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Stream Algal Biomass Associations with Environmental Variables in a Temperate Rainforest

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Abstract: Benthic algae and autotrophic seston are important bases of stream food webs, and several different environmental factors may influence their biomass. We explored how benthic algae and autotrophic seston biomass (using chlorophyll-*a* as a proxy for algal biomass) were associated with stream temperature, channel width, canopy cover, stream cardinal orientation, benthic macroinvertebrate functional feeding group abundance, salmonid biomass, and water velocity in 16 small, fish-bearing streams in the temperate rainforest of the Olympic Peninsula in Washington State, USA, in the summer of 2020. We performed a mixed-effects regression analysis of extracted chlorophyll-*a* (chl-*a*) and then used model averaging to determine significant ($\alpha = 0.05$) algal–environmental associations for benthic algae and autotrophic seston separately. We found that benthic algae chl-*a* concentration increased significantly with stream temperature ($p = 0.0085$) and decreased significantly with water velocity ($p = 0.0053$). For autotrophic seston, we found that chl-*a* concentration increased significantly with benthic macroinvertebrate predator abundance ($p = 0.0007$) and stream temperature ($p = 0.0160$). This study underscores the need to consider a broad range of environmental variables when making research and management decisions concerning stream ecology.

Keywords: algal biomass; environmental associations; Olympic Peninsula; benthic algae; autotrophic seston; temperate rainforest

Citation: Toskey, E.K.; Bollens, S.M.; Rollwagen-Bollens, G.; Kiffney, P.M.; Martens, K.D.; Bormann, B.T. Stream Algal Biomass Associations with Environmental Variables in a Temperate Rainforest. *Water* **2024**, *16*, 1533. https://doi.org/10.3390/w16111533

Academic Editors: Marina Marcella Manca, Moshe Gophen and Dariusz Halabowski

Received: 25 April 2024
Revised: 23 May 2024
Accepted: 24 May 2024
Published: 27 May 2024

1. Introduction

Autochthonous primary production is an important but often overlooked base of stream food webs in addition to the well-studied base of allochthonous riparian inputs in forested streams [1–3]. The autotrophic members of periphyton form the dominant source of primary production in forested streams [4]. The autotrophic portion of seston forms a smaller albeit still important part of stream primary production [5].

Benthic algae and autotrophic seston provide high-quality food, rich in essential fatty acids, for vertebrates and macroinvertebrates [2,6]. Benthic algae are consumed by fish and collector–gatherer and scraper macroinvertebrates, and autotrophic seston is consumed by filter-feeding macroinvertebrates [1]. In streams flowing through conifer forests, benthic algae and autotrophic seston can be particularly important to the food web, given conifer leaf litter's relatively poor nutritional quality compared with broadleaf litter [7]. Stream algae are also important in biogeochemical cycles because of their role in nutrient uptake [8] and remineralization [9]. Understanding the factors associated with primary producer biomass in streams will aid in predicting how stream algae will respond to current and future environmental changes like restoration, logging, and climate change.

Several abiotic and biotic factors have been shown to affect stream algal growth, including temperature via influence on physiological (e.g., growth and respiration) rates [10,11], macroinvertebrates via grazing [12,13], fish predation through trophic cascades [14], anadromous fish carcass nutrient enrichment [15,16], water velocity via scouring [17], and sunlight and nutrients [18–20]. Additionally, some of these variables may have interacting effects (e.g., the temperature-mediated metabolism of macroinvertebrate grazers) [21]. Despite this large array of potentially influential environmental variables that can mediate algal biomass in streams, studies have largely focused on the role of nutrients and light (but see several studies on macroinvertebrate grazing, e.g., [12,13]). Of the multivariate studies of stream algae, many have used categorical comparisons (e.g., low-light versus high-light [13,22–24]) rather than gradients of environmental conditions (but see [25–27]), thereby limiting the exploration of the complex associations of stream algae with the environment. Moreover, most previous studies consider only benthic algae, leaving the environmental associations of autotrophic seston biomass in streams relatively unknown.

