ALGAL COLONIZATION AND RECOLONIZATION RESPONSE RATES DURING EXPERIMENTAL LOW SUMMER STEADY FLOWS

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TABLE OF CONTENTS

	PAGE NO.
LIST OF FIGURES	ii
LIST OF TABLES	iii
ACKNOWLEDGMENTS	iv
INTRODUCTION	1 - 3
METHODS	4 - 9
Study Area	4
Experimental Design	5
Phytobenthic Colonization	6
Algal and Invertebrate Accretion Rates	7
Production Estimates	8
Statistical Analysis	9
RESULTS	9 - 21
Phytobenthic Colonization	9
Phytobenthic Response to Experimental Treatments	11
Phytobenthic Response of the Control	13
Macroinvertebrate Response to Experimental Treatments	16
Spike Flow Effect	20
Estimated Production Rates	21
DISCUSSION	23 - 31
Colonization	23
Snail Herbivory	26
Sloughing	32
CONCLUSION	33
LITERATURE CITED	34 - 40

LISTOFFIGURES

FIGURENO.	TITLE	PAGE
Figure1.	Theexperimentalhydrograph,consistedofastableflowreleaseof227 $m^3 s^{-1}$ that extended from 01 June through 30 September, 2000. Typical discharges fluctuate between a minimum of 142 $m^3 s^{-1}$ and a maximum of 710 $m^3 s^{-1}$ flow.	41
Figure 2.	Plot of the average periphyton biomass accreted for treatments (T1, T2 and T3), across 11 sampling periods, representative of (A) T1 and T2, total mean periphyton biomass, (B) T3, mean biomass for Cladophora and MAMB. Values are expressed in AFDM (g m^2 ± 1 SE, n = 20)	42
Figure 3.	Plot of the average detrital accumulation for the Control and T3, across 11 sampling periods, representative of (A) mean detritus, (B) variance around the mean detrital biomass for a given sampling period. Values are expressed in AFDM (g m^2 ± 1 SE, n = 20)	43
Figure 4.	The distribution of the phytobenthic biomass (AFDM, g m^2) for the Control, across 11 sampling periods, (A) total mean phytobenthic biomass, (± 1 SE, n = 20), (B) compositional separation representing; *Cladophora* (Clad), muscillagenous algae (MUSC), miscelllaneous algae (MA) and bryophytes (BRYO).	44
Figure 5.	Plot of snail biomass, and density distributed across 11 sampling periods among treatments T1 and T2, (A) mean biomass AFDM (g m^2), (B) mean density (org * 10^3 m^{-2}). Standard error (± 1 SE, n = 20).	45
Figure 6.	Intra-sampling variance plotted for Cladophora biomass and snail biomass and density across 11 sampling periods reflecting differences among treatment T3 and the Control, (A) T3 variance , (B) Control variance. Standard error (± 1 SE, n = 20) for AFDM (g m^2) and density (org * 10^3 m^{-2}).	46
Figure 7.	Plot of snail biomass and density distributed across 11 sampling periods among treatments T3 and the Control, (A) mean biomass AFDM (g m^2), (B) mean density (org * 10^3 m^{-2}). Standard error (± 1 SE, n = 20).	47
Figure 8.	Plot of *Cladophora* and snail biomass distributed across 11 sampling periods among T3 and the Control, (A) Control mean biomass , (B) T3 mean biomass. Values are expressed in AFDM (g m^2 ± 1; SE, n = 20)	48

LIST OF FIGURES

FIGURE NO.	TITLE	PAGE
Figure 9.	Intra-sampling variance plotted for *Cladophora* biomass and snail biomass and density across 11 sampling periods reflecting differences among treatment T3 and the Control, (A) T3 variance , (B) Control variance. Standard error (± 1 SE, n = 20) for AFDM (g m^2) and density (org * 10^3 m^{-2}).	49
Figure 10.	Plot of the sampling distribution for the Control, across 11 sampling periods between average *Cladophora* and snail biomass (AFDM g m^2), (A) mean biomass, (± 1 SE, n = 20), (B) variance around the mean biomass for a given sampling period.	50
Figure 11.	Plot of planaria biomass distributed across 11 sampling periods among the different treatments (T1, T2, and T3) and Control, (A) T1 and T2 mean sample biomass , (B) T3 and Control mean sample biomass. Values are expressed in AFDM (g m^2 ± 1; SE, n = 20)	51

LIST OF TABLES

Table 1.	Categorical listing of most common taxon collected in the field and sorted to 15 categories using a modified method developed by [1]Blinn *et al* (1998). Conversions for ash-free dried mass (AFDM) values (g m^{-2}) used were developed by [2]Shannon *et al.* (2000).	52
Table 2.	Results of primary production rates are derived from empirical measurements of quantum oxygen yield relative to underwater irradiance, biomass and temperature. Production estimates are modeled from gross production and respiration rates (light and dark) using equivalent environmental conditions present at the site. Parameters took into account apparent optical properties (K_N = 0.28), PPFD: μmol m^{-2} s^{-1}, angle of incidence (θ_i), transect depth (m), 12 °C, and quantum efficiency 1.2. Reported here are the mean rate estimates of production relative to both biomass-specific and area-specific production estimated for the three different treatments and Control.	53

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INTRODUCTION:

In lotic systems, the countervailing affect between rates of algal production and loss ultimately determine the persistence of benthic communities (Peterson 1986; Stewart 1987; Peterson and Boulton 1999). The structure and function of these communities are regulated by the interaction of different abiotic and biotic factors: growth rates are typically influenced by a combination of temperature, light and nutrients (Cuker 1983; Mulholland *et al.* 1991; Hogg and Williams 1996; Falkowski and Raven 1997; Shaver *et al.* 1997) whereas loss rates are often affected by, herbivory, pathogens and hydrological disturbance (Cuker 1983; Stewart 1987; Blinn *et al.* 1995). In regulated rivers, flow variation on a daily, weekly or seasonal basis increases the total wetted area available for phytobenthic production (Blinn *et al.* 1995). The areal extent of benthic production is primarily determined by flow regulation (Blinn *et al.* 1995; Stevens *et al.* 1997; Blinn *et al.* 1998) an increase in wetted channel can be substantial at higher discharges (Blinn *et al.* 1995). A number of investigators have evaluated the affects of desiccation (Usher and Blinn 1990; Blinn *et al.* 1995) and phytobenthic response to long-term atmospheric exposure, results have demonstrated how temporary reduction in total wetted area, negatively effects the phytobenthos (Peterson 1986; Angradi and Kubly 1993; Blinn *et al.* 1995; Shaver *et al.* 1997; Benenati *et al.* 1998). While considerable information has been compiled regarding benthic community response to fluctuating flow patterns, little understanding exists on how the benthos might respond to stable flow conditions (Benenati *et al.* 1998).

This study was conducted in the Colorado River, a system that is biologically regulated by cold, clear hypolimnetic release ($9 \pm 2\,^{\circ}C$) patterns. This system supports a phytobenthic community of sizeable standing biomass; yet reduced benthic diversity (Stevens *et al.* 1997).

Flows temporarily inundate hard substrata, where variation in river stage result from diel, seasonal and annual changes in hydroelectric generation, unregulated inflow and reservoir level (Stevens *et al.* 1997; Shannon *et al.* 1996). The conditions present in this desert biome are further exacerbated by the canyon morphology where certain physical processes lead to either rapid or delayed loss of exposed or submerged benthos. Substrate scouring or desiccation occurs through periodic or prolonged exposure to seasonal variation in shoreline temperature (0° to 45°C), winds, and sediment deposition (Shaver *et al.* 1997; Parnell and Bennett 1999) and abrasion (Wilson *et al.* 1999).

Periodic inundation of the channel has been presumed to be temporarily beneficial to the phytobenthic community due to the expansion the wetted-area (BOR 1995), yet the validity of this hypothesis is contingent on whether or not newly wetted substrates are colonized at sufficient rates upon inundation. Three possible colonization mechanisms account for the establishment and growth of the phytobenthos, they are fragmentation, sporogenesis (zoospore and akinetes), and residual holdfast structures. In the Colorado River, fragmentation has been considered the most common mode of colonization through surface adhesion by large single or multi-branched thallus (>3 mm) carried in the drift (Blinn and Cole 1991; Shannon *et al.* 1996; Benenati *et al.* 1998). Alternately, zoospores and akinetes colonize the leading substrate edge, forming dense, small micro-filamentous strands. Yet, it has rarely been observed in this system (Benenati *et al.* 1998; Shaver *et al.* 1997) and presumed to be limited by environmental factors, primarily temperature (Bellis and McLarty 1967; Bellis 1968; Lester *et al.* 1988). Lastly, under certain environmental conditions, residual algal holdfast structures are known to regenerate rapidly after ecological disturbance (e.g., light limitations, sediment scouring, and desiccation) and are

thought to be responsible for the rapid in-stream response after hydrological disturbance (Blinn *et al.* 1995; Benenati *et al.* 1998; Wilson *et al.* 1999).

Numerous studies have increased our ecological understanding of benthic response, recovery and recolonization relative to variable flow regimes (Usher and Blinn 1990; Hardwick *et al.* 1992; Angradi and Kubly 1993; Shannon *et al.* 1994; Shannon *et al.* 1996; Blinn *et al.* 1995; Shaver *et al.* 1997; Stevens *et al.* 1997). As a result of these studies, it has been hypothesized that steady flows would have an affect of increasing algal biomass in the varial-zone (Benenati *et al.* 1998). However, little information regarding actual flow stabilization for large regulated rivers exists to validate this ecosystem response. Also, these past studies have not addressed the affects of stabilized inundation after substrate scouring, nor possible interactions that might influence colonization rates due to the benthic community response under stable flows.

To date, very few large ecosystem-scale experiments have been conducted in lotic systems (Hogg and Williams 1996; Blinn *et al.* 1999; Parnell and Bennett 1999). The relevance of these large-scale experiments are contingent on how well natural conditions, incidental to manipulated flows are maintained or exist during the experimental period (Hill and Knight 1987). An experimental hydrograph was developed for Glen Canyon Dam to simulate certain flow characteristics and temporal patterns that corresponded to the Colorado River's natural hydrograph (Ralston, *et al.* 2000; Valdez *et al.* 2000). The primary objective of this ecosystem-scale experiment was to test a series of nested hypotheses that low steady flow conditions at a constant 227 m^3 s^{-1} would provide low-velocity habitat and near shoreline warming for young-of-year native fish (Valdez *et al.* 2000). Secondary hypotheses were developed to test abiotic and

biotic responses to these stable flow conditions. This particular study has taken the opportunity afforded by steady flow conditions to address the underlying mechanisms of colonization.

We report here detailed analysis on substrate colonization response of the phytobenthos and macroinvertebrates to a steady flow experiment. We examined variations in density and biomass accretion rates under the premise that rates should relate closely to colonization modes. In particular, we used experimental treatments to evaluate hypotheses that the degree of substrate conditioning and atmospheric exposure to desiccation influenced the mode of colonization, developmental rates of benthic composition, density and biomass. Our data suggested that grazing pressure may have differential affects on colonization modes, benthic cobble structure and composition, and on rates of macroinvertebrate density and biomass accretion, at least under the constant hydraulic conditions of this experiment.

METHOD

Study Area

The Colorado River on the Colorado plateau of northern Arizona originates from Lake Powell's reservoir as a cold, clear and variable flow. The downstream tail-water section is conducive for primary production owing to the hypolimnetic and optical characteristics (Blinn and Cole 1991; Shaver *et al.* 1997; Benenati *et al.* 1998). Variable flows are released from Glen Canyon Dam (GCD) hydroelectric facility, and fluctuate between a minimum 142 $m^3 s^{-1}$ and maximum 710 $m^3 s^{-1}$ discharge. These operational constraints limit daily variation to a maximum change of ± 227 $m^3 s^{-1}$ in a 24h period. Our study area, Lees Ferry cobble bar (36°56′06″N, 111°28′53″W; RM 0.8) was physically located above any major tributary influence. Glen

Canyon, the first 26 km downstream from GCD are consistently clear water and represent 60% of the total phytobenthic standing biomass produced throughout the remaining 390 km corridor in Colorado River (Glen and Grand canyons) (Blinn *et al.* 1995). The phytobenthic community consists primarily of macroalgae, *Cladophora glomerata*, *Ulothrix sp.*, *Mougeotia sp.*, *Spirogyra sp.*, *Chara contraria*, bryophytes, *Fontinalis sp.*, and macrophyte, *Potomogeton pectinatus*. *Cladophora*, is a green filamentous and branched alga, that functions as the structural attachment for epiphytes and habitat for macroinvertebrates (Shannon *et al.* 1994; Blinn *et al.* 1995). This epiphytic assemblage is composed almost entirely of diatomaceous species. The dominant taxa are *Diatoma vulgare*, *Cocconeis placentula*, and *Rhoicosphenia curvata* (Czarnecki *et al.* 1976; Czarnecki and Blinn 1978; Hardwick *et al.* 1992; Benenati *et al.* 1998), and are the primary source of autotrophic energy for higher trophic levels, and that comprise the majority of invertebrate diet (Pinney 1991; Blinn and Cole 1991; Blinn *et al.* 1995).

Experimental Design

Experimentally, we used cobble substrate as our experimental unit and compared differences in rates of benthic colonization using a stratified random design consisting of three treatments and one control. Cobbles consisted of fine grain sedimentary material (calcareous limestone and sandstone) and all were similar in surface area (300 ± SE 75 cm^2). Three exposure levels were applied to cobble substrate. These treatment types consisted of T1, substrate exposed > 100 yr (never colonized); T2, substrate known to have been previously colonized, benthos mechanically scraped and desiccated for 1 yr; and T3, substrate previously colonized, benthos mechanically scraped but never desiccated. A control group was established using untreated

cobble substrate that supported the local composition of phytobenthic and macroinvertebrate community.

Figure 1, identifies the experimental hydrograph and sampling period that extended from 1 June to 12 September 2000. Treatments and control cobbles were assigned to 44 transects, containing 20 replicate samples per transect for a total of 880 cobbles. Each transect's sampling date was preassigned randomly; as well as the distribution of the different treatments and control within the overall experimental plot. For each sampling period, three treatments and one control were sampled at a 10-11 d interval for a total of 11 sampling periods. The sources of cobbles were all locally obtained and depending on the treatment type were collected directly from the Colorado River or adjacent Pleistocene deposits. Where applicable, cobbles were mechanically scraped clean of filamentous algae using safety edge razors. To distinguish from different treatment types, cobbles were marked (bottom surface) and positioned on 5 m cable transects oriented perpendicular to shoreline at 1 to 1.2 m depths. All transects had comparable flow velocities (0.25 $m^{-1}s^{-1}$, ± SE 0.06) measured at 6/10 depth.

