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# Decay of Macroalgae and Leaves and Their Relation to Detrital Food Webs

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# DECAY OF MACROALGAE AND LEAVES AND THEIR RELATION TO DETRITAL FOOD WEBS

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DECAY OF MACROALGAE AND LEAVES AND THEIR RELATION TO DETRITAL FOOD WEBS

Megan E. Grandinetti May 2016 64 Pages

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This project addressed if decaying macroalgae and leaf detritus play a major role in the detrital pool of a 7$^{th}$-order karst riverine system. Decay rates, macroinvertebrates colonization patterns, and change in $\delta^{13}C$ values of *Cladophora, Platanus occidentalis,* and a mix of *Acer negundo* and *A. saccharinum* were tracked during summer and autumn months for portions of multiple years.

Packs of air-dried *Cladophora, Acer*, and *P. occidentalis* were placed in mesh bags and put in groups (n=4) in wire baskets. Seven baskets were submerged in riffle (0.5 m) and deeper run (2 m) habitats. Benthic organic matter was collected with each pack to see if there was a correlation with $\delta^{13}C$ signatures of decaying macroproducers to help understand what is entering the detrital food web.

Summer 2014 *Cladophora* and *Acer* were significantly faster to breakdown than *Platanus* in both habitats. In autumn–spring 2014–2015, *Cladophora* was significantly faster to breakdown than leaves. Isotopic values of *Cladophora* were not significantly different than leaves in summer 2014 but were significantly more $\delta^{13}C$-depleted in the autumn–spring 2014–2015. There were no significant differences in macroinvertebrate abundance between the macroproducers for either season. *Cladophora* had significantly lower macroinvertebrate richness in both seasons, lower shredder abundance, but a significantly higher abundance of clingers. The mean $\delta^{13}C$ values of

benthic detritus were significantly different than all three macroproducers in the summer and significantly different than *Cladophora* in the run treatment for autumn–spring.

Seasonality had a strong influence on breakdown rates, leading to greater mass loss of all three species in the warm summer months compared to the cooler autumn–spring months. The low macroinvertebrate richness and shredder abundance on the decaying macroalga suggests *Cladophora* may not be consumed by macroinvertebrates but used strictly as habitat. The implication of rapid *Cladophora* decay during warm seasons, plus few colonizing macroinvertebrate taxa, is that the decaying macroalgae may not pass through a decomposer food web before being remineralized as $CO_2$.

# Introduction

## *Detrital processing*

Organic carbon sources in lotic systems come from either allochthonous or autochthonous origins. As stream channel size increases, the importance of allochthonous inputs decreases, placing more reliance on in-stream primary producers to support reach-scale food webs (Vannote et al. 1980, Naiman 1983, Conners and Naiman 1984). The combination of these organic carbon sources can vary greatly in flowing water systems (Webster and Meyer 1997, Fausch et al. 2002, Power and Dietrich 2002, Bunn et al. 2003).

Traditionally it has been thought that allochthonous sources directly enter stream detrital pools, but autochthonous sources are consumed solely as live material (Vannote et al. 1980, Webster and Benfield 1986). It was dismissed as a non-essential resource until proposed as detrital "ooze" by Lindeman (1942), but is now a well-known energy source for consumers (Wiegert and Owen 1971). Most consumers rely directly or indirectly on detrital material as a food resource (Fisher and Likens 1973, Wetzel 1995), because 70–90% of primary production enters the detrital food webs (O'Neill and Reichle 1980). The detritus can be a limited resource (Wallace et al. 1999), due to timing and seasonal patterns. The size of the detrital pool can control food web stability, where there is more detritus continually available there is a more stable food web (DeAngelis 1975). In mid-reach streams, detrital material is constantly being processed (Vannote et al. 1980), allowing a regular flow of carbon through the system.

In lotic systems, the processing of detritus is known to be faster than in terrestrial systems (Enriquez et al. 1993, Cebrián and Duarte 1995), which can be a factor of

discharge and geomorphology (Finlay et al. 2002). In-stream processing is controlled by biotic and abiotic stream characteristics, leaf litter amount, species, and season (Webster and Benfield 1986, Gessner et al. 2007). Shredders are macroinvertebrates which directly feed on coarse detrital material, often referred to as detritivores (Cummins 1973), breaking it down and fragmenting it during consumption into smaller particles such as fine particulate organic matter (FPOM) (Anderson and Sedell 1979, Wallace and Webster 1996). As stream size increases, the importance of shredders decreases (Vannote et al 1980), suggesting that most of the FPOM is from upstream. Breakdown rates of detritus and detritivore activity can be influenced by a number of abiotic factors including flow, temperature (Irons et al. 1994), and pH (Griffith and Perry 1993). Detritus has been found in many studies to support autumn and winter food chains (Minshall 1967, Cummins 1974, Swan and Palmer 2004).

The focus on detrital food webs has primary been on leaf processing studies (Petersen and Cummins 1974, Grafius and Anderson 1980), with little focus on macrophyte decomposition. Aquatic plants may represent a large source of autochthonous detritus because they are not extensively grazed upon while living (Hynes 1966). Abrasion and sediment are large factors which contribute to the sloughing and initial decomposition of some macroalgae (Salovius and Bonsdorff 2004). Once the detached mass of algae reaches bottom it is assumed that microbes from the sediment assist in the decomposition process (Rosenberg and Diaz 1993). Macrophytes make up a large percentage of the biomass in summer streams (Fisher and Carpenter 1976), but the rapid decomposition suggests macrophytes are broken down close to where they grow (Jewell 1971). Aquatic plants tend to have a lot of fibrous material, including lignin and

cellulose, yet macroalgae may completely lack (e.g., *Cladophora;* Mann 1988, Martone et al. 2009).

*Cladophora*

The ubiquitous filamentous macroalga *Cladophora* is found on every continent except Antarctica (Guiry and Guiry 2007). *Cladophora* is abundant during periods of ample sunlight and low flow, growing back from basal cells which survived winter scouring (Power et al. 2009). During times of high productivity and base flow hydrology, the water column can be dominated by *Cladophora* in temperate lotic systems (Whitton 1970, Dodds and Gudder 1992, Power et al. 2009).

The growing season of *Cladophora* starts in early summer and can last until later autumn (Whitton, 1970, Higgins et al. 2008). As water velocity increases with higher flow events, dam releases, or directly from precipitation, *Cladophora*'s cell wall is compromised (Bergey et al. 1995) causing the algae to break off of its holdfast (Power 1990, Power et al. 2009). Physical abrasion and sediment are large factors which contribute to sloughing and processing (Salovius and Bonsdorff 2004). When filamentous alga becomes detached, it can sink below the photic layer where the decomposition begins (Salovius and Bonsdorff, 2004). It is largely unknown what influence *Cladophora* has in the detrital pool of lotic systems.

*Stable isotopes*

One useful way to track food pathways through a detrital system is by using stable isotope analysis. Stable isotopes are non-radioactive elements which are found in nature

at specific proportions. These isotopes break down at specific rates called fractionation (Fry 2007), making them detectable throughout a system. Fractionation can be altered depending upon the environment and trophic level (Fry 2007). Isotopes can be tracked through a food web through consumers depending upon the change in these ratios (DeNiro and Epstein 1981).

Isotopic ratios are expressed in terms per mil and compared to a standard where the values of heavy to light isotopes can be either higher, where the heavier isotopic value is enriched, or lower where the heavier isotopic value is depleted.

Living and detrital organic matter can be differentiated by looking at the $\delta^{13}C$ values (Delong and Thorp 2006), helping to distinguish what is being assimilated by consumers. There is a distinctive difference in $\delta^{13}C$ between allochthonous and autochthonous material (Finlay 2001). This is important in understanding the carbon pathways. It can be problematic to identify at the base of the food web due to the high turnover rate for primary producers (Cabana and Rasmussen 1996). *Cladophora* has a short life span making it difficult to track through generations (Bronk and Glibert 1993, Rolff 2000, Dore et al. 2002). Other processes that can alter aquatic plant $\delta^{13}C$ values include location in the water column, temperature, season, light, turbulence, and water chemistry (France 1995). Dissolved inorganic carbon (DIC) can be available to aquatic plants in the form of atmospheric $CO_2$ (France 1995), biogenic $CO_2$, and weathered bicarbonate (Rounick and James 1984), creating a variable combination of carbon sources among plants in lotic systems. Benthic detritus may be an accumulation of multiple origins, with changing mixtures across seasons (Benner et al. 1987).

*Study Purpose*

The overall goal of this study was to compare macroinvertebrate colonization patterns, processing rates, and isotopic signatures of the filamentous algae *Cladophora* to allochthonous leaf resources in a detrital pathway in the upper Green River, Kentucky. The specific inputs of the detrital food web to the Green River are unknown, but it was expected that *Cladophora* would have a large influence in detrital signatures in the summer months but lesser of an influence compared to leaves in autumn. Three questions were addressed in this study.

*Research Questions*

*1) Are macroinvertebrate colonization patterns different between Cladophora and decaying leaves?*

It is well studied that leaves can be heavily colonized by macroinvertebrates (Petersen, and Cummins 1974), but it is not well known if *Cladophora* is similarly colonized as a detrital material. *Cladophora* in freshwater systems has been found to be colonized by few macroinvertebrate taxa, namely gastropods, oligochaetes, amphipods, and Chironomidae larvae (Carothers and Minckley 1981, Leibfried and Blinn 1987, Hardwick et al.1992, Blinn et al. 1995, Stevens et al. 1997).

*2) Does the rate of processing differ temporally with habitat for Cladophora and leaves?*

The current literature on *Cladophora* processing is limited to one study in the Baltic Sea (Paalme et al. 2002). Processing rates of *Cladophora* and its contributions to detrital pools in a riverine system are unknown. However, for 40 years, leaf processing

has been well studied in rivers for several leaf and aquatic macrophyte species (Webster and Benfield 1986).

*3) Does stable isotopic ratio change temporally with habitat and is there concordance between stable isotopic signatures of benthic detritus and either Cladophora or decaying leaves?*

Stable isotopic composition of macroproducers changes little during processing (Benner et al. 1987, Fry and Sherr 1989), providing an advantage when tracking detrital food webs. *Cladophora* is an abundant macroproducer and it was expected that this had a major isotopic signature within benthic organic matter (BOM) during late summer and autumn. The $\delta^{13}C$ of BOM was compared to the $\delta^{13}C$ of decaying *Cladophora* and leaves to see if there was sufficient amount of the decaying macroalga present within the Green River. The presence of $\delta^{13}C$ signatures of *Cladophora* in BOM would suggest that it is available as a potential food source for detritivores.

## Methods

### *Study Area*

The research took place in a 7$^{th}$-order reach of the Green River (37.24789, -85.98574) located in central Kentucky, U.S.A. at the Western Kentucky University Green River Preserve (GRP). The Green River originates in Lincoln County, Kentucky, and flows ca. 600 km west to the Ohio River. The Green River Basin is the largest of Kentucky's primary river basins, draining approximately 23,000 km$^2$ and ca. 23% of the commonwealth (Fenneman 1938, Palmer and Palmer 2009).

The study reach is characterized by an open canopy and shallow run habitats underlain by small cobbles and gravel substrates, and is positioned within the Crawford-Mammoth Cave Upland Level IV Ecoregion. This ecoregion is underlain by Mississippian-age limestone and Chesterian-age fractured bedrock formations with low surface stream density and nitrogen-rich groundwater (Woods et al. 2002). Base-flow nitrogen and phosphorous levels at GRP are high (Penick et al. 2012).

There are several aquatic macroproducers present within the study reach, namely *Cladophora* and a dense bed of the vascular plant *Podostemum ceratophyllum* Michx. High productivity of *P. ceratophyllum* is typically indicative of high quality, well-oxygenated rivers in the southeastern U.S. (Hill and Webster 1984), and provides stable habitat for macroinvertebrate communities (Hutchens et al. 2004). During low-flow conditions between late summer and autumn, a dense matting of *Cladophora* can rapidly proliferate and reaches maximum standing stocks prior to high-flow scouring events (Penick et al. 2012). *Fontinalis* sp., *Potamogeton* sp. and *Spirogyra* sp. are also present, but markedly less abundant.

The riparian edges of the Green River are dominated by red elm (*Ulmus rubra* Muhl.), silver maple (*Acer saccharinum* L.), box elder (*A. negundo* L.), and American sycamore (*Platanus occidentalis* L.). In the spring and summer there is very little leaf retention in the channel itself, with leaf packs present mainly along the margins on emergent rocks, branches, or snags. During the study period the Green River rose several times above base flow (Fig. 1), creating multiple high flow events throughout the study period that prevented wadable access.