The current study examined the associations of chlorophyll-a (chl-*a*) concentration as a proxy for the biomass of autotrophic components (primarily algae) in periphyton and seston with various environmental variables in temperate rainforest streams on the Olympic Peninsula in Washington state, USA. We hypothesized that variables associated with light availability, temperature, benthic macroinvertebrate functional feeding group abundance, fish biomass, and hydrodynamic conditions would be significant predictors of both benthic algae and autotrophic seston chl-*a* concentration. More specifically, we hypothesized the following:

(1) Benthic algal chl-*a* concentration would be positively associated with water temperature, bankfull width (related to light availability and stream size), salmonid biomass, macroinvertebrate scraper–grazer abundance (consumers of benthic algae), macroinvertebrate predator abundance, and sample-level canopy cover. The effect of canopy cover would depend on channel orientation, as streams oriented north–south may be exposed to sunlight during midday, whereas canopy cover on the south bank of east–west-oriented streams may block sunlight. Water velocity would be negatively associated with benthic algal chl-*a* concentration.

(2) Sestonic algal biomass would be positively related to water temperature, bankfull width, salmonid biomass, macroinvertebrate collector–filterer abundance, macroinvertebrate predator abundance, and reach-level canopy cover, similarly modulated by stream orientation. Water velocity would be negatively associated with sestonic algal chl-*a* concentration.

2. Materials and Methods

2.1. Study Sites

We sampled a total of 29 sites from 16 different streams (2 sites in each of 13 streams, 1 site in each of 3 remaining streams) in the Olympic Experimental State Forest (OESF) on the western side of the Olympic Peninsula in Washington State, USA (Figure 1). All 16 streams were small, fish-bearing streams between orders one and three. These sites were selected as part of the study design for the larger, longer-term “T3 Watershed Experiment” in the OESF, which is investigating the effects of various forest management practices on riparian and stream ecology [28]. The OESF is part of the Pacific Coastal Ecoregion and is characterized as a temperate rainforest with typical annual precipitation ranging from 203 to 355 cm [29]. The riparian forests in the OESF mainly consist of 30- to 50-year-old conifer forests dominated by Douglas fir (*Pseudotsuga menziessii*), which have primarily been left to recover from historic timber harvest practices through passive restoration because of regulation changes in the 1990s.

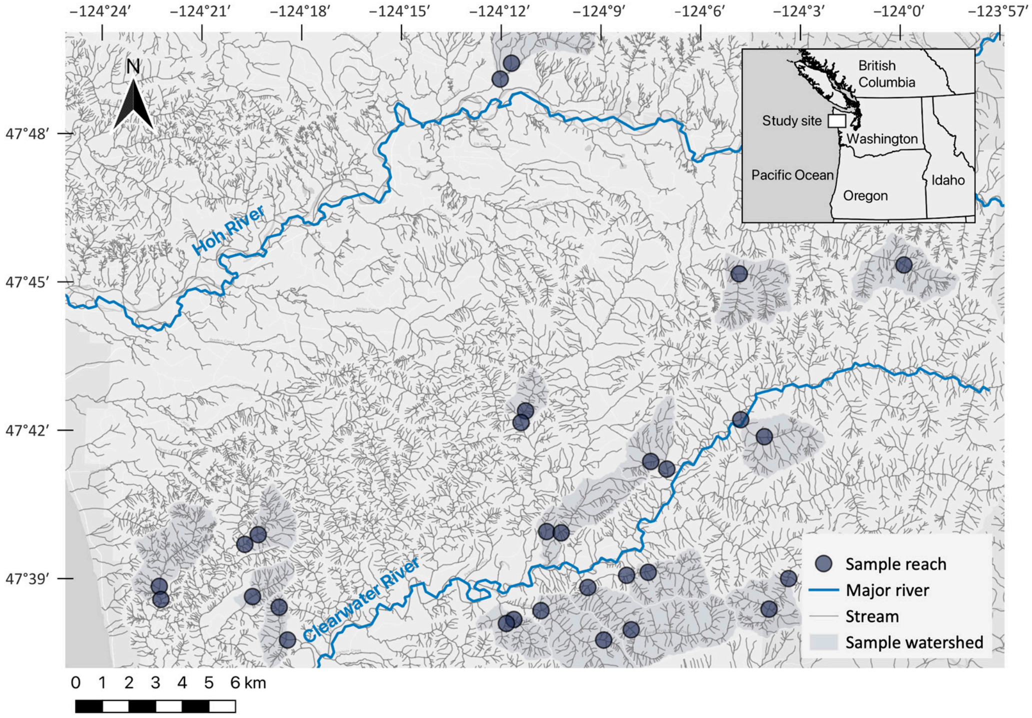

Figure 1. Map of the study area showing the 29 sites spanning 16 watersheds that we sampled for benthic algae (n = 98) and autotrophic seston (n = 58) chl-*a* and corresponding environmental variables in 2020.

