J. N. Am. Benthol. Soc., 1995, 14(4):465–509

Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments

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Abstract. This review summarizes the state of knowledge regarding herbivory in stream ecosystems by quantitatively analyzing the results of 89 experimental studies published between 1972 and 1993. Our primary objective was to determine if general patterns exist among stream ecosystems in the type and strength of interactions occurring between herbivores (grazers) and their primary food source, periphyton. We conducted two types of meta-analyses of the published literature: (1) analyses of the proportion of studies showing significant effects for three types of interactions (effects of grazers on periphyton, effects of periphyton on grazers, and effects of grazers on other grazers and benthic animals) and (2) analyses of factors influencing the magnitude of effect that grazers had on periphyton. For effects of grazers on periphyton, we also determined (1) if the likelihood of observing significant effects varied with the spatial and temporal scale at which experiments were done and (2) if the magnitude of effect by grazers on periphyton abundance varied with spatial and temporal scale, grazer taxon, grazer abundance, and periphyton accrual based on the difference in treatments with and without grazers.

Grazers held at ambient densities usually reduced periphyton biomass (70% of experiments) and altered algal taxonomic or physiognomic structure (81%) relative to grazer removal treatments, whereas grazers had slightly lower effects on periphyton productivity (usually <70% of experiments, depending on productivity measure). Experiments conducted in laboratory streams and at two spatial scales in the field (few or single habitat units and stream reaches or basins) were equally likely to report significant effects of grazers. Both short-term (≤4 wk) and long-term (>4 wk) experiments also were equally likely to report significant effects of grazers on periphyton. However, the magnitude of effect grazers had on periphyton biomass varied with the amount of periphyton accrual, grazer taxon, and grazer population biomass. Grazer effects also were higher for longer studies conducted under laboratory conditions than for shorter studies conducted in the field.

A high proportion of the experiments that manipulated periphyton abundance significantly affected grazer densities and growth. Reduction in periphyton abundance usually reduced grazer density and growth. Experimental manipulations of dominant grazers typically had strong and usually negative effects on densities and growth of other species of benthic animals, either from direct (e.g., interference) or indirect (e.g., resource exploitation) mechanisms.

Results of these analyses suggest that stream herbivores regulate their food resources as or more frequently than herbivores in other ecosystems, and strongly contradict the view held by many ecologists that stream communities are regulated primarily by abiotic factors. Although publication bias (i.e., the tendency for journals to publish positive results) appears minimal, we cannot yet generalize from these results to the entire universe of stream ecosystems because (1) most studies were conducted during summer base flow conditions and (2) results do not adequately represent interactions during the more physically stressful conditions that occur during periods of flooding, drought, or extreme cold. If rapid progress in the development of general stream ecosystem theory is to occur, we believe (1) future studies should be explicitly designed within the context of general ecological questions, (2) as much background information as possible describing environmental conditions should be collected, and (3) journals should permit and urge inclusion of tabular data describing both experimental conditions and treatment means and variances.

Key words: algae, food webs, foraging, grazers, grazing, herbivory, lotic, meta-analysis, periphyton, streams.

Ecological interest in plant-herbivore relationships can be traced back several decades. Much early work in terrestrial systems stemmed from an interest in the impact of herbivores on their food plants in terms of plant and herbivore abundance, population dynamics, nutrient cycling, and system productivity (reviewed by Harper 1969, Hodkinson and Hughes 1982, Crawley 1983, Strong et al. 1984, Abrahamson 1989). Parallel studies of benthic habitats in freshwater lakes (e.g., reviewed by Porter 1977, Lodge 1991) and marine intertidal zones (e.g., reviewed by Lubchenco and Gaines 1981, Duffy and Hay 1990, Steneck and Dethier 1994) examined effects of herbivores on plant morphology, turnover rates, succession, and diversity. From the collective literature on herbivory, it appears that herbivores (1) have a greater effect on their food resources in aquatic than in terrestrial ecosystems and (2) more frequently affect the trophic level below them than carnivores do (see Sih et al. 1985, Menge and Sutherland 1987, Cyr and Pace 1993). The second generalization contrasts strongly with the idea that herbivory plays a secondary role in structuring natural communities relative to that of competition, predation (i.e., carnivory), and abiotic factors (see Hairston et al. 1960, also fig. 8 in Shorrocks 1993).

Perhaps the earliest correlative evidence that herbivores regulate plant abundance in streams was that of Douglas (1958), who reported an inverse relationship between grazing caddisflies and periphyton, and Hynes (1961), who described a large algal bloom immediately downstream of an insecticide release (see Ide 1967 for a similar example). Compared with other ecosystems, interest in examining lotic herbivore-plant interactions using controlled experiments has been slow to develop, with few studies being published before the mid-1980s. Decade-old reviews of benthic herbivory in streams (Gregory 1983) and freshwater ecosystems (Lamberti and Moore 1984) cited only a handful of studies where controlled experiments were used to elucidate the effects of lotic herbivores on plants (i.e., Kehde and Wilhm 1972, Eichenberger and Schlatter 1978, Gregory 1980, Sumner and McIntire 1982, Lamberti and Resh 1983). Further, in a review of experimental studies of predation (sensu latu) and competition published before 1984, Sih et al. (1985) included only one study (Lamberti and Resh 1983) under the topic 'lotic herbivory'.

Since the mid-1980s, over 100 experimental studies of stream herbivory have been published, and at least three recent reviews exist that summarize a portion, but not most, of this research explosion: Lamberti (1993), for research in laboratory streams; Allan (1994), for a quantitative review of selected studies; and Steinman (in press), for a qualitative analysis of selected studies with emphasis on plant responses. These reviews notwithstanding, to date there has been no comprehensive, quantitative synthesis of this literature. The lack of such a synthesis likely has contributed to the meager acknowledgement of stream herbivory research in comparisons with other ecosystems. For example, Cyr and Pace (1993) compared effects of mass-specific herbivory on primary productivity between terrestrial and aquatic communities. Their aquatic data base included information on both planktonic and benthic herbivores from marine and freshwater lake communities, but contained no data from streams.

Here, we summarize the current state of knowledge regarding plant-herbivore interactions in streams by quantitatively analyzing data from the primary literature. Our main objective was to determine if general patterns exist among stream ecosystems with respect to the type, frequency, and strength of interactions between stream herbivores and their plant resources. We specifically addressed the following questions:

1. What types of experiments have been done to quantify plant-herbivore interactions in streams?
2. How pervasive are effects of stream herbivores on plant abundance, productivity, and assemblage structure, and what are the magnitudes of these effects?
3. Are effects of stream herbivores on their plant resources related to herbivore taxon?
4. What effects do plants have on stream herbivores?
5. What effects do stream herbivores have on conspecific herbivores or other associated animals?
6. Do inferences regarding the strength of interactions depend on the spatial and temporal scales at which observations are made?
7. Based on the above questions, what can be

generalized about the importance of plant-herbivore interactions in streams?

Methods

Definitions and scope

Herbivory is generally defined as the consumption by a heterotrophic organism of all or part of a living, autotrophic organism (sensu Begon et al. 1990). In this paper, we restrict our analyses to stream herbivores (or grazers) that consume periphyton, one of the two dominant food sources available to consumers in streams (Cummins 1973, Minshall 1978). We consider the terms 'periphyton', 'lithophyton', 'biofilm', and 'aufwuchs' as synonyms, all referring to the algal, bacterial, and fungal species complex that inhabits stream benthic substrates. Periphyton occurs in virtually all lotic ecosystems from the smallest tributaries to the largest rivers (Whitton 1975), and forms the primary diet of a wide variety of lotic species (Lamberti and Moore 1984, Allan 1994). For practical reasons we have not attempted to separate the autotrophic and heterotrophic components of this resource. Studies that examined organisms that largely consume allochthonous inputs (wood and leaves from terrestrial vascular plants) or submersed macrophytes were not included. We also considered only macroscopic consumers widely recognized as periphyton grazers or scrapers (sensu Merritt and Cummins 1984).

Data sources

For our quantitative analyses, we included all studies published through 1992 (and four studies published in 1993 and 1994 available as manuscripts during data compilation) that used controlled field or laboratory experiments to manipulate a single population or species assemblage of grazers, their periphyton food resource, or other environmental factors related to herbivory that were predicted to affect either grazers (e.g., predators) or periphyton (e.g., irradiance, nutrients, current, etc.). By focusing on experimental rather than correlative studies, we could more confidently attribute results to the manipulated variable rather than to other, uncontrolled variables (Connell 1975, Hairston 1989). Data were compiled from the following sources: (1) published articles in refereed ecological journals; (2) unpublished theses and dissertations; and (3) book chapters containing original data. Specific studies within these categories were identified from a variety of sources including CD-ROM and diskette-based searches (i.e., ACRICOLA—National Agricultural Library; CAB—Commonwealth Agricultural Bureau; Current Contents on Diskette©—Institute of Scientific Information), local on-line computer searches (i.e., DSCI: Auburn University Library User Information System), prior knowledge of published papers, bibliographic pyramiding from recently published papers, and personal communications.

Data compilation and scoring

For each study, we compiled the following information: (1) specific interaction (described below); (2) type of experiment (field or lab); (3) geographic location of study; (4) grazer taxon studied; (5) treatment and response variables; (6) spatial scale of experiment; (7) season of experiment; (8) duration of experiment; (9) ambient density of target grazers (i.e., those subject to manipulation); (10) size of target grazers; and (11) values (usually means) of response variables within treatments. Appendix 1 lists the data used in our analysis and summarizes categories 1–10 for each study.

Types of interactions examined

We summarized three main interactions: (1) effects of grazers on periphyton (G→P); (2) effects of periphyton on grazers (P→G); and (3) effects of grazers on other grazers or benthic animals (G→G). Most experiments involving the G→P interaction produced contrasting grazer densities by physically removing grazers from experimental areas and reducing immigration, while allowing densities in control areas to vary naturally (e.g., Lamberti and Resh 1983, Feminella et al. 1989, Creed 1994). Experiments involving P→G and G→G interactions produced contrasting periphyton treatments (i.e., high- versus low-periphyton levels) by altering periphyton abundance in several ways. In some cases, differences were created by simultaneously culturing periphyton in the presence and absence of grazers (e.g., McAuliffe 1984a, Lamberti et al. 1987b, Feminella and Resh 1991). Other researchers mechanically altered periphyton

abundance (e.g., by scraping or brushing) on a subset of previously cultured substrates (e.g., Kohler 1984, Ogilvie 1988, Hart et al. 1991). Still others manipulated light or nutrient regimes to alter periphyton (e.g., Elwood et al. 1981, Fuller et al. 1986, Hershey et al. 1988, Hill and Knight 1988a, Lamberti et al. 1989, Dudgeon and Chan 1992). In each case, periphyton was then exposed to target grazers and their responses were measured.

Types of response variables compiled

Investigators used several different measures to quantify grazer-periphyton interactions, and often several response variables to quantify each measure (e.g., the *variables* density and biomass were often used to *measure* abundance). Therefore, for each interaction we analyzed only the most common measures and their response variables. Moreover, because many studies quantified more than one independent variable, were conducted over > 1 spatial scale (e.g., > 1 stream) or temporal scale (e.g., > 1 season), and examined responses of > 1 grazer species, the number of possible comparisons of effects (sensu Sih et al. 1985) among response variables greatly exceeded the number of studies. If multiple streams, seasons, years, or grazer species were examined in experiments, we considered each comparison as a separate replicate. For studies in which time-series experiments were done (e.g., multiple measures within one season), grand means were computed from means of individual sampling periods. We chose to use grand means rather than single end points in these cases because they were more representative of the average response to experimental manipulations during each study.

G→P interaction.—We compiled treatment-specific estimates of periphyton abundance (as ash-free dry mass [AFDM] or chlorophyll *a*), primary production (as areal- or biomass-specific productivity), and assemblage structure to examine effects of grazers on periphyton. For periphyton abundance data, we calculated two derived response variables that described the magnitude of grazer effects on periphyton (see below). Differences in assemblage structure were quantified by comparing either abundances of individual periphyton taxa (i.e., as cell density or biovolume) or community-based measures of diversity (i.e., as richness, evenness, or heterogeneity) among grazed and ungrazed (i.e., grazer exclusion) periphyton assemblages.

An index of experiment-specific grazing pressure was developed by computing grazer population dry weight biomass, derived from all studies providing grazer biomass data and population density (see Appendix 1). If not directly reported by authors, we used regression equations to estimate population biomass from known measures of grazer length, wet weight, or AFDM. Regression equations were taken from the literature, provided by authors, or based on our own empirically derived estimates (unpublished data). Most experiments used ambient levels of grazing as controls and lower (i.e., exclusion) or higher levels as treatments. For those experiments that used multiple grazer densities (e.g., low, intermediate, high densities) we used the difference in periphyton between the lowest and intermediate treatment densities. In these cases, intermediate densities of grazers were usually reported by investigators as those closest to ambient conditions.

The number of studies describing the G→P interaction (n = 70) was sufficient to allow us to assess if the spatial or temporal scale at which experiments were conducted, or the grazer taxon of choice, affected the difference in periphyton abundance between grazed and ungrazed treatments. To examine effects of spatial scale, we subdivided experiments into three categories: (1) laboratory experiments conducted in artificial streams; (2) field experiments conducted at a scale of sub-unit to channel unit (sensu Hawkins et al. 1993); and (3) field experiments conducted at the reach, section, or interbasin scale (sensu Gregory et al. 1991). For the temporal scale analysis, comparisons were subdivided into either short-term (≤ 4 wk) or long-term (> 4 wk) studies. We chose 4 wk as our cut-off point because it closely represented the average duration of experiments (i.e., median = 4.25 wk; mode = 4 wk), and it also provided similar sample sizes per interval (n = 23 comparisons of periphyton abundance for short-term intervals; n = 26–31 for long-term intervals, depending on response variable). For the grazer taxon analysis, results of experiments were analyzed at two taxonomic levels of resolution. At one level, six of the most commonly studied groups of grazers were used (i.e., fish, anurans, crustaceans, snails, caddisflies, and

mayflies). The second level consisted of grouping grazers by genus.

P→G and G→G interactions.—For these two interactions that described target and non-target grazer (and other animal) response to periphyton manipulations or that of other grazers, we focused only on the most frequently examined measures and their response variables: grazer or animal abundance (as density or biomass) and feeding/development (as growth).

Data analyses

Meta-analyses are statistical methods that use data from independently conducted studies as independent replicates to test general hypotheses (Hedges and Olkin 1985, Gurevitch and Hedges 1993, Arnqvist and Wooster 1995). Different types of meta-analyses have been used in ecology to elucidate trends in experimental studies of competition (Connell 1983, Schoener 1983, Sih et al. 1985) and predation (Sih et al. 1985), and more recently to summarize data from experimental studies of nutrient limitation of phytoplankton (Elser et al. 1990), field competition (Gurevitch et al. 1992), accuracy of artificial substrates for estimating periphyton abundance (Cattaneo and Amireault 1992), sampling variability in freshwater periphyton (Morin and Cattaneo 1992), and lotic predation (Cooper et al. 1990, Wooster 1994).

We used two types of meta-analyses to test hypotheses about the prevalence and magnitude of treatment effects: "vote counts" to determine the prevalence of grazer effects and analyses of "effect size" to examine how different factors influence the magnitude of grazer effects on their periphyton resource.