Phytobenthic Colonization

All replicate samples were visually observed in the field for the presence/absence, species composition, mode of attachment (zoospore, fragmentation, holdfast structure), spatial distribution, point of colonization, areal coverage, density and filament length. The experimental design used a hierarchical approach to falsify hypotheses. Depending on the experimental outcome, certain hypotheses were mutually exclusive; therefore, outcomes were contingent on the order of falsification. It were assumed that if algal establishment was due to fragmentation or

zoospore production, than rates of colonization would have been equal among treatments. Particularly since transect layout and sample assignment for each treatment had the same likelihood of being colonized. However, if colonization were due to zoospore production it would be apparent owing to the algal growth pattern (filament size and substrate distribution). Alternately, if colonization rates and secondary growth were due to holdfast structures and differential viability, we would have expected to observe a significant difference in rates of biomass accretion among treatments. Especially, since treatments T2 and T3 were known to have had originally a substantial algal standing crop prior to substrate removal. Macroalgal identification was performed in the field using a field microscope (100x).

Algal and Invertebrate Accretion Rates

For each sampling period, cobbles were sampled without replacement to avoid sampling bias among and within treatments. Circular sampling templates (12.57 cm^2) were used to sample cobble surfaces. So as to avoid preferential placement, cobble surface was subdivided into eight quadrants with sampling point location preassigned randomly. All benthic material were macroscopically identified and sorted by periphyton and invertebrate taxon into 15 field categories using a similar method developed by Blinn *et al* (1998) (Table 1). A broad category referred to as miscellaneous algae, macrophytes, and bryophytes (MAMB) has been used in the past (Benenati *et al.* 1998) to distinguish a combined group of phytobenthic taxon (*Ulothrix sp.*, *Mougeotia sp.*, *Spirogyra sp.*, *Gomphonema sp.*, *Batrachospermum sp.*, *Rhodochorton sp.*, *Chara contraria*, *Fontinalis sp.*, and *Potomogeton pectinatus*).

Sorted samples were stored in pre-weighed glass vials (25 x 13 mm), dried, re-weighed and converted to ash-free dried mass (AFDM) values (g m^{-2}) using conversions established by Benenati *et al.* (1998) (Table 1). Owing to the destructive nature of biomass determination, reference samples were collected and preserved in Lugol's solution (Greenberg *et al.* 1985). Additionally, during each sampling period, periphyton samples were collected for each treatment (n=10), filtered (Whatman GF/F 0.7 µm pore) and desiccated for 48-h at 60 °C and stored. Further enumeration for diatom composition has not been completed to date.

Production Estimates

By definition, net primary production (NPP) is equal to the net photosynthetic rate plus the difference associated with the metabolic cost of both light and dark respiration. Whereas, estimates for net photosynthetic rate (NPR) is the net organic production that occurs during the daylight period, essentially the difference between gross production and light respiration. We have intentionally made a distinction between these two rates because they are often inadvertently confused and misreported in the literature (Falkowski and Raven 1997). Secondly we have reported rate estimates of production relative to both biomass-specific and area-specific production (Lamberti *et al.* 1989).

We used two separate methods to estimate net primary production: 1) cross-sampling rates of biomass accrual, and 2) production rates based on oxygen generation. The first method, we used a SLR and cross-sampled between sampling periods, by calculating regression coefficients between each sampling interval, to determine an interval estimate of biomass change (±) in response to time. Owing to the experimental design, biomass response was considered

independent of the preceding and following sampling period. The sum of interval rate estimates was used to calculate total change in biomass for experimental period. Whereas, the second production method was based on empirically derived production irradiant curves.

Production estimates are modeled using equivalent environmental conditions present at the site. The different model parameters took into account the apparent optical properties, average photosynthetic photon flux density (PPFD: μmol m^{-2} s^{-1}) estimated at 15 min intervals, direct insolation, angle of incidence (θ_i), transect depth (m), water temperature (12 °C), gross production and respiration rates (light and dark), and quantum efficiency 1.2 (Kirk 1983; Falkowski and Raven 1997). Modeled assumptions were that nutrients were constant and non-limiting, transmissivity was constant during experiment, normalized light attenuation ($K_N = 0.28$) was considered constant between days (i.e., although diel variability in light attenuation was adjusted for by using, $\cos(\sin \theta_i) / 1.33 \cdot K_N$). Lastly, all primary production in excess of meeting metabolic costs was transferred to structural growth, as biomass. The assumption was that no mechanical loss occurred from autogenic sloughing, structural damage, loss of metabolites (DOC), or herbivory.

Statistical Analysis

We used a combination of univariate and multivariate tests to determine the affect specific treatments and sampling intervals had on the phytobenthic community. The statistical tests used included ANOVA (Model I) (Kruskal-Wallis), simple linear regressions, and multiple linear regressions for determining temporal trends and rates. All periphyton and macroinvertebrate densities and AFDM were transformed ln (x+1) to assure for homogeneity of

variance. Tukey HSD and Spjotvoll-Stolline tests were used for multiple *post-hoc* comparisons among treatments and within sampling periods. Density and AFDM levels are reported as mean values (± SE m^{-2}). Statistical analysis was performed using STATISTICA 5.1 (StatSoft, Inc. 1997) statistical software.

RESULTS

Phytobenthic Colonization

Algal colonization and growth was minimal for two of the three exposure treatments during the 105-d colonization period. The initial quantitative source of phytobenthic material observed to accumulate on T1 (100 yr. or greater) and T2 (1 yr.) was due to fragmentation. Fragments consisted of *Cladophora*, *Ulothrix*, *Mougeotia*, *Spirogyra*, *Chara, Fontinalis*, and *Potomogeton*. Although intermittently present on substrate, visual observations did not indicate a significant increase in the quantity of fragments ($p > 0.1$) through the sampling period, nor was their substantial accretion of secondary growth following fragment establishment. Only, 36.4% ± 3.9 of all cobble treatments (T1 & T2) contained fragments during the course of the experiment. Although viable, this propagation mode did not appear to be responsible for, or as rapid in response to substrate colonization as other propagation modes.

Source of colonization for T1 and T2, appeared to have been primarily due to zoospore production, and of all cobbles observed during the course of the experiment zoospores were present 72% ± 8.0 ($n = 440$) of the time. The colonization response was rapid where 50-60% of cobbles had detectable filaments within a 10-d period. Colonization occurred on the leading stream edge of the cobble, and within 30-d over 90% of cobbles had filaments distributed over

most of the cobble surface. Taxonomic composition of these filaments was predominantly *Ulothrix* and *Cladophora*. Treatments T1 and T2, began to increase in phytobenthic biomass by 60-d into the experiment, and had maintained an average AFDM value of 2.6 g m^{-2} ± 0.86, and 5.7 g m^{-2} ± 1.14.

Whereas, treatment T3 demonstrated a rapid recolonization response (i.e., relative to the other two treatments) owing to the viability of the periphyton's original basal holdfast structure and began to accrete measurable quantities of biomass by 21-d. This treatment had been originally scrapped free of all standing biomass similar to T2; however, was never exposed to atmospheric conditions. The initial taxa to colonize T3 was *Cladophora*, followed later by unbranched mucilaginous filamentous greens (*Ulothrix*, *Mougeotia* and *Spirogyra*). The initial colonization response pattern for periphyton growth exhibited a linear trend. This rapid growth phase became asymptotic by 60-d, where the total sum of phytobenthos maintained a mean AFDM of 55.8 g m^{-2} ± 4.3 for the duration of the experiment. The secondary colonists, were delayed in their establishment until 80-d into the experiment. The predominant mode of colonization for these mucilaginous algal forms was probably fragmentary, adhering loosely to the filamentous under-storage formed by *Cladophora*. Yet once established, overall accretion by these algae was rapid, occurring at a rate of 670 mg m^{-2} d^{-1} ($p < 0.001$).

Phytobenthic Response to Experimental Treatments

Results indicated that there were significant differences among treatments in overall phytobenthic AFDM ($p < 0.001$). Yet, *post-hoc* tests indicated there was no significant differences among treatments T1 and T2 ($p > 0.1$). The maximum mean AFDM for T1 and T2

periphyton attained during the entire sampling period was 4.2 g m^{-2} ± 1.98 (92-d) and 8.4 g m^{-2} ± 3.8 (82-d), respectively. For treatment T3, the mean maximum biomass in phytobenthos had an AFDM of 66.6 g m^{-2} ± 15 (71-d). Although, these two treatments had significantly lower phytobenthic AFDM than T3 ($p < 0.001$), there was a trend for greater biomass accretion for cobbles having been exposed to atmospheric conditions no greater than 1yr. Trends suggested a possibility of substrate conditioning and viability of residual holdfast structures. Rates of accretion for treatments T1 and T2 were delayed and did not begin to accrue with sizeable quantities of AFDM until 60-d into the experiment (Fig. 2A). We pooled treatment T1 and T2 data since rates were not significantly different between treatments. Results indicated that after 60-d AFDM for periphyton began to accrete at a rate of 67 mg m^{-2} d^{-1}.

Treatment T3 was unlike the other two treatments, and showed a rapid colonization that was predominantly *Cladophora*, with an overall AFDM accretion rate of 930 mg m^{-2} d^{-1} ($p < 0.001$) (Fig. 2B). *Cladophora* represented 85.8% of the entire phytobenthic biomass accrued, and was significantly different in proportion to the overall periphyton found on T1 ($p < 0.001$) and T2 ($p < 0.001$). Although, *Cladophora* was present in these other treatments, its overall percent composition was considerably less and represented 3% for T1, and 16% for T2. Further *post-hoc* comparisons showed that there was no significant difference in percent composition ($p = 0.17$) between these two treatments, which were comprised of predominantly mucilaginous, filamentous green algae.

Results for MAMB indicated that there were significant differences in AFDM among the three different treatments ($p < 0.001$). *Post-hoc* comparisons indicated that the differences among T1 and T2 were not significant ($p > 0.1$). Mean AFDM for MAMB attained during the

entire sampling period for T1 was 430 mg m^{-2} ± 0.18, and T2 was 810 mg m^{-2} ± 0.2. In the case of T3, it was significantly different than the other two treatments ($p < 0.001$), where MAMB AFDM values averaged 2.7 g m^{-2} ± 0.57. Although T3 MAMB, represented only 8% of the phytobenthic composition for the entire sampling period, there were significant differences within sampling periods ($p < 0.001$). *Post-hoc* tests (Fig. 2B), revealed that within sampling differences for mean T3 MAMB was due to the last series of sampling period's (105-d), where mean AFDM increased rapidly and attained levels of 16 g m^{-2} ± 3.6.

Fragmentary growth was more often than not absent on treatments T1 and T2, with the exception of some fragments from macrophytes. Additionally, the proportion of miscellaneous algae in T1 and T2 did not accrete significant quantities ($p > 0.05$) AFDM among treatments. This was also the case for bryophytes ($p = 0.91$), and macrophytes ($p = 0.24$). However, macrophytes for treatment T3 had an average AFDM value of 597 mg m^{-2} ± 33. T3 was also significantly greater in the quantity of bryophytes ($p = 0.02$) and other algae ($p < 0.004$); however, there were no within treatment differences for either bryophytes ($p = 0.64$) or other algae ($p = 0.34$).

Detritus accumulation differed significantly among treatments ($p < 0.001$), yet *post-hoc* differences were only attributed to T3. Detritus accumulation was not significant among ($p = 0.56$) and within treatments for T1 ($p = 0.57$) and T2 ($p = 0.51$). Although, cobble substrate was typically devoid of detrital material, and averaged AFDM values of 24 mg m^{-2} ± 16.8 for T1, and 10 mg m^{-2} ± 8.5 for T2. Treatment T3 detrital accumulation averaged 12.5 g m^{-2} ± 2.2, yet differed significantly within sampling periods ($p < 0.001$). A trend existed where once T3 began to accrue sufficient enough standing periphyton as of 31-d (Fig. 3A), detritus proceeded to

accumulate in significant quantities ($p < 0.001$), at a rate of 1.1 g m^{-2} d^{-1}. Detrital accumulation reached mean maximum AFDM levels at 49.4 g m^{-2} ± 19 ($n = 20$) as of 60-d. However, by experimental closure it had decreased just as rapidly to AFDM values of 9.2 g m^{-2} ± 1.8 (105-d). Also, we observed a trend of increasing variance around the sample mean, with greatest variance at 60-d into the experiment (Fig. 3B).

Phytobenthic Response of the Control

Phytobenthic AFDM increased significantly during the duration of the experiment ($p < 0.001$) at a rate of 20 mg AFDM m^{-2} d^{-1}. The average phytobenthic AFDM was 176 g m^{-2} ± 5 (Fig. 4A). In comparison, *Cladophora* on average represented 53.4% of the Control's cobble composition, and was significantly different then the three other treatments ($p < 0.001$) when tested for among treatment differences. Standing biomass of *Cladophora* increased during the entire experiment with an overall accretion rate of 0.36 g m^{-2} d^{-1} ($p < 0.004$) in AFDM. It was notable that AFDM alternated frequently between sampling period's (10-d), and demonstrated an oscillating periodicity that increased in amplitude as it approached experimental closure (Fig. 4B). Additionally, this oscillating pattern was observed for an alternate category referred to as miscellaneous algae, and consisted primarily of a colonial aggregate (i.e., primarily the diatom *Gomphonema sp.*).

Miscellaneous algae associated with the Control, had AFDM values that were significantly higher than values attained among other treatments ($p < 0.001$), as well as significant within variability ($p < 0.001$). This miscellaneous algal group represented 17.3% ± 1.2 ($n = 220$) of the mean phytobenthic composition, yet by experimental closure had decreased from of 24 to 5% of

total composition (Fig. 4B). Results indicated a significant trend in biomass reduction through the experimental period ($p < 0.001$), and where the maximum mean AFDM value decreased from 67 g $m^{-2} \pm 16$, to 4.6 g $m^{-2} \pm 1.4$. By the end of the experiment, the biomass loss represented a negative AFDM rate of 393 mg m^{-2} d^{-1}. This miscellaneous alga was composed predominantly of *Gomphonema*. It demonstrated a periodicity that was both negatively correlated, and asynchronous in periodicity to *Cladophora* AFDM ($p < 0.05$). Whereas, it was significantly ($p < 0.001$) and positively correlated to the presence of bryophytes and in synchrony with its oscillating periodicity. For all the possible interactions tested, Bryophyte x *Cladophora*, were found to be significant ($p < 0.001$). Miscellaneous algae responded more positively under an increase in overall phytobenthic biomass and compositional difference, favoring a greater proportion of bryophytes over *Cladophora*, but not of an exclusive bryophyte composition.

During the experimental period, the Control MAMB averaged an AFDM value of 85.8 g $m^{-2} \pm 0.2$, and was significantly higher in comparison to the other treatments ($p < 0.001$), as well as differences during the sampling periods ($p < 0.001$). *Post-hoc* tests revealed that this periodic variation between sampling periods began to increase mid-way into the experiment and continued to closure. Overall MAMB represented 46.6% ± 2.1 ($n = 220$) of the mean phytobenthic composition (Fig. 4B).