2.2. Field Data Collections

Between 5 August and 8 October 2020, we collected 2 autotrophic seston samples and 3 to 5 (initially five but then reduced to three later in the season due to time constraints) benthic algae composite samples from each of the 29 sites for a total of 58 autotrophic seston and 98 benthic algae composite samples. More samples of benthic algae were taken than seston to reflect the greater spatial variability we expected in benthic algae. Autotrophic seston was collected at each site by filling two 1 L amber bottles just below the water surface. Each of the three to five benthic algae composite samples was collected approximately 30 m upstream by scrubbing periphyton from three representative cobbles from the same riffle (within approximately 0.5 m^2) using a brass-bristled brush and a 24 × 36 mm slide frame (for consistency of area sampled) and then rinsing with deionized water into an amber bottle [30]. Qualitative observations indicated that there were no submerged macrophytes in the streams where samples were taken. The majority of the autotrophic seston samples were collected between 9:00 and 11:00, and the majority of the benthic algal samples were collected between 12:00 and 14:00, thereby minimizing potential bias due to diel periodicity in algal drift [31] as much as possible. Both types of algae samples were kept in a cooler until filtered, approximately two to eight hours after collection.

Along with each algal sample, we made a single measurement each of water temperature using an encased stream thermometer and canopy cover using a densiometer [32], which we used as a proxy for light availability [33]. Also, with every algal sample, we measured water temperature using an encased thermometer and determined the dominant substrate size class using a ruler. Approximately 10 m downstream from the periphyton sampling, we also collected three Hess (mesh size = 363 µm; diameter = 0.33 m) samples of benthic macroinvertebrates from individual riffles [34]. Macroinvertebrates were preserved in the field with 70% ethanol. Approximately 10 m further downstream, live salmonid biomass was estimated using multiple-pass removal electrofishing in 100 m reaches, where bottom and top nets confined fish movement, following the methods described in Martens and Connolly [35]. While only quantitative measurements of salmonids were made, qualitative observations of other fish, including lampreys and sculpins, were also made [35]. At each site, we also measured water velocity with a propeller current meter placed in the thalweg at a narrowing of the stream (thus likely to represent the maximum velocity for a given stream reach). We used topographic LiDAR (Light Detection and Ranging) to map and thus calculate the cardinal orientation of each sampled stream section. In 20 m intervals along the 100 m reach that we surveyed for salmonids, we made further stream habitat measurements, including median substrate grain size using a gravelometer, bankfull width, gradient, elevation, water depth, and canopy cover using hemispherical photos. We averaged each of these reach-level measurements to obtain quantitative measurements of the overall stream habitat [36]. Note that the location-specific canopy cover measurements using a densiometer differ from the reach-level measurements using hemispherical photos.

2.3. Lab Analyses

Benthic algae and autotrophic seston subsamples were filtered through GF/F filters immediately upon return from the field (within 2 to 8 h of collection) and then frozen. Once a week (within one to seven days of collection), we extracted the pigments from the filters in 90% acetone for 24 h in a freezer. We brought samples to room temperature and then used a fluorometer to measure chl-*a* concentration using the acidification method [37]. Chl-*a* is commonly used as a proxy for algal biomass in both lotic and lentic environments, as chl-*a* has been found to be positively correlated with primary productivity in streams, rivers, lakes, and oceans [38]. While traditional methods that directly measure algal biomass, such as measuring ash-free dry mass and enumerating algal cells under a microscope [39–41], are more exact, chl-*a* measurements offer a less complex and time-consuming method of estimating biomass [42,43]. Using a dichotomous key, we identified and enumerated all macroinvertebrates in a functional feeding group (i.e., collector–filterer, collector–gatherer, scraper–grazer, shredder, and predator) in each Hess sample under a dissecting microscope (10× magnification) [44]. The genus with the greatest abundance of organisms in each macroinvertebrate functional feeding group was as follows: *Hydropsyche* (Trichoptera: Hydropsychidae; collector–filterer), *Baetis* (Ephemeroptera: Baetidae; collector–gatherer), *Cinygmula* (Ephemeroptera: Heptageniidae; scraper–grazer), *Pomoleuctra* (Plecoptera: Leuctridae; shredder), and *Rhyacophila* (Trichoptera: Rhyacophilidae; predator).