Vote counting analyses.—For all three interactions we used a "vote counting" procedure that has been previously used in ecology (e.g., Connell 1983, Schoener 1983, Sih et al. 1985) to quantify the proportions of studies meeting different types of criteria (e.g., the percent of studies showing effects and no effects) and test the simple hypothesis that the proportions (P) of studies reporting significant effects were greater than would be expected by chance alone (i.e., H_o: $P = 0$, $\alpha = 0.05$). The null hypothesis of 0 studies showing effects was conducted as a formality, because it was obvious from the literature that many, if not most, studies reported significant effects. We used log-likelihood ratios (G tests, Zar 1984) to test hypotheses based on effects/no effects frequencies. It is important to note that vote counting procedures are conservative and biased toward finding no overall effect (Gurevitch et al. 1992, Bushman 1994), and they provide no information about the magnitude of effects that factors of interest have on response variables.

For all three sets of interactions, we considered effects 'significant' if they were reported as such by investigators based on inferential statistics. In addition, for the G→P interaction data set that contained a reasonably large sample size ($n = 70$ studies), we also re-examined the results of each experiment and ignored any statistically based significance. Here, we considered an effect significant if the difference between treatment and control group means was $> 1.5\times$. Although our $1.5\times$ standardized significance criterion is somewhat arbitrary, we chose it based on both ecological and statistical grounds. If real, a 1.5-fold difference between treatments is almost certainly of ecological significance. However, the replication ($n = 3$ or 4) and the type I error rate ($\alpha = 0.05$) used in most studies were usually so low that the power of these individual studies to detect real differences was extremely low, i.e., many differences were probably real but suffered from high type II error rates. Standardization eliminated the bias of highly variable sample size on the likelihood of reporting significant differences, a potential problem for data we compiled because the number of replicates reported varied from 1 to 12.

Both Allan (1984) and Resh and McElravy (1993) show that stream ecologists seldom take enough samples (i.e., $n > 20$) to detect less than a 1.5 difference in treatment means at $\alpha = 0.05$. We therefore assumed that (1) the reported treatment means were unbiased estimates of the true means and (2) if more samples would have been taken the investigator would have been able to detect a 1.5-fold difference. This standardized significance criterion also allowed us to use data from several unreplicated or pseudoreplicated studies (sensu Hurlbert 1984) as legitimate replicates for statistical analyses (Hawkins 1986, see also Statzner and Resh 1993). Finally, our $1.5\times$ factor was in the range of criteria used in other ecological meta-analyses (i.e., between 1.25- and $2\times$, Elser et al. [1990] and Sih et al. [1985], respectively). Because fewer studies

existed describing either P→G (n = 29) or G→G (n = 23) interactions (and these translated to even fewer numbers of comparisons with similar response variables), we used only statistically based measures of significance.

Effect size analyses of G→P interaction.—In addition to vote counting analyses, sample size for the G→P interaction was sufficient to allow us to quantify effect size of grazers on periphyton. Two sets of analyses of effect size were conducted across studies based on spatial and temporal scale of the experiment, grazer taxon, population biomass of the grazer, and accrual of periphyton in the absence of grazers (termed *potential periphyton abundance*). We used these data to test several hypotheses that we developed based on our knowledge of the literature, our own experiences, and discussions with colleagues. Our hypotheses were: (1) effect size decreases with increasing spatial scale, being highest under laboratory conditions and lowest for field experiments conducted at the reach scale, (2) effect size decreases with increasing temporal scale, (3) effect size varies with grazer taxon, (4) effect size decreases with increasing potential periphyton abundance, (5) effect size increases with increasing grazer population biomass; and (6) grazer taxonomic group and potential periphyton abundance interact to determine effect size. In general, we expected increasing environmental heterogeneity associated with increasing spatial and temporal scale to ameliorate the effects of grazers, large or highly specialized grazer taxa to be more effective at removing periphyton than small or less specialized taxa, and grazer control of the periphyton resource to decrease with the capacity of the resource to accrue new biomass. Hypothesis 6 was based on the idea that large-bodied taxa would be more efficient at harvesting large accumulations of periphyton and small taxa would be more efficient harvesting small periphyton accumulations.

Gurevitch and Hedges (1993) describe procedures for conducting meta-analyses of effect size on ecological data (see also Arnqvist and Wooster 1995). An important assumption of any meta-analysis is that the data represent an unbiased sample of the studies that have been conducted (Begg 1994). The tendency for journals to preferentially publish studies reporting statistically significant results over those describing nonsignificant relationships is a potentially important source of bias in all scientific literature. Therefore, prior to conducting the meta-analysis of effect size, we used the graphical procedure described by Begg (1994) to determine if the compiled data were a biased sample. In this analysis, sample size (n) of each study is plotted on the y-axis against means and variances of effect size (x axis). Data that have no-to-little publication bias will show a cone shaped pattern and no skew (Begg 1994). Our data showed this general pattern (unskewed, roughly cone shaped) and thus appeared to not suffer from significant publication bias.

Gurevitch and Hedges (1993) recommend transforming the raw effect sizes reported in each study prior to conducting a meta-analysis. This transformation (difference between treatment means/pooled standard deviation) creates a standardized variable describing effect size. Such transformations are required for analyses that report results in different "currencies" (e.g., abundance, growth, behavior) or use different scales of measurement, but can introduce artifacts into analyses that are difficult to interpret (Rosenthal 1994). Because the magnitude of a transformed effect depends on both the difference between treatment means (numerator) and the pooled standard deviation (denominator), two estimates of similar raw effect size but having different within treatment variances will yield different standardized effect sizes (S. D. Cooper, University of California, Santa Barbara, personal communication). For our analyses, the response variables (periphyton chlorophyll *a* and AFDM) did not vary among studies, thus there was no need to calculate a standardized effect size. We did however, conduct tests using two different measures of effect size: (1) the simple absolute difference between ungrazed and grazed treatments (D), and (2) an index of "herbivore impact" (HI) based on the method used by Cooper et al. (1990) to quantify effects of predators on their prey:

$$HI = -\log_e(P_g/P_{ug})$$

where P_g is the amount of periphyton in the grazed treatment and P_{ug} is the amount in the ungrazed treatment. HI values can theoretically vary from − to + infinity. Positive values of this index mean herbivores reduce periphyton abundance and vice versa. Cooper et al. (1990) suggested the use of this index because it removes

the potentially confounding effect of differences among experiments in prey (i.e., periphyton) abundance.

To test our hypotheses, we conducted simultaneous multiway analyses of variance based on general linear model procedures (Neter and Wasserman, 1974). Use of general linear models allowed us to include categorical data as well as continuous data in these analyses, and facilitated analysis of unbalanced data. All analyses were carried out with SYSTAT® statistical programs, and statistical tests were based on type III sums of squares (Shaw and Mitchell-Olds 1993). We used a type I error rate (α) of 0.10 as the criterion for concluding statistical significance of these tests as a means of more equitably spreading the risks of committing type I and type II errors (Toft and Shea 1983, Peterman 1990).

After conducting statistical tests of hypotheses, we then used stepwise multiple regressions to identify the best predictive models possible and identify any relationships that were not detected by the multifactor ANOVAs. These latter analyses were not used to test hypotheses but instead to describe relationships and refine hypotheses.

Results

Trends in experimental studies of stream herbivory

We found 100 experimental studies of stream herbivory distributed among 22 ecological journals and other sources (Table 1). Publications have increased steadily since the early 1980s, reaching a peak in 1992 (Fig. 1). Of the 89 studies through mid-1993 that were included in our meta-analysis (see Appendix 1), nearly three-quarters (74%) were conducted in the field and the remainder (26%) were done in laboratory streams. Of the laboratory studies, only about 5% also included a field component, either to determine appropriate experimental densities or to verify experimental results (e.g., Hill 1992, Kohler 1992). The vast majority of studies were conducted in north-temperate streams (93%), particularly those within North America (89%, see Appendix 1).

Field experiments were conducted at several spatial scales, including manipulations within single channel units (56% of studies), 2–3 channel units (9%), > 3 units distributed over a stream reach (29%), and across > 1 stream (i.e., interbasins, 6%). Studies involving field experiments at small scales (subunits and units, 65% of studies) were almost twice as frequent as those done at large scales (reaches and interbasins, 35%). Only six studies (Elwood et al. 1981, Yasuno et al. 1982, Hershey et al. 1988, Hinterleitner-Anderson et al. 1992, Peterson et al. 1993, and Hershey et al. 1993) conducted whole-stream manipulations of periphyton or grazer abundances (see also Eichenberger and Schlatter [1978] and Yasuno et al. [1985] for examples of large-scale experiments in artificial

TABLE 1. List of journals and other sources containing experimental studies of lotic herbivory through 1994. Inclusive years refer to time studies were published or date unpublished theses or dissertations were completed (n = 100).

Journal/Source	Number of studies	Inclusive years
Ecology	18	1981–1994
Journal of the North American Benthological Society	15	1986–1992
Oecologia	11	1983–1993
Oikos	9	1981–1993
Freshwater Biology	9	1986–1994
Unpublished theses or dissertations	7	1980–1992
Canadian Journal of Fisheries and Aquatic Sciences	6	1990–1994
Hydrobiologia	4	1982–1994
American Midland Naturalist	3	1972–1992
Journal of Phycology	2	1988–1991
Limnology and Oceanography	2	1984–1988
Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie	2	1987–1988
Environmental Biology of Fishes	2	1989–1992
New Zealand Journal of Marine and Freshwater Research	2	1994
Australian Journal of Marine and Freshwater Research	1	1993
Ecological Monographs	1	1992
Science	1	1990
New Zealand Natural Sciences	1	1989
Journal of Freshwater Ecology	1	1985
Environmental Pollution (Series A)	1	1985
Archiv für Hydrobiologie	1	1982
Book chapter	1	1983

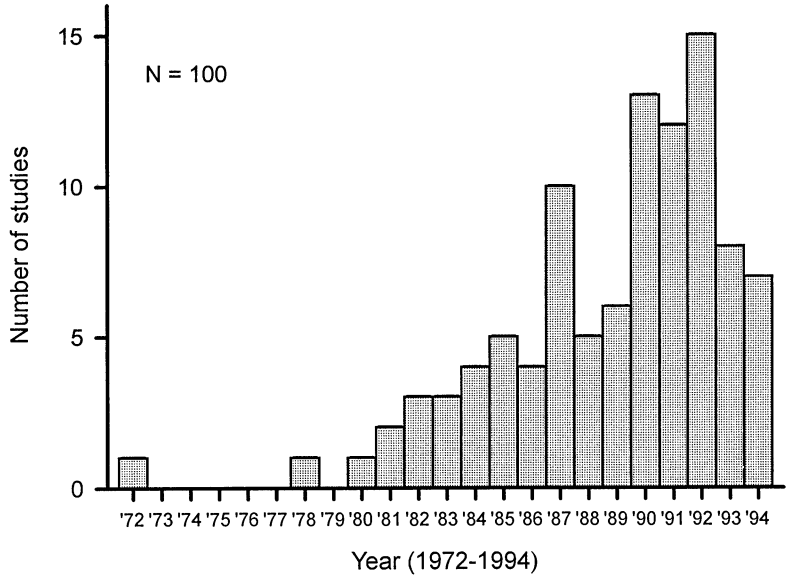

FIG. 1. Publication history of experimental studies of stream herbivory from 1972 through 1994.

streams). Most field and laboratory experiments were conducted within a single season (79%), with fewer studies conducted over two (15%) or 3–4 seasons (2%). Less than 5% of short-term field studies were repeated over several years (e.g., Feminella and Resh 1990, Rosemond et al. 1993), or were conducted continuously for 1 yr or more (e.g., Furnish 1990, Kohler 1992). The average duration of experiments across all studies was about 1 mo (median = 4.25 wk, mode = 4 wk, n = 84).

The most frequently used measures of periphyton response to herbivory (i.e., G→P interaction) were periphyton abundance, assemblage structure, and productivity. Although nine different variables were used to quantify periphyton abundance, most studies measured either AFDM or chlorophyll *a* concentration (Table 2). In contrast, effects of grazing on periphyton condition (e.g., use of chlorophyll *a*—phaeophytin ratios; Martin et al. 1991, Gelwick and Matthews 1992), export or drift (Sumner and McIntire 1982, Lamberti et al. 1989, Barnese and Lowe 1992; see also McCormick et al. 1994), composition as bacteria (e.g., Lamberti and Resh 1983, Mulholland et al. 1991), and chemistry (i.e., Steinman et al. 1987b) were rarely quantified. Only a small percentage of studies used alternative measures of macroalgal abundance such as algal percent cover (e.g., Hart and Robinson 1990, Creed 1994), damp weight (e.g., Power 1991), algal height (e.g., Power 1990a, Feminella and Resh 1991), and number of algal tufts or thalli (e.g., Dudley and D'Antonio 1991, Creed 1994).

The most frequently examined measures of grazer (or other animal) response to herbivory (i.e., P→G and G→G interactions) were grazer abundance (as density), and measures associated with feeding and development (i.e., growth; Table 2). In contrast, effects of herbivory on grazer survivorship (e.g., Hart 1987, Lamberti et al. 1987b, McCormick 1991), behavior (e.g., Hart 1981, Lamberti and Resh 1983, Kohler 1984, Kohler and McPeek 1989), chemistry (e.g., Hill 1992, Hill et al. 1992b), size (e.g., Hart and Robinson 1990, Hill et al. 1992b), fitness (e.g., Feminella and Resh 1990, Martin et al. 1991), secondary production (e.g., Furnish 1990, Vaughn et al. 1993), and species composition (e.g., Hawkins and Furnish 1987, Dudgeon and Chan 1992, Gelwick and Matthews 1992) were examined infrequently (Table 2).

Herbivores spanning six taxonomic categories at or above the level of Class were used in experiments (Insecta: 66 studies; Gastropoda: 33; Crustacea: 13; Osteichthyes: 9; Amphibia: 1; Protista: 1). Invertebrates, principally caddisfly larvae (Trichoptera, 41% of studies), snails (prosobranch and pulmonate Gastropoda, 38%),

TABLE 2. List of measures and variables used to quantify periphyton (n = 76 studies) and target grazer (n = 54 studies) responses from stream herbivory experiments. Number of studies shown in parentheses.

Measure	Response variable	
	Periphyton	Grazer
Abundance	Ash-free dry mass (43) Chlorophyll *a* (39) Cell density (25)[a] Percent cover (7) Export (6) Number of thalli (4) Algal height (filamentous) (4) Dry weight (3) Damp weight (2)	Density (28)[d] Biomass (12)
Feeding and development	— — — — —	Growth (14) Development (4) Ingestion rate (3) Assimilation (1) Diet (1)
Assemblage structure	Species composition (38)[b] Diversity (9)[c]	Species composition (4)
Productivity and metabolism	GPP, NPP, P:$\overline{B}$ (23) ATP, phosphatase activity (5)	Secondary production (2)
Chemistry	C:N (3) Lipid, fatty/amino acid content (1)	Lipid content (2)
Condition and fitness	Chl-*a*:AFDM (4) Senescence (3)	Size of pupae or adults (8) Survivorship (6) Adult emergence (1) Fecundity (2)
Behavior	—	Spatial distribution (7) Activity (4) Movement rate (4) Export (drift) (2)

[a] Includes biovolume or cell counts, for either algae (19 studies) or bacteria (5 studies).
[b] Includes either percent dominance (26 studies) or community similarity (e.g., SIMI; 9 studies).
[c] Includes species richness (S), McIntosh diversity, Shannon diversity (H'), evenness (J), or heterogeneity (H'') indices.
[d] Includes colonization or recruitment (3 studies).

mayfly nymphs (Ephemeroptera, 24%), and crustaceans (Decapoda or Isopoda, 14%) were studied most frequently (totals exceed 100% because some studies used > 1 herbivore). Studies involving herbivorous fishes were less common (9%), and two-thirds of these studies examined the effects of a single, common north temperate species (*Campostoma anomalum*, e.g., Power et al. 1985, 1988a, Gelwick and Matthews 1992). The remaining fish studies were designed to examine effects of herbivorous fish assemblages in tropical streams (e.g., Power et al. 1989, Power 1990b, Wootton and Oemke 1992).