Also, results indicated that there were significant differences that existed among treatments ($p < 0.001$) in bryophyte biomass; yet, *post-hoc* tests revealed that only the control was significantly greater ($p < 0.001$) in AFDM. The frequency of bryophytes occurrence (i.e., fragments) on the three treatments was extremely rare, and represented from 1-8% for all treatment cobbles ($n = 660$). In comparison, the Control cobbles were observed to have a 75%

frequency of occurrence. Results indicated that bryophyte AFDM on the Control was significantly higher than mean values attained among other treatments ($p < 0.001$); however, no significant difference existed between sampling periods ($p < 0.14$) for the Control. Mean AFDM value for bryophytes was 46.5 g $m^{-2} \pm 0.26$ ($n = 220$) and represented 24.8% of the total composition (Fig. 4B). Bryophytes, not unlike *Cladophora*, demonstrated a periodic pattern throughout the duration of the experiment; however, its compositional proportion and overall biomass was negatively correlated to *Cladophora* ($p < 0.001$).

This same pattern was observed for Control macrophytes, where AFDM was significantly higher than mean values attained among other treatments ($p < 0.001$) and no significant differences were detected between sampling periods ($p < 0.16$). Additionally, mucilaginous filamentous algae on the Control consisted primarily of *Ulothrix*, *Mougeotia*, and *Spirogyra*, and as a categorical group were found to be significantly different in AFDM among all three treatments ($p < 0.001$). However, unlike bryophytes and macrophytes there were within sampling differences ($p < 0.001$). *Post-hoc* tests indicated that mean AFDM for mucilaginous filamentous algae attained maximum levels of 14.2 g $m^{-2} \pm 3.4$ ($n = 20$) by the end of the experimental period. However, it maintained typically averaged an AFDM value of 7.4 g $m^{-2} \pm$ 1.1 ($n = 220$), and represented 4.5% of the total composition of Control cobbles.

Detritus for the Control cobbles differed significantly among the three different treatments ($p < 0.001$), and as well between sampling efforts ($p < 0.001$). On average detritus for the entire sampling period had an AFDM of 65.2 g $m^{-2} \pm 9.1$, consisting primarily of sloughed or senescent algal material (Fig. 3A). Detritus attained a mean maximum AFDM level of 177.9 g $m^{-2} \pm 72$, although there was considerable variation between and within sampling periods (Fig. 3B). *Post-*

hoc comparisons demonstrated that within sampling differences for detritus were temporally linked to changes that occurred mid-way into the experiment. Detritus descended to AFDM levels of 10.2 g m^{-2} ± 2.1 (105-d) by the end of the experiment. These lower detrital levels were similar to those observed for T3.

Macroinvertebrate Response to Experimental Treatments

There was no significant difference in overall *Physella sp.* (snails) mean density between T1 and T2 ($p > 0.1$); *post-hoc* comparisons revealed that by 72-d mean densities ($p < 0.05$) and mean AFDM ($p < 0.05$; 41 d) were significantly greater for treatment T2 (Fig. 5A; Fig. 5B). The maximum mean densities attained during the entire sampling period for T1 and T2, were $25.8 \cdot 10^3$ org m^{-2} ± $8.2 \cdot 10^3$ (92-d), and $35.5 \cdot 10^3$ org m^{-2} ± $9.3 \cdot 10^3$ (105-d), respectively. AFDM for gastropods were also consonant to observed density patterns. Maximum mean AFDM attained by snails for T1 and T2 were 5.9 g m^{-2} ± 1.8 (92-d) and 11.2 g m^{-2} ± 3.6 (105-d), respectively. Pooled data for both treatments demonstrated that snail density ($p < 0.001$) and biomass ($p < 0.001$) were positively and significantly correlated to *Cladophora* and mucilaginous filamentous algal AFDM. A strong linear relationship existed between snail biomass and density but not *Cladophora*. Although, correlated the corresponding pattern in intra-sampling variance for theses three benthic constituents indicated that variation in periphyton biomass did not explain the variance observed in snail biomass or density for either treatment, T1 (Fig. 6A) and T2 (6B).

Alternately, treatment T3 was significantly greater for both snail density ($p < 0.01$) and algal AFDM ($p < 0.01$) than T1 and T2, and had attained a maximum mean density of $129.7 \cdot 10^3$ org m^{-2} ± $22 \cdot 10^3$ (49 d) and AFDM of 49.0 g m^{-2} ± 6.7 (80 d) (Fig. 7A; Fig. 7B). Also, results

indicated that T3 snail densities ($p < 0.001$) and biomass ($p < 0.001$) were positively and significantly correlated to periphyton AFDM (*Cladophora,* miscellaneous and mucilaginous filamentous algae). T3 snail AFDM tracked *Cladophora* at a rate of 0.86 g m^{-2} d^{-1} ($p < 0.001$) and became asymptotic after 60-d.

For the Control, snails rapidly responded to stable flows conditions and increased from an initial density of $32 \cdot 10^3$ org $m^{-2} \pm 7.9 \cdot 10^3$, and AFDM 15.4 g $m^{-2} \pm 3.5$ to maximum levels within a 60-d period of $217 \cdot 10^3$ org $m^{-2} \pm 19.5 \cdot 10^3$, and AFDM and 104 g $m^{-2} \pm 11.2$ (Fig. 7A; Fig. 7B). This represented approximately a six-fold increase in density and biomass. During this expansion phase snail density and AFDM increased at a rate of $3.5 \cdot 10^3$ org m^{-2} d^{-1} ($p < 0.001$), and 1.5 g m^{-2} d^{-1} ($p < 0.001$). The overall mean snail density and AFDM maintained during the entire experiment was $151 \cdot 10^3$ org $m^{-2} \pm 7.4 \cdot 10^3$ and 68.1 g $m^2 \pm 3.6$, respectively (n=220).

For treatment T3, *Cladophora* was significantly correlated with snail density ($p < 0.001$), although not significantly correlated to snail biomass ($p = 0.054$). Findings indicated that under stable flow condition snails responded to algae, yet appeared non-exploitive, and by 60-d into experiment snail densities and biomass had stabilized and were synchronous with the observed variation for *Cladophora* biomass (Fig. 8A, Fig. 8B). For T3, a linear relationship existed for intra-sampling variance between *Cladophora* and snail biomass and density. This linear correspondence indicated a pattern of resource tracking, where variation between samples for *Cladophora* AFDM explained the observed variation in snail biomass and density (Fig. 9A). By the end of the experiment snail AFDM had increased from 73% to over 95% of the total macroinvertebrate biomass. Whereas for the Control, intra-sampling variance increased with sampling periods reaching maximum variation around the sample mean by 50-d. However,

neither snail biomass nor density demonstrated as strong of a correspondence to *Cladophora* (Fig 9B) as had T3. The proportion of snail biomass to total benthic (autotrophs and macroinvertebrates) biomass for the three different treatments and Control represented for T1, 82% ± 16; T2, 73% ± 21; T3, 47% ± 20; and Control, 31% ± 8.2. The Control attained snail densities ($p < 0.01$) and AFDM ($p < 0.01$) levels that were significantly greater than those observed among other treatments. Additionally, for the Control, snails far exceeded other macroinvertebrate densities and biomass levels (Fig. 10A, Fig. 10B).

In regards to these other larger macroinvertebrates, there was an apparent colonization lag (60-d) observed for tubificids, lumbriculids, and amphipods occupying available substrate. However, no other macroinvertebrates were found to be as abundant in density or biomass as were snails. During the entire experiment the only other invertebrate observed on cobbles for treatments T1 and T2 were flatworms (Turbellaria) (Fig. 11A). Test for differences in mean organism density ($p < 0.001$) and AFDM ($p < 0.001$) among treatments indicated that only T3 was significantly different. Mean densities and AFDM levels of flatworms for T1 and T2 were respectively 214 org m^{-2} ± 46 and 107 mg m^{-2} ± 38.2, and 326 org m^{-2} ± 62 and 106 g m^{-2} ± 30.6. Alternately, the mean density and AFDM of flatworms for T3 was $1.2 \cdot 10^3$ org m^{-2} ± $0.14 \cdot 10^3$ and 313 mg m^{-2} ± 38 (Fig. 11B). Average rate of increase for treatments were: T1, 6.7 org m^{-2} d^{-1} and 3.7 mg m^{-2} d^{-1}; T2, 8 org m^{-2} d^{-1} and 2.4 mg m^{-2} d^{-1}; and T3, 25.1 org m^{-2} d^{-1} and 6.2 mg m^{-2} d^{-1}.

Regarding other macroinvertebrates, these were associated with T3 and only once algal biomass had sufficiently accrued. Macroinvertebrates included lumbriculids, tubificids, gammarids, simulids, and chironomids. Results for T3, lumbriculids showed an increase in density ($p < 0.001$) and AFDM ($p < 0.001$) throughout the experiment, and attained maximum

mean densities of 478 org m^{-2} ± 134 and AFDM of 3.3 g m^{-2} ± 1.2 (91-d). Results for tubificids were similar, where densities ($p < 0.001$) and AFDM ($p < 0.001$) increased throughout the experiment; although, no appreciable increase had occurred until mid-way into the experiment (60-d). Once tubificids were established they attained a maximum mean density of 557 org m^{-2} ± 200, and by 92 d had an AFDM of 362 mg m^{-2} ± 142.

However, response patterns for gammarids were not similar. *Gammarus lacustris*, was found to be extremely rare for T3, occurring in 3% of all sorted samples (n = 220). Additionally, simulids were extremely rare and were not detected for any of the three treatments, whereas chironomids were temporally variable upon colonizing T3 substrate. Overall mean chironomid density and AFDM levels for T3 during the experimental period was 362 org m^{-2} ± 69 and 912 mg m^{-2} ± 57. Results showed that during the colonization phase (50 d) chironomid density ($p < .001$) and AFDM ($p < .05$) increased significantly. Organism densities and AFDM increased until mid-way into the experiment and attained maximum mean density of $1.1 \cdot 10^3$ org m^{-2} ± $0.45 \cdot 10^3$ and AFDM of 5.4 g m^{-2} ± 5.2. However, following the period of growth, chironomids just as rapidly decreased to undetectable levels by the end of experiment.

In comparison, *post-hoc* tests for within sampling differences in the Control indicated that changes in mean biomass for lumbriculids ($p < 0.001$) and tubificids ($p < 0.001$) had increased significantly; whereas chironomids exhibited a significantly negative decline ($p < 0.001$). Lumbriculids increased over the study period to a density of 388 org m^{-2} ± 93 and AFDM of 12.0 g m^{-2} ± 2.9, at a rate of 106 mg m^{-2} d^{-1}. Lumbriculid AFDM was significantly and positively correlated to increased detrital accumulation on cobbles for T3 ($p < 0.001$), and the Control ($p < 0.02$). In regards to the Control tubificids, they demonstrated within sampling variability ($p <$

0.001), and by experimental closure tubificids had increased in density to 4 org m^{-2} ± 0.17 and AFDM of 544 mg m^{-2} ± 27. However, they were not significantly correlated to detrital accumulation.

Spike Flow Effect

Tests were performed to address questions concerning the affect of a short duration spike flow of 896 $m^3 s^{-1}$ on the benthic community following a period of stable flow conditions. This flow event occurred between 4-8 September 2000. Using univariate tests, a series of comparisons were made between trip number 10 and 11, to evaluate the benthic response of the Control relative to changes in flow. Results showed that following the spike flow event, a significant decrease was detected for both macroinvertebrates ($p < 0.01$) and the phytobenthos ($p < 0.02$). However, single *post-hoc* tests for macroinvertebrates indicated that only lumbriculids density ($p < 0.002$), and AFDM levels ($p < 0.01$), as well as snails densities ($p < 0.001$) and AFDM levels ($p = 0.02$) had decreased. For the phytobenthic component, AFDM levels differed significantly for *Cladophora* ($p < 0.01$) and mucilaginous algae ($p < 0.01$); as well as the detrital component ($p < 0.001$). Although the effect between sampling periods was significant, reductions in macroinvertebrate density and phytobenthic biomass cannot be attributed solely to the spike flow since trends toward reduction had been previously detected. Lastly, in regards to questions concerning cobble displacement due to hydraulics, it was determined that the frequency of cobbles displaced for all treatments and Control were not significant following this event ($p > 0.1$).

Estimated Production Rates (Biomass accretion and oxygen generation)

We used two separate methods to estimate net primary production, 1) cross sampling rates, and 2) production rates based on primary production irradiant curves (unpublished data). Estimates of standing biomass accretion for *Cladophora* based on cross-sampling biomass rate remained relatively constant. The average accretion rate showed an increase in AFDM across all sampling periods and was on average 3.5 gC m^{-2} d^{-1}. Conversely, rates of biomass loss between sampling intervals decreased overtime from 2.0 to 5.1 g m^{-2} d^{-1} AFDM. The average rate of decrease was 3.3 g m^{-2} d^{-1}. The rate in biomass loss was sequentially regressive throughout the extent of the study period and sharply increased with time. The difference between average biomass accretion and loss rates indicated that 90% to 95% of the total standing biomass production was potentially lost. The mechanisms that could have accounted for this loss were drift from hydraulic turbulence, epiphytic loads, sloughing of senescent growth, and loss of extra-cellular metabolites in the form of DOC. Lastly, loss of biomass through herbivory. Based on the cross-sampling method the total gross quantity of standing biomass produced over a 105-d period amounted to 367 g C m^{-2}.

The second production method was based on empirically derived rate curves for oxygen generation under varying thermal, irradiance and biomass levels. Production-irradiant rates were derived from experimental data using phytobenthic covered cobbles, comprised predominantly of *Cladophora* and associated epiphytes (unpublished data). The total average daily amount of underwater photosynthetic photon flux density (PPFD) available during the experimental period was estimated as 41.57 mol m^{-2} d^{-1} (± 0.33). The average daily instantaneous underwater PPFD

estimated at depth was at 787 μmol m^{-2} s^{-1}. Cumulative hour duration of photoperiod totaled 14-h (± 1.5 h, civil twilight) and had a daily underwater maximum of 1439 μmol m^{-2} s^{-1}.

Net primary production estimates (NPP) based on an average hourly rate for the entire day, varied relative to the quantity of biomass accrued on cobbles (Table 2). Results indicated that production estimates for the Control based on the average total phytobenthic biomass of 176 g m^{-2} (± 5.0) had an average hourly NPP of 2.03 mg O_2 gC^{-1} m^{-2} h^{-1}. This biomass-production estimate was considerably less than estimates derived for the other treatments, where a combined estimate for treatments T1 and T2 had an estimated NPP of 7.93 mg O_2 gC^{-1} m^{-2} h^{-1}, based on an AFDM of 0.145 g m^{-2} (first 50 d of experiment); whereas, T3 had an estimated NPP of, and 5.84 mg O_2 gC^{-1} m^{-2} h^{-1}, based on an AFDM of 55.8 g m^{-2}.