2.4. Statistical Analyses

Since our data were nested by site within each watershed, we used a linear mixed effects regression model to build a random intercept model of the chl-*a* concentration as a function of environmental variables for benthic algae and autotrophic seston separately. The environmental fixed effects in the benthic algal model were water temperature, above-sample canopy cover, bankfull width, salmonid biomass, maximum water velocity, macroinvertebrate predator abundance, scraper–grazer abundance, and the interaction between orientation and above-sample canopy cover. The environmental fixed effects in the sestonic algal model were water temperature, reach-level canopy cover, bankfull width, salmonid biomass, maximum water velocity, macroinvertebrate predator abundance, collector-filterer abundance, and the interaction between orientation and above-sample canopy cover. To account for any minor multicollinearity introduced by the inclusion of interaction terms, we mean-centered all fixed effects [45]. We used an ln(x) transformation of the chl-*a* data to achieve normally distributed model residuals for both the benthic algae and autotrophic seston models. Environmental variables were included as fixed effects, and site and watershed were included as random effects, with the site nested within the watershed, to account for inherent similarities within sites and watersheds. Interactions between fixed effects were included based on our hypotheses, rather than all possible interactions, to prevent overparameterization.

We compared second-order Akaike's Information Criteria (AIC_C) among candidate models for benthic algae and autotrophic seston chl-*a* concentration separately. To determine the most relevant environmental predictors, we used model averaging based on an information-theoretic approach and considered only the top-ranked models with $\Delta AIC_C \leq 2$ [46,47]. Finally, we standardized all fixed effects by dividing the values of each mean-centered parameter by its standard deviation and then refit each model to compare the standardized effect sizes between model parameters [48].

3. Results

Environmental conditions across the 29 sites varied considerably, exhibiting the following ranges: benthic algal chl-*a* (0.017–16.4 mg m^{-2}), autotrophic seston chl-*a* (0.00259–0.117 µg L^{-1}), temperature (11.0–14.0 °C), canopy cover above sample (33.4–100%), average canopy cover of sampled stream reach (86.8–94.3%), bankfull width (2.3–11.0 m), salmonid biomass (0.35–18.3 g m^{-1}), average macroinvertebrate predator abundance (6.4–132.6 individuals m^{-2}), average macroinvertebrate scraper/grazer abundance (12.8–345.8 individuals m^{-2}), average macroinvertebrate collector–filterer abundance (0.6–116.2 individuals m^{-2}), maximum water velocity (0.00588–1.06 m s^{-1}), and stream orientation (6.13–180° to N) (Supplementary Table S1).

Benthic algal chl-*a* concentration was best explained by water temperature and maximum water velocity (Table 1). Benthic algal chl-*a* concentration increased with water temperature and decreased with maximum water velocity (Table 1; Figure 2). Based on the 95% confidence intervals of the standardized coefficients of the fixed effects, there was a significantly non-zero, positive association between water temperature and a non-zero, negative association between maximum water velocity and benthic algal chl-*a* concentration (Figure 3). Of the significant environmental variables, maximum water velocity had the greatest effect size (Figure 3).

Table 1. Benthic algal chl-*a* model-averaged estimates of significant (*a* = 0.05) fixed-effect coefficients and associated p-values based on 98 samples from 29 sites spanning 16 streams on the Olympic Peninsula in 2020.

Parameter	β	*p*-Value
Water temperature	0.3459	0.0085
Maximum water velocity	−0.0139	0.0053