*Field Methods*

Leaves of three riparian tree species, slow-processed *P. occidentalis* and medium-processed *A. negundo* and *A. saccharinum,* were collected from the riparian area immediately adjacent to the study reaches during summer and autumn. In summer, green leaves were taken directly from trees in July, whereas in autumn, freshly-abscised leaves were collected from the riparian floor in October (*Platanus*) or November (both *Acer* species). Leaves were air-dried for at least 10 d prior to constructing 4.0 ± 0.1 g dry mass packs. Leaves from the two *Acer* species were combined in packs. Dried mass packs corresponded to 3.7 ± 0.1 g ash-free dry mass (AFDM) for both *Acer* and *Platanus*.

*Cladophora* was hand-collected from the study reach in June and October, air-dried in the lab for at least 20 d, and subsequently picked free of snails (mainly *Leptoxis praerosa* Say), leaf detritus, twigs, *P. ceratophyllum,* and *Fontinalis*. Air-dried *Cladophora* packs were 15.0 ± 0.1 g, which corresponded to 7.4 ± 0.9 g AFDM.

Each individual pack was placed in a 7-mm nylon mesh bag, and four packs each of *Platanus, Acer,* and *Cladophora* were put into a rubber-coated steel cage. Seven cages each were placed on the river bottom in a separate riffle and slow-moving run. The riffle was located on the side of the channel where cages were continually exposed to fast flow. Minimum depth during base-flow conditions was 0.5 m with a mean velocity of 0.23 $m/s^2$ and mean DO level of 10.19 mg/L. The run was located upstream with a minimum depth of 2 m, mean velocity of 0.04 $m/s^2$, and mean DO level of 10.41 mg/L.

Cages were placed in-stream separately during summer (mid-June 2014) and autumn (mid-November 2014). One cage per habitat was retrieved after two days to serve as a 48 hour post-leach control and one cage per habitat was subsequently retrieved

approximately every two (summer) or four (autumn–spring) weeks. Upon removal from the cage, each pack was placed into an individual Whirl-Pak© bag, put in a cooler, returned to the lab, and placed in a refrigerator at 4°C.

BOM samples were collected using a PVC coring sampler (diameter: 0.005 $m^2$) immediately upstream of where cages were placed. Four BOM samples were obtained from each habitat, poured into a Nalgene jars, and immediately refrigerated at 4°C in the laboratory prior to separation and stable isotope processing.

*Lab Methods*

In the laboratory, macroinvertebrates and extraneous sediment were gently washed off leaf packs with tap water and into a 500-µm sieve. *Cladophora* packs were hand-picked in a shallow enamel pan clean of sediments and macroinvertebrates. Macroinvertebrates were preserved in 95% ethanol and identified to the lowest possible level, namely genus or species, and assigned to individual functional feeding groups and habits according to Hauer and Lamberti (2006) and Merritt et al. (2008).

Leaf and *Cladophora* packs were placed in a drying oven at 65°C for 48 h, cooled to room temperature, and weighed to the nearest 0.01g to quantify dry mass (DM). Each pack was then combusted at 550°C for 4 h in a muffle furnace, cooled to room temperature, and reweighed to the nearest 0.01g. AFDM was determined by subtracting the mass of the ashed materials from DM. A sample, between 0.1 and 0.7 g, from each dried pack was removed prior to ashing and placed in a crucible to prepare for stable isotope analyses. Breakdown rates of *Cladophora* and leaf packs, as processing coefficients (-*k*), were calculated with AFDM using a negative exponential model

(Webster and Benfield 1986). All AFDM data were log-transformed and the negative exponential model was calculated by taking the slope of the regression line for the natural log mean of percent AFDM remaining per time in-stream.

Whole BOM samples were poured through a nested series of sieves to separate into several size fractions: >1000 µm, 1000–500 µm, and 500–100 µm. An ultrafine BOM fraction (100–1µm) was obtained by filtering the remaining sample through a 1-µm Gelman glass fiber filter (GFF). Each BOM fraction was placed in a separate crucible and dried at 65°C to be prepared for stable isotope analyses. Unlike *Cladophora* and leaf pack, the entire BOM fraction was processed for isotopic analyses.

The subsamples of oven-dried *Cladophora* packs, leaf packs, and BOM samples were pulverized to a fine powder with a Wig-L-Bug®. Approximately 4.5 mg portions were packed in 5x9-mm tin capsules. Carbon stable isotopic analysis on decaying *Cladophora*, decaying leaves, and BOM were performed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California, Davis Stable Isotope Facility, USA. Stable isotope ratios were expressed in δ format in parts per mil (‰) as: $\delta X = ([R_{sample}/R_{standard}]-1) * 1000$, where X = $^{13}C$ and R = $^{13}C$:$^{12}C$ ratios. Vienna Pee Dee Belemnite was used as the carbon standard.

*Statistical Methods*

A non-parametric analysis of covariance (ANCOVA; including separate slopes analysis, R version 3.0, package Geomorph, Adams et al. 2016), followed by a pair-wise comparison to assess differences between riffle vs. run habitats was used to compare

breakdown rates, macroinvertebrate colonization patterns, and $\delta^{13}C$ isotopic changes between the three macroproducers. The covariate for all models was time (i.e., days), and prior to analysis, data were checked for normality and homogeneity of variance.

Shredders were chosen because they feed mainly on decaying vascular plant tissue (Cummins 1973), and would be a good indicator if *Cladophora* were entering into a consumer detrital pool. Gathering-collectors were also analyzed because this functional group typically is found in high abundance during high algae productivity in the summer (Power 1992). For habits, clingers were analyzed due to their adaptations to attach to hard surfaces with the tarsal claws and sprawlers to see if *Cladophora* was a suitable habitat for an insect that prefers a flat surface (Hauer and Lamberti 2006, Merritt et al. 2008).

## Results

### *Macroinvertebrate colonization*

There were no significant differences between decaying macroproducers in macroinvertebrate abundance in either summer 2014 (ANCOVA, $F_{1,5}=2.9$, $P = 0.159$) (Table 1, Fig. 2) or autumn–spring 2014–2015 ($F_{1,5}=1.9$, $P= 0.207$, Table 1, Fig. 3). *Cladophora* had similar abundances of macroinvertebrates across seasons (Fig. 4). *Acer* also showed similar abundances of macroinvertebrates between seasons (Fig. 5). During summer 2014, *Platanus* had a higher abundance of macroinvertebrates compared to autumn–spring 2014–2015 (Fig. 6).

Mean macroinvertebrate richness on *Cladophora* was similar between seasons and habitats. *Acer* and *Platanus* also showed similar richness patterns in both habitats (Table 2). *Cladophora* had significantly lower richness than *Acer* and *Platanus* on all

decaying macroproducers in both summer 2014 ($F_{1, 5}$ =16.2, P = <0.001, Table 1, Fig. 2) and autumn–spring 2014–2015 ($F_{1, 5}$=3.4, P=0.001, Table 1, Fig. 3).

In summer 2014, *Cladophora* and *Acer* in both habitats had a significantly lower mean number of shredders compared to *Platanus* ($F_{1, 5}$ =5.7, P=0.001, Table 1, Fig. 7). In autumn–spring 2014–2015, *Cladophora* had a significantly lower amount of shredders than *Acer* and *Platanus* in both habitats ($F_{1, 5}$ =7.6, P<0.001, Table 1, Fig. 7). The most abundant shredder in summer 2014 was *Berosus* and in autumn–spring 2014–2015 was *Taeniopteryx.* Shredders were more abundant in the fall, making up ≥50% of the macroinvertebrates found on *Acer* and *Platanus* than on *Cladophora* (Fig. 8). The most abundant functional group found across the study were gathering-collectors (Table 3), which were significantly higher in *Cladophora* run habitat for both summer 2014 ($F_{1, 5}$ =4.4, P<0.008) and autumn–spring 2014–2015 ($F_{1, 5}$ =3.9, P<0.005, Fig. 9). Gathering-collectors were numerically dominated by non-Tanypodinae chironomid larvae.

The mean abundance of clingers throughout the seasons was higher than any other macroinvertebrate habit (Table 4). In the run habitat, there were 10–30% more clingers present on decaying macroproducers than in the riffle (Fig. 10). *Cladophora* had the highest average abundance of clingers, significantly higher than both leaf species in summer 2014 ($F_{1,5}$ =3.7, P=0.038, Table 1, Fig. 11) and autumn–spring 2014–2015 ($F_{1,5}$ =3.3, P<0.008, Table 1, Fig. 11). Sprawlers were not as abundant on *Cladophora* and significantly lower than leaves for summer 2014 ($F_{1,5}$ =5.0, P=0.003) and autumn–spring 2014–2015 ($F_{1,5}$ =6.0, P<0.001, Table 1, Fig. 12).

The most abundant macroinvertebrate to colonize *Cladophora* in both habitats and across seasons were Chironomidae. *Acer* in the summer of 2014 in the run habitat was also dominated by chironomids, where *Platanus* did not have the highest amount in any season or habitat.

*Processing Rates*

All mass loss models were significant (Table 5). For all species, there was faster processing during summer and slower during autumn–spring. *Cladophora* was processed at the fastest rates across the study periods (Table 6) with packs in the riffle treatment in summer 2014 exhibiting the fastest rate ($k$ = 0.235). In general, processing was intermediate and slowest for *Acer* and *Platanus*, respectively. *Cladophora* had the largest processing range within a species ($k$ = 0.010–0.235), but similar processing rates within seasons (Fig. 13). *Acer* and *Platanus* were processed at comparable rates between seasons and habitats (Figs. 14–15).

During the summer, leaves showed similar processing rates in 2014 (Table 5). *Platanus* was the slowest to be processed in both habitats. *Acer* showed similar processing rates as *Cladophora*, with slower processing in the run and faster processing in the riffle habitats. In summer 2014, *Cladophora* and *Acer* were significantly faster to process than *Platanus* in both habitats (ANCOVA, $F_{1,5} = 11.8$, $P < 0.004$, Table 1, Fig. 16). During autumn–spring 2014–2015, stream discharge was greater than the summer months (Fig. 17) but all macroproducers were processed at slower rates in both habitats. *Cladophora* was processed significantly faster than both leaf species ($F = 184.1$, $P < 0.001$, Table 5) in both habitats.

*Cladophora and leaf isotopic data*

The mean $\delta^{13}C$ values for decaying leaves remained similar between seasons, between habitats, and over the study period. During summer 2014, *Cladophora* had similar mean $\delta^{13}C$ values to decaying leaves (Table 7, Fig. 18). The $\delta^{13}C$ values for *Cladophora* changed little between habitats, but were more $^{13}C$-depleted during the autumn–spring 2014–2015 (Table 8). *Cladophora* in autumn–spring 2014–2015 was significantly more $^{13}C$-depleted than both leaf species ($F_{1,7} = 6.6$, $P < 0.001$, Table 7, Fig 19). Both *Cladophora* and *Acer* did not change in mean $\delta^{13}C$ values with % AFDM remaining, but had variability between seasons (Figs. 20–23). *Platanus* exhibited similar $\delta^{13}C$ values over time, showing little variation with AFDM remaining (Figs. 24–25).

*Benthic organic matter*

Mean $\delta^{13}C$ values of BOM were not different between the riffle and run habitats (Figs. 18–19, Table 7). Mean $\delta^{13}C$ values of BOM from summer 2014 were significantly more $^{13}C$-enriched than all three decaying macroproducers (ANCOVA, $F_{1,7} = 6.4$, $P < 0.001$). In autumn–spring 2014–2015, BOM was again more $^{13}C$-enriched compared to *Cladophora* but no different than decaying leaves ($F_{1,7} = 50.6$, $P < 0.001$).

## Discussion

There have been very few studies that have addressed the processing dynamics of macroalgae (e.g., Paalme et al. 2002, Salovius and Bonsdorff 2004, Olafsson et al. 2013) and none with *Cladophora* in freshwater systems. The study by Paalme et al. (2002) appears to be the only research comparable to the processing dynamics of this project yet this was conducted in the Baltic Sea. Primary productivity in aquatic systems can be

dominated by *Cladophora* when present (Power et al. 2009). *Cladophora* is abundant in many different habitats with the ecology of the species varying significantly with locality (Dodds and Gudder 1992). *Cladophora* is the dominant macroproducer in the Green River during summer and autumn but relatively little is known when the macroalga enters into a detrital pool. It has been assumed that when *Cladophora* becomes detached it becomes a food source for detritivores (Patrick et al. 1983, Dudley et al. 1986, Brönmark et al. 1991, Dodds and Gudder 1992). Shannon et al. (1994), however, suggested that *Cladophora* serves only as habitat, implying that senescent *Cladophora* may only be entering a microbial loop during decomposition (Hein et al. 2003) instead of being consumed by detritivores (Blinn et al. 1995). This study addressed *Cladophora* macroinvertebrate colonization patterns, processing rates, and stable isotopic signatures, while comparing them to the same aspects of processing dynamics of leaves of three well-studied riparian tree species common to the study system.