A large number of interactions relevant to herbivory were examined (see Appendix 1), although the three main interactions (G→P: 79% of studies; P→G: 33%; or G→G: 26%) were studied most frequently. Relatively few studies examined grazer-periphyton interactions in relation to effects of other environmental variables such as nutrients (21% of studies, e.g., Mulholland et al. 1991, Rosemond 1993a, 1993b), irradiance (14%, e.g., Gregory 1980, Hawkins and Furnish 1987, Steinman 1992), carnivory (8%, e.g., Power 1990a, Harvey and Hill 1991, Bechara et al. 1992), and stream hydraulics (2%, e.g., DeNicola and McIntire 1991, Poff and Ward 1992).

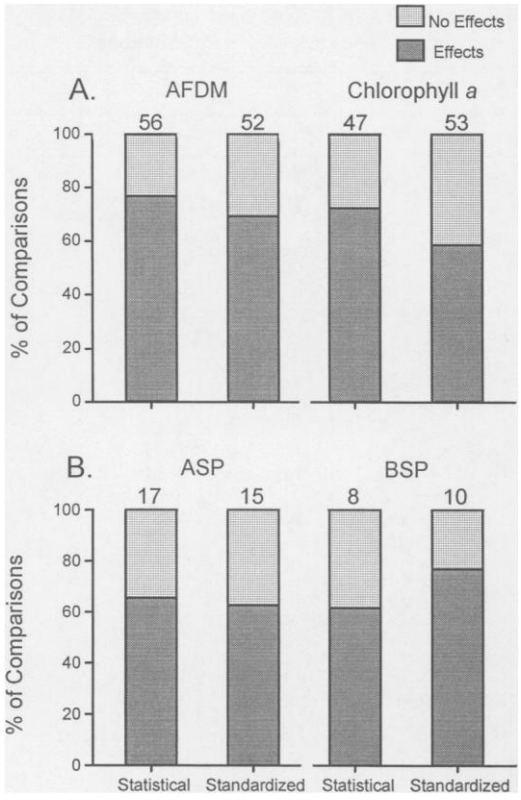

FIG. 2. Proportion of comparisons (experiments) that showed significant effects of grazers on periphyton (A) biomass, as ash-free dry mass (AFDM) and chlorophyll *a*, and (B) areal- and biomass-specific productivity, based on statistical and standardized significance criteria. Numbers above bars are sample sizes (number of comparisons).

Effects of grazers on periphyton (G→P interaction): vote counting analyses

Periphyton abundance.—Close to 70% of comparisons reported significant effects of grazers on periphyton AFDM for both statistically based (77%) and standardized (69%) significance criteria (Fig. 2A). Both proportions were much higher than the null hypothesis of no grazer effects. Of these studies, only McCormick (1990) reported that grazed treatments yielded higher periphyton biomass than ungrazed treatments; in all other cases grazers reduced AFDM. We found slightly lower frequencies of effects for studies that measured chlorophyll *a* abundance, although the proportions of both statistically based (72%) and standardized (58%) comparisons showing effects by grazers were also much larger than zero (Fig. 2A). Only two studies (Kehde and Wilhm 1972, Hart 1985a) reported that grazed treatments had higher periphyton chlorophyll *a* than ungrazed treatments; all others reported that grazers reduced chlorophyll *a*. Choice of significance criterion (statistical or standardized) did not alter effects/no effects frequencies for either periphyton chlorophyll *a* ($G = 2.12$, $p = 0.15$) or AFDM ($G = 0.78$, $p = 0.38$, Fig. 2A). However, of the 23 experiments that measured both chlorophyll *a* and AFDM, 18 (78%) found higher differences between grazed and ungrazed treatments for AFDM than for chlorophyll *a* ($\chi^2_c = 6.3$, $p < 0.025$).

Periphyton productivity.—Twenty-two studies were designed to examine effects of grazers on areal-specific productivity (ASP) of periphyton ($n = 26$ comparisons), and one-half of these also examined biomass-specific productivity (BSP, $n = 13$ comparisons). Over 60% of comparisons reported significant effects of grazers on ASP for both statistical and standardized criteria (Fig. 2B). Six of the nine studies (67%) that reported no effects of grazers on ASP used snails (*Juga* spp. or *Elimia* spp.). Of the ASP comparisons that showed effects ($n = 17$), only one (Lamberti et al. 1989, for the snail *Juga silicula*) found that grazers increased ASP; in all other cases (94%), grazers decreased ASP. Proportions of studies reporting significant effects of grazers on BSP were similar to that observed for ASP for both statistical and standardized criteria (Fig. 2B). Nearly all studies that reported significant decreases (statistical criterion) in BSP in grazed treatments used snails (*Elimia clavaeformis*) as target grazers (i.e., Steinman et al. 1990, Hill et al. 1992a, Rosemond et al. 1993). No differences existed between the two significance criteria in the frequencies of studies reporting significant effects on either ASP ($G = 0.04$, $p = 0.83$) or BSP ($G = 0.73$, $p = 0.39$, Fig. 2B).

Periphyton assemblage structure.—Forty-seven studies were designed to examine effects of grazers on periphyton assemblage structure, with emphasis on algal species composition and relative abundance. Eighty-one percent of the comparisons showed that grazers had some effect on structure of the algal assemblage. Statistical significance for individual comparisons was difficult to judge, because many studies reported differences in percent abundance be-

tween treatments without using statistical analyses, or they reported qualitative differences (e.g., from SEM micrographs) between grazed and ungrazed treatments. However, in many of these studies, grazed and ungrazed assemblages were so different that statistical analyses appeared superfluous. Of the eight comparisons (five studies) that yielded no effects on assemblage structure, four (50%) used tadpoles (Lamberti et al. 1992), three (38%) used mayflies (Lamberti et al. 1987a, Jacoby 1987, DeNicola et al. 1990), and one (12%) used snails (Kehde and Wilhm 1972) as target grazers.

The main effect of grazing on algal assemblage structure (76% of all comparisons) was the reduction of one or more numerically dominant algae, such as the diatoms *Achnanthes minutissima, Gomphonema, Melosira,* and *Nitzschia* spp., and the concomitant increase in abundance of more grazer-resistant taxa, such as the chlorophyte *Stigeoclonium,* the diatoms *Achnanthes lanceolata* and *Cocconeis placentula,* and the cyanobacterium *Calothrix* (i.e., Sumner and McIntire 1982, Steinman et al. 1987a, Hill and Knight 1987, Power et al. 1988a, Dudley 1992, Hill et al. 1992b, Steinman 1992, Rosemond 1993a, 1993b). Of the 17 comparisons (nine studies) examining effects of grazers on algal species diversity (Table 2), 82% reported significant effects. However, comparisons were nearly evenly divided between grazers increasing (43%) and decreasing (57%) algal diversity.

Effects of grazers on periphyton (G→P interaction): effects size analyses

The multiway hypothesis tests yielded somewhat different results depending on the measure of periphyton abundance or the index of effect size (Table 3). The most consistent results were that (1) potential periphyton abundance (accrual in ungrazed treatments) and grazer taxonomic group interacted to influence the effect grazers had on periphyton abundance and (2) effect size increased with grazer biomass. The latter result was consistent with our initial hypothesis, but the former result only partly fit our predictions. The significant interaction between potential periphyton abundance and taxon implies that both grazer taxon and periphyton abundance influence effect size, but that their effects cannot be understood independently of one another. This result, however, was not consistent with our hypothesis about how effect size would vary with periphyton abundance. The general relationship between effect size and potential periphyton abundance was actually opposite to our original hypothesis in that effect size generally increased rather than decreased with increasing periphyton abundance (Fig. 3).

The magnitude of differences in effect size among grazer taxa was only partially consistent with our hypotheses. Inspection of ungrazed and grazed chlorophyll *a* means for the four grazer taxa for which chlorophyll *a* data existed showed that caddisfly larvae, tadpoles (Anura), and mayfly nymphs affected periphyton biomass most strongly, with caddisflies having a much greater effect on periphyton than either tadpoles or mayflies (Fig. 4A). Comparisons based on AFDM revealed that fish and crustaceans, like caddisflies, also had stronger effects on resources than tadpoles, snails, and mayflies (Fig. 4B). All taxa appeared to reduce AFDM standing crops to < 1 mg/cm^2 on average even though the capacity of these streams to accrue periphyton biomass in the absence of grazers varied from nearly 0 to about 8 mg/cm^2. We point out though that for most grazer taxa (fish, crustaceans, anurans, and mayflies), these relationships were based on small sample sizes and should therefore be viewed with some caution.

Although the high number of grazer taxa combined with low number of within-taxon replicates precluded statistical analysis at the taxonomic level of genera, we visually examined trends among genera for consistency with broader taxonomic groups (Fig. 5A, B). Genera usually showed consistent effects on periphyton irrespective of the measure of periphyton abundance used, and we were able to identify three arbitrary groupings based on their effect sizes. Four taxa had large effects on periphyton (*Campostoma, Dicosmoecus, Orconectes,* and *Helicopsyche*), nine taxa had intermediate or highly variable effects on periphyton (*Glossosoma, Baetis, Juga, Neophylax, Elimia = Goniobasis, Ascaphus, Ameletus, Centroptilum,* and *Gumaga*), and three taxa had small or no effect on periphyton (*Physella = Physa, Ephemerella,* and *Nixe*).

Tests of our other hypotheses were clearly rejected. Although we found a significant temporal scale effect for chlorophyll *a* and no spatial scale effect for either measure of periphyton (Table 3), the statistical tests on both scale variables are suspect because experiments conducted at

TABLE 3. Results of tests of hypotheses regarding factors influencing grazer effect size (*D* and *HI*) on periphyton abundance. Separate results given for *D* and *HI* based on periphyton chlorophyll *a* and AFDM. PPA = potential periphyton abundance and TG = grazer taxonomic group. $\alpha = 0.10$.

Source of variation	SS	df	MS	*F*	*p*
D (chlorophyll *a*):					
Spatial scale	2.070	2	1.035	0.315	0.733
Temporal scale	10.679	1	10.679	3.246	0.084
TG	2.011	3	0.670	0.204	0.893
Grazer biomass	9.285	1	9.285	2.822	0.105
PPA	413.597	1	413.597	125.715	<0.001
TG × PPA	114.588	3	38.196	11.610	<0.001
Error	82.249	25	3.290		
D (AFDM):					
Spatial scale	0.196	2	0.098	0.410	0.668
Temporal scale	0.533	1	0.533	2.232	0.148
TG	1.790	5	0.358	1.499	0.226
Grazer biomass	0.907	1	0.907	3.798	0.063
PPA	0.336	1	0.336	1.413	0.246
TG × PPA	10.680	5	2.136	8.941	<0.001
Error	5.972	25	0.239		
HI (chlorophyll *a*):					
Spatial scale	0.518	2	0.259	0.375	0.691
Temporal scale	4.017	1	4.017	5.815	0.024
TG	1.093	3	0.365	0.528	0.667
Grazer biomass	2.101	1	2.101	3.042	0.093
PPA	7.464	1	7.464	10.804	0.003
TG × PPA	5.786	3	1.929	2.792	0.061
Error	17.270	25	0.691		
HI (AFDM):					
Spatial scale	0.353	2	0.177	0.290	0.751
Temporal scale	0.011	1	0.011	0.018	0.895
TG	6.943	5	1.389	2.279	0.078
Grazer biomass	2.078	1	2.078	3.411	0.077
PPA	3.465	1	3.465	5.688	0.025
TG × PPA	12.126	5	2.425	3.981	0.009
Error	15.231	25	0.609		

different spatial and temporal scales did not appear to be independent of one another. For example, we found that laboratory stream studies were also those of longest duration (i.e., median of 5.5 wk, vs. 4 wk for field experiments conducted at both subunit-unit and reach-basin scales). This apparent lack of independence appeared to confound our ability to distinguish their separate effects, and the statistical results for the tests on both factors must therefore be interpreted with extreme caution. For these reasons, we present the trends for both factors.

Inspection of treatment means suggested that long-term studies resulted in stronger effects of grazers than short-term studies, and that the outcome of field experiments generally was stronger than that of laboratory experiments (Fig. 6). In both sets of comparisons, responses were opposite to that predicted. Values of the two effect size measures based on comparing treatment means for short- and long-term studies, respectively, were: $D = 1.63$ and 5.52 and $HI = 0.74$ and 0.81 for chlorophyll *a*, and $D = 0.22$ and 1.39 and $HI = 0.10$ and 0.98 for AFDM. Respective differences among laboratory, field habitat-unit scale, and reach scale studies were: $D = 14.37$, 2.67, and 2.03 and $HI = 0.80$, 0.71, and 0.68 for chlorophyll *a* and $D = 1.29$, 1.18,

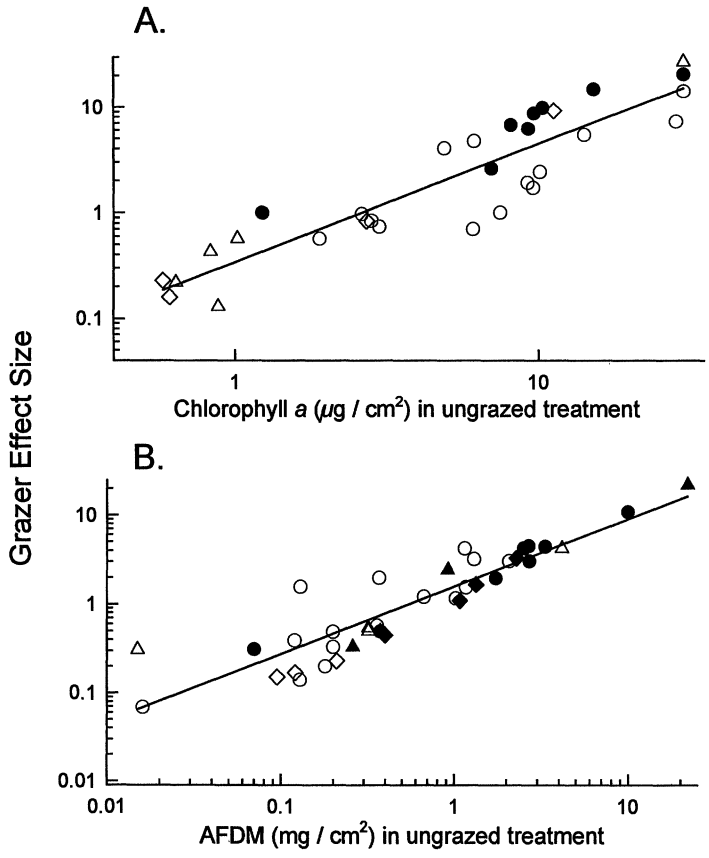

FIG. 3. Relationship between grazer effect size (D = difference between ungrazed and grazed treatments) and periphyton in ungrazed treatments (potential periphyton abundance) as (A) chlorophyll *a* and (B) AFDM. Data were plotted on log scales to separate heavily clumped points near the origin, and thus facilitate visual interpretation of the overall relationship and the position of different grazer taxa. Values of r^2 for the untransformed data were 0.83 (A) and 0.82 (B) for the relationships between D and potential periphyton abundance (also see Table 4). Symbols for plotted points are six broad taxonomic groupings of grazers used in the analysis: ●—caddisfly larvae; △—mayfly nymphs; ▲—fish; ○—snails; ◇—anurans (tadpoles); and ◆—decapod, amphipod, and isopod crustaceans. Relationships were based on the following studies: **Chlorophyll *a***—Kehde and Wilhm 1972, Hom 1982, Lamberti and Resh 1983, Hawkins and Furnish 1987, Jacoby 1987, Hill and Knight 1987, Lamberti et al. 1987a, 1987b, Steinman et al. 1987a, Hill and Knight 1988b, Lamberti et al. 1989, Feminella and Resh 1990, Furnish 1990, Hill and Harvey 1990, Feminella and Resh 1991, Martin et al. 1991, Mulholland et al. 1991, Bechara et al. 1992, Hill et al. 1992a, Lamberti et al. 1992, Rosemond et al. 1993, Rosemond 1993a, 1993b; **AFDM**—Kehde and Wilhm 1972, Gregory 1980, Hom 1982, Sumner and McIntire 1982, Lamberti and Resh 1983, Power and Matthews 1983, Murphy 1984, Hill and Knight 1987, Jacoby 1987, Lamberti et al. 1987a, 1987b, Stewart 1987, Hill and Knight 1988b, Feminella et al. 1989, Lamberti et al. 1989, Creed 1990a, 1990b, Furnish 1990, Hill and Harvey 1990, Steinman et al. 1990, Mulholland et al. 1991, Steinman 1991, Bechara et al. 1992, Gelwick and Matthews 1992, Hill et al. 1992a, Kohler 1992, Lamberti et al. 1992, Steinman 1992, Rosemond et al. 1993, Rosemond 1993a, 1993b, Creed 1994.

and 2.68 and HI = 0.75, 1.50, and 1.87 for AFDM. Although the absolute difference (i.e., D in chlorophyll *a* between grazed and ungrazed treatments was greatest in laboratory studies, values of HI varied little among the three spatial scales.