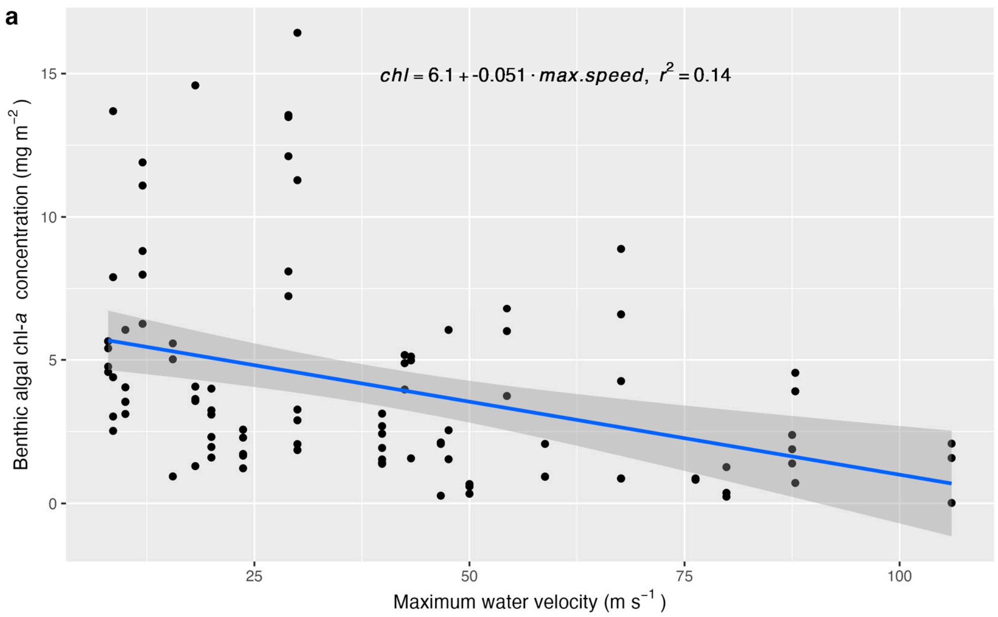

Figure 2. *Cont.*

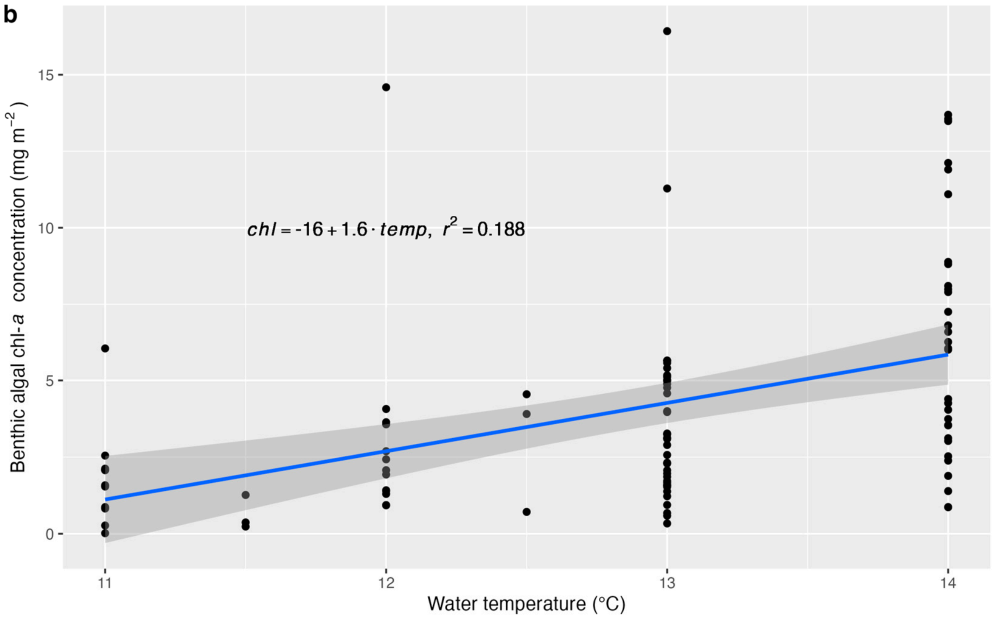

Figure 2. Scatter plots with a simple linear regression line and 95% confidence interval showing the relationship between benthic algal chl-*a* concentration and significant environmental variables: (**a**) water velocity and (**b**) temperature ($a = 0.05$; $n = 98$).