Although there was a reduction in biomass-specific NPP (i.e., generation of O_2 gC^{-1} m^{-2} h^{-1}), overall area-specific NPP production was greatest for cobbles having the largest accretion of biomass per area. NPP for the Control was estimated as having an average hourly NPP of 300 mg O_2 gC^{-1} m^{-2} h^{-1}; whereas, the other treatments NPP were an of 1.28 mg O_2 gC^{-1} m^{-2} h^{-1} for T1 & T2 (combined estimate), and 340 mg O_2 gC^{-1} m^{-2} h^{-1}. Carbon conversions based on a conservative photosynthetic quotient of 1.2 were calculated for the different treatments and Control (Kirk 1983; Falkowski and Raven 1997). Daily rates for NPP carbon syntheses were 25.72 mg C m^{-2} d^{-1}, 6,814 mg C m^{-2} d^{-1}, and 6,066 mg C m^{-2} d^{-1}, for treatment T1 & T2 (combined), T3 and Control, respectively. Extrapolated estimates for total net carbon production (area-specific NPP) for the duration of the experiment (105-d) were 2.7 gC m^{-2} (T1 & T2), 715.5 gC m^{-2} (T3) and 637 gC m^{-2} (Control). The daily production to biomass ratio (PB) was four times as high for T1 & T2 (0.19) as for T3 and Control (0.05).

It is notable, that NPP production rates for T3 are greater than the Control. During our experiment, the onset of decreased photosynthetic efficiency under high irradiant levels was estimated to begin at 115 g m^{-2} AFDM, and NPP production rates become asymptotic once biomass levels attained AFDM of 230-240 g m^{-2}. This photosynthetic response was indicative of allometric constraints on NPP, perhaps in response to light and nutrient limitations or the accumulation of senescent growth. The ecological consequences for periphyton are that the biomass compensation point between photosynthesis and respiration will be dependent on seasonal incidence, substrate depth and the optical properties of water. Therefore, the maximum amount of accreted biomass will vary on a temporal and spatial scale based on limitations to primary production occurring within the channel.

DISCUSSION

Colonization

Our results indicated that differences in colonization modes influenced algal establishment, growth rates and composition. Although, flow stabilization allowed for colonization of periphyton, differential response in biomass accretion among treatments may have been attributed to developmental differences in algae and increased grazing pressures by herbivores that equally responded to these stabilized conditions. Numerous studies have demonstrated that grazing reduces area-specific productivity (Stewart 1987; Mulholland *et al.* 1991); as well as altered phytobenthic composition (Cuker 1983). Alternately, other investigators have shown that grazing has increased biomass and production levels by the removal of senescent under-storage (Gregory 1983; Sarnelle *et al.* 1993), increased PPFD availability (Hill and Harvey 1990;

Mulholland *et al.* 1991), reduction in epiphytes (Cuker 1983; Hill and Knight 1987) and nutrient recycling by grazers (Cuker 1983; Mulholland *et al.* 1983; Grimm and Fisher 1989; Vanni and Layne 1997). In particular, *Cladophora* has been shown to respond positively to snail grazing (Dudley 1992; Sarnelle *et al.* 1993).

Results indicated that the mode of algal establishment and response rate were dependent on the nature of the cobble treatment. Following substrate inundation, colonization occurred within a 10 to 20-d period. Fragmentation was initially the most observable mode, yet it was not the primary colonization mode. Although, all colonization modes (fragmentation, zoospores, and residual holdfast structures) were present the most affective means of establishment were related to viable holdfast structures, zoospores, and lastly fragmentation. Shaver *et al.* (1995) identified slow recolonization rates for *Cladophora* and considered colonization to be entirely due to fragmentation or viability of residual holdfast structures. Their results for translocation experiments showed that only 25% of the standing mass had accrued after 11-mo of recovery. In other aquatic systems, total recovery has been observed to occur within a two-mo period (Blum 1982). This slow recovery response in the Colorado River has been attributed to the affects of cold stenothermic (9° C ± 2°) conditions, which are suggested to be the major inhibitor of sporogenesis (Shannon *et al.* 1994, Shaver *et al.* 1995; Blinn *et al.* 1998).

Nevertheless, this study has indicated that the colonization mode using zoospore propagules are perhaps more common than once thought. The overall periphyton composition of the different treatment cobbles was dominated by green filamentous algae, composed primarily of *Ulothrix* and *Cladophora*. Yet, the differences in the propagation modes used, their viability and ultimate establishment may favor certain species over others. Alternately, the colonization

for other mucilaginous macroalgae such as *Mougeotia* and *Spirogyra* occurred only on treatment T3 once a substantial amount under-storage had developed. It appeared that their predominant mode of colonization was probably fragmentary since these two taxa do not propagate by zoospores, and formed by adhering loosely to the filamentous under-storage of the previously established phytobenthic mat.

Although both *Ulothrix* and *Cladophora* utilized zoospores in colonizing treatment cobbles (T1 &T2), it appeared that the greatest colonization success favored *Ulothrix*. However, algal growth rate for cobbles colonized by zoospores appeared to have been much slower in response than the alternate colonization mode that relied on the use of viable basal holdfast structures. Perhaps this phytobenthic response reflected developmental and compositional differences that existed between mature and intermediate growth and its susceptibility to herbivory. Also, we presume that either grazing susceptibility or grazer preference may be a responsible for the different colonization responses and that the observed algal growth from *Cladophora* utilizing basal holdfast structures provided resistance to grazing. This latter treatment (T3), under steady flow conditions responded in pattern similar to that of other recolonization experiments using cobbles desiccated for 3-mo (Benenati *et al.* 1998). Benenati *et al.* (1998) reported that periphyton consisting primarily of *Cladophora* and epiphytes had only partially recovered to 35% of the control. As mentioned, our results were similar, indicating that by experimental closure (15-week period), *Cladophora* and associated periphyton for the three treatments had attained less than 0.4, 0.9 and 39.4% of the biomass associated with the Control. However, this slow response is contrary to other desert streams where algal biomass quickly accrues after seasonal re-wetting of previously dry channel (Peterson and Boulton 1999).

Apparently, this colonization mode favored *Cladophora*; even so its establishment as the initial colonist may not reflect differences in algal propagation mode or reliance, but rather the original benthic composition of the cobble prior to the physical removal of periphyton. Although compositionally, bryophytes were one of the principal components of the phytobenthic Control's community, they demonstrated no effective colonization on any of the three treatments during the experimental period. This response supported the premise that bryophytes are much slower to colonize than are periphyton. However, once established bryophytes may have equivalent primary production rates to the other macroalgal constituents. Additionally,

Snail herbivory

Previous colonization experiments in the Colorado River performed by Angradi *et al.* (1993), showed that in absence of snail grazing pressure, *Ulothrix* responded rapidly in accreting biomass (Log_{10} biomass = 0.09 (d), $r^2 = 0.96$). Clearly we cannot say with certainty that the sequential pattern observed for biomass accretion in phytobenthos and macroinvertebrates was in response to herbivory. However, these response differences among treatments would suggest that susceptibility to snail grazing was dependent on the different modes at earlier stages of algal colonization. In considering benthic colonization response by all treatments, it appears there was insufficient time for the benthos to reach density or biomass levels that were equivalent to that of the Control. Of all the treatments, T3 colonized the fastest owing to the viability of holdfast structures. Yet, in comparison the autotrophic and invertebrate AFDM for T3 had attained only 40% and 60% of the Control's biomass.

Herbivory has been shown to be a major mechanism maintaining aquatic systems in early successional stages (Dudley and D'Antonio 1991). High algal turnover rates can support high herbivore biomass (Lamberti and Resh 1983; Lamberti *et al.* 1989) resulting in an inverted trophic pyramid (Gregory 1983). Lamberti *et al.* (1989) showed that rate of primary production, biomass accretion and export were greatest under high irradiant levels, and demonstrated that algae production exposed at high irradiant levels for both grazed and ungrazed algae had a broad range of abundance. This indicated that grazing at high light intensities did not influenced GPP rates and standing biomass. However, under lower light intensities, there was no significant relationship between GPP and biomass because the influence of grazing modified algal biomass. For low production the primary process reducing standing biomass was due to grazer consumption; whereas at higher production loss was primarily through sloughing and dislodgment, with only 5% of algal biomass consumed at high irradiant levels.

We suspect that if intermediate, successional propagules such as *Cladophora*, as well as other macroalgae were consumed directly by snails, the physiognomic structure should have remained similar to the initial epilithic state (fast growing, adnate diatoms) (Cuker 1983; Hill and Knight 1987). This appeared to have been the case for treatments T1 and T2, where cobbles consisted of bare desiccated substrate (T1 and T2). Although, within a 10-d period we had

an insufficient detected 50-60% zoospore presence on cobble treatments, there appears to have bee

ıely high snail time for algal establishment to have escaped snail grazing pressure owing to extrem

)ose that snail densities (10-fold increase) on bare substrata following flow stabilization. We prop

l development foraging behavior may have been more effective on bare substrata, yet the structura

that of the under-story may have provided structural integrity and functional complexity

increased the foraging area, and attenuated flow velocities allowing for greater densities to accrue and persist.

Under intense grazing pressure, the successional establishment of *Ulothrix* and *Cladophora* appeared to have proceeded only once substrate conditions were suitable for propagule settlement (Dudley and D'Antonio 1991). Ultimately, filamentous algae appeared to have outdistanced the presence of snail grazing by increased biomass production after 60-d. This lag-time in biomass accretion has been observed in other experimental and natural systems, and has been attributed to an algal enhancement response to the effects of grazing (Peterson and Boulton 1999). For treatment T3, the rapid increase in biomass with time, may have been related to the difference in colonization mode. Findings from other studies have indicated that snails don't preferentially graze on mature *Cladophora* owing to their large, thick cell walls, and filamentous structure (Calow and Calow 1975; Skoog 1978), yet early in their development snails are known to crop young filamentous growth (Hill and Knight 1987; Lamberti *et al.* 1989; Sarnelle *et al.* 1993; Peterson and Boulton 1999). This response appeared to be the case for treatments T1 and T2.

Interspecific competition has been shown to influence the distribution and abundance of benthic macroinvertebrates (McAuliffe 1984). In particular snails have been shown to have a negative affect on densities of periphytic grazing larvae (Cuker 1983; Hawkins and Furnish 1987). One would expect that when populations expand to high densities they would have a major structuring affect. Competition for resources by exploitation or agonistic behavior should exist only when predators are absent (Bronmark *et al.* 1991). Ecologically, we are unsure why, such high snail densities were observed in the Colorado River; however, we recognize that this would be expected if snails were predominantly invulnerable to predation (i.e., speculated for

Colorado River system lacks moluscivores). Also, it would be expected once populations reached some critical density, where taxa would exploit certain resources (Osenberg 1989). However, this resource exploitation was never observed, except for a temporary suppression of early macroalgal development during the initial colonization of treatment T1 and T2.

Exploitive competition was not observed for *Cladophora*; however, a negative correlation was observed between gastropods and miscellaneous algae (i.e., primarily gelatinous stalks of the diatom *Gomphonema sp.*). Although we presume that epiphytes attached to *Cladophora* were influenced by grazing, there was little if any trend of snails limiting the structural component of the host-plant. In the Colorado River, epiphytes function as the primary source of autotrophic energy available for higher trophic levels (Blinn and Cole 1991; Blinn *et al.* 1995). Typically, phytobenthic biomass represents only a small proportion of the total stream production (Gregory 1983). Their trophic importance to this system cannot be overstated (Czarnecki *et al.* 1976; Czarnecki and Blinn 1978; Hardwick *et al.* 1992; Benenati *et al.* 1998). Epiphytic-host relationships have been identified as beneficial to macroalgal host plants by different mechanisms, such as nutrient exchange, protection from high solar incidence of visible and UV light, and desiccation (Harlin 1973; Usher and Blinn 1990: Blinn *et al.* 1995). Even so there is considerable evidence to the contrary. Accumulation of epiphytic biomass has been shown to increase hydrological drag (Stevenson and Stoermer 1982; D'Antonio 1985; Mulholland *et al.* 1994), competition for light and nutrients (Whitton 1970; Phillips *et al.* 1978; Dudley 1992). Stevenson and Stoermer (1982) and others (Dudley 1992; Cuker 1983; Mulholland *et al.* 1983; Stewart 1987) have indicated that under nutrient limitations *Cladophora* was unable to outgrow

its epiphytic load. This resulted in encrustation of epiphytes and increased susceptibility to sloughing.

For this reason, *Cladophora* may require grazing to suppress excessive epiphytic loads (Dudley 1992). The build up of a large overstory of epiphytes can be reduced by grazing (Nicorti 1977) favoring adnate epiphytic and epilithic species (Cuker 1983; Lamberti and Resh 1983; Hill and Knight 1987). Our experimental observation supports this response, where high *Cladophora* biomass was maintained and responded positively to snail biomass and densities and negatively to colonial aggregates comprised predominantly of *Gomphonema* (miscellaneous algae). High algal production rates have been shown to escape the negative effects of herbivory (Whitton 1970). Differences between treatments potentially explained how biomass accretion may have escaped regulation by grazers; however this response would have been expected to be constrained at some point when grazing numbers had increase (Lamberti *et al.* 1989), since epiphyte availability has been shown to limit snail production (Osenberg 1989). In comparison, cross-sampling biomass production estimates for the Control were considerably less at 368 gC m^{-2}, than those derived from biomass-specific NPP, based on O_2 generation, estimated at 637.0 gC m^{-2} (Table 2). The latter NPP estimate for algal production, should have been sufficient to have maintained snails at AFDM levels of 104 g m^2 (± 11.2). Secondly, our derived estimates of 13.22 mg O_2 m^{-2} h^{-1}, based on biomass-specific NP rates for *Cladophora* and epiphytic diatoms (high irradiance and low biomass) were equivalent to other documented biomass-specific production levels (13.5 mg O_2 m^{-2} h^{-1}), under grazed conditions (Lamberti and Resh 1983; Hart *et al.* 1991).