Stepwise multiple regression analyses showed that over 90% of the variation in grazer effect size as D was associated with potential periphyton abundance and the interaction between potential periphyton abundance and taxon (Table 4, see also Fig. 3). D increased with

both increasing chlorophyll *a* and AFDM abundance in the ungrazed treatments. Only the analysis based on AFDM and using *HI* to measure effect size, however, revealed that other factors might have also influenced the effect of grazers on periphyton. Here, *HI* also increased with increasing grazer biomass as observed in the previous multiway hypothesis tests. The stepwise analyses based on *HI* accounted for much less variation (37 and 60%) than those based on *D*. These results are consistent with the suggestion by Cooper et al. (1990) that *HI* (*PI* in their study) removes the direct influence of resource abundance. However, we point out that for both the AFDM and chlorophyll *a* analyses, potential periphyton abundance was still an important predictor of grazer effect size either alone (for chlorophyll *a*) or together with grazer taxon (AFDM and chlorophyll *a*).

Responses of grazers to herbivory

P→G interaction (vote counting analyses).—Forty-one studies quantified the effects of periphyton, sometimes in combination with other factors, on grazers or other benthic animals (Appendix 1). Most investigators (80%) manipulated only periphyton abundance (cf. compositional or patchiness measures) to evaluate grazer response (see Kehde and Wilhm 1972, Hart 1981, Kohler 1984, Dudley et al. 1986, Vaughn 1986, Ogilvie 1988, Richards and Minshall 1988, McCormick 1991 for exceptions). The main response variables used were grazer density and growth (Table 2). Nearly all animals considered were benthic invertebrates. Caddisflies (29% of comparisons), mayflies (29%), and chironomid midges (17%) were the most frequently used invertebrates in density studies, whereas snails (32%), caddisflies (24%), and midges (24%) were used most often in growth studies.

Manipulation of periphyton abundance had pronounced effects on grazers in most studies, affecting both grazer density (63% of studies, n = 92 comparisons) and growth (70%, n = 41). Proportions of significant effects between these two response variables were not different (G = 0.75, p = 0.37). Of the comparisons that yielded significant effects on grazer density, most (83%) found higher grazer densities in the high-periphyton treatments. Only 10 comparisons (17%) reported highest grazer densities in low-periphyton treatments (i.e., Hart 1985b, Dudley et al. 1986, Ogilvie 1988, Gelwick and Matthews 1992, Kohler 1992, Creed 1994). Of the comparisons that found significant effects on grazer growth, two (Bechara et al. 1992, for the mayfly *Baetis*; Vaughn et al. 1993, for the snail *Physella*) reported highest growth in low-biomass periphyton treatments; all others (93%) reported highest growth in high-biomass treatments.

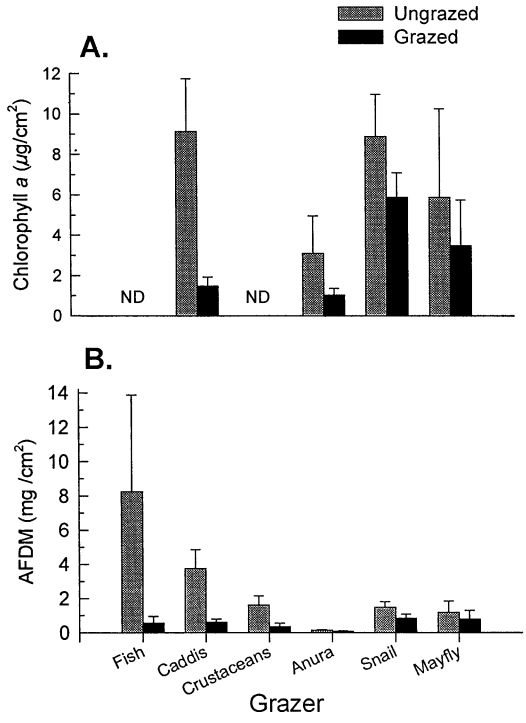

FIG. 4. Periphyton abundance as (A) chlorophyll *a* and (B) AFDM in ungrazed and grazed treatments for the six most frequently studied groups of grazers. Raw means (+1 SE) are plotted. ND = no data. Data are from studies listed in Fig. 5 legend.

P→G interaction (regression analyses).—The abundance of grazers in grazed treatments (i.e., representing ambient conditions as reported by investigators) was significantly related to the productive capacity of a stream (potential periphyton abundance) in only one of four possible comparisons. Grazer dry weight biomass ($\log_{10}$) was directly related to the amount of periphyton chlorophyll *a* in ungrazed treatments (r^2 = 0.19, $p < 0.007$, n = 37), but was unrelated to periphyton AFDM ($p > 0.520$, n = 41). Moreover, grazer numerical density was not related to either periphyton chlorophyll *a* ($p > 0.197$, n = 37) or AFDM ($p > 0.879$, n = 40).

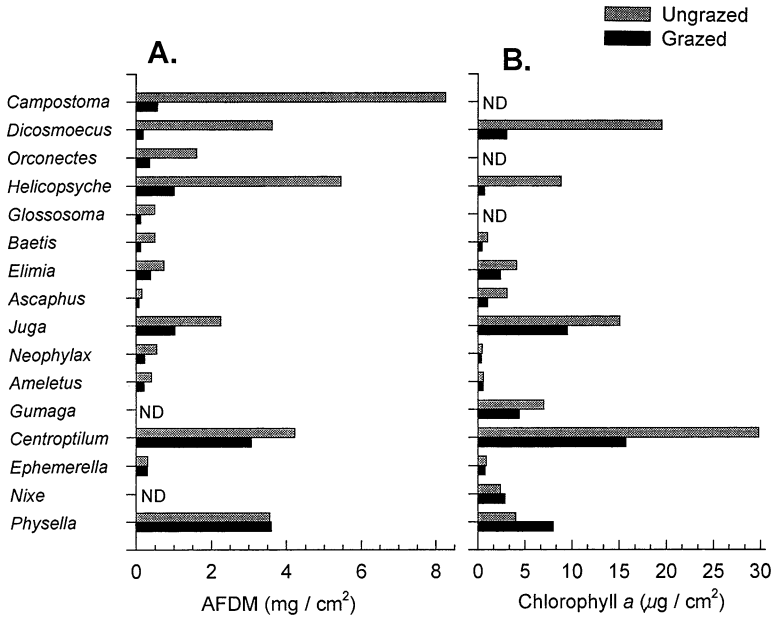

FIG. 5. Mean periphyton abundance as (A) chlorophyll *a* and (B) AFDM in ungrazed and grazed treatments for 16 genera of grazers included in the meta-analysis of grazer effect size. Genera are listed in general decreasing order of difference in periphyton chlorophyll *a* or AFDM between grazed and ungrazed treatments. Data were based on the following studies: *Ameletus* (Hill and Knight 1987, 1988b), *Ascaphus* (Lamberti et al. 1992), *Baetis* (DeNicola et al. 1990, Bechara et al. 1992, Kohler 1992), *Campostoma* (Power and Matthews 1983, Stewart 1987, Gelwick and Matthews 1992), *Centroptilum* (Lamberti et al. 1987a), *Dicosmoecus* (Jacoby 1987, Lamberti et al. 1987a, Steinman et al. 1987a, DeNicola et al. 1990), *Elimia* = *Goniobasis* (Hom 1982, Hill and Harvey 1990, Hill et al. 1992a, McCormick 1990, Mulholland et al. 1991, Steinman 1991, 1992, Steinman et al. 1990, 1991b, Rosemond 1993a, 1993b, Rosemond et al. 1993), *Ephemerella* (Bechara et al. 1992), *Glossosoma* (Kohler 1992), *Gumaga* (Feminella and Resh 1991), *Helicopsyche* (Lamberti and Resh 1983, Lamberti et al. 1987b, Feminella et al. 1989, Feminella and Resh 1990), *Juga* (Gregory 1980, Sumner and McIntire 1982, Hawkins and Furnish 1987, Lamberti et al. 1987a, 1989, Steinman et al. 1987a, DeNicola et al. 1990, Furnish 1990), *Neophylax* (Hill and Knight 1988b, Martin et al. 1991), *Nixe* (Jacoby 1987), *Orconectes* (Creed 1990a, 1990b, 1994, McCormick 1990, Hart 1992, Vaughn et al. 1993), and *Physella* = *Physa* (Kehde and Wilhm 1972, Vaughn et al. 1993). ND = no data.

G→G interaction.—Twenty studies quantified the direct or indirect effects of grazer manipulations on conspecific grazers (7 studies) or other benthic animals (13 studies). The usual treatment variable was grazer density (i.e., ambient versus low) and the main response variables were density, growth, biomass, and survivorship of conspecifics or other benthos (Table 2, see also Appendix 1). However, several studies also examined effects of grazers on animal feeding rate (Kohler 1992), condition factor (Hill 1992), size structure (Kohler 1992), and spatial distribution (Lamberti and Resh 1983, McAuliffe 1984b). Only one study (Harvey and Hill 1991) examined the response of a benthic vertebrate (i.e., the salamander *Desmognathus fuscus*) to grazers; all other studies quantified responses only for invertebrates.

For intraspecific experiments (n = 8 comparisons), all but one (Rosemond 1993a, for the snail *Elimia clavaeformis*) reported significant effects of grazers on growth of conspecifics. In these cases, higher growth occurred at lower grazer density. For experiments involving interspecific interactions between grazers and other benthic animals, we also found that most studies reported significant effects on growth (80%, n = 5 comparisons). In three of four comparisons, animal growth was higher under lower densities of target grazers. A smaller proportion of studies reported interspecific effects on animal density (60%, n = 84 comparisons). Of

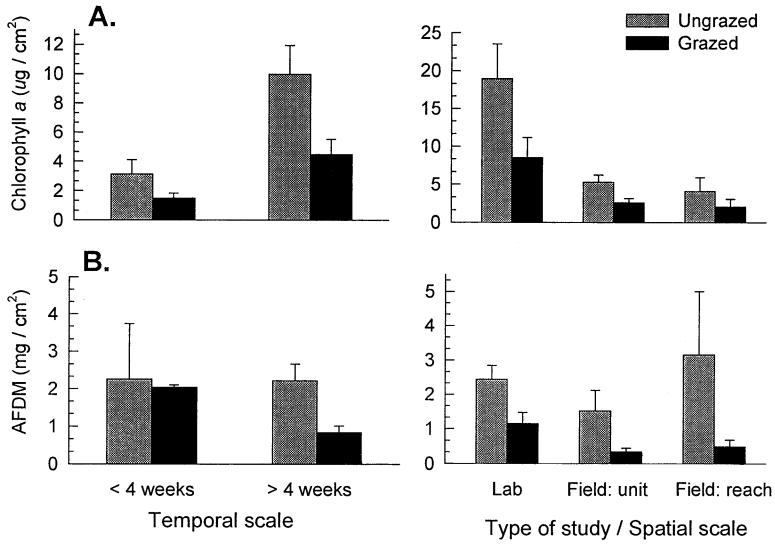

FIG. 6. Periphyton abundance as (A) chlorophyll *a* and (B) AFDM in ungrazed and grazed treatments based on temporal scale of experiments (left panels), and type and spatial scale of experiments (right panels). Raw means (+1 SE) are plotted. Data were based on the following studies: **Temporal scale, ≤4 wk**—Power and Matthews 1983, Murphy 1984, Hill and Knight 1987, Jacoby 1987, Stewart 1987, Hill and Knight 1988b, Creed 1990a, 1990b, Feminella and Resh 1990, 1991, Martin et al. 1991, Steinman 1991, Bechara et al. 1992, Kohler 1992, Hill et al. 1992a, Lamberti et al. 1992, Creed 1994; **Temporal scale, >4 wk**—Kehde and Wilhm 1972, Gregory 1980, Hom 1982, Sumner and McIntire 1982, Lamberti and Resh 1983, Hawkins and Furnish 1987, Lamberti et al. 1987a, 1987b, Steinman et al. 1987a, Feminella et al. 1989, Lamberti et al. 1989, Furnish 1990, Hill and Harvey 1990, Steinman et al. 1990, Mulholland et al. 1991, Gelwick and Matthews 1992, Kohler 1992, Lamberti et al. 1992, Steinman 1992, Rosemond 1993a, 1993b, Rosemond et al. 1993. **Spatial scale, lab**—Kehde and Wilhm 1972, Gregory 1980, Hom 1982, Sumner and McIntire 1982, Lamberti et al. 1987a, Steinman et al. 1987a, Lamberti et al. 1989, Creed 1990a, Steinman et al. 1990, Mulholland et al. 1991, Steinman 1991; **Spatial scale, field subunit/unit**—Lamberti and Resh 1983, Hawkins and Furnish 1987, Hill and Knight 1987, Jacoby 1987, Lamberti et al. 1987b, Hill and Knight 1988b, Creed 1990b, Feminella and Resh 1990, Furnish 1990, Feminella and Resh 1991, Martin et al. 1991, Bechara et al. 1992, Hill et al. 1992a, Kohler 1992, Steinman 1992, Rosemond 1993a, 1993b, Rosemond et al. 1993, Creed 1994; **Spatial scale, field reach/basin**—Power and Matthews 1983, Murphy 1984, Stewart 1987, Feminella et al. 1989, Hill and Harvey 1990, Gelwick and Matthews 1992, Lamberti et al. 1992.

those comparisons that reported significant effects of grazers ($n = 50$), only three (6%) showed that densities of some taxa (i.e., crane flies, caddisflies, and chironomid midges) were higher under ambient rather than under low grazer density (Hawkins and Furnish 1987, Kohler 1992, and Creed 1994). All other studies reported that benthic animals were more abundant when grazer density was lower.