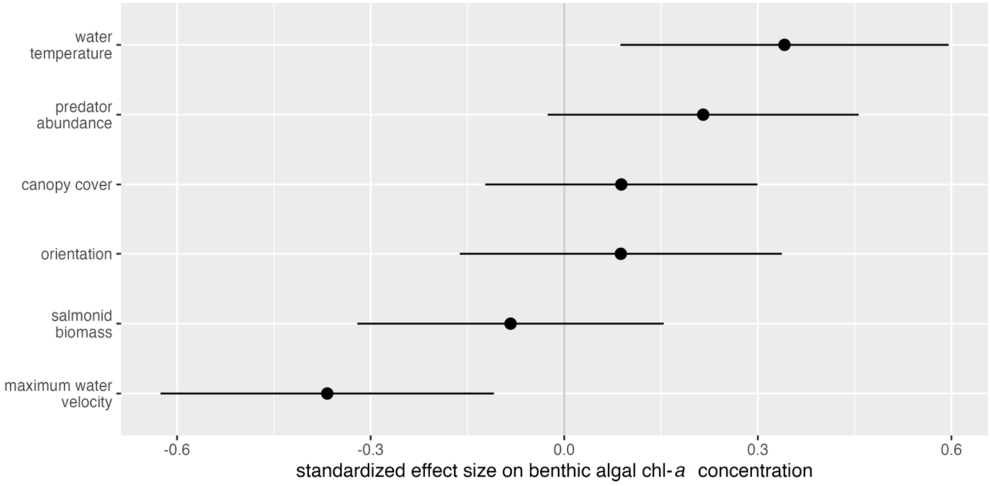

Figure 3. Standardized mean and 95% confidence intervals for the coefficients of environmental variables retained in the averaged model predicting the concentration of benthic algal chl-*a* from 29 sites over 16 fish-bearing streams on the Olympic Peninsula in the summer of 2020 ($n = 98$). Effect sizes are in units of standard deviation of benthic algal chl-*a* concentration per standard deviation increase in x_j.

The autotrophic seston chl-*a* concentration was best explained by macroinvertebrate predator abundance and water temperature. The autotrophic seston chl-*a* concentration significantly increased with macroinvertebrate predator abundance and water temperature (Table 2; Figure 4). Of the significant environmental variables, macroinvertebrate predator abundance had the largest effect on autotrophic seston chl-*a* concentration (Figure 5).

Table 2. Autotrophic seston chl-*a* model-averaged estimates of significant (a = 0.05) fixed-effect coefficients and associated p-values based on 58 samples from 29 sites spanning 16 streams on the Olympic Peninsula in 2020.

Parameter	**β**	***p*-Value**
Water temperature	0.2979	0.0160
Macroinvertebrate predator abundance	0.0119	0.0007