The maintenance of epiphytes at lower levels may reduce the frequency of mature algal mats from sloughing (Mullholand *et al.* 1983). In comparison to the Control, we observed no periodicity in algal standing biomass for the three other treatments. The density of T3 snails had stabilized mid-way into the experiment, yet were 43% less than Control density (Fig 7B). The distributional differences in both density and biomass would imply that greater productivity was occurring in these mature cobbles, even though our areal-production estimates for NPP were slightly greater for T3. Grim and Fisher (1986) suggested that lag-time in biomass accretion was due to nutrient fluxes in primary production rates. Although, it has been suggested that once sufficient biomass and detritus had accrued, it would facilitate nutrient cycling and buffer fluxes in nutrient supply for streams having low nutrient concentration (Mulholland *et al.* 1991). Previous work by Benenati *et al.* (2000) had identified that the hypolimnetic flows of Colorado River were at or below detectable levels. Disturbance (flooding, flow variation and desiccation) may arrest successional shifts in phytobenthic composition (Whitton 1970; Power and Stewart 1987; Dudley and D'Antonio 1991; Blinn *et al.* 1998). However, nutrient supply was considered less important in systems with frequent disturbance because limitations in availability would not function as the primary factor precluding biomass accretion from reaching its steady state condition (Mulholland *et al.* 1991). As a result of stabilized flows conditions, the higher detrital and snail levels exhibited on the Control may have provided greater nutrient availability and cycling.

Sloughing

Export of algae via drift was high in grazed streams, under high irradiant levels where snails sloughed and dislodged periphyton (Lamberti *et al.* 1989). This was considered a major mechanism responsible for algal export. Although, the sloughing process has been attributed to seasonal loss in standing biomass and shifts in community physiognomy (Stevenson and Stoermer 1982; Osenberg 1989); as well as facilitating enhanced growth due to increased light, nutrient cycling and removal of epiphytes. Mulholland *et al.* (1991) identified that biomass accretion varied episodically due to large-scale sloughing of periphyton. Yet, it does not seem likely that snail grazing was the major factor responsible for the oscillating periodicity in loss and growth of biomass. Variation in discharge can result in turbulent flow that exert shear forces directed onto algal mats sufficient enough to cause substantial biomass loss (Lamberti *et al.* 1987; Osenberg 1989; Blinn *et al.* 1995). However, episodic or incremental drift due to variation in hydraulic force could not have been responsible for the periodic oscillations observed for *Cladophora* (Mulholland *et al.* 1994; Shannon *et al.* 1996). Since during most of the experimental period discharge remained constant (227 $m^3 s^{-1}$). Rather, it is possible that incremental accretion and encrustation of epiphytes could have structurally altered the turbulent flow characteristics (i.e., surface roughness and load), or increased cumulative damage to supporting filaments by shear forces (Dudley and D'Antonio 1991; Power and Stewart 1987). Mature algal mats of *Cladophora* developed thicker cellular walls (Bronmark *et al.* 1991; Wilson *et al.* 1999) and were more resistant to herbivory (Moore 1975). Yet, were also more prone to sloughing of senescent growth (Dudley and D'Antonio 1991), especially highly epiphytized clumps of *Cladophora* (Dudley 1992).

CONCLUSION

Results from these experiments have provided us with a better understanding how the phytobenthic and macroinvertebrate community might respond to flow conditions during periods of inundation and re-inundation. These differential rates in colonization will improve our capabilities to predict benthic response. The colonization experiments have demonstrated that viable holdfast structures are the most probable mode of recolonization in the varial zone, following effects from atmospheric exposure or physical abrasion due to variation in flow or sediment discharge. Although, it does not preclude colonization to occur by other modes such as zoospore production, neither colonization mode will lead to a rapid recovery response after a hydrological disturbance. However, it is unclear, though probable that the recovery response for both the phytobenthic and macroinvertebrate community was attenuated to some degree by the presence of herbivorous snails. Differences among treatments would suggest that algal susceptibility to snail grazing was dependent on the different colonization modes at earlier stages of development. In considering benthic colonization response by all treatments, it appears there was insufficient time for the benthos to reach density or biomass levels that were equivalent to that of the Control. At present, we can only postulate whether the observed response demonstrated an interaction between herbivore, structural substrate and a potential food resource. For this reason, additional studies need to be conducted to determine whether or not this taxon will continue to demonstrate an ecological release to flow stabilization.

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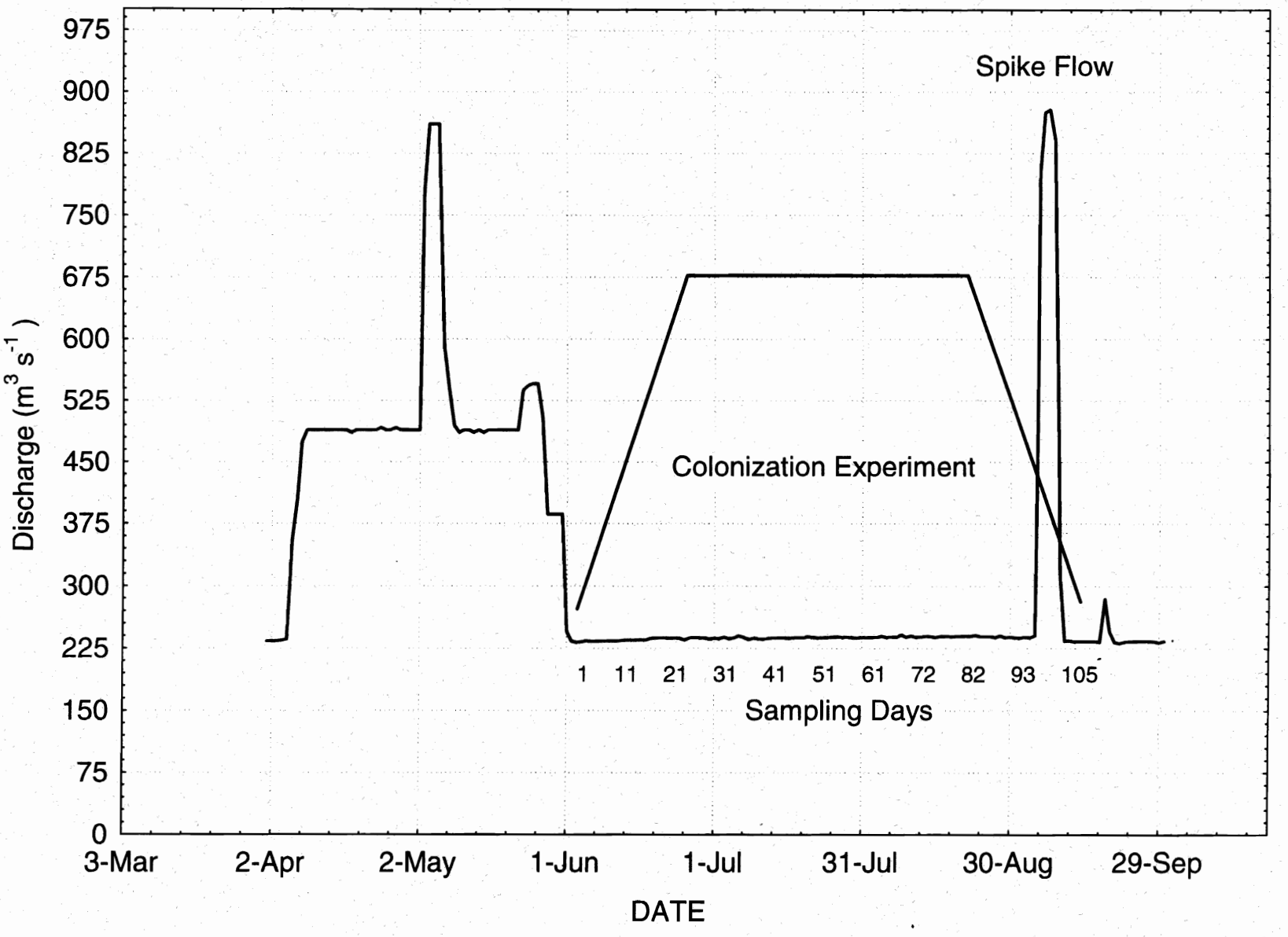

Spike Flow
Colonization Experiment
Discharge (m3 s-1)
975
900
825
750
675
600
525
450
375
300
225
150
75
0
1 11 21 31 41 51 61 72 82 93 105
Sampling Days
3-Mar
2-Apr
2-May
1-Jun
1-Jul
31-Jul
30-Aug
29-Sep
DATE

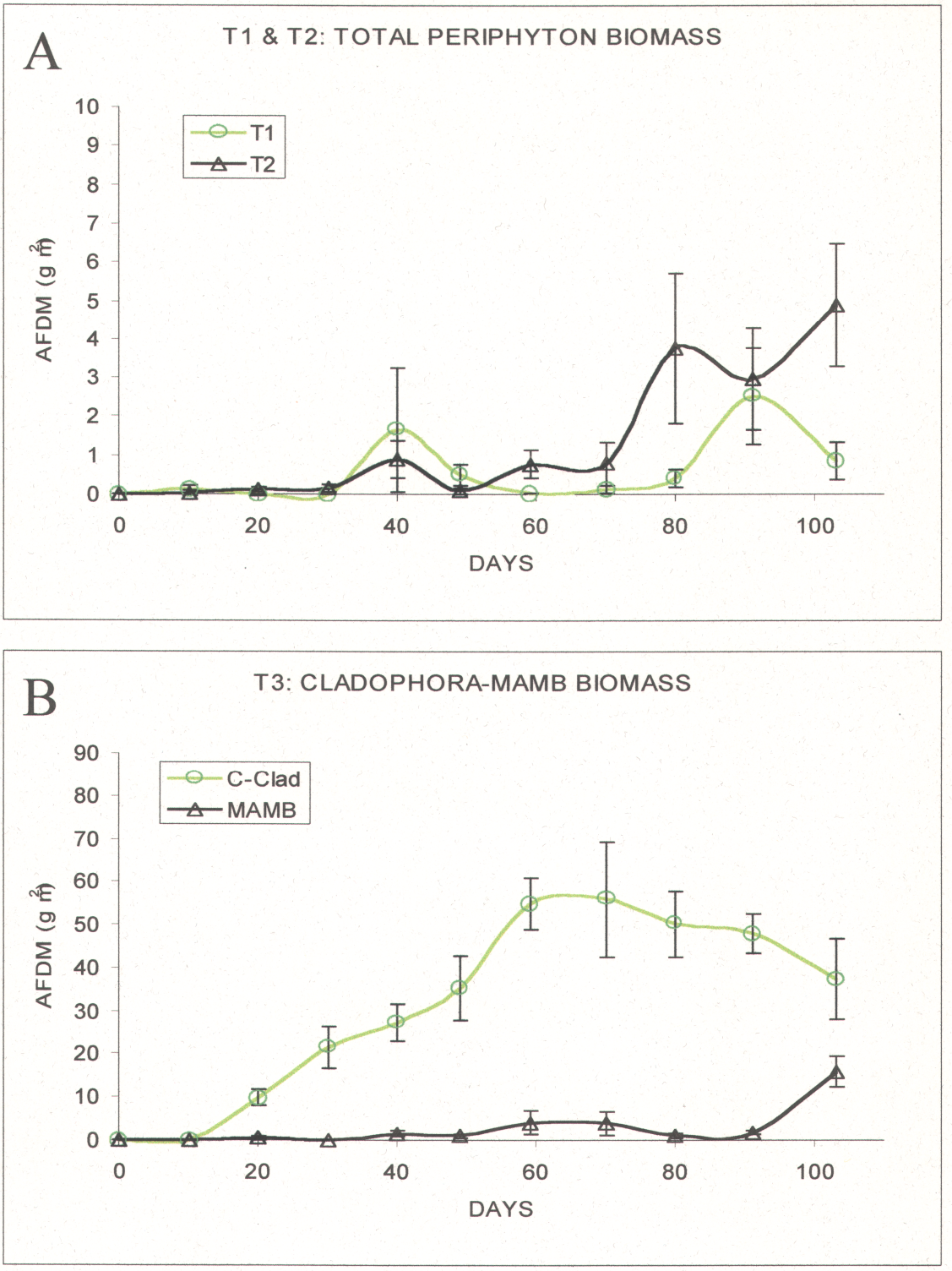


Fig. 2. Plot of the average periphyton biomass accreted for treatments (T1, T2 and T3), across 11 sampling periods, representative of (A) T1 and T2, total mean periphyton biomass, (B) T3, mean biomass for Cladophora and MAMB. Values are expressed in AFDM (g m^2 ± 1 SE, n = 20)

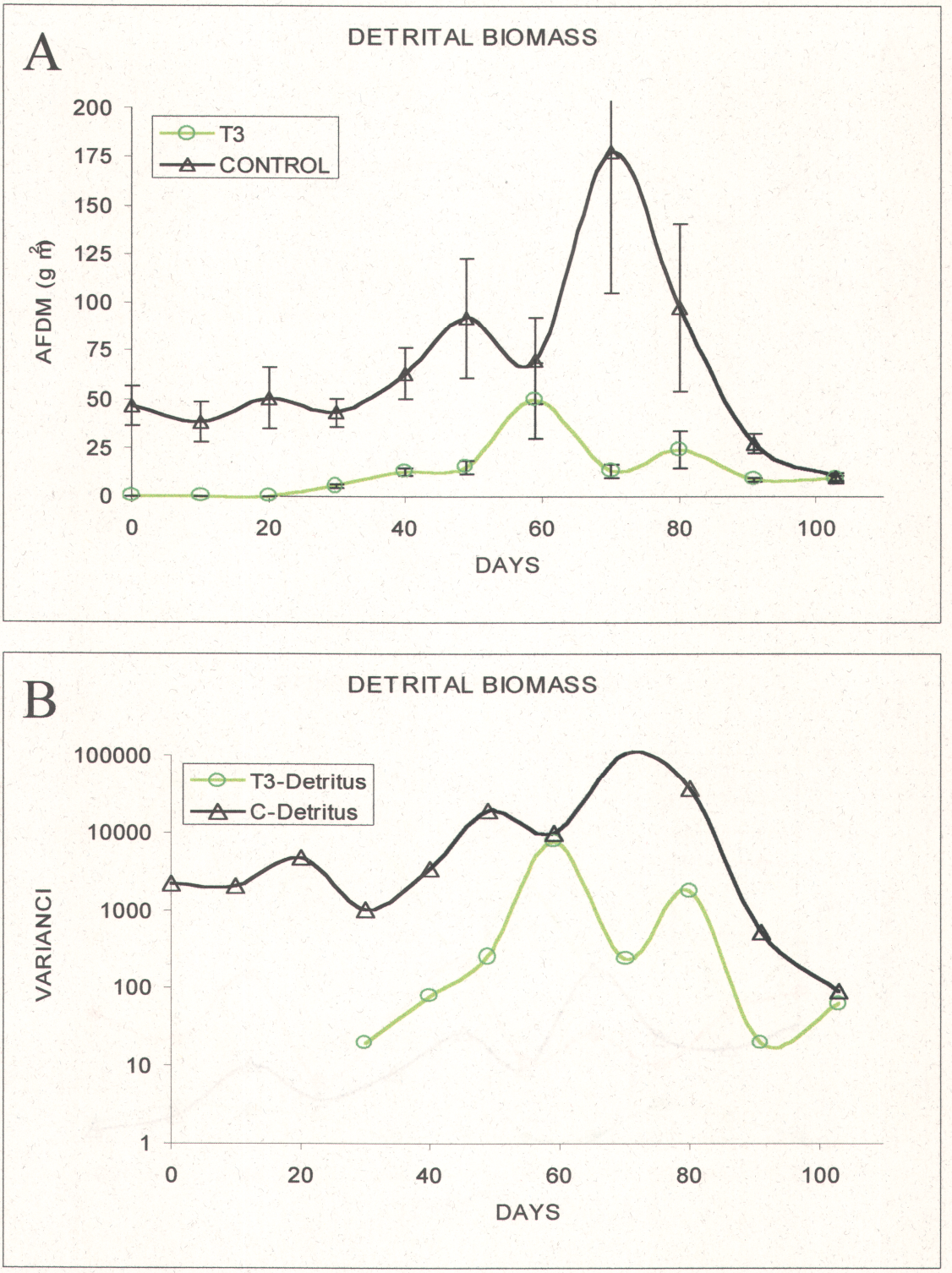


Fig. 3. Plot of the average detrital accumulation for the Control and T3, across 11 sampling periods, representative of (A) mean detritus, (B) variance around the mean detrital biomass for a given sampling period. Values are expressed in AFDM (g m^2 ± 1 SE, n = 20)