Discussion

A central goal of ecology is to determine the degree to which patterns and underlying processes in nature can be both identified and generalized across space and time. Controlled experiments that manipulate factors thought to produce patterns represent a critical step toward meeting this objective. Although results of isolated experiments often cannot be safely extrapolated beyond the bounds of their own environmental conditions, empirical and theoretical advances in science are made by integrating information from individual studies (Cooper and Hedges 1994). Qualitative summaries of data have helped synthesize our collective knowledge, but such efforts are sometimes compromised by lack of analytical rigor and, hence, objectivity (Arnqvist and Wooster 1995). In the present study, we examined several fundamental questions about herbivory in stream ecosystems by compiling a quantitative analysis of re-

TABLE 4. Results of the stepwise regressions of grazer effect size (*D* and *HI*) on the six independent variables listed in Table 3. Separate results given for data based on periphyton chlorophyll *a* and AFDM. R^2 given for total model, and independent variables listed in order of the amount of variance explained in the dependent variable. Only those variables contributing significantly to regression models are shown.

Source of variation	SS	df	MS	*F*	*p*	R^2
D (chlorophyll *a*):						0.926
PPA	639.648	1	639.648	192.549	<0.001	
PPA × TG	266.713	3	88.904	26.762	<0.001	
Error	106.304	32	3.322			
D (AFDM):						0.983
PPA × TG	17.933	5	3.587	13.260	<0.001	
PPA	2.505	1	2.505	9.260	0.005	
Error	9.196	34	0.271			
HI (chlorophyll *a*):						0.365
PPA	5.536	1	5.536	7.387	0.011	
PPA × TG	8.284	3	2.761	3.685	0.022	
Error	23.982	32	0.749			
HI (AFDM):						0.601
PPA × TG	28.320	5	5.664	7.889	<0.001	
Biomass	4.536	1	4.536	6.318	0.017	
Error	24.409	32	0.718			

sults from independently conducted experimental studies. Below, we discuss the adequacy of the existing data base for addressing general questions regarding herbivory in streams and the implications of our analyses for understanding the nature and importance of stream herbivory. We also identify questions and hypotheses we believe should be addressed in future research.

Do the compiled data represent an unbiased appraisal of the importance of stream herbivory?

Collection of the empirical data necessary to test for generality in ecology is clearly beyond the scope of any single research endeavor, and generality therefore must be assessed by compiling information from separate studies. At least three types of bias may limit our ability to generalize accurately from the published literature. First, there are tendencies among scientists to seek positive results (i.e., confirmation bias, sensu Loehle 1987) and among journals to publish positive results (Connell 1983). Second, the way in which sites and specific habitats were chosen by investigators could bias experiments toward finding effects. Third, the published data may not represent a random collection of the possible sites, geographic regions, and seasons available for study.

We were encouraged to find that publication and confirmation bias do not appear to compromise the data from available literature on herbivory in streams. Furthermore, any tendency that might have existed to select sites based on their likelihood of showing strong herbivore effects did not appear to result in a biased sample, since this type of bias would also have generated a skewed sample size versus effect size relationship (Begg 1994). As such, we assumed that the experiments we examined represented a random sample of those streams studied to date. However, this sample clearly did not represent a random sample of the entire universe of possible stream conditions, and this bias limits the extent to which we can presently generalize from these data.

Most (73%) field experiments were conducted during spring and summer seasons, usually during benign, low-flow periods and in small to medium sized streams. These are times when benthic animals are usually concentrated in streams, and temperatures are favorable for high consumption and growth by grazers. Grazing animals also may be less abundant in larger stream systems where animal assemblages are

TABLE 5. Proportion of experimental studies showing significant effects of consumers in different trophic levels and ecosystems on their resources. Table modified from Sih et al. (1985).

Ecosystem	Herbivores	Pooled carnivores	Primary carnivores	Secondary carnivores
Intertidal	68	58	—	—
Other marine	59	41	—	—
Lotic	70–81[a]	53[b]	67	49
Lentic	—	72[b]	73	64
Terrestrial	63	40[b]	53	29

[a] This study. Range represents results based on differences in frequencies of effects on periphyton biomass (70) and assemblage structure (81).

[b] Calculated as the weighted (by number of studies) average of studies examining primary and secondary carnivores from data in table 7 of Sih et al. (1985).

often dominated by fine-particle feeders (Vannote et al. 1980). Further, the predominance of experiments conducted in streams from north-temperate latitudes (see Appendix 1) also could have introduced a strong geographic bias in interpreting the prevalence of herbivory. These biases probably exaggerate the importance of herbivory in stream ecosystems in general, and hence constrain our ability to understand how periphyton–herbivore interactions vary among all streams. Ultimately, achieving this goal will require that stream ecologists (1) conduct future experiments in larger stream systems, during hydrologically variable seasons, and in areas outside the north-temperate latitudes and (2) that authors describe and journals publish data describing the environmental settings of their study in as much detail as possible.

How may we generalize about effects of herbivores in the streams studied?

Relative importance of herbivores in streams compared to other ecosystems.—The proportion of studies that reported biotic control of resources by consumers at different trophic levels in streams are close to or higher than that found in all other ecosystems examined (Table 5). This trend is startling considering the view by many stream ecologists that structure and function of stream ecosystems are largely determined by abiotic processes such as physical disturbance (Minshall 1984, Reice 1985, 1994; also see discussions in Power et al. 1988b, Resh et al. 1988, Poff and Ward 1989). Our study filled a critical gap in the comparisons among ecosystems and trophic levels in patterns of predation (sensu latu) conducted by Sih et al. (1985) and Menge and Sutherland (1987). Our estimates of between 70 and 81% of comparisons showing significant effects by stream herbivores on periphyton are similar to or higher than those reported for intertidal and terrestrial herbivores, and considerably higher than those reported for 'other marine' herbivores (Table 5). This estimate also concurs with that reported for benthic herbivores from experiments in both freshwater lotic and lentic ecosystems (76%, Steinman, in press). The high frequency of effects by lotic herbivores relative to those of primary and secondary carnivores in streams is also similar to trends reported from other ecosystems (Sih et al. 1985). This is consistent with the predictions of Menge and Sutherland (1987), who hypothesized that impact of consumers is greatest at lower trophic levels (cf. Hairston et al. 1960) because of disproportionately lower effects of abiotic stress on these versus higher trophic levels.

Do experimental results describe naturally occurring patterns?—Although stream ecology has benefitted greatly from manipulative experiments, few of the reviewed studies provided rationale that either tied their experimental design to patterns known to occur in nature or considered how experimental manipulations were representative of natural conditions. For example, we found only eight studies (Power and Matthews 1983, Power et al. 1985, Power 1991, Hawkins and Furnish 1987, Hart 1992, Hill 1992, Kohler 1992, Creed 1994) that were explicitly designed to determine if the activities or response of grazers produced patterns observed in the field, although in some cases investigators did conduct laboratory experiments to supplement or confirm results of field experiments (e.g., Kohler 1984, Hart 1987). Furthermore, we found only three studies (Vaughn 1986, Hill 1992, Hill et al. 1992b) that conducted supplementary field sampling following lab or field experiments to evaluate if experimental results were actually manifested in nature (see also Feminella and Resh 1990, Rosemond 1994).

To date, most stream ecologists studying herbivory have not combined experimental results with quantitative assessments of natural patterns. Until this is done, the generality of much

experimental data of the type reviewed here will remain suspect. Although individual experiments often suffer from low statistical power, we believe empirical understanding in stream ecology will grow most rapidly by both (1) conducting field experiments as a means of identifying or discovering mechanisms that can produce patterns in nature and (2) sampling nature to determine if patterns are consistent with either theoretical predictions or results obtained from highly controlled experiments.

How large and how long should experiments be?—Ecologists are concerned with scales of observation, because many patterns and processes in natural ecosystems appear to be scale dependent (Wiens 1989, Crowl and Schnell 1990, Downes et al. 1993, see also Schneider 1994). In practical terms, scale dependency means that observations made at one scale may provide limited insight about the same phenomenon at another scale. For logistical reasons stream ecologists often must conduct experiments within spatially small (usually < 1 m^2) enclosures and over temporally short (< 4 wk) periods. How well do the results of herbivory experiments represent patterns and processes operating at larger scales (e.g., whole stream, different seasons, etc.)?

The most striking patterns to emerge from the comparisons of scale were the tendency for laboratory studies to show lesser effects of grazers on periphyton than field studies, and for short-term experiments to show lesser effects than long-term experiments (Fig. 6). These trends surprised us because we initially suspected that laboratory and short-term experiments, because of their higher degree of control, would show the strongest effects of grazer manipulations on periphyton. What mechanisms could produce these trends?

The trend for longer experiments to show stronger effects may be due to (1) animals in grazed treatments having a longer time period to forage and thus reduce the periphyton initially present in the experiment, (2) periphyton in ungrazed treatments having more time to accrue biomass, or (3) a combination of these processes. Indeed, the typical design used in quantifying the G→P interaction was to expose preexisting periphyton growths on substrates to grazers, and measure changes in periphyton relative to ungrazed treatments (e.g., Eichenberger and Schlatter 1978, Murphy 1984, Power et al. 1985, Lamberti et al. 1987b, Feminella and Resh 1991, Creed 1994). It thus appears that, on average, 4 wk is an insufficient period for periphyton assemblages within treatments to attain an equilibrium between processes creating cells (immigration, local growth) and those responsible for removing them (grazing, export).

Although experiments conducted for > 4 wk elicited stronger effects than those conducted for < 4 wk, our analyses could not determine the optimal length of experiments, just that 4 wk may be too short. We do not know, for example, if experiments conducted for 12 wk would show different effects than those conducted for 8 wk. We surmise, however, that the 'optimal' length for an experiment will strongly depend on stream conditions and the grazer used in the experiment. For example, many lotic grazers may have dramatic and immediate effects on their food resources, reducing periphyton standing crops to extremely low levels in a matter of hours or days (Lamberti and Resh 1983, Power and Matthews 1983, Feminella and Resh 1991, Creed 1994). We also note that under some circumstances, experiments conducted over long time periods (e.g., > 8 wk) may actually show low to moderate effects compared with shorter-term experiments. Several experiments conducted for >2 mo in our review showed an indirect negative effect on impact of grazers because other factors (e.g., disturbance, nutrient declines, senescence, seasonal succession, etc.) appeared to reduce or increase variation in periphyton abundance in ungrazed treatments (e.g., Lamberti et al. 1989, Mulholland et al. 1991, Gelwick and Matthews 1992, see also Grimm and Fisher 1986). These latter experiments may actually provide the most realistic description of the role of herbivores in streams, because their ungrazed treatments capture more of the natural temporal variability periphyton would exhibit in the absence of herbivores.

That field experiments tended to show stronger effects than laboratory experiments was puzzling, especially given that laboratory studies lasted about a week longer than field experiments. We advance four possible reasons why this trend emerged. First, temperatures, and hence algal production, may have been higher in laboratory streams and thus ambient densities of grazers less able to control this production (Phinney and McIntire 1965). Second, cur-

rent speeds may have been lower or less variable in laboratory streams than those typically encountered under field conditions, and export of periphyton associated with grazer foraging or movement also may have been lower. Third, light intensities and thus productive capacity of periphyton may have been higher in laboratory than under field conditions, although natural light regimes are often mimicked in most laboratory experiments. Fourth, assemblage structure of periphyton in laboratory experiments may have been more resistant to grazers than that found in the field. Unfortunately, the majority of studies used in our meta-analysis did not report data on some or most of these environmental variables to allow tests of these hypotheses. However, the first three hypotheses are consistent with our observations of higher chlorophyll *a* accruing in laboratory streams than under field conditions, with the AFDM data for laboratory versus habitat-unit field studies, but are inconsistent with the large estimate of mean AFDM in ungrazed treatments for reach-level field studies (Fig. 6). Differences among laboratory and field experiments in the amounts of both chlorophyll *a* and AFDM present in grazed treatments are consistent with the fourth hypothesis, i.e., periphyton abundances in grazed treatments in laboratory studies were 2.8 (AFDM) to 3.6 (chlorophyll *a*) times higher than those in grazed treatments under field conditions.

Regardless of the mechanisms responsible for temporal and spatial temporal patterns, it appears that both short-term and laboratory experiments may misrepresent outcomes of the very interactions they are designed to mimic in nature. It may therefore be difficult to extrapolate either from the results of laboratory studies to real ecosystems or from short-term experiments to the longer time periods over which natural populations of both periphyton and grazers interact. We recognize that some laboratory experiments were designed to elucidate possible mechanisms, and extrapolation to real ecosystems was never a stated objective. We simply emphasize that such extrapolations, if attempted, should be approached with extreme caution (see also Lamberti and Steinman 1993). Studies explicitly designed to examine the combined effects of spatial and temporal scale are sorely needed.

Specific effects of herbivores on periphyton

The results of our analyses imply that at least some aspect of periphyton in streams is nearly always affected by herbivores, with frequency of effects falling in the order: periphyton assemblage structure > periphyton biomass > periphyton productivity.

Effects on periphyton assemblage structure.— Stream grazers appear to have pervasive effects on periphyton assemblage structure. The ability of grazers to affect assemblage structure is apparently related to taxon-specific differences among algae in vulnerability to grazing associated with differences in physiognomy or microdistribution. Upright, overstory species or those in loose, upper periphyton layers often decrease in relative abundance in response to grazing (Hill and Knight 1987, 1988a, Creed 1994; but see Dudley et al. 1986, Feminella and Resh 1991, Sarnelle et al. 1993), whereas adnate species that adhere tightly to hard substrata often increase in relative abundance (Colletti et al. 1987, Hill et al. 1992b).

Shifts in assemblage structure also may occur from consumption of particular algae by herbivores and their indirect effects on unconsumed algal taxa. Grazing caddisflies (*Gumaga nigricula, Helicopsyche borealis*: Feminella and Resh 1991, Bergey and Resh 1994, *Leucotrichia pictipes*: Hart 1985a, *Agapetus*: Dudley 1992, Poff and Ward 1992, *Psilotreta*: Karouna and Fuller 1992), mayflies (*Baetis*: Dudley 1992), chironomid midges (*Orthocladius*: Hershey et al. 1988), and fish (*Campostoma anomalum*, Power et al. 1988a) all show preferences for particular algal species or growth forms, presumably based on differences among algal species in their availability (Moore 1977, Gray and Ward 1978, Scrimgeour et al. 1991) or quality (Peterson 1987, Kupferberg et al. 1994, Lester et al. 1994). There remains a debate about whether such "preference" represents differential efficiency of grazers consuming particular periphyton growth forms or true selection (Gregory 1983, Steinman, in press), although some examples of selection or specialist herbivores have been found in streams (Resh and Houp 1986, Feminella and Resh 1991, McCormick 1991, Becker 1994). Irrespective of the mechanism of consumption, removal of particular algal taxa by grazers may alter assemblage structure in two ways: (1) by directly reducing the dominant alga, if con-

sumed, and (2) by indirectly increasing other algal species with poorer competitive abilities (Hart 1985a, Power et al. 1988a, Feminella and Resh 1991).

It is not clear why grazing increased algal diversity in some studies and decreased it in others. We found no consistent pattern in types of grazers, predominant algal assemblages present, or other conditions that would account for this result. Steinman (in press) hypothesized that a combination of low grazer preference for dominant algae and loose algal competitive hierarchies resulting from ample space (both benthic and epiphytic) in benthic habitats may explain why grazers do not consistently reduce algal diversity, although this idea remains to be tested. Interactions between density of grazers (i.e., intensity) and time (i.e., duration) used in experiments also may explain some of the differences. For example, Colletti et al. (1987) found that intermediate densities (2800/m^2) of the grazing mayfly *Heptagenia criddlei* decreased diatom diversity (as Shannon's H') in 10 d to levels that high-density (>7100/m^2) treatments produced in only 24 h. In contrast, low-density (800/m^2) treatments had no effect on diversity throughout their 28-d experiment.

