. We thank Nancy Glozier for helpful comments on earlier drafts, Jamie Dixon for assistance with statistical analyses, and two anonymous reviewers. This research was funded by summer support to GJS from Environment Canada, grants to JMC and FJW from the National Sciences and Engineering Research Council of Canada, and funds to MLB from Weyerhaeuser Canada, Ltd.

References

Allan JD, Flecker AS, McClintock NL (1986) Diel epibenthic activity of mayfly nymphs and its nonconcordance with behavioural drift. Limnol Oceanog 31:1057–1065

Andrzejewska L, Wojick Z (1970) The influence of Acridoidea on the primary production of a meadow (Field experiment). Ekol Polska 18:89–109

Bothwell ML (1989) Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. Can J Fish Aquat Sci 46:1293–1301

Colletti PJ, Blinn DW, Pickart A, Wagner VT (1987) Influence of different densities of the mayfly grazer *Heptagenia criddlei* on lotic diatom communities. J N Am Benthol Soc 6:270–280

Downing JA (1981) In situ foraging responses of three species of littoral cladocerans. Ecol Monogr 51:85–103

Friedman MI (1980) Deterministic mathematical models in population ecology. Pure and Applied Mathematics, vol. 57. Marcel Dekker Inc, pp 254

Gregory SV (1983) Plant-herbivore interactions in stream systems. In: Barnes JR, Minshall GW (eds). Stream ecology, application and testing of general ecological theory. Plenum, New York, pp 157–189

Hart DD (1985) Grazing insects mediate algal interactions in a stream benthic community. Oikos 44:40–46

Hatto J, Harper JL (1969) The control of slugs and snails in British cropping systems, specially grassland. Int Copper Res Assoc Proj 115(A):1–25

Harper JL (1977) Population biology of plants. Academic Press Inc., London, England, 892 p

Hill WR, Knight AW (1987) Experimental analysis of the grazing interaction between a mayfly and stream algae. Ecology 68:761–769

Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can Entom 91:295–320

Lamberti GA, Resh VH (1983) Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64:1124–1135

Lamberti GA, Ashkenas LR, Gregory SV, Steinman AD (1987) Effects of three herbivore on periphyton communities in laboratory streams. J N Am Benthol Soc 6:92–104

Lamberti GA, Gregory SV, Ashkenas LR, Steinman AD, McIntire CD (1989) Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. Ecology 70:1840–1856

McAuliffe JR (1984) Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. Oikos 42:327–333

McCormick PV, Stevenson RJ (1989) Effects of snail grazing on benthic algal community structure in different nutrient environments. J N Am Benthol Soc 8:162–172

Morikawa K (1988) Differences in plating efficiency of bacteria from river epilithon sampled from upper and lower surfaces of artificial substrata. Microbiol Ecol 15:217–225

Power ME, Stewart AJ, Mathews WJ (1988) Grazer control of algae in an Ozark stream: effects of short-term exclusion. Ecology 69:1894–1898

Schowalter TD, Hargrove WW, Crossley DA Jr (1986) Herbivory in forested ecosystems. Ann Rev Entomol 31:177–196

Stockner JG, Shortreed KRS (1978) Enhancement of autotrophic production by nutrient addition in a coastal stream on Vancouver Island. Can J Fish Aquat Sci 35:28–34

Steinman AD, McIntire CD, Gregory SV, Lamberti GA, Ashkenas LR (1987) Effects of herbivore type and density on taxonomic structure and physiognomy of algal assemblages in laboratory streams. J N Am Benthol Soc 6:175–188

Trexler JC, McCulloch CE, Travis J (1988) How can the functional response best be determined? Oecologia 76:206–214

Underwood AJ, Jernakoff P (1981) Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oecologia 48:221–233

Walde SJ, Davies RW (1984) The effect of intra-specific interference on *Kogotus nonus* (Plecoptera) foraging behaviour. Can J Zool 62:2221–2226

Wiley MJ, Kohler SL (1984) Behavioral adaptations of aquatic insects. In: Merritt RM, Cummins KW (eds) An introduction to the aquatic insects of North America. 2nd edition. Kendall/Hunt, Dubuque, Iowa, pp 101–133

Wilkinson L (1988) SYSTAT: the system for statistics. SYSTAT Inc. Evanston, Illinois

Williams FM, Juliano SA (1985) Further difficulties in the analysis of functional-response experiments and a resolution. Can Entomol 117:631–640

Winterbourn MJ, Hildrew AG, Box A (1985) Structure and grazing of stone surface organic layers in some acid streams of southern England. Freshwat Biol 15:363–374