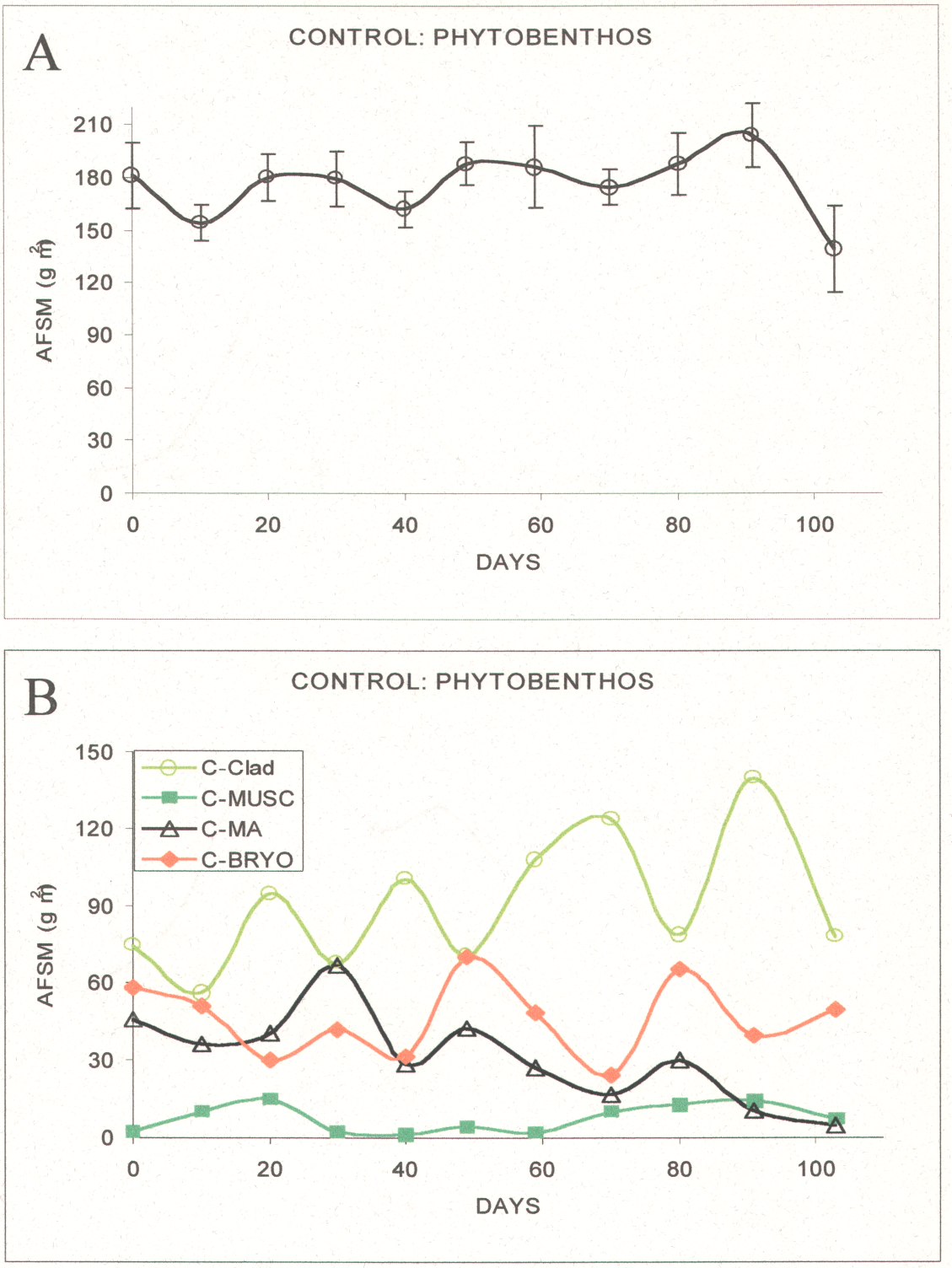


Fig. 4. The distribution of the phytobenthic biomass (AFDM, g m^2) for the Control, across 11 sampling periods, (A) total mean phytobenthic biomass, (± 1 SE, n = 20), (B) compositional separation representing; *Cladophora* (Clad), muscillagenous algae (MUSC), miscelllaneous algae (MA) and bryophytes (BRYO).

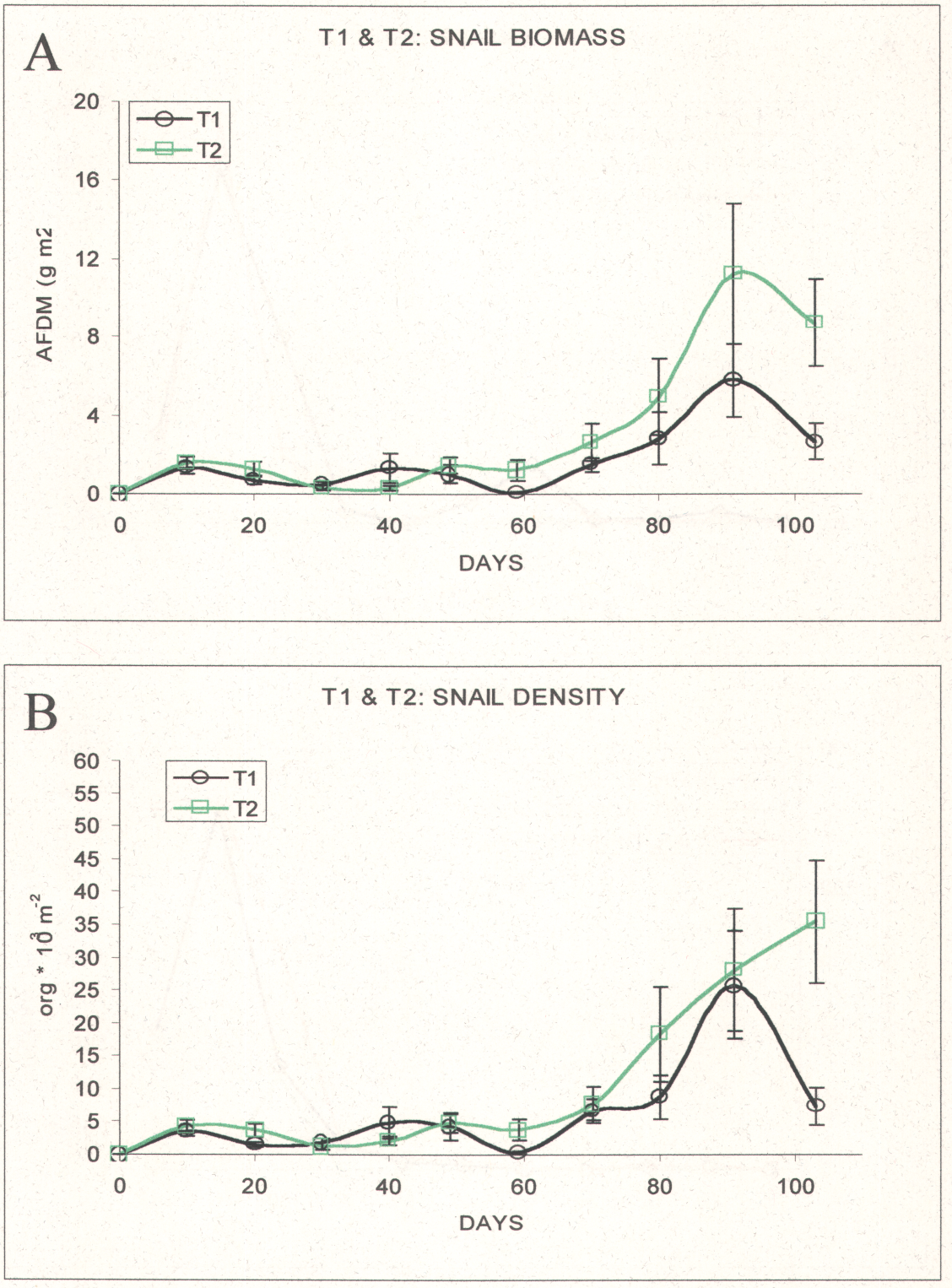


Fig. 5. Plot of snail biomass, and density distributed across 11 sampling periods among treatments T1 and T2, (A) mean biomass AFDM (g m^2), (B) mean density (org * 10^3 m^{-2}). Standard error (± 1 SE, n = 20).

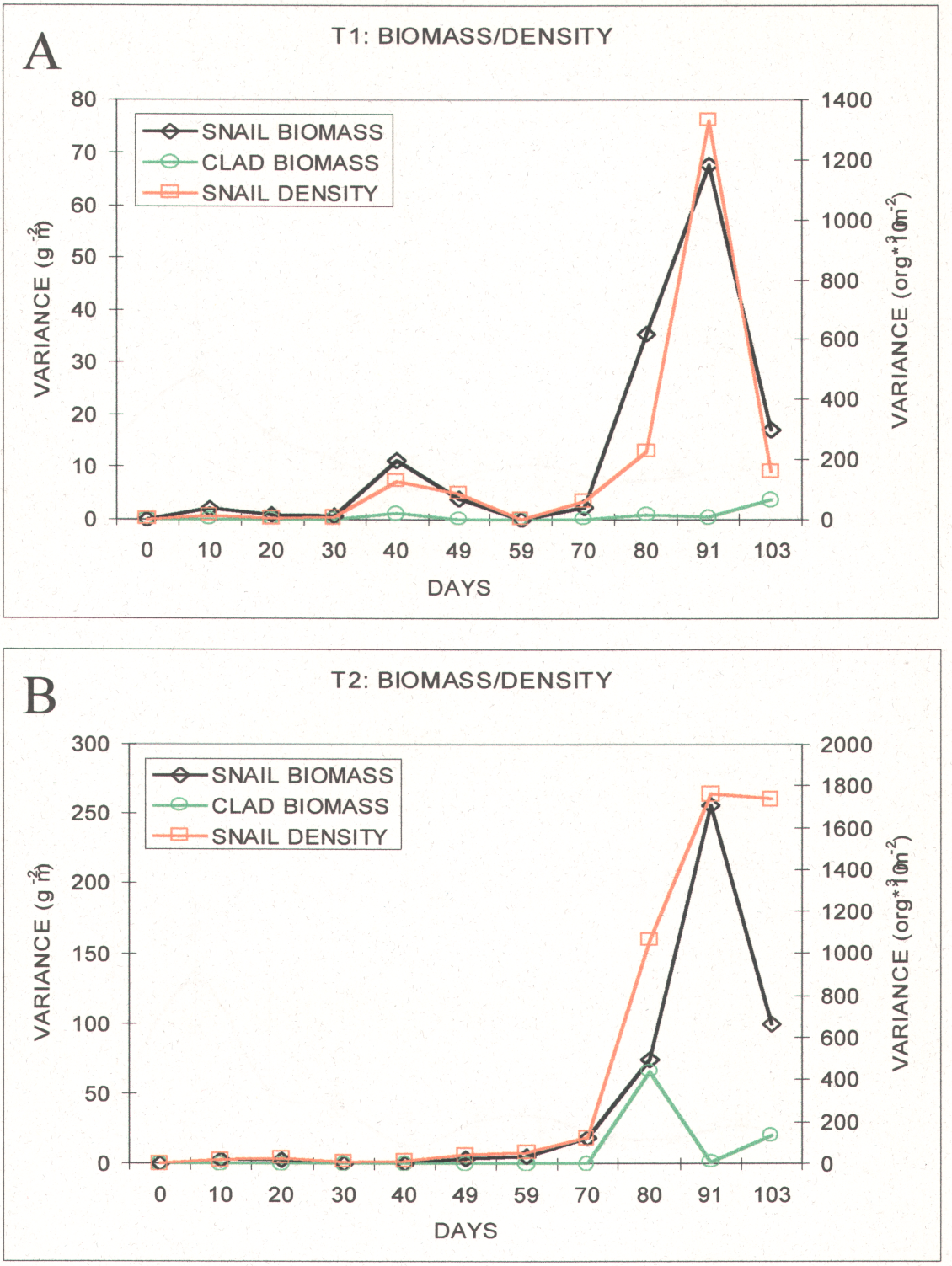
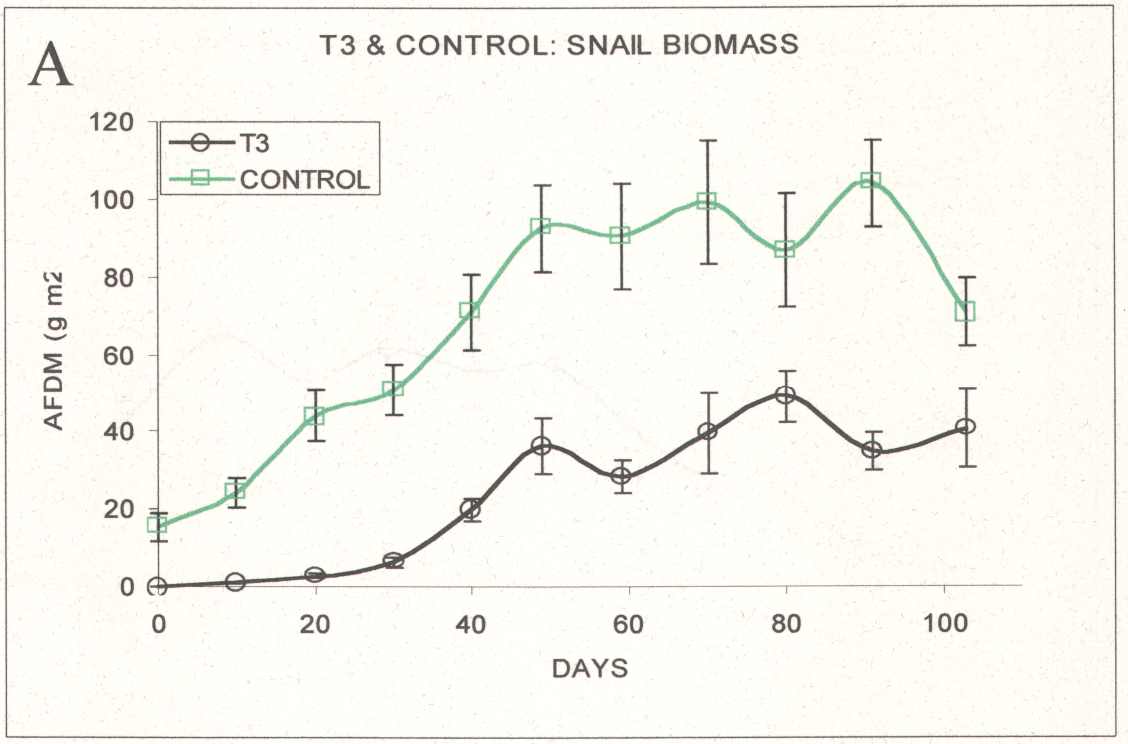


Fig. 6. Intra-sampling variance plotted for Cladophora biomass and snail biomass and density across 11 sampling periods reflecting differences among treatment T3 and the Control, (A) T3 variance , (B) Control variance. Standard error (± 1 SE, n = 20) for AFDM (g m^2) and density (org * 10^3 m^{-2}).