Of those studies finding effects of grazers on algal diversity, only two provide empirical support for Connell's (1978) intermediate disturbance hypothesis (see also Lubchenco 1978). McCormick and Stevenson (1989) reported highest diversity (as Shannon's H' and Pielou's J') at intermediate grazer density of the snail *Goniobasis* (= *Elimia*). DeNicola et al. (1990) studied three grazer species (i.e., *Dicosmoecus, Juga, Baetis*) in separate experiments, each having a different effect on periphyton biomass and thus producing different levels of disturbance. They observed highest periphyton diversity (as species heterogeneity, H'') in treatments containing *Juga,* the grazer whose presence had intermediate effects on biomass. Unfortunately, too few studies quantified diversity using the same index to allow us to explicitly test this hypothesis using data compiled across studies.

Effects on periphyton biomass.—Perhaps the most striking result that emerged from our effect size analyses was that the amount of periphyton removed in grazed treatments was mostly a function of potential periphyton abundance available to grazers, as measured by periphyton biomass in the ungrazed treatments. Although more variable for chlorophyll *a* data, uniformly low standing crops in grazed treatments occurred for periphyton AFDM, irrespective of potential periphyton abundance, grazer taxon, and grazer population density and biomass (Fig. 4). The ecological implication of this pattern is profound because it suggests that herbivores in streams are generally capable of controlling resource levels across nearly three orders of magnitude of potential periphyton abundance. In many ecosystems, plant production can be high enough to swamp the consumptive losses due to grazing (Slobodkin et al. 1967, Ricklefs 1990, Cyr and Pace 1993). In the present study, evidence for swamping across studies would have been manifested by the amount of periphyton removed by grazers either reaching an asymptote (i.e., type II total response, Hassell 1981) or declining with increasing periphyton abundance after an initial increase. The outcome of the relationships we found was the presence of low and remarkably uniform (< 1 mg AFDM/cm^2) periphyton standing crops in grazed treatments across systems and grazer taxa studied (cf. Figs. 3, 4). At least one of two possible mechanisms may account for this relationship. First, grazer taxonomic composition may have varied among studies such that the specific taxa present were those most efficient at harvesting the type and amount of periphyton present. Large-bodied grazers, often with greater consumptive demands (e.g., the minnow, *Campostoma*) or mechanical abilities to harvest large standing crops (e.g., cased caddisflies and decapod crustaceans) were usually found in streams with the greatest productive capacity (see Fig. 4B). In contrast, low production systems were often dominated by smaller-bodied taxa (e.g., mayflies and physid snails) capable of harvesting only thin biofilms. Second, densities or population biomasses of grazers may have varied directly among sites in relation with the amount of food potentially available. The latter response would suggest efficient tracking of variation in productive capacity of resources by grazers (sensu Power 1984, see also Hawkins et al. 1982, Fuller et al. 1986, Wallace and Gurtz 1986), either behaviorally or from differential survivorship in stream sections of contrasting periphyton availability.

The results of our analyses were at least partially consistent with both of these potential

mechanisms in that grazer biomass did vary directly with potential periphyton abundance as measured by chlorophyll *a*, and grazer taxonomic group was related to the degree to which periphyton standing crops were reduced. Together with the data showing frequent food limitation on grazer growth rates (see below), these relationships imply that grazer populations strongly reduce available periphyton abundance and are in turn limited by food availability. We know of no other ecosystem in which grazers appear to exert such a pervasive effect on their resource base (but see Morrow and Lamarche [1978] for a case of consistent strong effects of terrestrial herbivores on some south-temperate *Eucalyptus* forests).

Taxon-specific effects on periphyton biomass.— That grazer taxon and biomass emerged as important factors in effect size analyses was not surprising, given large differences in ambient biomass and density of the species used in experiments and their abilities to harvest periphyton. However, interactions among these factors in terms of effects on periphyton biomass varied strongly with the species in question. For example, high mean numerical densities (ca. 5500/m^2) of the caddisfly *Helicopsyche borealis* had large effects, even though mean biomass density was relatively low (ca. 1.4 g/m^2, Lamberti and Resh 1983, Lamberti et al. 1987b, Feminella and Resh 1990). In contrast, another caddisfly (*Dicosmoecus gilvipes*) showed large effects at low numerical density (ca. 150/m^2) but high biomass density (ca. 18 g/m^2, Jacoby 1987, Lamberti et al. 1989, Steinman et al. 1987a). Interestingly, two large-bodied grazers with both low numerical and biomass density had large effects on periphyton: the crayfish *Orconectes propinquus* (1–5 individuals and 1–5 g/m^2, numerical and biomass density, respectively, Creed 1990a, 1990b, 1994), and the minnow *Campostoma anomalum* (2 individuals and 1.1 g/m^2, Power and Matthews 1983, Stewart 1987, Gelwick and Matthews 1992). Mayflies were the only taxonomic group to have consistently low effects on periphyton relative to other grazers, although most mayfly experiments also were conducted at low densities. Mayflies typically appear to exert low effects relative to other grazers (Jacoby 1987, Lamberti et al. 1987a, Hill and Knight 1988b, Feminella et al. 1989, DeNicola et al. 1990, Bechara et al. 1992), but we found some exceptions (e.g., *Baetis* spp. [Dudley 1992, Kohler 1992], *Ameletus validus* [Hill and Knight 1987], see Fig. 5). Snails usually had intermediate effects relative to other grazers even though they spanned a large range of ambient population densities (120–1400/m^2) and biomass (0.6–14 g/m^2) across experiments. Effects of lotic prosobranch snails (*Elimia* and *Juga*) were considerably greater than lotic pulmonates (e.g., *Physella*). Interestingly, this pattern was exactly the opposite of that reported for lakes, in which pulmonate snails were more effective at removing periphyton than prosobranch snails (Barnese and Lowe 1990).

Taxon-specific differences in effects on periphyton are a complex function of differences in grazer mouthpart or other food-gathering features (McAuliffe 1984a, McShaffrey and McCafferty 1986, 1988, Karouna and Fuller 1992, but see Arens 1994), consumption rates (Lamberti et al. 1989), movement rates (Wiley and Kohler 1981, Kohler 1984, Kohler and McPeek 1989, Li and Gregory 1989, Poff and Ward 1992), energetic demands (Calow 1974, Lamberti et al. 1989), feeding efficiency (Lamberti et al. 1987a, Steinman et al. 1987a, Scrimgeour et al. 1991), and body size (Steinman 1991). Magnitude of grazer impact also may be associated with differences among grazers in their vulnerability to predators. We observed that most grazers having large effects on periphyton in individual experiments were also those not commonly consumed by local predators (*Helicopsyche*: Lamberti et al. 1987b, *Dicosmoecus*: Jacoby 1987, *Juga*: Hawkins and Furnish 1987, *Elimia*: Hill and Harvey 1990, *Glossosoma*: Kohler 1992). In contrast, other, more vulnerable species had their greatest effects on periphyton only at low predator densities (*Campostoma*: Power et al. 1985, *Baetis*: Kohler and McPeek 1989, *Pseudochironomus*: Power 1990a). There are some important experimental studies that assessed the role of predation in determining abundance and feeding behavior of some grazing mayflies (e.g., Culp et al. 1991, Bechara et al. 1992, Culp and Scrimgeour 1993, Cowan and Peckarsky 1994) and tadpoles (Feminella and Hawkins 1994) but more research on a greater variety of grazers is needed.

Most experiments that examined relative effects of more than one grazer taxon did so with widely different grazer population densities or biomasses, thereby confounding effects of individual taxa and abundance. We found only four

studies that examined effects of different stream grazers at equivalent density or biomass, and each only studied taxonomically related groups (i.e., mayflies: Scrimgeour et al. 1991, Bechara et al. 1992, Karouna and Fuller 1992; caddisflies: Feminella and Resh 1991). In each case, strong differences in periphyton removal rates were observed among most taxa. Carefully controlled experiments are clearly needed that quantify density- or biomass-specific effects across a range of grazer taxa.

Differences between AFDM and chlorophyll a measures of periphyton abundance.—It is not clear from our analyses nor those of others which periphyton abundance measure is the most ecologically meaningful index of periphyton response to grazers. For the strongest responses, both measures showed the same trends. In other cases, one or the other measure appeared to be sensitive to factors to which the other was not. We therefore believe stream ecologists should carefully consider how they measure periphyton abundance in future studies. Although the overall proportion of studies reporting significant effects appeared to be independent of whether AFDM or chlorophyll *a* was used, the two variables did not always lead to the same conclusions in the effect size analyses. We suspect chlorophyll *a* may provide less accurate, or more variable, estimates of true periphyton abundance than AFDM, but urge researchers to consider the theoretical advantages and disadvantages of the two measures when designing experiments. An advantage of chlorophyll *a* is that it provides a measure of the abundance of living plant tissue; however, chlorophyll *a* may be too sensitive to other environmental factors to detect real (i.e., ecologically relevant) differences among treatments in the abundance of the entire periphyton food source (see Hawkins and Furnish 1987). The amount of chlorophyll *a* per unit algal biomass can vary up to three fold as a function of algal taxon, irradiance, and grazing pressure (Wetzel and Westlake 1969, Hunter 1980, Antoine and Benson-Evans 1983, Richardson et al. 1983). In their review, Morin and Cattaneo (1992) found that chlorophyll *a* was inherently more variable than AFDM, with the magnitude of variation dependent on type of experiment (lab versus field incubation) and substrate (artificial versus natural) used. This tendency for chlorophyll *a* to exhibit high variation might bias chlorophyll-based studies toward finding no effect of a treatment, a prediction that we did not observe. Concurrent measurement of both variables would probably facilitate interpretation of results from individual experiments, and provide data for subsequent comparisons and analyses.

Effects on periphyton production.—In contrast to their frequent effects on periphyton assemblage structure and biomass, grazers appeared to have less frequent effects on productivity, although low sample size limited the statistical power of these tests too. Those experiments that found effects on productivity reported that grazers usually decreased areal-specific production (ASP). This observation is consistent with the magnitude and direction of effect found for periphyton biomass, and would thus be expected given the strong positive correlation that exists between algal biomass and ASP (Gregory 1983). As long as biomass-specific production (BSP) remains relatively constant within the grazed periphyton matrix, removal of algal cells by grazers should decrease ASP. However, BSP also responds to grazing, which potentially creates a feedback that can influence ASP. BSP can either increase or decrease with grazing, depending on environmental conditions and the intensity of grazing. For example, grazing of high-biomass assemblages (e.g., Gregory 1983, Lamberti and Resh 1983, Stewart 1987, Gelwick and Matthews 1992) appears more likely to enhance BSP than grazing of low-biomass assemblages, which are often under strong light or nutrient limitation (e.g., Steinman et al. 1990, 1991a, Hill et al. 1992a, Rosemond et al. 1993). Assemblages in these latter cases may already be at or near their maximum BSP in the presence of these other environmental constraints (Hill and Boston 1991). Grazers appear to increase BSP by the following mechanisms: (1) disproportionately removing moribund algal cells, (2) increasing diffusion rates and light within the biofilm, (3) supplementing or regenerating limited nutrients, and (4) selecting for fast-growing, early successional taxa (Lamberti and Resh 1983, Mulholland et al. 1991, Hill et al. 1992a, Steinman 1992). Although grazers clearly can increase BSP, observed increases do not seem large enough to normally compensate for the concomitant loss of biomass. Of those experiments in which grazers increased BSP, only one (Lamberti et al. 1987a, for the snail *Juga*) found that, on an areal basis, grazed as-

semblages had higher net production than ungrazed assemblages, a result occasionally observed in other aquatic (Cooper 1973, Flint and Goldman 1975, Kesler 1981) and terrestrial (McNaughton 1976) ecosystems.

Do herbivores affect other herbivores and benthic species in streams?

Relative to the number of studies that examined G→P interactions, there were few studies of P→G and G→G interactions. However, we can draw a few tentative generalizations from these studies. Grazer abundance, distribution, and growth all appear to be strongly affected by periphyton abundance. Higher grazer densities in food-supplemented treatments (versus grazed controls) suggests bottom-up control of herbivore populations (Elwood et al. 1981, Hart and Robinson 1990), which may occur in conjunction with strong top-down control of periphyton by herbivores (Steinman 1992, Peterson et al. 1993, Rosemond et al. 1993, Biggs and Lowe 1994, Hill et al. 1995, but see Junger and Planas 1993). Large numerical responses by grazers apparently occur because of their ability to recognize food-rich patches, and a combination of (1) increased immigration into these areas by drift, oviposition, or crawling (Lamberti and Resh 1983, Kohler 1985, Richards and Minshall 1988, Feminella et al. 1989, Winterbourn 1990), and (2) decreased emigration from food-rich patches by reductions in movement rates, and increased foraging time and consumption rates (Calow 1974, Hart 1981, Kohler 1984, Kohler and McPeek 1989, Scrimgeour et al. 1991, Poff and Ward 1992). However, studies that quantified such responses usually did so at extremely small spatial scales (i.e., grazed patch) or under artificial conditions in laboratory streams. Thus, we do not know the degree to which patch-specific periphyton conditions (e.g., biomass, productivity, physiognomy, chemistry, presence of certain algal species, etc.) interact with environmental variables (e.g., shading, flow, detrital load, etc.) at larger scales to influence grazer abundance (see Dudgeon and Chan 1992, Poff and Ward 1992). Moreover, there is no consensus about what specific cues associated with periphyton-rich sites at these scales trigger numerical responses, nor do we know the degree to which cues vary with grazer species.

Grazers at high density are often food limited in streams, and numerous studies have invoked competition, either intraspecific (Hart 1981, Lamberti and Resh 1983, Hart 1987, Lamberti et al. 1987b, Hill and Knight 1987, 1988b, Hershey et al. 1988, Furnish 1990, Feminella and Resh 1990, Martin et al. 1991, Kohler 1992) or interspecific (McAuliffe 1984a, 1984b, Hart 1985b, Hawkins and Furnish 1987, Lamberti et al. 1987b, Dudley and D'Antonio 1991, Feminella and Resh 1991, Kohler 1992, Hill 1992, Hill et al. 1992b, Vaughn et al. 1993, Biggs and Lowe 1994), as a mechanism responsible for observed patterns of low growth, survivorship, or abundance. A typical effect of periphyton reduction by dominant grazer species was lower abundances of other grazers relative to ungrazed, high-periphyton treatments. Exploitative (i.e., consumptive, sensu Schoener 1983) competition appears to be more common than interference (i.e., pre-emptive or territorial, sensu Schoener 1983) competition, but experiments specifically designed to discriminate between these mechanisms are rare (but see McAuliffe 1984a, 1984b, Hart 1985a). Sessile or sedentary species appear more likely to engage in interference competition than more mobile species (e.g., Hawkins and Furnish 1987, Hemphill 1988), although some large, mobile species (e.g., snails) may reduce densities of other species by accidentally displacing them from substrates rather than reducing availability of a limiting resource (Hawkins and Furnish 1987).

Despite the clear existence of competition within and between species of grazers, several key issues remain unresolved that are central to understanding the importance of competition on grazer population dynamics. We do not know if populations experience chronic competition for resources over many generations (see Keddy 1989, Feminella and Resh 1990) and if intense competition within one generation can carry over and affect quality of subsequent generations (sensu Anderbrant et al. 1985). Moreover, we have such a limited understanding of the niche relationships of most stream species that we cannot evaluate if a central principle of competition theory generally applies to streams—i.e., is the magnitude of competition between species directly related to niche overlap (Hawkins and Furnish 1987)?