*Macroinvertebrate colonization patterns*: Macroinvertebrate abundance was not different between decaying *Cladophora* and leaves, but macroinvertebrate richness was significantly lower on *Cladophora*. This lower richness but high abundance has been found in other studies examining macroinvertebrates colonizing live *Cladophora* (Hardwick et al. 1992, Blinn et al. 1995, Stevens et al. 1997).

A major role of shredders in streams is the breakdown of leaf litter into smaller particles (Cummins et al. 1989). Some shredders can supplement their diet with algae when microbially-conditioned leaves are not available (Jacobsen and Sand-Jensen 1994). Bird and Kaushik (1984), however, found shredders would prefer other algae instead of decaying *Cladophora*. Mean shredder abundance on *Cladophora* was significantly lower

than on leaves in both summer 2014 and autumn 2014–2015. Low shredder abundance on decaying *Cladophora* suggests these detritivores are preferentially choosing leaves for a combination of higher habitat and food quality, and potentially leading to lessened contribution of macroinvertebrates to overall processing. *Cladophora* packs were present in the same basket with both *Acer* and *Platanus* packs. This further suggests that macroinvertebrates may bypass decaying *Cladophora* in favor of conditioned leaves, leading to the macroalga never entering into detritivore food webs and instead only entering a microbial detrital pool.

In the Green River, gathering-collectors easily comprised the highest proportions of macroinvertebrate functional feeding groups colonizing decaying *Cladophora* and leaves. This is similar to studies showing decreasing proportions of shredders as stream size increases (Vannote et al. 1980, Minshall et al. 1985). Decaying *Cladophora* itself has been found to be less preferred as a food source by macroinvertebrates over leaf material (Patrick 1983, Bird and Kaushik 1984). This suggests that it is used only as habitat for macroinvertebrates. Salovius and Kraufvelin (2004) found that even as *Cladophora* decayed it was being used as a preferred habitat over fresh green *Cladophora*.

Decaying *Cladophora* was colonized by a significantly higher abundance of clingers across seasons and habitats. Clingers were dominated by non-tanypodinae Chironomidae, especially on *Cladophora*. Clingers are more adapted to holding onto *Cladophora* strands with their single tarsal claw to hold onto rock surfaces, woody debris, and in some cases moss or vascular plants (Wisseman 2012). Small macroinvertebrates, including clingers, will colonize *Cladophora* faster and more successfully than sprawlers (Highsmith 1985). The filamentous nature of *Cladophora*

creates large surface area with strands, compared to a single flat surface on decay leaves. *Cladophora* strands may provide attachment space and protection from predators for smaller, immature macroinvertebrates (Dudley et al. 1986). In contrast, sprawlers were found on leaves more than *Cladophora*. This is because sprawlers spread out on a single solid surface such as vascular plant material, wood, or sediment (Merritt et al. 2008).

Other studies have also found high densities of Chironomidae larva on fresh *Cladophora* (Carothers and Minckley 1981, Leibfried and Blinn 1987), and decaying *Cladophora* in the Baltic Sea (Olafsson et al. 2013). The run habitat had the highest percentage of chironomids between habitats. This may be due to *Cladophora* filaments being more stable in the run than the riffle (Brown and Brussock 1991).

*Macroproducer processing*: Macroproducer processing rates were faster during the summer and in the riffle habitat. This matches previous studies where processing rates of leaves were faster in the summer than autumn, as well as riffles compared to pools or runs. This difference in processing rates between a similar pair of distinct habitats has been noted in other studies with both *Cladophora* (Salovius and Bonsdorff 2004) and many times with leaves (e.g., Cummins et al. 1980, Benfield et al. 2000, Swan and Palmer 2004).

*Cladophora* in the Green River had similar processing rates as reported in Paalme et al. (2002) and Olafsson et al. (2013). *Acer* and *Platanus* both lost mass at different rates between seasons and habitats. The breakdown rates of the leaves in this study partially matched those of previous studies (Table 9) with the *Acer negundo-saccharinum* mix being processed faster than most studies that have used leaves of *Acer saccharum* Marsh or *Acer rubrum* L. Using the breakdown categories classified by Peterson and

Cummins (1974), *Acer* was placed in fast processing category ($k$ = 0.010–0.015) for autumn–spring 2014–2015 (run: $k$ = 0.014; riffle: $k$ = 0.015) (Table 7) and even faster in summer 2014 (run: $k$ = 0.047; riffle: $k$ = 0.152). *Platanus* was in the slow category ($k \leq$ 0.005) for both seasons and depths. In summer 2014, *Cladophora* was categorized as processing fast in the run habitat, but very fast in the riffle (run: $k$ = 0.142; riffle: $k$ = 0.235).

The processing of aquatic plants is typically rapid following senescence (Puriveth 1980, Webster and Benfield 1986, Moran and Hodson 1989), but the processing of leaves can vary depending upon species. The amount of extracellular lignocellulose activity is typically correlated with processing rates (Sinsabaugh et al. 1992, 1994, Sinsabaugh and Linkins 1993). Leaves with lower lignin content tend to have faster processing rates (Cromack and Monk 1975), and faster microbial colonization rates (Mathuriau and Chauvet 2002). Unlike leaves, however, *Cladophora* lacks lignin (Martone et al. 2009), suggesting that the very fast processing rates are due to high levels of microbial activity (Webster and Benfield 1986). The rapid processing of *Cladophora* may additionally be due to its large surface area of fine filamentous strands, with higher colonization rates of bacteria and fungi (Suberkropp and Klug 1976, Zhuang et al. 2000).

*Stable isotopic ratio changes*: As *Cladophora* was processed the mean $\delta^{13}C$ values remained similar over time (Fig. 20). This trend was also found in the leaves. Neither *Acer* (Fig. 22) nor *Platanus* (Fig. 24) exhibited changing mean $\delta^{13}C$ values over time. There was very little temporal change in mean $\delta^{13}C$ values for *Cladophora* between treatments, but there was a difference between seasons. Processed *Cladophora* in the

autumn–spring 2014–2015 became more $^{13}C$-depleted compared to summer 2014. There were no studies to compare mean $\delta^{13}C$ values of decaying *Cladophora*.

Aquatic macroproducers can have greater variability in their $\delta^{13}C$ values (Fry 1984, Kendall et al. 2001). Decaying *Cladophora* did not have significantly different $\delta^{13}C$ values than leaves in summer 2014 (Figure 18, Table 7). The large range in $\delta^{13}C$ values for *Cladophor*a (-35.4 to -25.7) (Plafkin 2007), overlaps with that of the average $\delta^{13}C$ values of $C_3$ plants -25‰ (-33.0 to -24.0 ‰) (Bender 1971). The indistinctive isotopic signals are one possible explanation why the there was no significant difference between macroproducers. The autumn–spring 2014–2015 *Cladophora*, however, was significantly different from the leaves, being more $^{13}C$ -depleted (-32.6 ± 0.6) compared to *Acer* (-29.1 ± 0.5) and *Platanus* (-28.5 ± 0.1). High growth rates of *Cladophora* creates variability in $\delta^{13}C$ values between growing periods due to abiotic conditions of low light, high flow, and temperature change (Finlay et al. 1999). This may be why there is very little change for the mean $\delta^{13}C$ values of leaves but varying $\delta^{13}C$ values *Cladophora* between seasons.

*Stable isotopic signatures of benthic detritus versus decaying Cladophora and leaves*: BOM collected in summer 2014 did not match the $\delta^{13}C$ values of decaying *Cladophora* or leaves. This strongly suggests, particularly for *Cladophora* and *Acer* with fast processing rates, that benthic detritus is comprised of slower-processed allochthonous materials. Similar results have been found by McArthur and Moorhead (1996), where benthic organic matter did not match the leaves. In autumn–spring 2014–2015 the $\delta^{13}C$ values of BOM was also significantly different than *Cladophora*, but not significantly different from processed leaves. Benthic organic matter may be an

accumulation of multiple species, of which changes materials and mixtures across seasons (Benner et al. 1987). This would mean that BOM during autumn–spring 2014–2015 was influenced by other allochthonous sources entering the Green River. Sourcing benthic detritus with stable isotopes can be a difficult task due to detritus accumulating multiple litter types and other detrital material (Benner et al. 1987). *Cladophora* was not found in the benthic organic matter, suggesting this autochthonous material is absent from the benthic organic matter in the Green River. Benthic organic matter in the Green River is probably a combination of allochthonous material such as slow processing leaf material and wood.

## Conclusion

Although decaying *Cladophora* and leaves were colonized by similar abundances of macroinvertebrates, the macroalga was not heavily colonized by shredders. This suggests that macroinvertebrates are not consuming *Cladophora*, but instead using it strictly as habitat. There was no evidence of similar isotopic signatures of *Cladophora* in BOM, further suggesting the rapidly-decaying macroalga is part of the detrital pool for a short time period before being mineralized by microbes.

## Figures and Tables

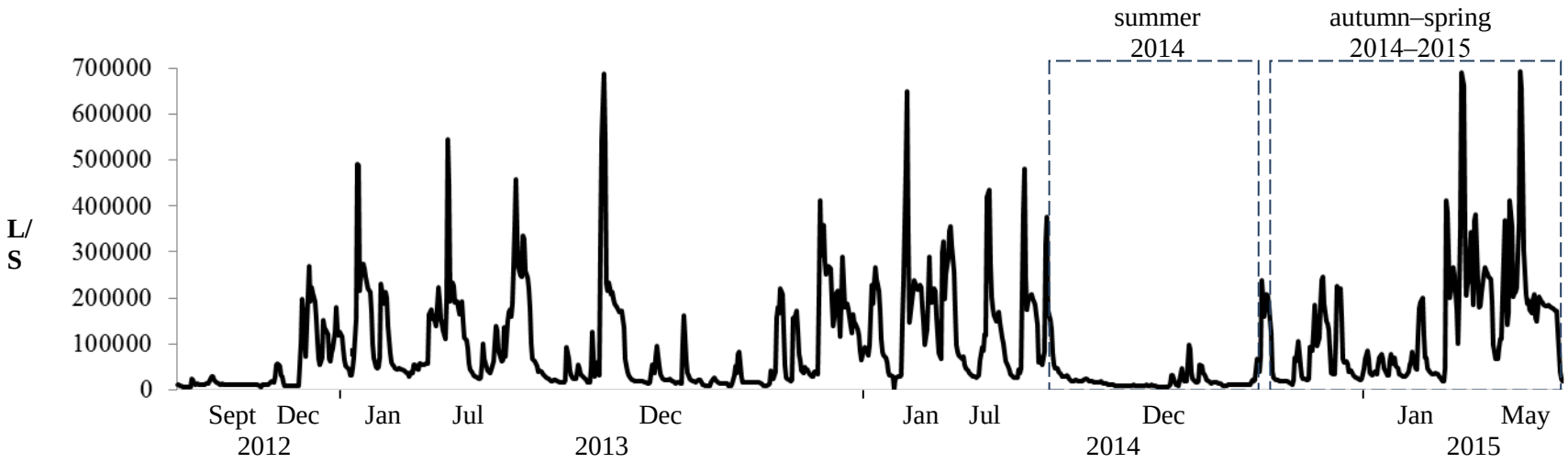


**Figure 1.** Discharge (L/S) throughout the study period. The rectangles outlined by dashed lines refer to the different study periods.