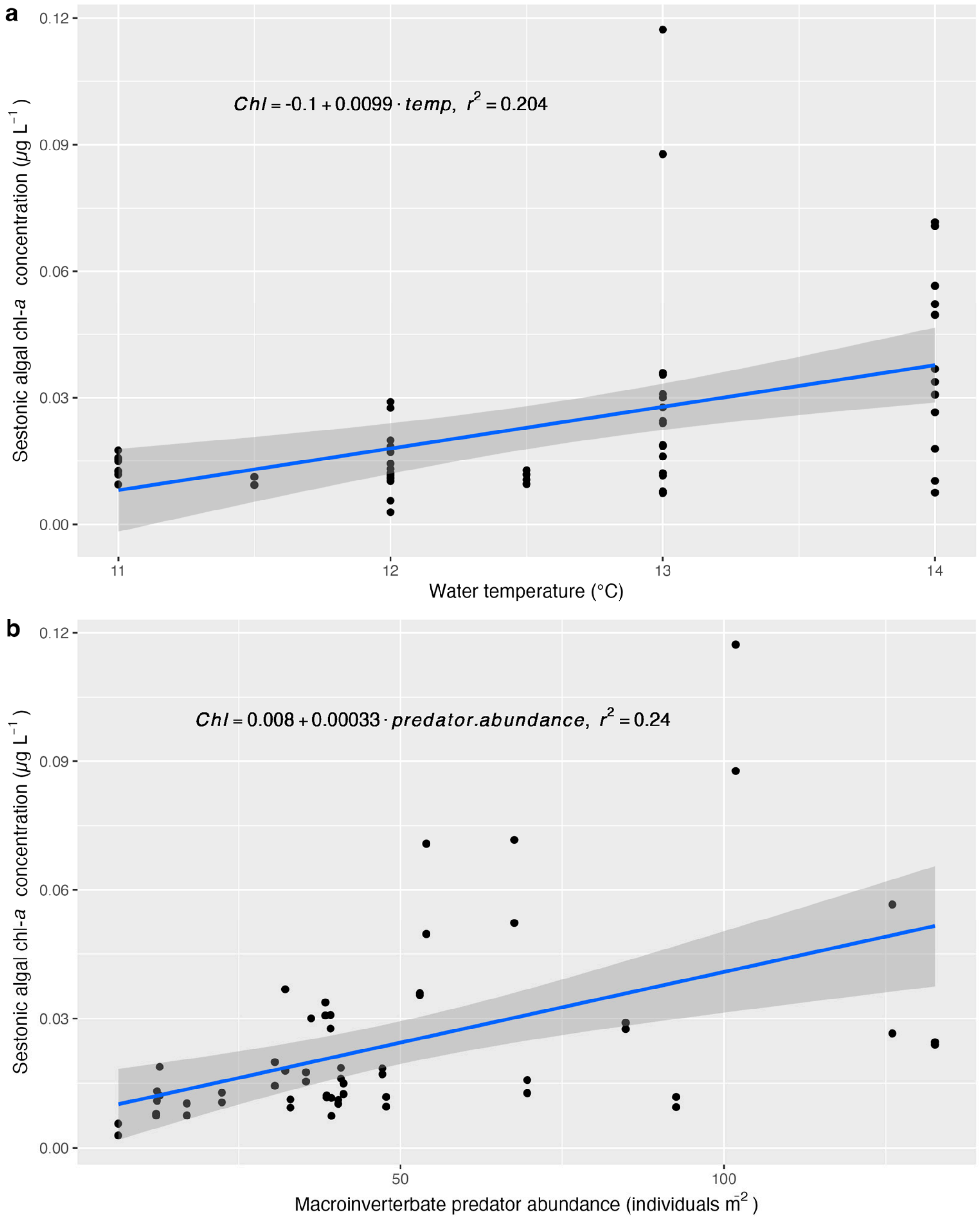

Figure 4. Scatter plots with a simple linear regression line and 95% confidence interval showing the relationship between sestonic algal chl-*a* concentration and significant environmental variables: (**a**) water temperature and (**b**) macroinvertebrate predator abundance (a = 0.05; n = 58).

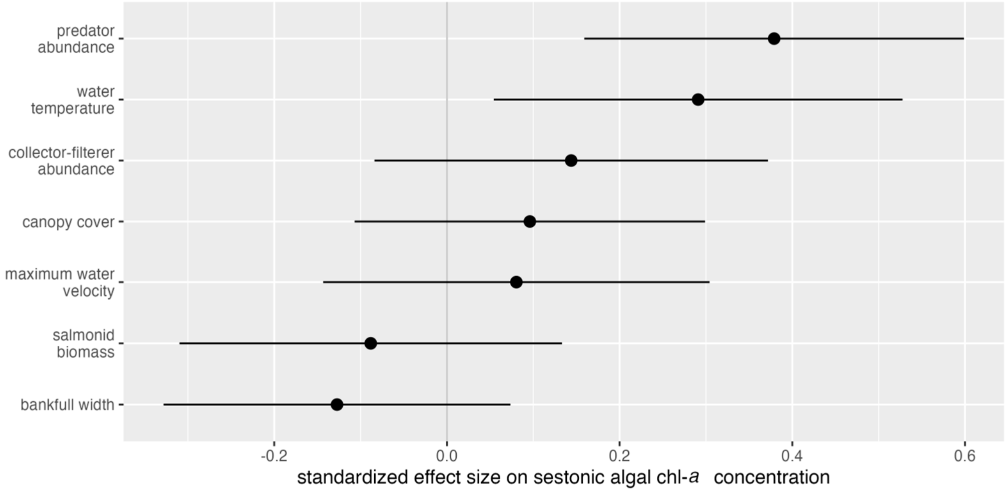

Figure 5. Standardized mean and 95% confidence intervals for the coefficients of each environmental variable and their interactions retained in the averaged model predicting the concentration of autotrophic seston chl-*a* from 29 sites over 16 fish-bearing streams on the Olympic Peninsula in summer 2020 (n = 58). Effect sizes are in units of standard deviation of autotrophic seston chl-*a* concentration per standard deviation increase in x_j.

4. Discussion

The range of benthic algal and autotrophic seston chl-*a* values we found for these small, oligotrophic streams in a temperate rainforest was on the low end of observed values from other stream ecosystem types across the world [49,50]. We found that macroinvertebrate predator abundance was a significant, positive predictor of sestonic algal biomass; water temperature was a significant, positive predictor of both benthic and sestonic algal biomass; and that maximum water velocity was a significant, negative predictor of benthic algae. This supports our hypothesis that macroinvertebrate predators, temperature, and water velocity are important drivers of stream algal biomass. Contrary to our expectations, we did not find evidence that canopy cover, salmonid biomass, bankfull width, stream orientation, macroinvertebrate scraper–grazer abundance, or macroinvertebrate collector–filterer abundance were significantly related to stream algal biomass.