It also appears that, in some cases, herbivore densities can increase (rather than decrease) when periphyton is decreased, or decrease

when periphyton is increased. Decreases by grazers in high food treatments ostensibly result either from active avoidance of complex, high-biomass assemblages by some species or preference for architecturally simple, grazed assemblages by others (Dudley et al. 1986, Ogilvie 1988, Feminella and Resh 1991, Gelwick and Matthews 1992, Vaughn et al. 1993). Both types of grazer responses appear to involve differences in feeding efficiency in high- and low-biomass assemblages (Steinman, in press); however, innovative experiments are needed to test if grazers inhabit these dissimilar assemblages to maximize growth rates, avoid competitors or predators, or for other reasons that may affect fitness (see Feminella and Resh 1991, Hill et al. 1992b, Kohler 1992, Vaughn et al. 1993). Density increases by some grazer species in low food treatments may occur from the indirect facilitation of a dominant grazer that enhances resource conditions for some grazer species at the expense of others (Hawkins and Furnish 1987, Feminella and Resh 1991, Gelwick and Matthews 1992, O'Connor 1993, Vaughn et al. 1993, Creed 1994). The mechanisms for facilitation may occur from (1) a grazer-induced change in habitat suitability for different grazer species due to physical alteration of substrate, or (2) a competitive release of one grazer species following the reduction in abundance of a strong competitor by a dominant grazer. Such higher order or indirect effects (see Billick and Case 1994) are known to occur among species, but their prevalence and importance in stream ecosystems are largely unknown.

Recommendations

Given the overall importance of periphyton as a food source in streams, we believe it is critical that stream ecologists develop (1) an accurate understanding of the overall importance of herbivory in stream ecosystems and (2) an understanding of the variability among streams in the importance of herbivory. Accomplishing the first task will depend primarily on how well stream ecologists reduce the site selection biases that currently characterize data now in the literature. Accomplishing the second task will require, in addition to unbiased site selection, that individual investigators collect ancillary data that can be used as covariables in subsequent meta-analyses. We recommend that future studies of herbivory in streams collect and report as much of the following data as possible: geographic location of the site; date and duration of the experiment; size of the stream studied; historical and contemporary discharge regimes; size of the experimental arenas used; mean, maximum, and minimum temperatures encountered during the study; solar irradiance or shade levels; water chemistry including concentrations of major ions; habitat type studied; type and size of stream substrates; current velocities within and outside experimental arenas; individual size, density, and biomass of animals used in experiments. Collection of some or all these data will undoubtedly lead to a more robust analysis than was possible here, and hence a more comprehensive understanding of the reciprocal interactions between grazers and their food resources in stream ecosystems.

Finally, improved understanding of the importance of herbivory in streams will occur when ecologists determine (1) if the frequency and strength of interactions vary with the magnitude of disturbance across longer time scales (several seasons and years) and geographic regions, (2) if the effect of different grazer species (i.e., phylogeny) is independent of grazer site and density, (3) the degree to which environmental factors influence effects of dominant grazers on other benthic species, and (4) the degree to which strong interactions between grazers and periphyton affect long-term ecosystem dynamics.

Acknowledgements

We thank Rob Creed, Fran Gelwick, Walter Hill, Steve Kohler, Bill Matthews, Amy Rosemond, Al Steinman, and Caryn Vaughn for providing unpublished manuscripts at the time we began the review. Amy Rosemond, Fran Gelwick, and Walter Hill provided unpublished regression equations for grazer size-biomass conversions. Comments from Rob Creed, Dennis DeVries, Steve Dobson, Gary Lamberti, Rosemary Mackay, Mark Ritchie, Al Steinman, Mike Chadwick, Joe Furnish, Jim Hogue, Chuck Howard, Stuart Ludsin and an anonymous reviewer greatly improved the manuscript, and Melanie Minor assisted with the appendix. Any remaining errors of fact or interpretation are ours alone. We apologize to individuals whose studies were unintentionally omitted from our re-

view. Finally, JWF gratefully acknowledges Vince Resh and Gary Lamberti for providing him the primary stimulus, sapient counsel, and moral support for stream grazing research, and CPH thanks Stan Gregory, the grandfather of stream herbivory, for many years of intellectual stimulation and challenges and his unselfish sharing of ideas. This work was supported in part by the Alabama Agricultural Experiment Station (JWF), the Utah State University Ecology Center (CPH), and the Anadromous Fish Habitat Project, Pacific Northwest Experiment Station, US Department of Agriculture Forest Service (CPH). This is contribution No. 15-954983 of the Alabama Agricultural Experiment Station.

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Received: 1 March 1995
Accepted: 19 September 1995

APPENDIX 1. Summary of experimental conditions for the 89 studies used in quantifying stream grazer–periphyton interactions. Symbols in interaction column are G = grazer, Gi = grazer intraspecific effects, P and Peri. = periphyton, L = light, N = nutrients, C = current, Pd = predator (carnivore), and '→' used to indicate direction of interaction (e.g., G→P = effects of grazers on periphyton). Specific names of target grazers were omitted to save space. Intervals in experimental duration column are those that best approximated the length of experiments (i.e., 'Days': < 1 wk; 'Weeks': < 2 mo; 'Months': < 1 Season). Ambient densities of target grazers were those used in experiments to mimic natural densities or were those reported to occur in situ during experiments. N/G = data not given. N/A = not applicable. len. = length. dw = dry weight. ww = wet weight. CL = carapace length. TL = total length. SL = standard length.

Study	Interaction	Type of study	Geographic region	Target grazer	Manipulation
Barnese & Lowe 1992	G→P	Lab	Michigan, USA	*Brachycentrus*	Grazer exclusion Substrate Time of day
Bechara et al. 1992	G→P Pd→G	Field	Quebec, Canada	*Baetis* *Ephemerella*	Grazer exclusion Predator exclusion
Colletti et al. 1987	G→P	Lab	Arizona, USA	*Heptagenia*	Grazer density
Creed 1990a	G→P G+P→G	Lab	Michigan, USA	*Orconectes* & misc. grazers	Grazer exclusion Peri. abundance
Creed 1990b	G→P G+P→G	Field	Michigan, USA	*Orconectes* & misc. grazers	Grazer exclusion Peri. abundance
Creed 1994	G→P G+P→G	Field	Michigan, USA	*Orconectes* *Leucotrichia* *Psychomyia*	Grazer exclusion Peri. abundance
DeNicola et al. 1990	G→P	Lab	Oregon, USA	*Juga* *Dicosmoecus* *Baetis*	Grazer exclusion Grazer species
DeNicola & McIntire 1991	G+L+C→P C+L+P→G	Lab	Oregon, USA	*Juga*	Current Light Peri. abundance Grazer movement
Dudgeon & Chan 1992	L+P→G	Field	Hong Kong	Misc. grazers	Light Peri. abundance
Dudley 1992	G→P	Field	California, USA	*Baetis* *Agapetus*	Grazer density
Dudley & D'Antonio 1991	G→P G→G+Gi	Field	California, USA	*Agapetus* *Micrasema*	Grazer exclusion Substrate
Dudley et al. 1986	P→G	Field	California, USA	Misc. species	Peri. abundance Peri. composition
Eichenberger & Schlatter 1978	G→P	Field	Zurich, Switzerland	Orthocladiinae	Grazer exclusion
Elwood et al. 1981	N→P P+N→G	Field	Tennessee, USA	*Goniobasis* (=*Elimia*)	Nutrients Peri. abundance
Feminella & Resh 1990	G→P P→G G→Gi	Field & Lab	California, USA	*Helicopsyche*	Grazer density Peri. abundance
Feminella & Resh 1991	G→P	Field	California, USA	*Helicopsyche* *Gumaga*	Grazer exclusion Grazer species

APPENDIX 1. Extended

Response variable	Experimental duration	Experimental season	Spatial scale	Size of grazer	Ambient density of target grazers (no./m²)
Peri. export Peri. composition	Days	Summer	Lab streams	10 mm (len.)	1243
Peri. abundance Grazer size	Weeks	Summer (1988 & 1989)	Streamside channels	*Baetis*: 6–8 mm (len.) *Ephemerella*: 5–7 mm (len.)	300 300
Peri. abundance Peri. composition	Weeks	N/G	N/G	4–9 mm (len.)	521–3800
Peri. abundance Grazer density	Days	Spring	Lab stream	*Orconectes*: 1.4 g (dw)	2.5
Peri. abundance Grazer density	Weeks	Summer	Riffle & pool units	*Orconectes*: 1.24 g (dw)	1–5
Peri. abundance Grazer density	Weeks	Summer–Autumn	Single unit?	*Orconectes*: 5 g *Leucotrichia*: N/G *Psychomyia*: N/G	2.4 370–1480 4630–14,815
Peri. abundance Peri. productivity Peri. composition	Weeks	Summer	Lab streams	N/G	*Juga*: 500 *Dicosmoecus*: 50 *Baetis*: 500
Peri. abundance Peri. composition Grazer growth	Weeks	Summer	Lab streams	10–15 mm (len.)	375
Grazer density Grazer composition	Weeks	Autumn	Five riffles	N/A	N/A
Peri. abundance	Weeks	Spring	In situ channels	*Baetis*: 3–8 mm (len.) *Agapetus*: 3–6 mm (len.)	50,000? 15,000?
Peri. abundance Grazer density	Seasons	Spring & Autumn	Single riffle	N/G	<1000–7000 (grazers combined)
Grazer density Benthic composition	Seasons	Summer & Winter	Single unit	N/G	>1000
Peri. abundance	Season	Summer	Single unit	Variable	>20,000
Peri. abundance Grazer density	Season	Winter–Spring	Reach	N/G	119
Peri. abundance Grazer growth Grazer development Grazer survivorship Grazer fecundity	Season	Winter & Spring	Single pool	0.4–0.8 mg (dw)	1200–3400
Peri. abundance Peri. composition	Weeks	Summer	Single pool	*Helicopsyche*: 0.16 mg (dw) *Gumaga*: 0.45 mg (dw)	5000 300

APPENDIX 1. Continued.

Study	Interaction	Type of study	Geographic region	Target grazer	Manipulation
Feminella et al. 1989	G→P	Field	California, USA	*Helicopsyche* *Gumaga* *Centroptilum* *Physella*	Grazer exclusion
Fuller et al. 1986	L→P P→G	Field	New York, USA	*Baetis*	Light Peri. abundance
Furnish 1990	G+L→P	Field & Lab	Oregon, USA	*Juga*	Light Grazer exclusion
	P→G				Peri. abundance
Gelwick & Matthews 1992	G→P+N	Field	Oklahoma, USA	*Campostoma* & misc. grazers	Grazer exclusion
	G+P→G				Peri. abundance
Gregory 1980	L+G→P	Lab	Oregon, USA	*Juga*	Light Grazer density
	P→G				Peri. abundance
Hart 1981	P→G	Field	California, USA	*Dicosmoecus*	Peri. patchiness
Hart 1985a	G→P	Field	Michigan, USA	*Leucotrichia*	Grazer exclusion
Hart 1985b	G→P P→G G→Gi	Field	Michigan, USA	*Leucotrichia*	Grazer exclusion Peri. abundance
Hart 1987	G→P P→G G→Gi	Field & Lab	Michigan, USA	*Glossosoma*	Grazer density Peri. abundance
Hart 1992	G→P	Field	Michigan, USA	*Orconectes* *Leucotrichia* *Psychomyia*	Grazer exclusion
Hart et al. 1991	G→P	Field	Michigan, USA	*Leucotrichia* *Elimia*	Grazer exclusion Grazer species
Hart & Robinson 1990	N→P+G P→G	Field	Michigan, USA	*Leucotrichia* *Psychomyia*	Nutrients Peri. abundance
Harvey & Hill 1991	Pd+G→G	Field	Tennessee, USA	*Elimia*	Predator exclusion Grazer exclusion
Hawkins & Furnish 1987	G→P P+G→G+Gi	Field	Oregon, USA	*Juga*	Grazer exclusion Light Substrate Peri. abundance

APPENDIX 1. Continued. Extended.

Response variable	Experimental duration	Experimental season	Spatial scale	Size of grazer	Ambient density of target grazers (no./m²)
Peri. abundance	Months	Summer	Reaches in three streams	N/G	141–1820
Peri. abundance Grazer density Grazer size Grazer movement	Season	Summer	Three riffles	0.42–0.86 mg (dw, adults)	21–700
Peri. abundance Peri. productivity Peri. composition Grazer growth Grazer movement Grazer production	Seasons	All	In situ channel & lab stream	Variable	2.1–26.5 (g AFDM)
Peri. abundance Peri. productivity Peri. composition Bacterial abundance Detritus Nutrients Grazer density	Season	Spring	Reach	N/G	1.8
Peri. abundance Peri. productivity Peri. composition Peri. condition Grazer growth	Weeks	Variable	Lab stream	8–11 mm (len.)	0–1020
Grazer activity Grazer distribution Grazer foraging	Month	Summer	Single pool	5th instar	70
Peri. composition	Days	N/G	Single riffle	5th instar	>10,000
Peri. abundance Grazer distribution	N/G	Summer	N/G	5th instar	>10,000
Peri. abundance Peri. chemistry Grazer movement Grazer survivorship Grazer biomass	Weeks	Summer	Single unit	4th instar	1289
Peri. abundance	Weeks	Summer	Riffle & run units	*Orconectes*: 28 cm (CL) *Leucotrichia*: 5th instar *Psychomyia*: variable	44 6000 5400
Peri. abundance Peri. productivity	Days	Summer	Single unit	N/G	N/G
Peri. abundance Grazer density Grazer biomass Grazer development	Season	Summer & Autumn	In situ channels & single riffle	Variable	N/G
Grazer density Benthic composition	Weeks	Summer	In situ channels	N/G	400
Peri. abundance Grazer density Benthic composition	Seasons	Spring–Summer	Single unit	>5 mm (len.)	1278

APPENDIX 1. Continued.

Study	Interaction	Type of study	Geographic region	Target grazer	Manipulation
Hershey et al. 1988	N→P+G	Field	Alaska, USA	*Orthocladius*	Nutrients
	P→G				Peri. abundance
Hill 1992	P→G	Lab & Field	Tennessee, USA	*Elimia* *Neophylax*	Peri. abundance
Hill et al. 1992a	G+L+N→P	Field	Tennessee, USA	*Elimia*	Grazer exclusion Nutrients Light
Hill & Harvey 1990	G→P	Field	Tennessee, USA	*Elimia*	Grazer exclusion
	Pd→G				Predator exclusion
Hill & Knight 1987	G→P	Field	California, USA	*Ameletus*	Grazer density
	P→G				Peri. abundance
Hill & Knight 1988a	L+N→P	Field	California, USA	*Glossosoma*	Nutrients
	P→G			*Ameletus* *Baetis* *Cinygma* & others	Light Peri. abundance
Hill & Knight 1988b	G→P	Field	California, USA	*Neophylax* *Ameletus*	Grazer density
	P→G				Peri. abundance
Hill et al. 1992b	P→G	Lab & Field	Tennessee, USA	*Elimia*	Peri. abundance
	G→G			*Neophylax*	Detritus Grazer size (*Elimia*)
Hom 1982	G→P	Lab	Tennessee, USA	*Elimia*	Grazer density
	P→G				Peri. abundance
Jacoby 1985	G→P	Field	Sweden	*Theodoxus*	Grazer density
Jacoby 1987	G→P	Field	Washington, USA	*Dicosmoecus* *Nixe*	Grazer exclusion Grazer species
Karouna & Fuller 1992	G→P	Lab	New York, USA	*Psilotreta* *Ephemerella* *Epeorus* *Paraleptophlebia*	Grazer exclusion Grazer species
Kehde & Whilm 1972	G→P	Lab	Oklahoma, USA	*Physa*	Grazer exclusion
Kohler 1984	P→G	Field & Lab	Michigan, USA	*Baetis*	Peri. patchiness Peri. abundance
Kohler 1992	G→P	Lab & Field	Michigan, USA	*Glossosoma* *Baetis*	Grazer species Grazer exclusion
	G→G+Gi				

APPENDIX 1. Continued. Extended.