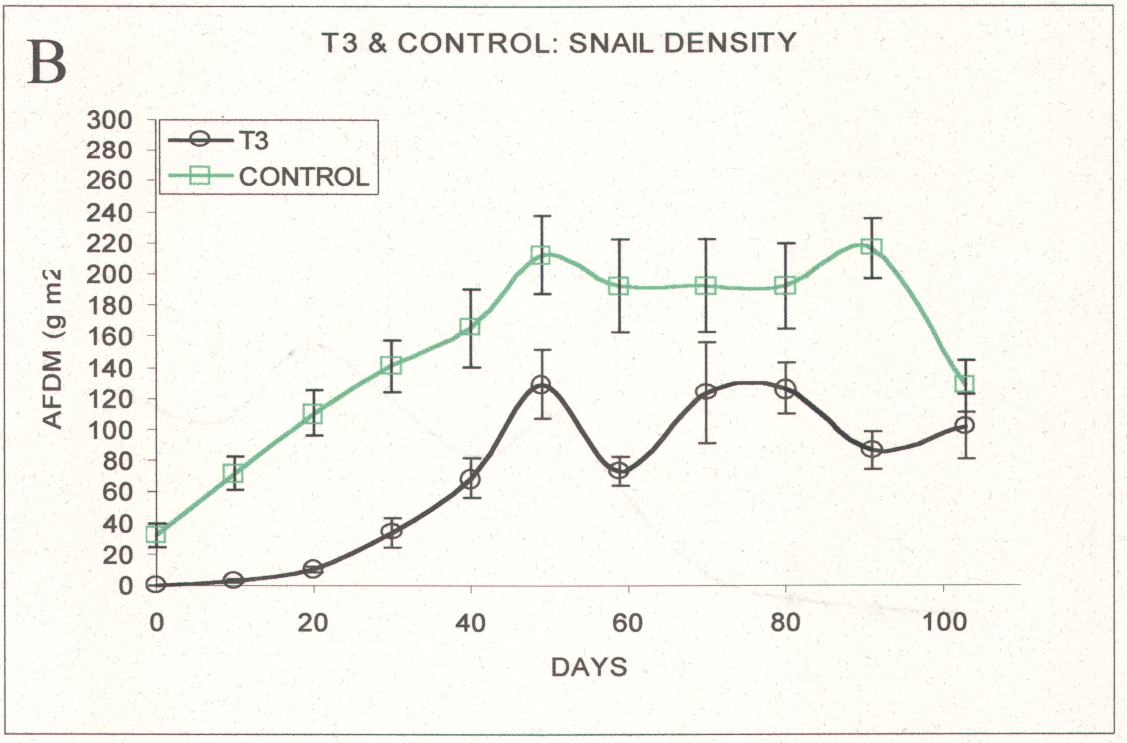


Fig. 7. Plot of snail biomass and density distributed across 11 sampling periods among treatments T3 and the Control, (A) mean biomass AFDM (g m^2), (B) mean density (org * 10^3 m^{-2}). Standard error (± 1 SE, n = 20).

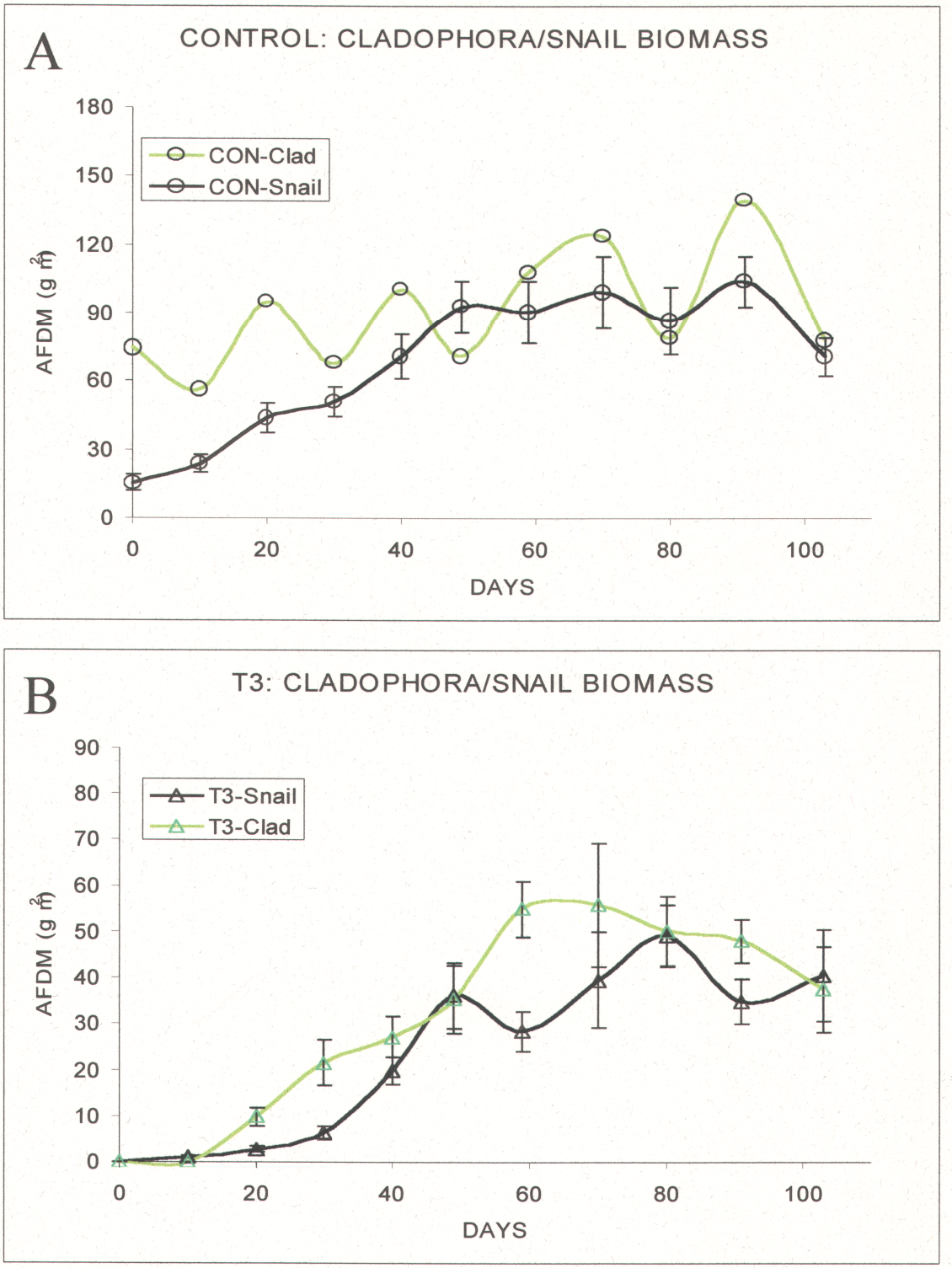
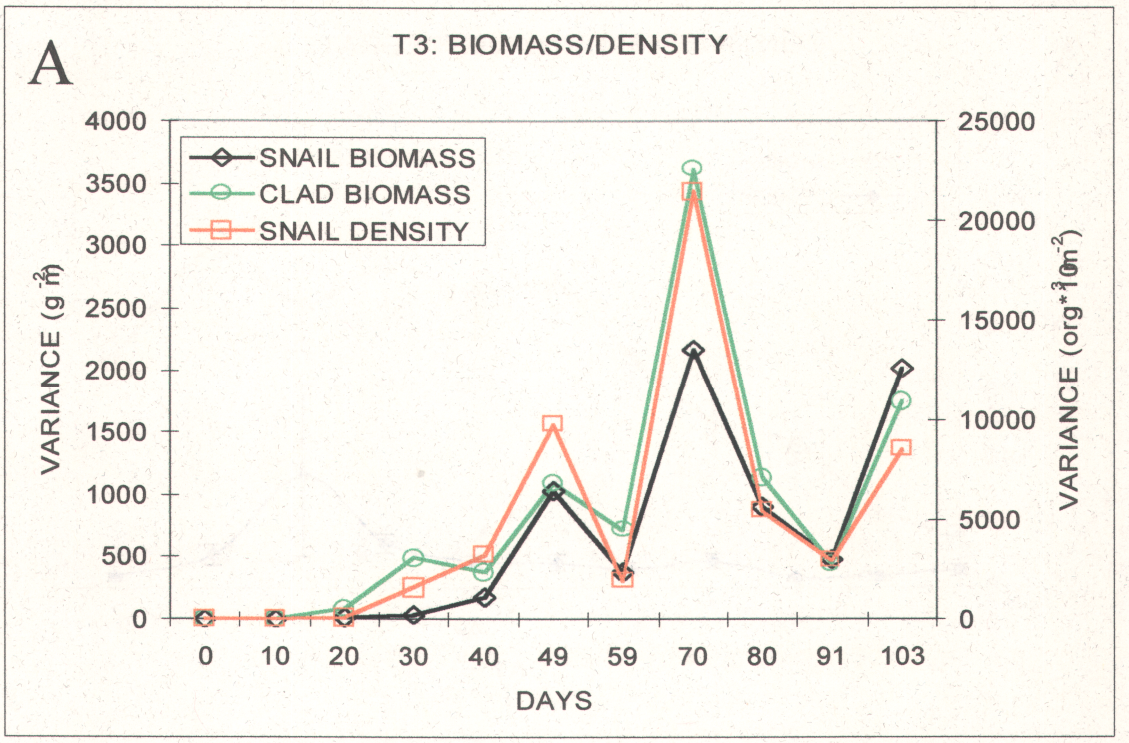


Fig. 8. Plot of *Cladophora* and snail biomass distributed across 11 sampling periods among T3 and the Control, (A) Control mean biomass , (B) T3 mean biomass. Values are expressed in AFDM (g m^2 ± 1; SE, n = 20)



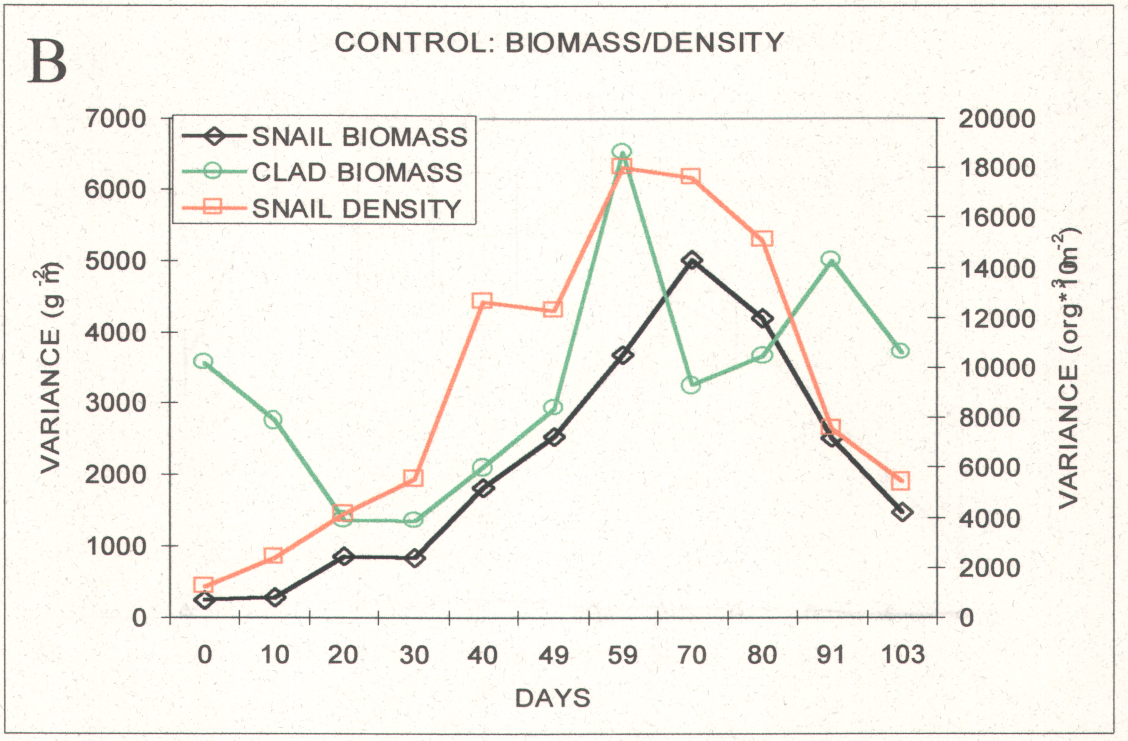
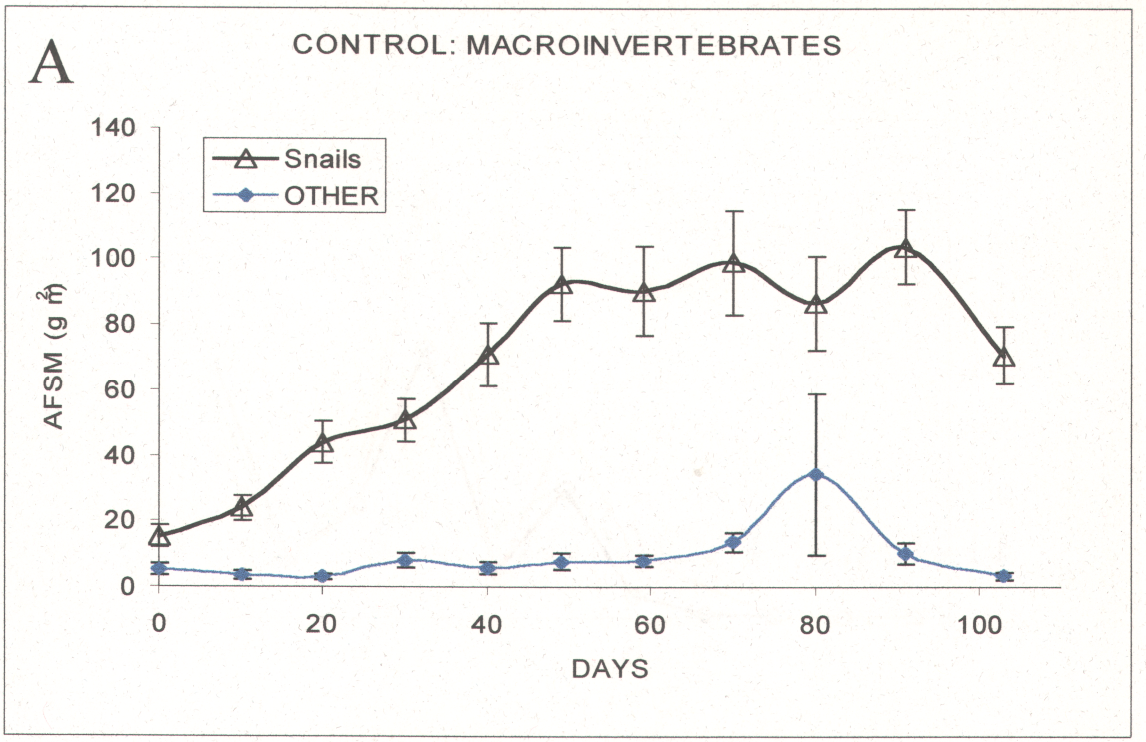