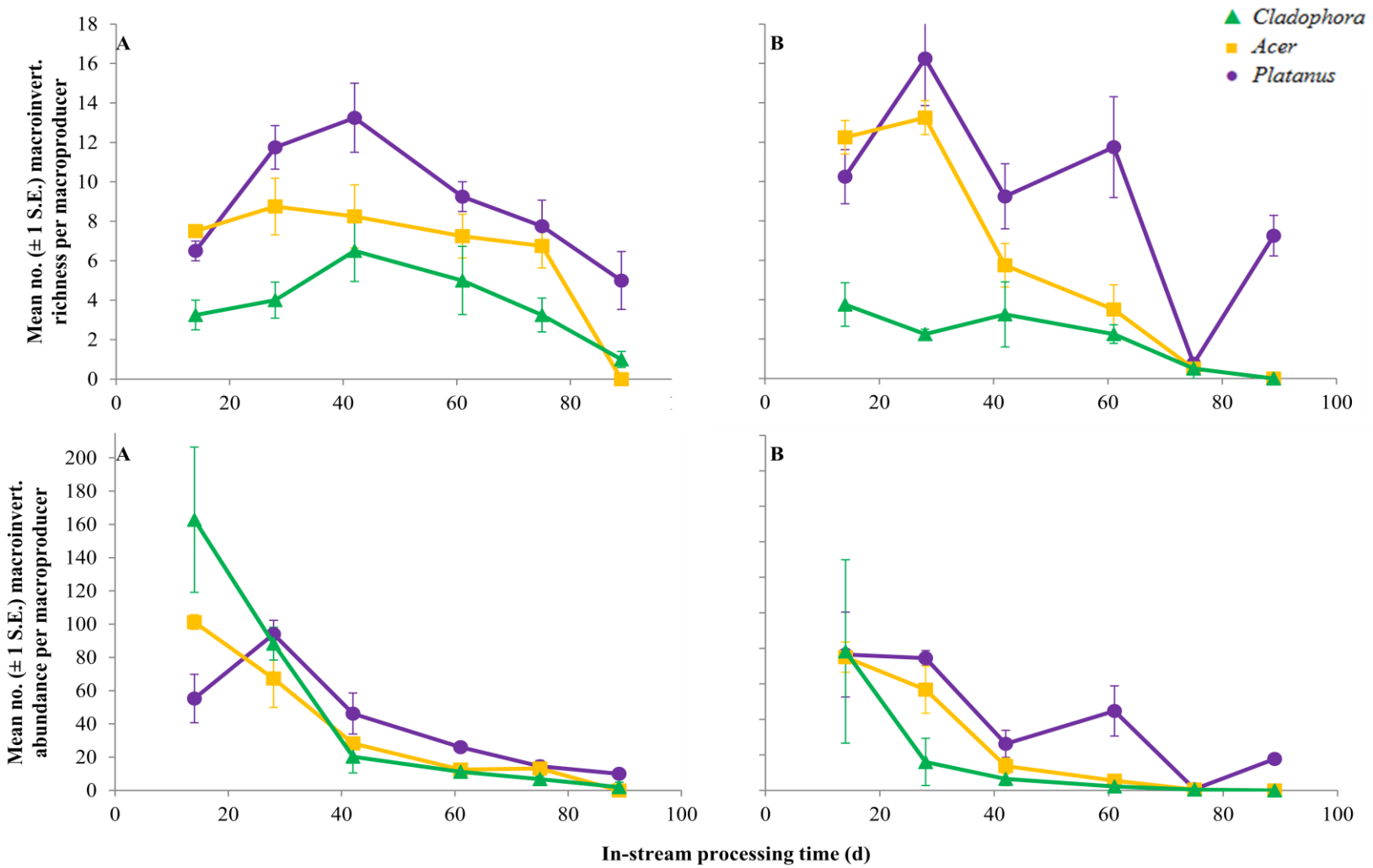


**Figure 2.** Mean richness (± 1 S.E.) and abundance (± 1 S.E.) of macroinvertebrates per macroproducer in the summer 2014 (A = run and B = riffle).

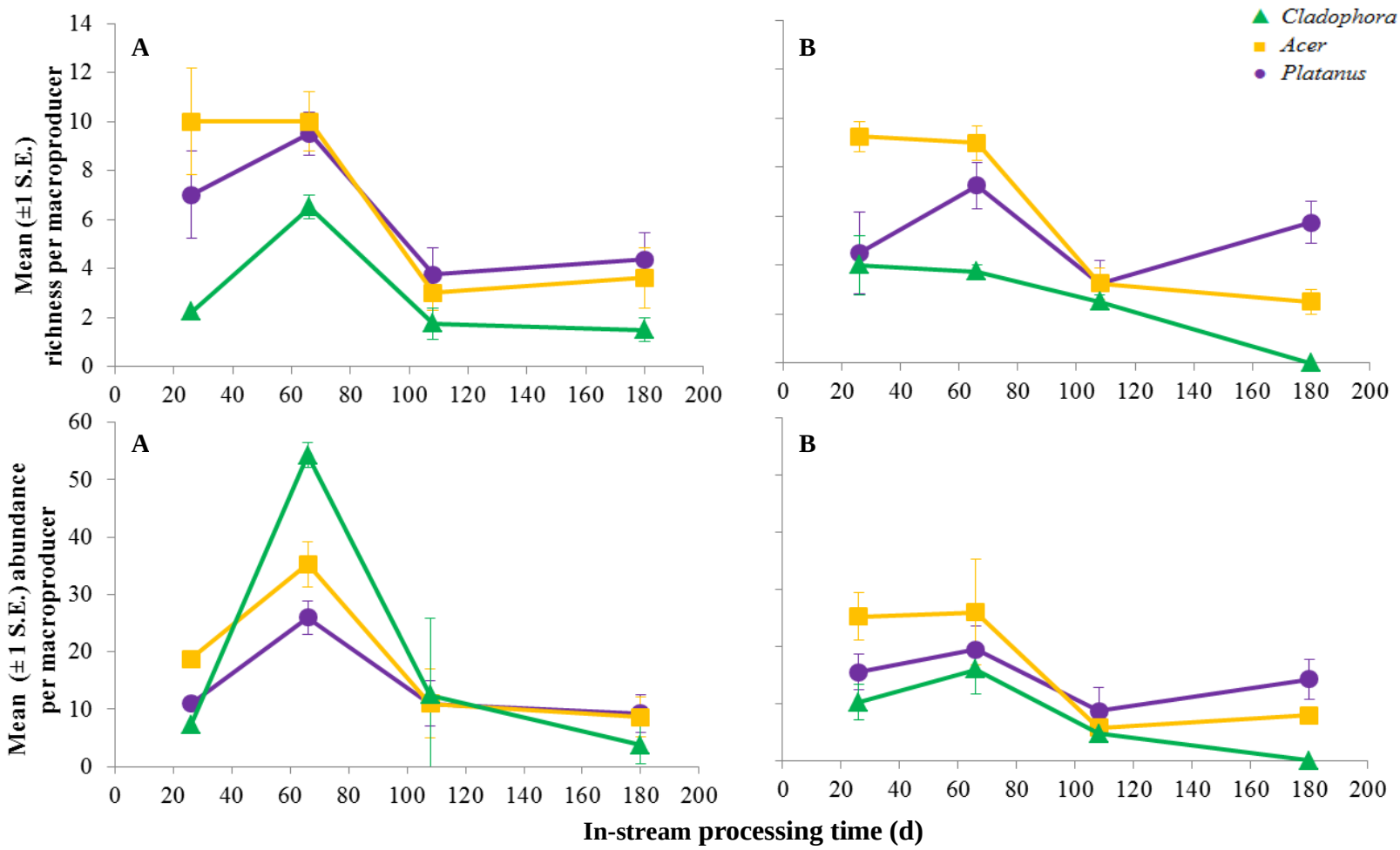


**Figure 3.** Mean richness (± 1 S.E.) and abundance (±1 S.E.) of macroinvertebrates per macroproducer in the autumn–spring 2014–2015 (A = run - and B = riffle).

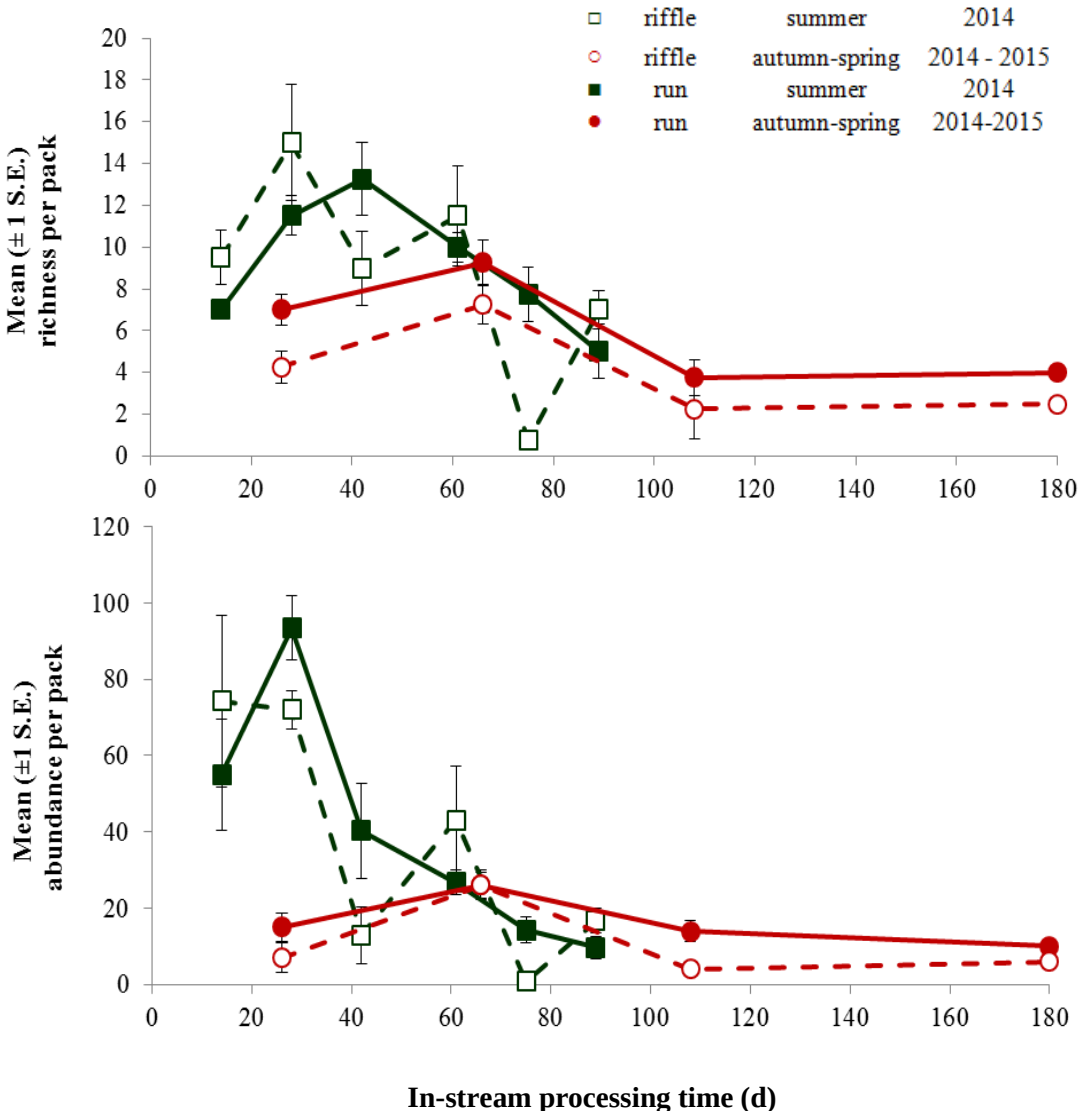


**Figure 4.** Comparison of mean richness (± 1 S.E.) and abundance (± 1 S.E.) of macroinvertebrates on *Cladophora* for summer 2014 and autumn–spring 2014–2015.