Temperate rainforest streams of the Olympic Peninsula are generally cold and close-canopied [51,52], suggesting that primary production here may be limited by temperature and light. Our results support the limiting nature of temperature on both benthic algae and autotrophic seston but not limitation by light (as reflected by canopy cover). Considering the findings regarding light as a primary limiting resource to stream primary production from a previous study in the nearby coastal rainforest of British Columbia [26], it may be that the small range of canopy cover data in the densely canopied second-growth forest of our current study area account for our lack of a significant relationship between canopy cover (and orientation) and algal biomass. Regardless, temperature may limit benthic algal biomass directly by limiting photosynthesis rates through temperature-dependent enzyme reaction rates [53] and indirectly by the temperature-dependent nutrient uptake rate [10].

Our observation of benthic algal biomass decreasing with water velocity aligned with our hypothesis based on high-velocity-associated scour and fits into a complex and sometimes contradictory scientific literature. Although our measurements likely represented maximum current speeds for each site at the time of sampling, our stream velocities were almost all below 1 m s^{-1}, an approximate threshold suggested by several (but not all) investigators, below which, the relationship between benthic algal biomass and water velocity has been reported as somewhat positive due, in part, to increased nutrient uptake at higher velocities [54–59]; however, see [60], who found a negative relationship between water velocity and periphytic algal biomass at these lower velocities. Because water velocity is directly proportional to turbulence [61], it is possible that this negative relationship was caused, in part, by the scouring of benthic substrate at high water velocities, which is commonly reported at velocities above approximately 1 m s^{-1} [54,56–59], although our measurements were below this threshold. It is also possible that our observed negative relationship was due to lower attachment rates at higher velocities, thus slowing the accumulation of benthic algae [56,62]. In any case, the relationship between benthic algal biomass and water velocity is complex, as evidenced by interacting environmental factors, including water velocity and streambed stability [63,64].

We expected that benthic macroinvertebrate abundance and algal biomass would be positively related due to the bottom-up effect of algae as an important food resource for macroinvertebrates (benthic algae consumed by scrapers–grazers; sestonic algae consumed by collector–filterers; and scrapers–grazers and collector–filterers consumed by predators) [65], but we found that only macroinvertebrate predator abundance increased with sestonic algal biomass. The positive relationship that we observed could indicate such a bottom-up control of a high proportion of algae relative to grazers, thus supporting grazer abundance and, through them, predators as well. However, why we only saw this reflected in predator abundance and not also scraper–grazer and collector–filterer abundance, which would presumably have a more direct relationship with algal biomass, is puzzling.

We offer three important caveats to our results. First, given that our labor-intensive data collection necessarily took place over the course of nine weeks, our results may be confounded due to seasonal patterns commonly exhibited by several of our explanatory variables, including riparian phenology, temperature, water velocity, and light availability. Second, we regret not being able to collect nutrients, as they have often been identified as important factors in determining stream algae biomass [4,6,18–20,53]. Finally, chl-*a* is a bulk proxy of algal biomass, and there may have been additional effects on benthic algae and autotrophic seston assemblage composition [66,67] that were beyond the scope of our study.

In summary, our results demonstrate a clear relationship between algal biomass and abiotic and biotic variables in small temperate rainforest streams of the OESF, especially water temperature, water velocity, and benthic macroinvertebrate predator abundance. We recommend that future research address the nature of nutrient and light limitation, including spectral differences and variation in photosynthetically available radiation in cold, close-canopied streams.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/w16111533/s1: Table S1: Chlorophyll-a and environmental data.

Author Contributions: Conceptualization, S.M.B., G.R.-B., P.M.K. and B.T.B.; methodology, E.K.T., S.M.B., G.R.-B., P.M.K. and K.D.M.; software, E.K.T.; formal analysis, E.K.T.; investigation, E.K.T. and K.D.M.; resources, S.M.B., G.R.-B., K.D.M. and B.T.B.; data curation, E.K.T. and K.D.M.; writing—original draft preparation, E.K.T. and S.M.B.; writing—review and editing, S.M.B., G.R.-B., P.M.K., K.D.M. and B.T.B.; visualization, E.K.T.; supervision, S.M.B.; project administration, S.M.B., K.D.M., P.M.K. and B.T.B.; funding acquisition, S.M.B., K.D.M. and B.T.B. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Washington State Department of Natural Resources (93102283; 93102544) and the United States Forest Service (20JV11261985044).

Data Availability Statement: The data presented in this study are available in Supplementary Table S1.

Acknowledgments: We thank the many members of the "T3" field crew for assistance with sample collection, the staff of the Olympic Natural Resources Center for access to housing and laboratory facilities, J. Zimmerman for advice on analytical methods, and Washington State University for support in the form of assistantships to E.K.T.

Conflicts of Interest: The authors declare no conflicts of interest.

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