Fig. 9. Intra-sampling variance plotted for Cladophora biomass and snail biomass and density across 11 sampling periods reflecting differences among treatment T3 and the Control, (A) T3 variance , (B) Control variance. Standard error (± 1 SE, n = 20) for AFDM (g m^2) and density (org * 10^3 m^{-2}).



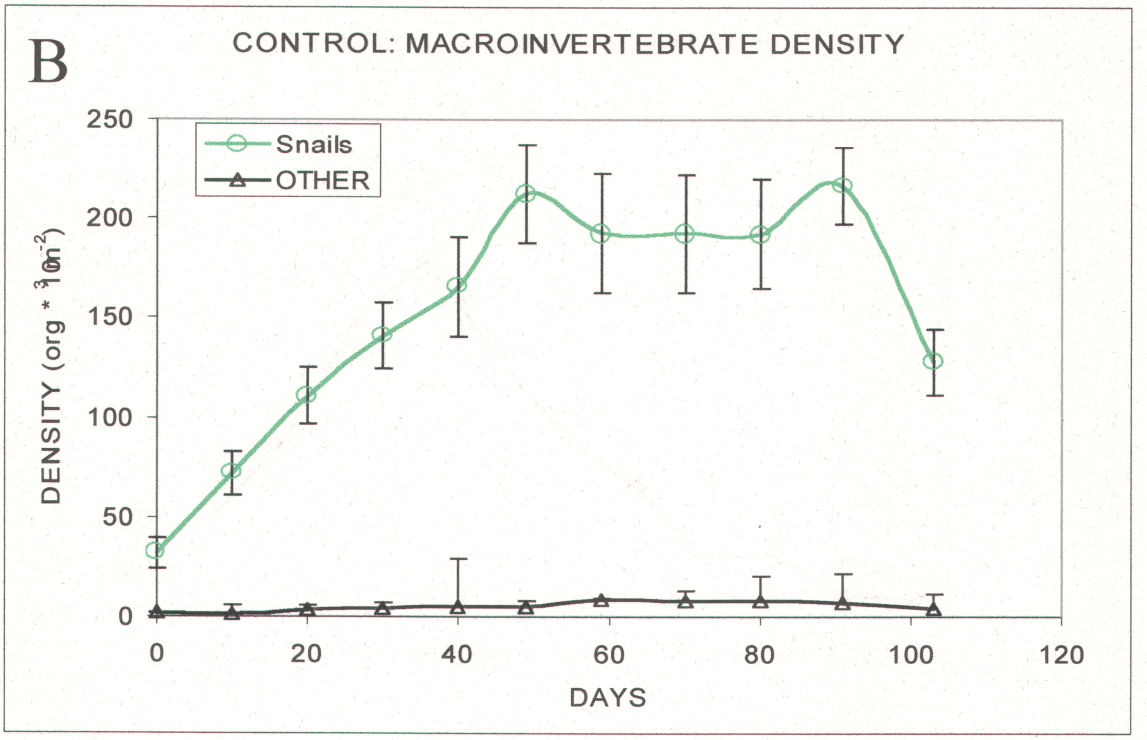


Fig. 10. Plot of the sampling distribution for the Control, across 11 sampling periods between average *Cladophora* and snail biomass (AFDM (g m^2), (A) mean biomass, (± 1 SE, n = 20), (B) variance around the mean biomass for a given sampling period.

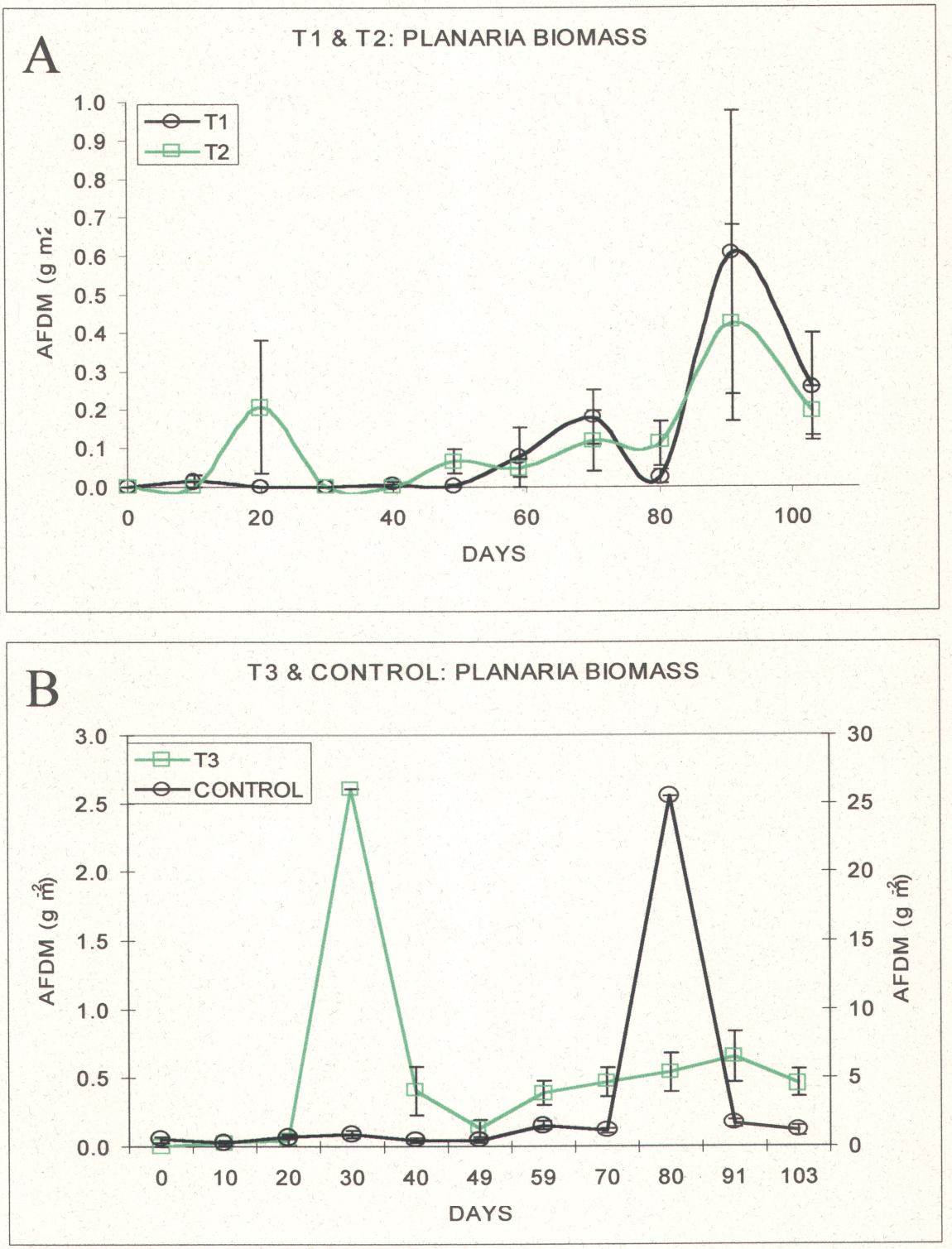


Fig. 11. Plot of planaria biomass distributed across 11 sampling periods among the different treatments (T1, T2, and T3) and Control, (A) T1and T2 mean sample biomass , (B) T3 and Control mean sample biomass. Values are expressed in AFDM (g m^2 ± 1; SE, n = 20)

Table 1. Categorical listing of most common taxon collected in the field and sorted to 15 categories using a modified method developed by [1]Blinn *et al* (1998). Conversions for ash-free dried mass (AFDM) values (g m^{-2}) used were developed by [2]Shannon *et al.* (2000).

TAXON	[1]CATEGORIES	COMMON NAME / CHARACTERISTICS	[2]AFDM CONVER.
INVERTEBRATES			
Annelida			
Lumbriculidae	1	Lumbriculids	0.73525
Oligochaeta			
Tubificidae	2	Tubificids	0.76251
Amphipoda			
Gammaridae			
Gammarus lacustris	3	Gammarus	0.69989
Diptera			
Simulidae	4	Black-flies	0.59603
Chironomidae	5	Chironomids	0.82593
Gastropoda			
Physella sp.	9	Snails	0.23328
MISCELLANEOUS INVERTEBRATES			
Ostracoda	6	Ostracods	0.60774
Trichoptera	6	Caddisfly	0.60774
Enchytraeidae	6	Flatworm (Turbellaria)	0.60774
PHYTOBENTHOS			
Chlorophyta			
Cladophoraceae			
Cladophora sp.	7	Filamentous branched algae	0.35606
Ulotrichaceae			
Ulothrix sp.	13	Mucilaginous filamentous branched algae (MAMB)	0.37312
Zygnemataceae			
Mougeotia sp.	13	Mucilaginous filamentous branched algae (MAMB)	0.37312
Spirogyra sp.	13	Mucilaginous filamentous branched algae (MAMB)	0.37312
Cyanophyta			
Oscillatoriaceae			
Oscillatoria	10	Blue-green algal crust	0.14839
MISCELLANEOUS ALGAE			
Chrysophyta			
Gomphonemaceae			
Gomphonema spp.	11	Colonial gelatinous stalks (MAMB)	0.37312
Rhodophyta			
Batrachospermaceae			
Batrachospermum spp.	11	(MAMB)	0.37312
Chantransiaceae			
Rhodochorton sp.	11	(MAMB)	0.37312
Chlorophyta			
Characeae			
Chara contraria	15	(MAMB)	0.37312
Bryophyta			
Fontinalaceae			
Fontinalis spp.	12	Bryophytes (MAMB)	0.37312
Potomogetonaceae			
Potomogeton pectinatus	14	Potomogeton (MAMB)	0.37312
DETRITUS	8	Detritus	0.45363

Table 2. Results of primary production rates are derived from empirical measurements of quantum oxygen yield relative to underwater irradiance, biomass and temperature. Production estimates are modeled from gross production and respiration rates (light and dark) using equivalent environmental conditions present at the site. Parameters took into account apparent optical properties (K_N = 0.28), PPFD: μmol m^{-2} s^{-1}, angle of incidence (θ_i), transect depth (m), 12 °C, and quantum efficiency 1.2. Reported here are the mean rate estimates of production relative to both biomass-specific and area-specific production estimated for the three different treatments and Control.

PRIMARY PRODUCTION RATES

	Net Photosynthesis Rate			**Net Primary Production Rate**		
Description		*NP Rate*			*NPP Rate*	*Total*
T1 & T2 AFDM: 0.145 gC m^{-2}	*Avg*	*Max*	*Daily*	*Avg*	*Daily*	*Carbon*
Biomass specific production						
mg O_2 gC^{-1} m^{-2} h^{-1}	13.22	16.82	-	7.93	-	
mg C gC^{-1} m^{-2} h^{-1}	11.02	14.01	-	6.61	-	
Area specific production						
mg O_2 m^{-2} h^{-1}	2.20	2.36	-	1.28	-	
mg C m^{-2} h^{-1}	1.83	1.96	-	-	-	-
mg C m^{-2} d^{-1}	-	-	27.83	-	25.72	
Total g C m^{-2}	-	-	-	-	-	2.7

	Net Photosynthesis Rate			**Net Primary Production Rate**		
Description		*NP Rate*			*NPP Rate*	*Total*
T3 AFDM: 55.8 gC m^{-2}	*Avg*	*Max*	*Daily*	*Avg*	*Daily*	*Carbon*
Biomass specific production						
mg O_2 gC^{-1} m^{-2} h^{-1}	9.98	13.59	-	5.84	-	
mg C gC^{-1} m^{-2} h^{-1}	8.32	11.33	-	4.87	-	
Area specific production						
mg O_2 m^{-2} h^{-1}	601.8	690.9	-	339.6	-	-
mg C m^{-2} h^{-1}	501.5	576	-	-	-	-
mg C m^{-2} d^{-1}	-	-	7,657	-	6,814	-
Total g C m^{-2}	-	-	-	-	-	715.5

	Net Photosynthesis Rate			**Net Primary Production Rate**		
Description		*NP Rate*			*NPP Rate*	*Total*
Control AFDM: 175 gC m^{-2}	*Avg*	*Max*	*Daily*	*Avg*	*Daily*	*Carbon*
Biomass specific production						
mg O_2 gC^{-1} m^{-2} h^{-1}	4.09	7.70	-	2.03	-	
mg C gC^{-1} m^{-2} h^{-1}	3.41	6.42	-	1.69	-	
Area specific production						
mg O_2 m^{-2} h^{-1}	679.4	1,099	-	300.03	-	-
mg C m^{-2} h^{-1}	566.2	916.9	-	-	-	-
mg C m^{-2} d^{-1}	-	-	8,867	-	6,066	-
Total g C m^{-2}	-	-	-	-	-	637.0