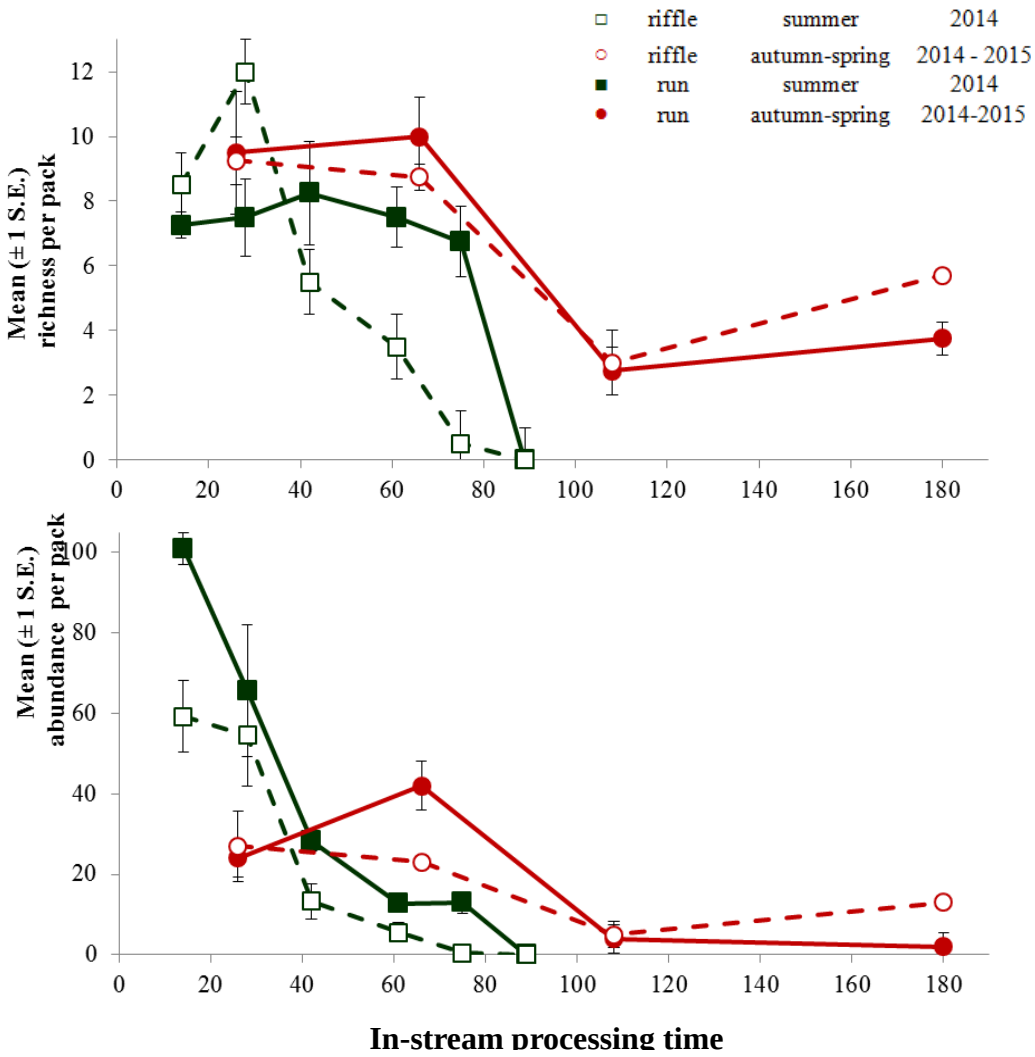


**Figure 5.** Comparison of mean richness (± 1 S.E.) and abundance (± 1 S.E.) of macroinvertebrates on *Acer* for summer 2014 and autumn–spring 2014–2015.

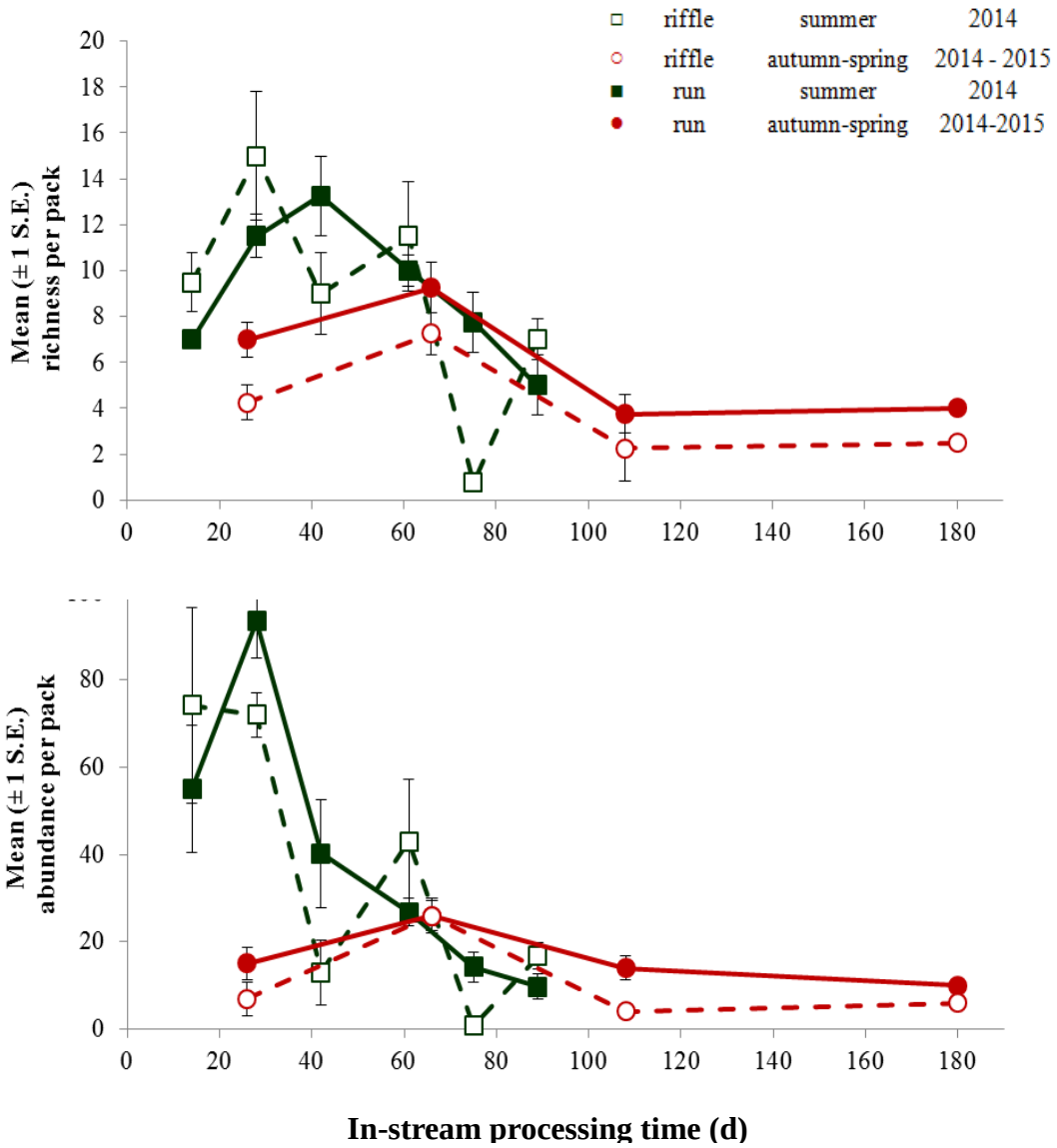


**Figure 6.** Comparison of mean richness (± 1 S.E.) and abundance (± 1 S.E.) of macroinvertebrates on *Platanus* for summer 2014 and autumn–spring 2014–2015.

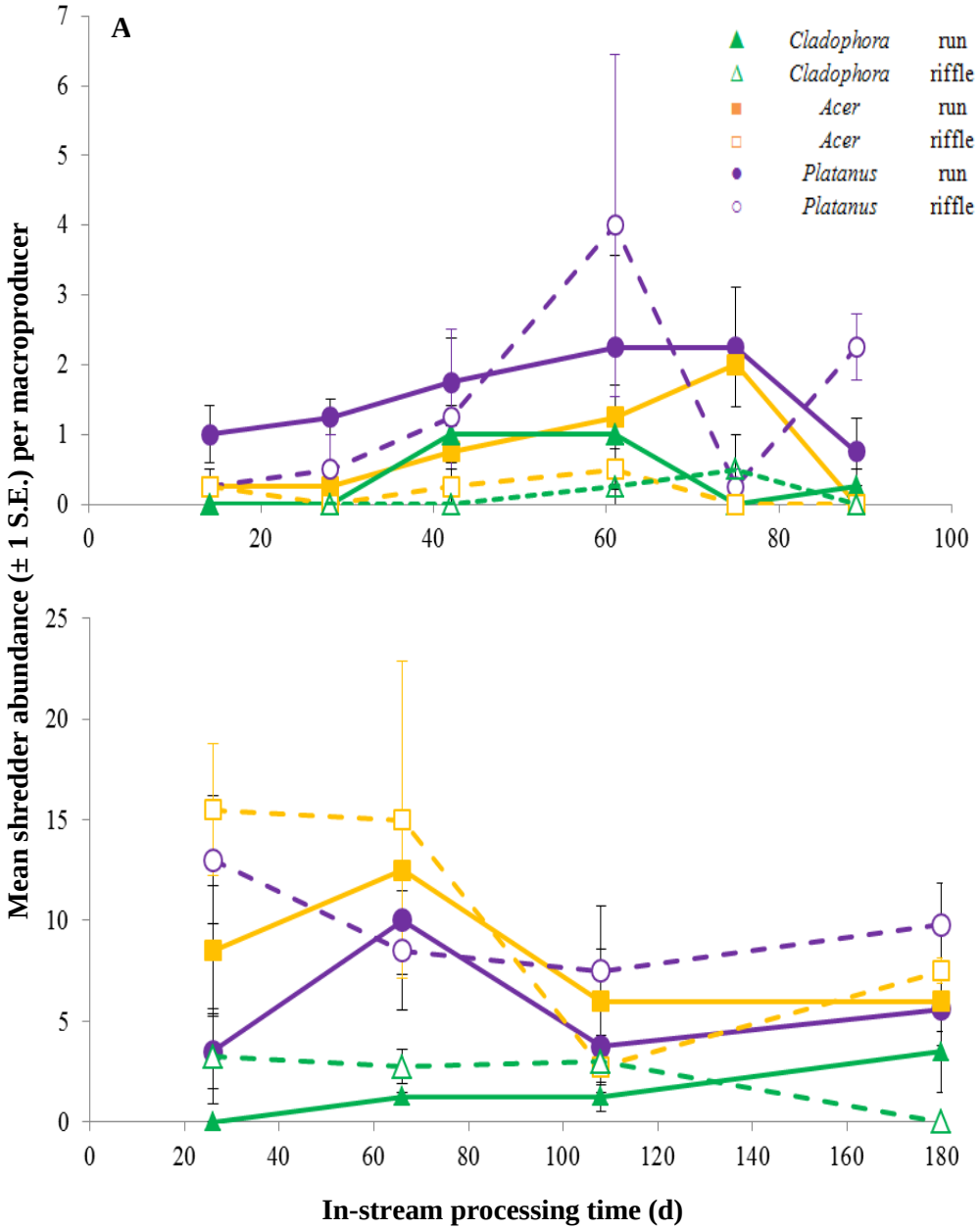


**Figure 7.** Comparison of mean shredder abundance (± 1 S.E.) per macroproducer. (A = summer 2014 and B = autumn–spring 2014–2015).

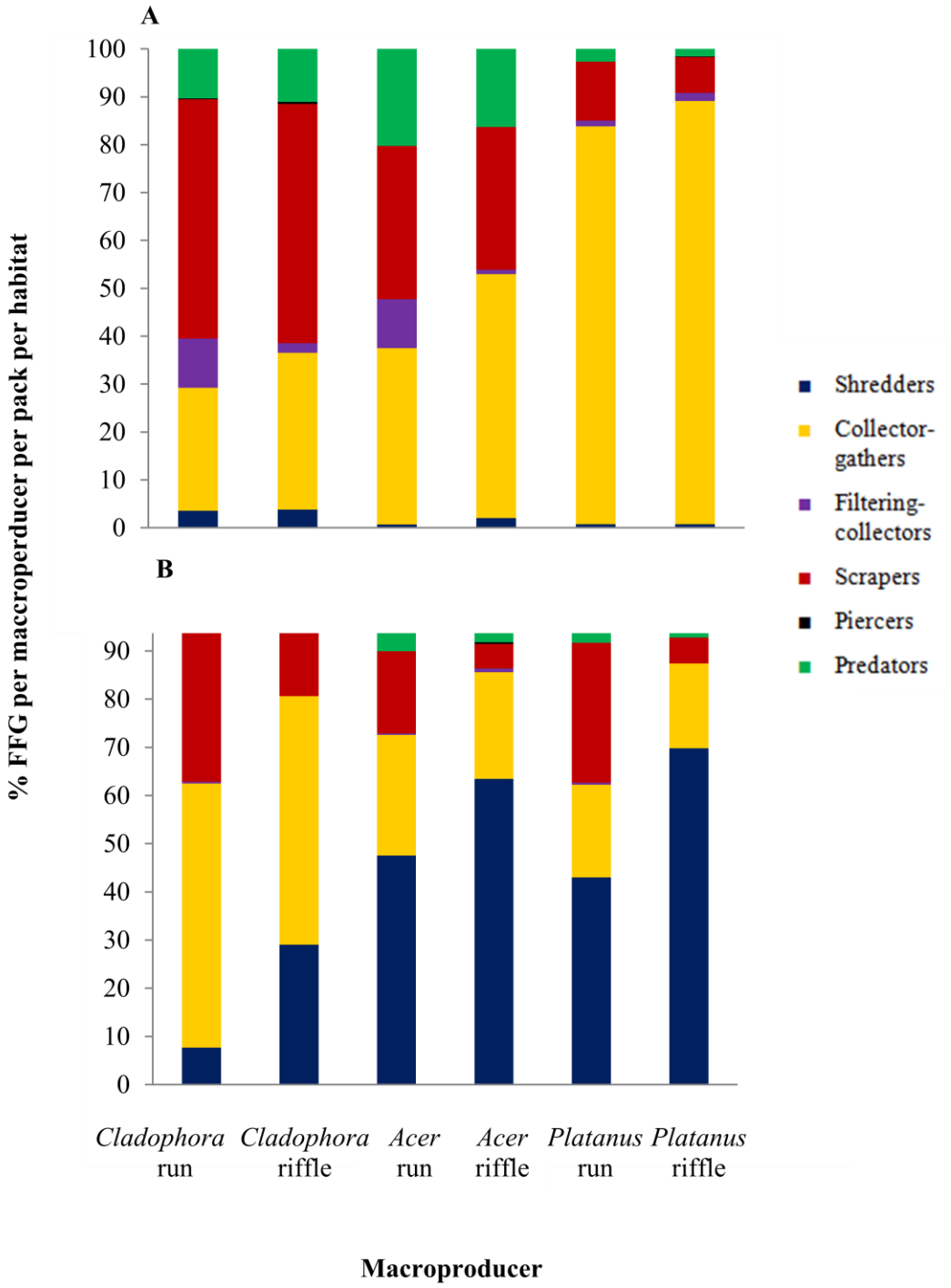


**Figure 8.** The percentage of Functional feeding groups for each macroproducer throughout the seasons (A = summer 2014 and B = autumn-spring 2014–2015).