Response variable	Experimental duration	Experimental season	Spatial scale	Size of grazer	Ambient density of target grazers (no./m²)
Peri. abundance Grazer density Grazer size	Month	Summer	Reach	3rd & 4th instar	138–1818
Grazer size Grazer chemistry Grazer development	Weeks	Spring	Lab streams	*Elimia*: 4.6 mm (shell width) *Neophylax*: 4th instar	1544 368
Peri. abundance Peri. productivity	Weeks	Autumn	In situ channels	N/G	200
Peri. abundance Peri. productivity Grazer growth	Weeks	Summer	Reaches	N/G	389
Peri. abundance Peri. composition Grazer growth	Weeks	Summer	Single unit	6.24 mm (len.)	192
Peri. abundance Peri. composition Grazer density	Weeks	Summer	Reaches in two streams	N/G	235 (grazer spp. combined; one stream)
Peri. abundance Peri. composition Grazer density	Weeks	Spring	Single unit	*Neophylax*: 5th instar *Ameletus*: 5–6 mm (len.)	38 85
Grazer growth Grazer chemistry Grazer development	Seasons	Winter, Spring & Autumn	Lab streams & in situ	*Elimia*: 28–59 & 62–188 mg (ww) *Neophylax*: 3rd instar	<500 N/G
Peri. abundance Peri. productivity Peri. composition Grazer growth	Weeks	N/G	Lab streams	0.9 mg (AFDM)	311
Peri. abundance	Weeks	Summer	Single unit	N/G	3850
Peri. abundance Peri. productivity Peri. composition	Weeks	Summer	Single pool	*Dicosmoecus*: 5th instar *Nixe*: 7–9 mm (len.)	41 286
Peri. abundance	Weeks	Autumn	Lab streams	*Psilotreta*: 5th instar *Ephemerella*: ~284 mg dw/m² *Epeorus*: ~284 mg dw/m² *Paraleptophlebia*: ~284 mg dw/m²	1300 1900–2200 1900–2200 1900–2200
Peri. abundance Peri. composition	Season	N/G	N/G	0.13 g (ww?)	120
Grazer activity Grazer distribution	Seasons	Spring & Summer	Single riffle	N/G	N/G
Peri. abundance Grazer foraging Grazer growth Grazer size (larvae & adults) Grazer survivorship Benthic composition	Weeks (lab) Seasons (field)	All	Lab streams & single riffle	Variable	Variable

APPENDIX 1. Continued.

Study	Interaction	Type of study	Geographic region	Target grazer	Manipulation
Kohler & McPeek 1989	P→G	Lab	Michigan, USA	*Baetis*	Predator exclusion
	Pd→G			*Glossosoma*	Peri. abundance
					Grazer hunger
Lamberti et al. 1987a	G→P	Lab	Oregon, USA	*Centroptilum*	Grazer density
				Juga	Grazer species
				Dicosmoecus	
Lamberti et al. 1987b	G→P	Field	California, USA	*Helicopsyche*	Grazer density
	P→G				Peri. abundance
	G→Gi				
Lamberti et al. 1989	L+G→P	Lab	Oregon, USA	*Juga*	Grazer exclusion
					Light
	P→G				Peri. abundance
Lamberti et al. 1992	G→P	Field	Washington, USA	*Ascaphus*	Grazer exclusion
				Dicosmoecus	
	G→G				Peri. abundance
Lamberti & Resh 1983	G→P	Field	California, USA	*Helicopsyche*	Grazer exclusion
	P→G				
	G→Gi				Peri. abundance
Martin et al. 1991	G→P	Field	Ontario, Canada	*Neophylax*	Grazer density
	G→Gi				Peri. abundance
McAuliffe 1983	G→P	Field	Montana, USA	*Glossosoma*	Grazer exclusion
	P→G				Peri. abundance
McAuliffe 1984a	G→P	Field	Montana, USA	*Glossosoma*	Grazer exclusion
	G→Gi				
McAuliffe 1984b	G→Gi	Field	Montana, USA	*Leucotrichia*	Grazer exclusion
McCormick 1990	G→P	Field	Kentucky, USA	*Elimia*	Nutrients
	Pd+N→G+P			*Orconectes*	Grazer exclusion
					Predator exclusion
McCormick 1991	G→P	Field	Kentucky, USA	*Stenonema*	Grazer density
	P+G→G			*Goniobasis* (=*Elimia*) & misc. protists (e.g. *Trithigmostoma*)	Peri. composition
McCormick & Stevenson 1989	G+N→P	Field	Kentucky, USA	*Elimia*	Nutrients
					Grazer density
Mulholland et al. 1991	G+N→P+N	Lab	Tennessee, USA	*Elimia*	Grazer exclusion
					Nutrients
	N+P→G				Peri. abundance

APPENDIX 1. Continued. Extended.

Response variable	Experimental duration	Experimental season	Spatial scale	Size of grazer	Ambient density of target grazers (no./m²)
Grazer movement Grazer foraging	Hours	Winter	Lab streams	N/G	N/G
Peri. abundance Peri. productivity Peri. export Peri. composition	Weeks	Spring	Lab stream	*Centroptilum*: late instar *Juga*: 10–15 mm (len.) *Dicosmoecus*: 3rd & 4th instar	500 350 200
Peri. abundance Peri. composition Grazer growth Grazer survivorship	Months	Summer & Autumn	Single pool	0.15–0.26 mg (dw)	8620
Peri. abundance Peri. composition Peri. productivity Peri. export Grazer growth Grazer assimilation	Season	Autumn & Winter	Lab stream	5 mg (dw)	1–500
Peri. abundance Peri. composition Grazer density Benthic density	Weeks	Summer	Reaches in 11 streams	*Ascaphus*: variable *Dicosmoecus*: 4th instar	Variable Variable
Peri. abundance Peri. productivity Grazer density Grazer distribution	Seasons	Spring & Summer	Single pool	Middle instars	4167
Peri. abundance Grazer growth Grazer development Grazer survivorship	Weeks	Spring	Single unit	5th instar	1433
Peri. abundance Grazer density	Season	Summer	Single riffle	N/G	100–300
Peri. abundance Grazer density	Month	Summer	Single riffle	N/G	13,600
Grazer density	Month	Summer	Reach	5th instar	12,000
Peri. abundance Grazer growth Grazer survivorship	Weeks	Summer	Pool mesocosms	*Orconectes*: 40 mm (TL?)	N/G
Peri. abundance Grazer density	Days	Spring	Streamside channels	N/G	*Stenonema*: 200 *Goniobasis*: 143
Peri. abundance Peri. composition	Weeks	Summer	Single pool	N/G	140
Peri. abundance Peri. productivity Peri. composition Nutrient uptake Bacteria production Detritus export Grazer growth	Season	Winter & Spring	Lab streams	N/G	1000

APPENDIX 1. Continued.

Study	Interaction	Type of study	Geographic region	Target grazer	Manipulation
Murphy 1984	G→P	Field	Alaska, USA	Amphipods & isopods	Grazer exclusion
Ogilvie 1988	P→G	Field	Alberta, Canada	*Oligophlebodes* *Neothremma* *Epeorus*	Peri. abundance Peri. patchiness
Poff & Ward 1992	P+C→G	Field	Colorado, USA	*Agapetus*	Peri. abundance Current
Power 1990a	G→P Pd→G	Field	California, USA	*Pseudochironomus* *Lavinia*	Grazer exclusion
Power 1990b	G→P	Field	Panama	Loricariidae	Grazer exclusion Sediment
Power 1991	G→P	Field	California, USA	*Pseudochironomus*	Grazer exclusion
Power et al. 1989	G→P	Field	Panama	Loricariidae	Grazer exclusion
Power & Matthews 1983	G→P	Field	Oklahoma, USA	*Campostoma*	Grazer exclusion
Power et al. 1985	G→P Pd→G+P	Field	Oklahoma, USA	*Campostoma*	Grazer exclusion Predator exclusion
Power et al. 1988a	G→P	Field	Oklahoma, USA	*Campostoma*	Grazer exclusion
Richards & Minshall 1988	P→G	Field	Idaho, USA	*Baetis*	Peri. patchiness Peri. abundance
Rosemond 1993a	G+N+L→P P+G→Gi	Field	Tennessee, USA	*Elimia*	Nutrients Light Grazer exclusion Peri. abundance
Rosemond 1993b	G+N+L→P P+G→Gi	Field	Tennessee, USA	*Elimia*	Nutrients Light Grazer exclusion Peri. abundance
Rosemond et al. 1993	G+N→P P+G→Gi	Field	Tennessee, USA	*Elimia*	Nutrients Grazer exclusion Peri. abundance
Scrimgeour et al. 1991	G→P	Field & Lab	Alberta, Canada	*Baetis* *Ephemerella* *Paraleptophlebia*	Grazer species Peri. abundance
Steinman 1991	G→P	Lab	Tennessee, USA	*Elimia*	Grazer exclusion Grazer hunger Grazer size
Steinman 1992	G+L→P	Field	Tennessee, USA	*Elimia*	Light Grazer exclusion
Steinman et al. 1987a	G→P	Lab	Oregon, USA	*Juga* *Dicosmoecus*	Grazer species Grazer density

APPENDIX 1. Continued. Extended.

Response variable	Experimental duration	Experimental season	Spatial scale	Size of grazer	Ambient density of target grazers (no./m²)
Peri. abundance Peri. productivity	Days & weeks	Spring & Summer	Freshwater & intertidal reaches	N/G	Freshwater: <4000 Intertidal: 38,000
Grazer density Grazer movement	Weeks	Summer	Riffle units	N/G	Variable
Grazer movement Grazer distribution	Hours	Summer	In situ channels	5th instar	≤3000
Peri. abundance Peri. condition Peri. composition Grazer density	Weeks	Summer	Reach	N/G	1100
Peri. productivity	Weeks	Winter & Spring	Reach	10 g (ww)	6
Peri. abundance	Weeks	Summer	Reach	6–9 mm (len.)	120,000
Peri. abundance	Days	Spring	Reach	N/G	0.36
Peri. abundance Peri. condition	Hours	N/G	Reach	N/G	2.1
Peri. abundance Peri. composition Peri. condition	Months	Autumn	Reach	2–8 cm (SL)	2–3
Peri. abundance Peri. composition	Weeks	Autumn	Single unit	N/G	<50
Grazer density	Hours	Summer	7–10 riffles	N/A	1000–2600
Peri. abundance Peri. productivity Peri. composition Grazer growth	Weeks	Summer	Streamside channels	3 mg (AFDM)	1100
Peri. abundance Peri. productivity Peri. composition Grazer growth	Weeks	Autumn	Streamside channels	3 mg (AFDM)	1300
Peri. abundance Peri. productivity Peri. composition Grazer growth	Weeks	Spring (1989 & 1990)	Streamside & in situ channels	3 mg (AFDM)	1200–1300
Peri. abundance Peri. export Grazer consumption	Weeks	Summer	Lab stream & three riffles	*Baetis*: 5.4 mm (len.) *Ephemerella*: 4.9 mm (len.) *Paraleptophlebia*: 5.2 mm (len.)	N/G N/G N/G
Peri. abundance Peri. composition	Days	N/G	Lab stream	Small snails: 3–5 mm (len.) Large snails: 8–12 mm (len.)	N/G
Peri. abundance Peri. productivity Peri. composition	Weeks	Autumn	Single pool	N/G	>2500
Peri. abundance Peri. composition	Weeks	N/G	Lab stream	N/G N/G	*Juga*: 66–500 *Dicosmoecus*: 25–200

APPENDIX 1. Continued.

Study	Interaction	Type of study	Geographic region	Target grazer	Manipulation
Steinman et al. 1987b	G→P	Lab	Oregon, USA	*Juga* *Dicosmoecus*	Grazer species Grazer density
Steinman et al. 1991b	N+G→P	Lab	Tennessee, USA	*Elimia*	Nutrients Grazer exclusion
Steinman et al. 1990	G→P	Lab	Tennessee, USA	*Elimia*	Nutrients Grazer exclusion
Stewart 1987	G+N→P	Field	Oklahoma, USA	*Campostoma*	Grazer exclusion Nutrients
Sumner & McIntire 1982	G+L+N→P	Lab	Oregon, USA	*Juga*	Light Nutrients Grazer exclusion
Vaughn 1986	P→G P+C→G	Lab & Field	Oklahoma, USA	*Helicopsyche*	Peri. abundance Current Peri. abundance Peri. composition
Vaughn et al. 1993	G→P	Lab	Oklahoma, USA	*Campostoma* *Orconectes* *Physella*	Grazer exclusion Grazer species
	P→G				Peri. abundance Grazer species
Winterbourn 1990	L+N+G→P	Field	New Zealand	Orthocladiinae & Diamesinae	Nutrients Grazer exclusion Light
	P→G				Peri. abundance
Winterbourn & Fegley 1989	G+N→P	Field	New Zealand	*Potamopyrgus*	Nutrients Grazer exclusion
	P→G				Peri. abundance
Wootton & Oemke 1992	G→P	Field	Costa Rica	Misc. fish species	Grazer exclusion
Yasuno et al. 1982	G→P	Field	Japan	Misc. species (usu. *Amphinemura*)	Grazer exclusion
Yasuno et al. 1985	G→P	Field	Japan	Misc. species (usu. *Thienemanniella*)	Grazer exclusion

APPENDIX 1. Continued. Extended.

Response variable	Experimental duration	Experimental season	Spatial scale	Size of grazer	Ambient density of target grazers (no./m²)
Peri. composition Peri. chemistry	Weeks	N/G	Lab stream	N/G N/G	*Juga*: 66–250 *Dicosmoecus*: 25–100
Peri. abundance Peri. composition Peri. productivity Bacteria abundance Bacteria productivity	Months	Winter & Spring	Lab stream	N/G	1000
Peri. abundance Peri. productivity Peri. composition Bacteria abundance	Months	Fall & Winter	Lab stream	N/G	1000
Peri. abundance Peri. productivity Peri. composition	Weeks	Summer	Reach	N/G	2.3
Peri. abundance Peri. productivity Peri. composition Peri. export Grazer growth Grazer density Grazer movement (drift) Grazer fecundity Adult emergence	Months	Summer	Lab stream	5.25 g (shell-free dw)	125–500
Peri. abundance Peri. productivity Peri. composition Grazer production Grazer recruitment Grazer growth	Weeks	All	Lab stream & single unit (?)	Variable	N/A
Peri. abundance Peri. composition Grazer density Grazer size	Weeks	Summer	Lab stream	*Campostoma*: 31–37 g (ww?) *Orconectes*: 1.59–8.71 g (ww?) *Physella*: 4–6 mm (len.)	7.75 7.75 77
Peri. abundance Peri. composition Grazer density	Weeks	Spring	Four reaches	N/G	N/G
Peri. abundance Peri. composition Grazer density	Weeks	Winter & Spring	Six reaches in two streams	N/G	8570
Peri. abundance Peri. productivity Detritus abundance	Weeks	Winter	Two units	N/G	N/G
Peri. abundance Peri. composition	Months	Winter	Reaches in three streams	N/G	Variable
Peri. abundance	Weeks	Spring & Summer	Paired stream channels	N/G	N/G