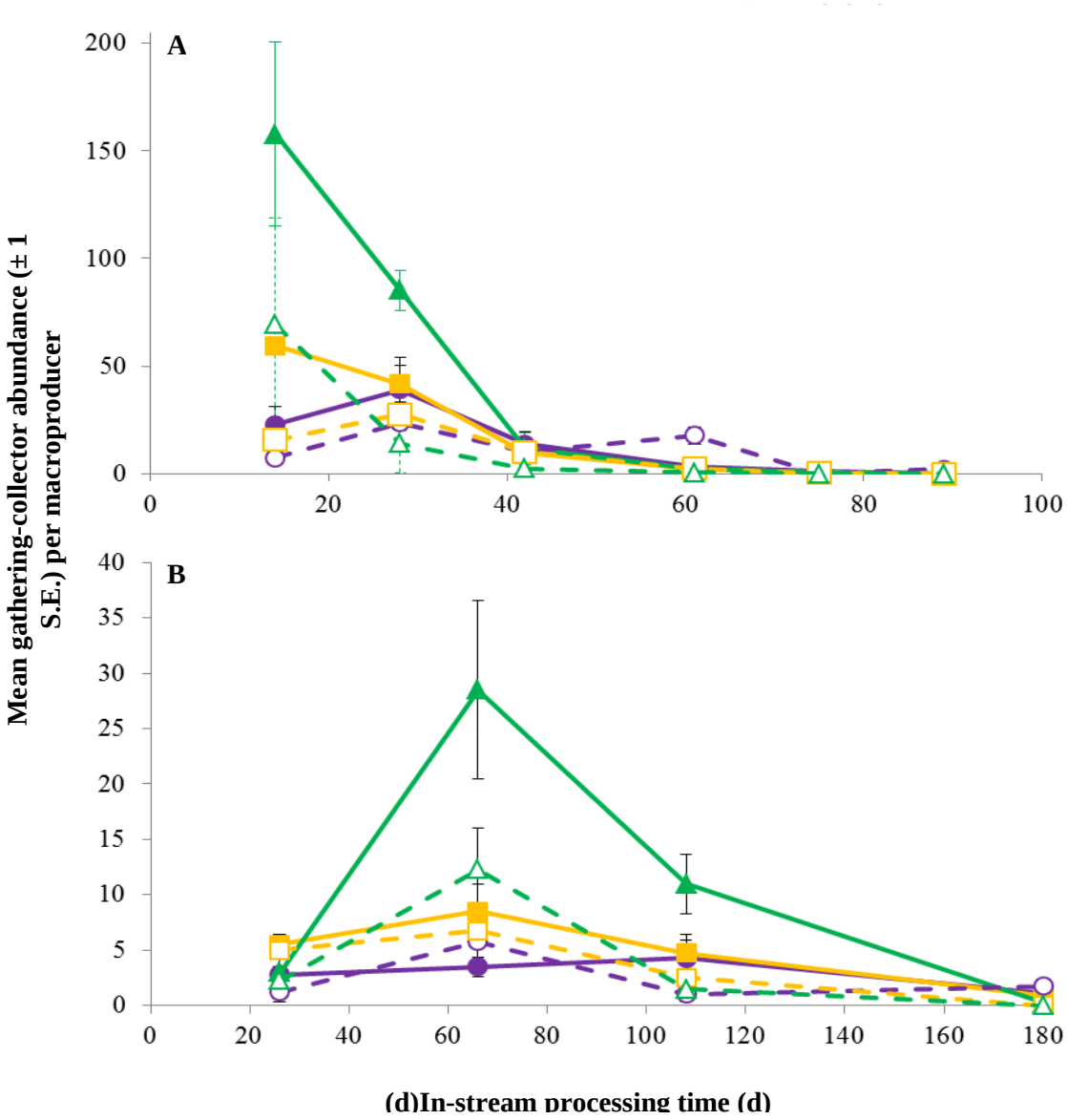


**Figure 9** Comparison of mean gathering-collector abundance (1 ±S.E.) per macroproducer. (A = summer 2014, B = autumn–spring 2014–2015).

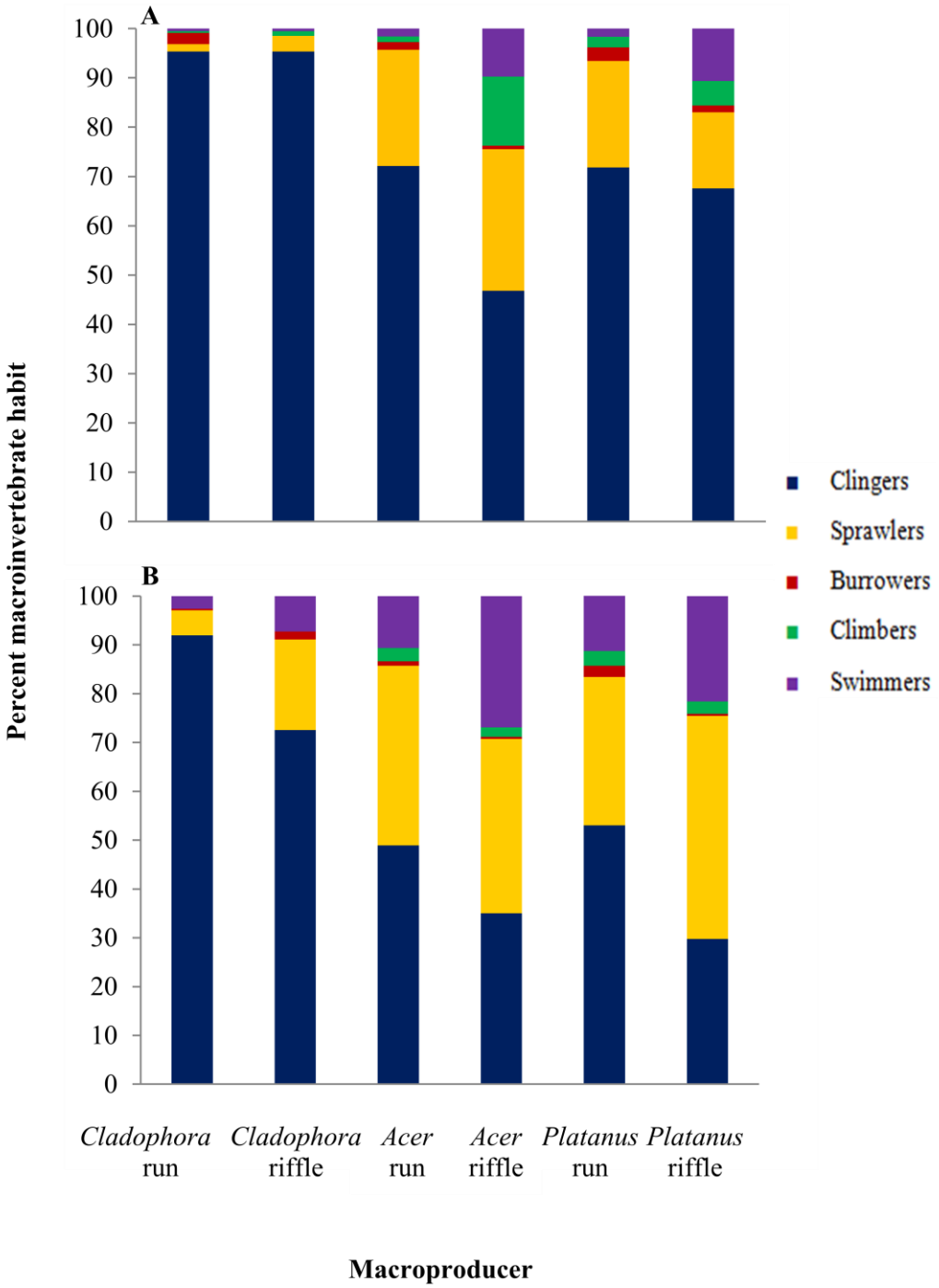


**Figure 10.** The percentage of macroinvertebrate habits for each macroproducer throughout the seasons. (A = summer 2014, and B = autumn–spring 2014–2015)

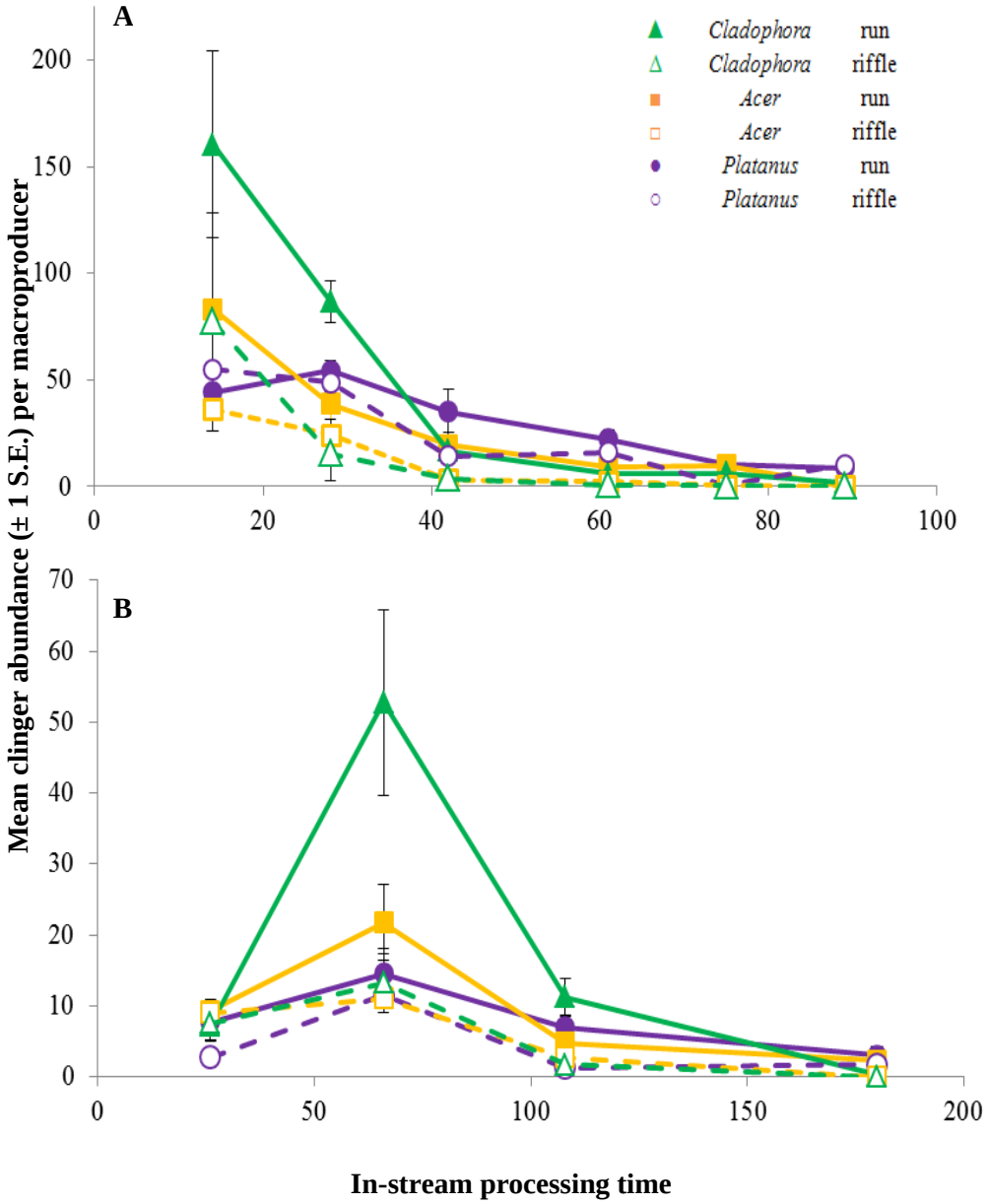


**Figure 11.** Comparison of mean abundance of clingers (± 1 S.E.) per macroproducer (A = summer 2014, B = autumn–spring 2014–2015).

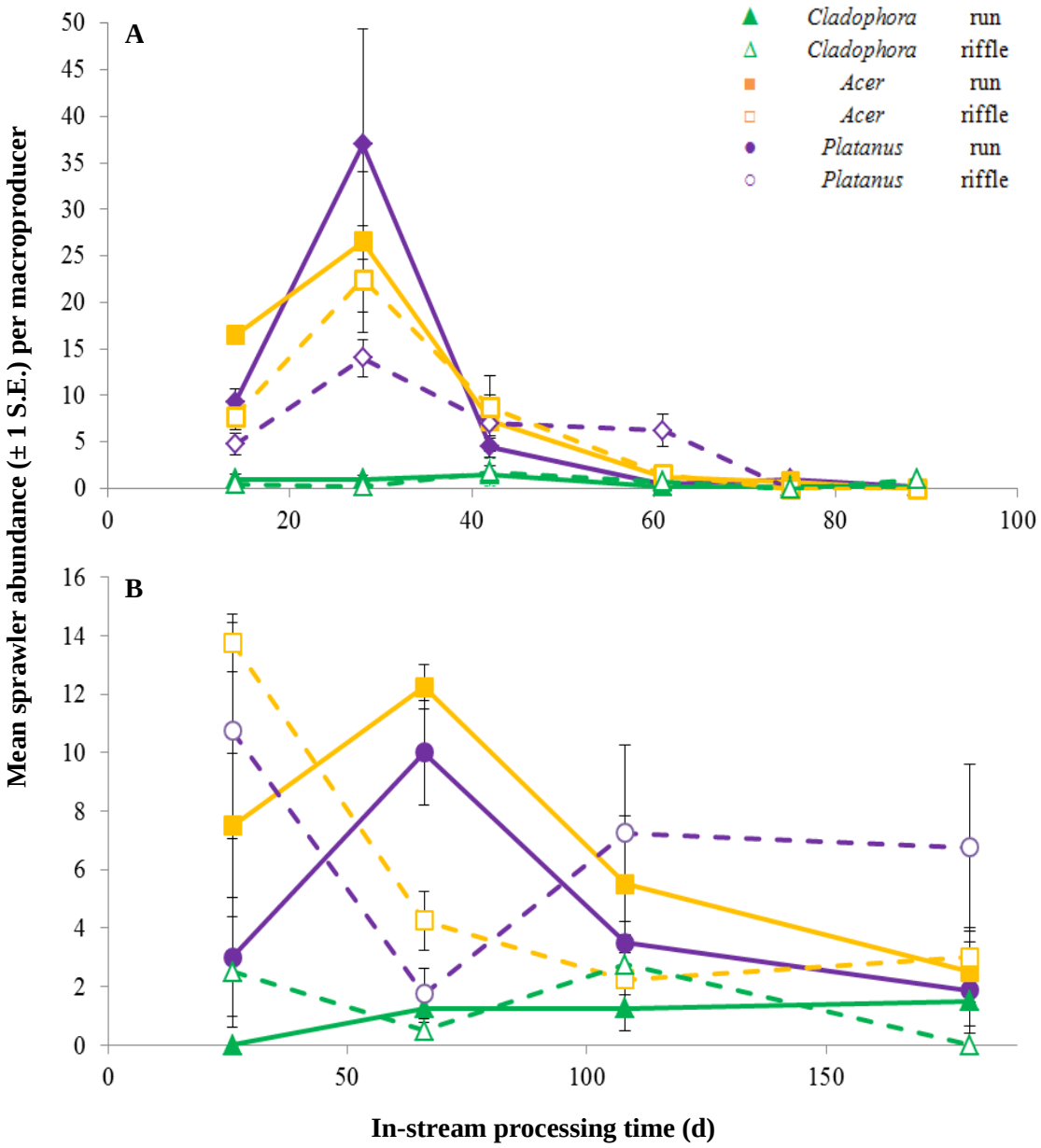


**Figure 12.** Comparison of mean abundance of sprawlers (± 1 S.E.) per macroproducer (A = summer 2014 and B = autumn–spring 2014–2015).

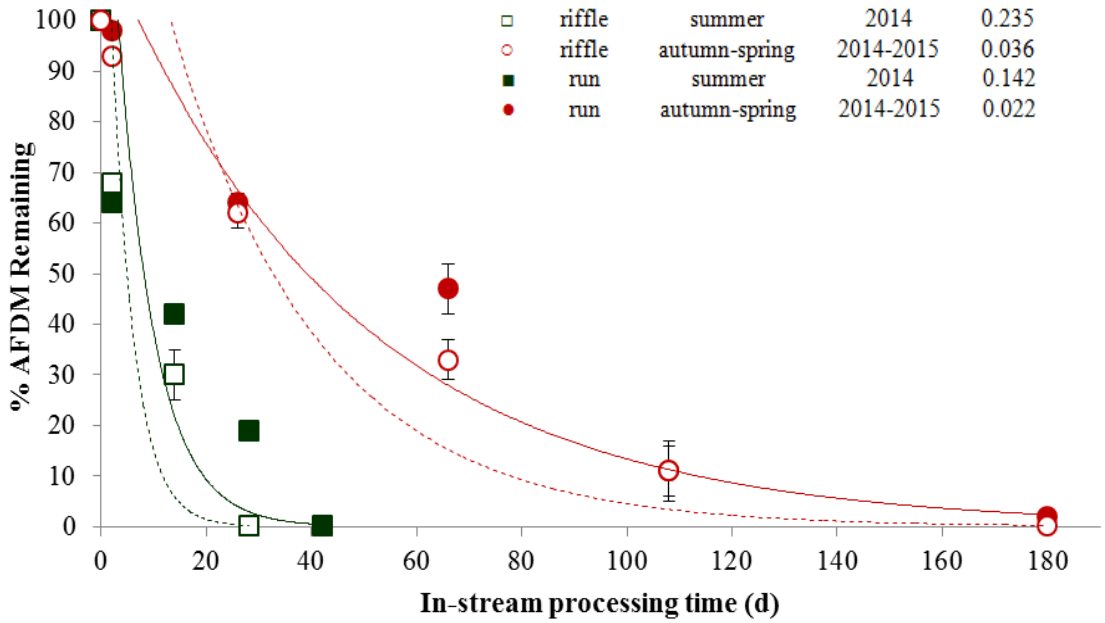


**Figure 13.** Comparison of mean *Cladophora* breakdown throughout the study. The breakdown rates are represented as $-k$ ($d^{-1}$) values. Lines represent lines of best fit.

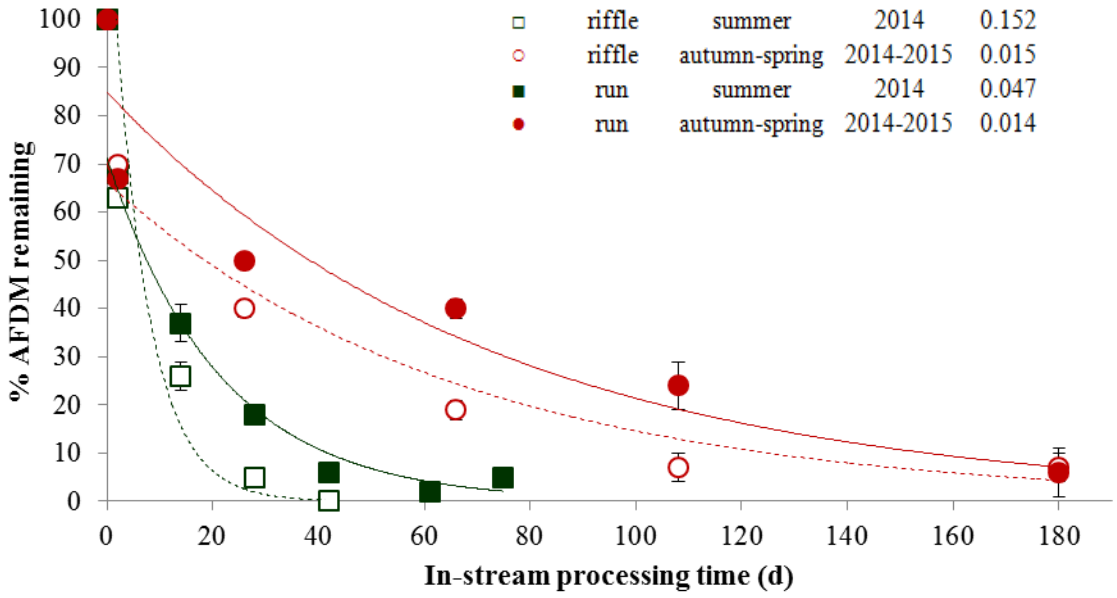


**Figure 14.** Comparison of *Acer* breakdown throughout the study. The breakdown rates are represented as $-k$ ($d^{-1}$) values. Lines represent lines of best fit.

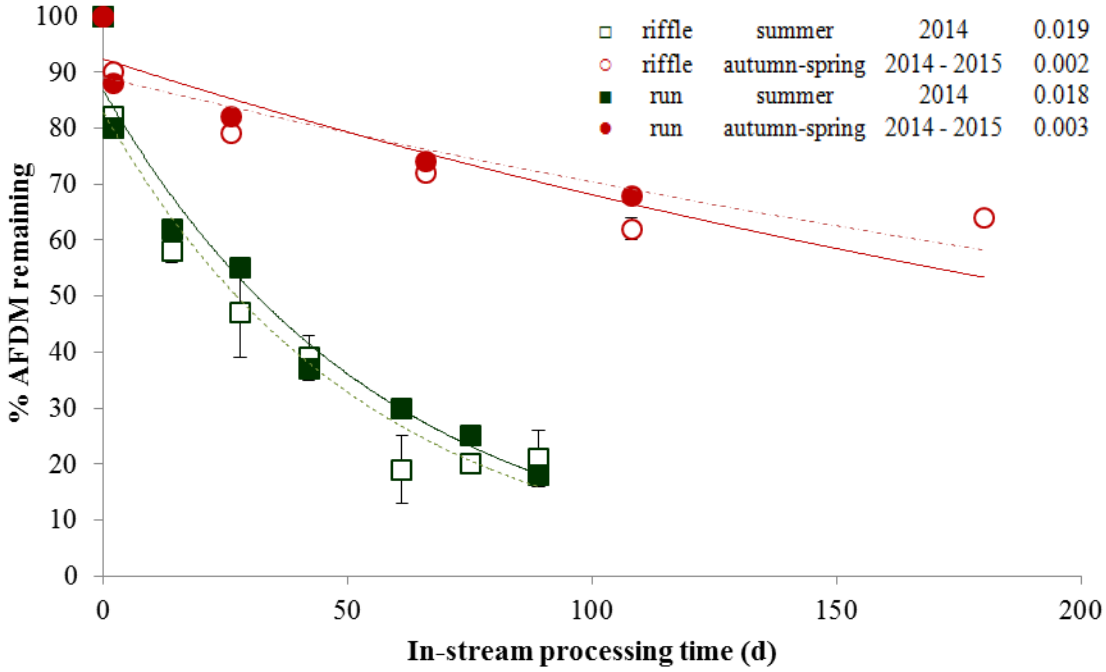


**Figure 15.** Comparison of mean *Platanus* breakdown throughout the study. The decay rates are represented as $-k$ ($d^{-1}$) values. Lines represent lines of best fit.

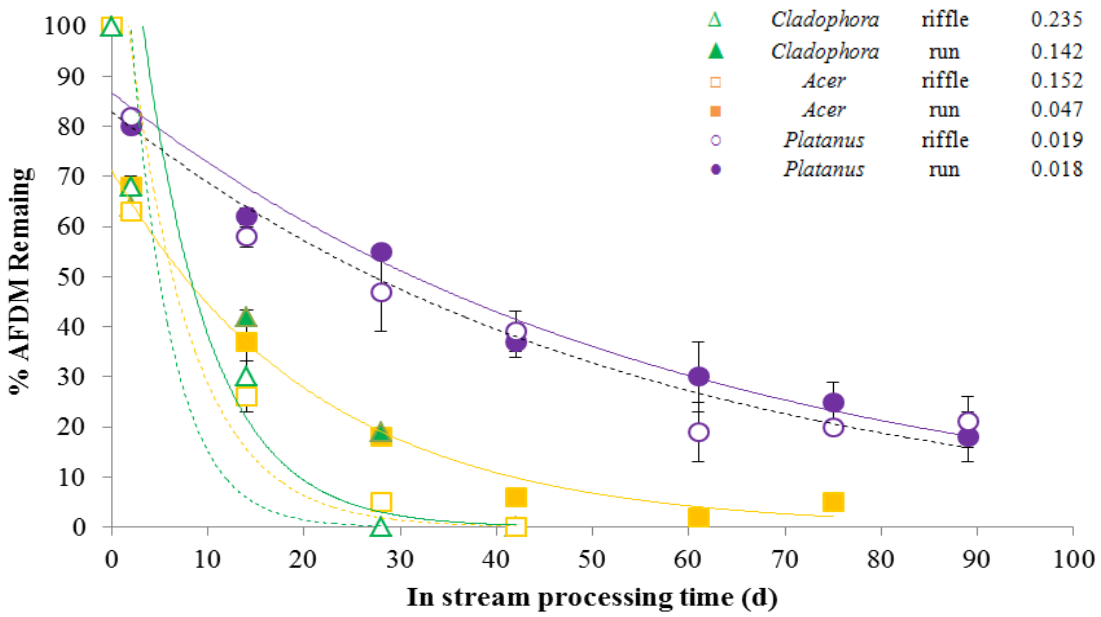


**Figure 16.** Comparison of mean AFDM remaining for each macroproducer during summer 2014. The breakdown rates are represented as $-k$ ($d^{-1}$) values. Lines represent lines of best fit.

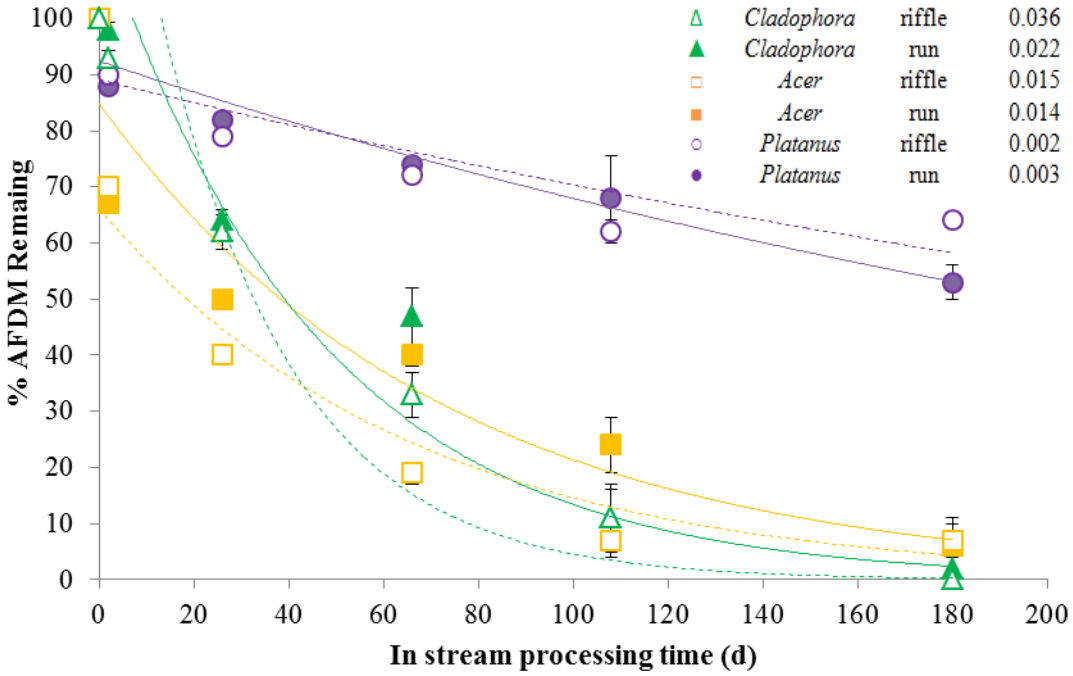


**Figure 17.** Comparison of mean AFDM remaining for each macroproducer during autumn–spring 2014–2015. The breakdown rates are represented as $-k$ ($d^{-1}$) values. Lines represent lines of best fit.

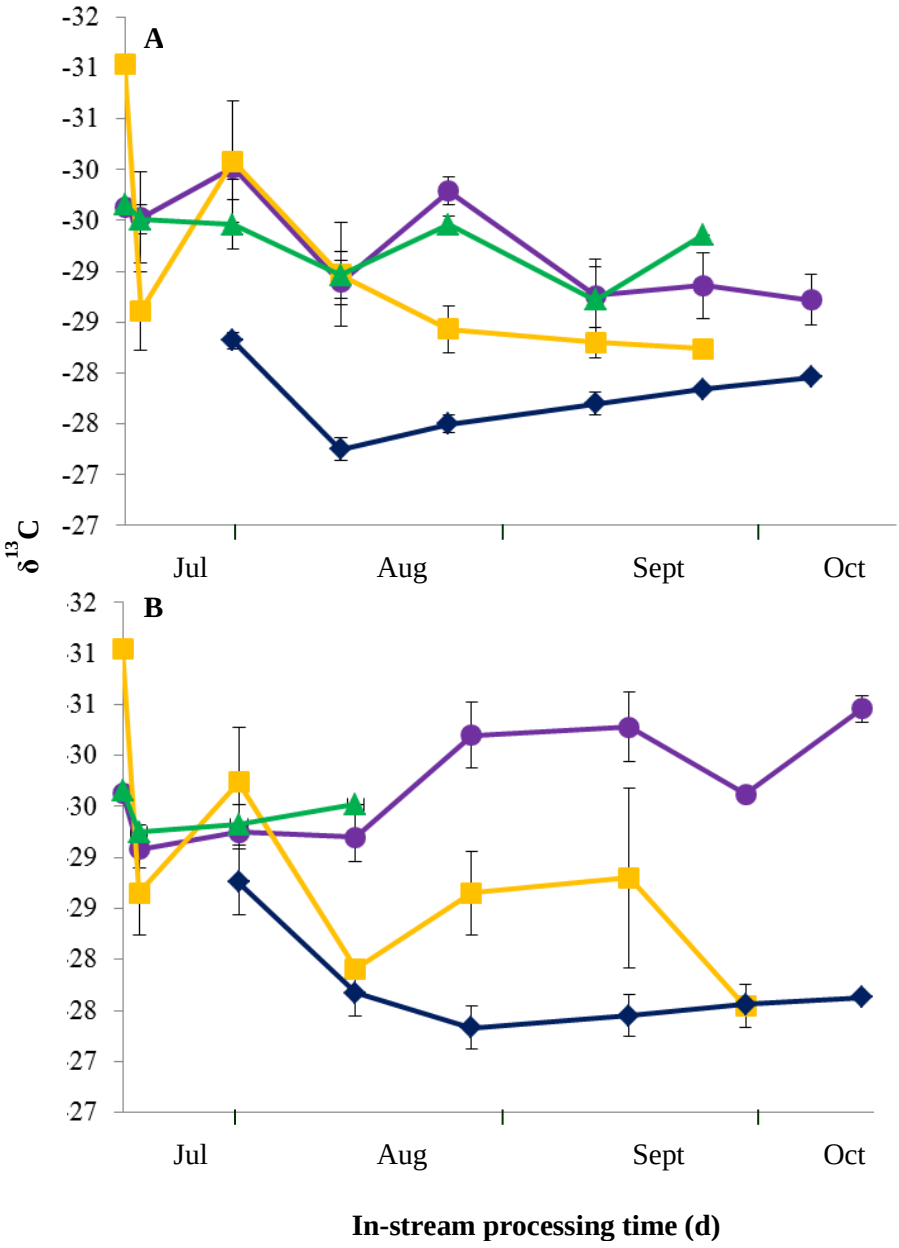


**Figure 18.** Comparison of mean $\delta^{13}C$ values during summer 2014 (A = run, B= riffle).

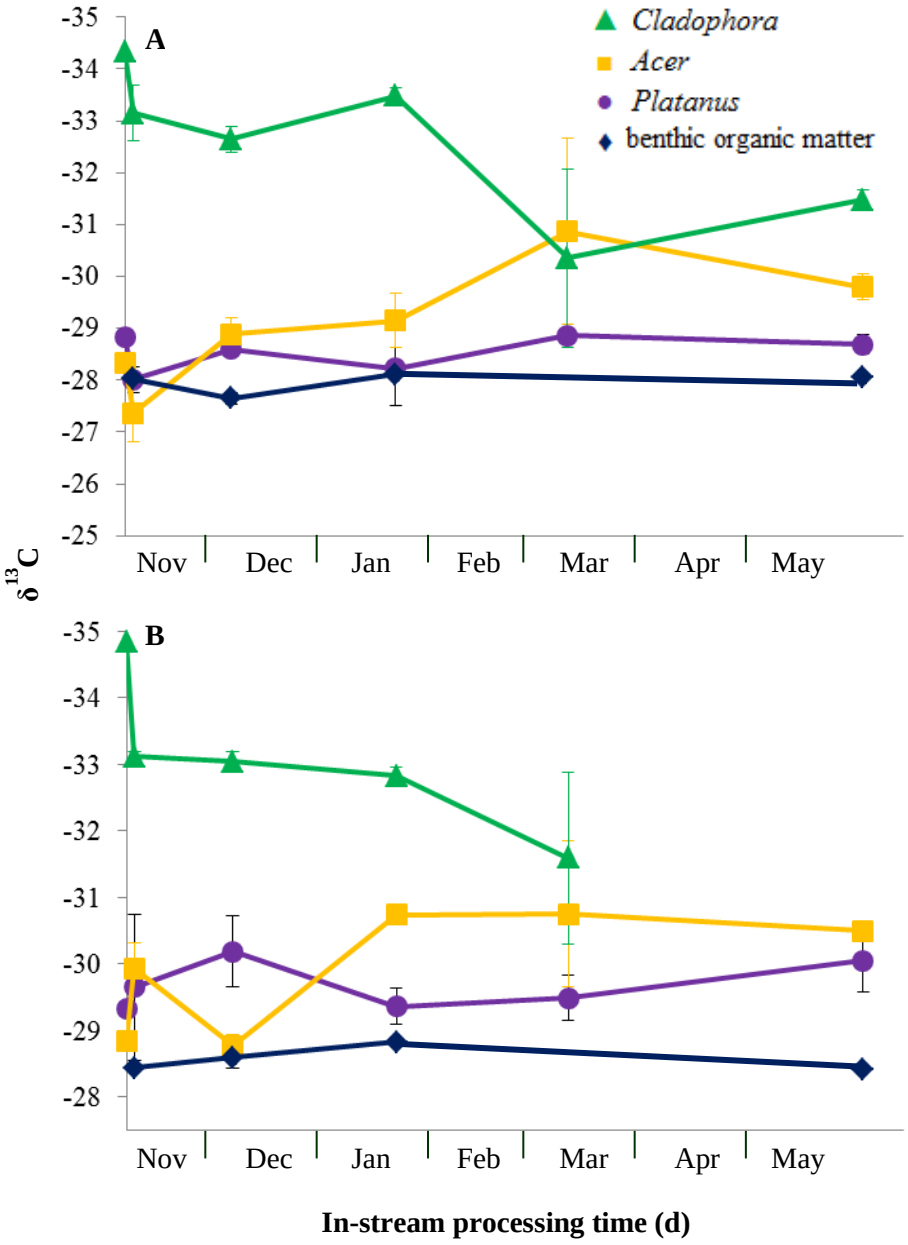


**Figure 19.** Comparison of mean $\delta^{13}C$ values during autumn–spring 2014–2015 (A = run, B= riffle)

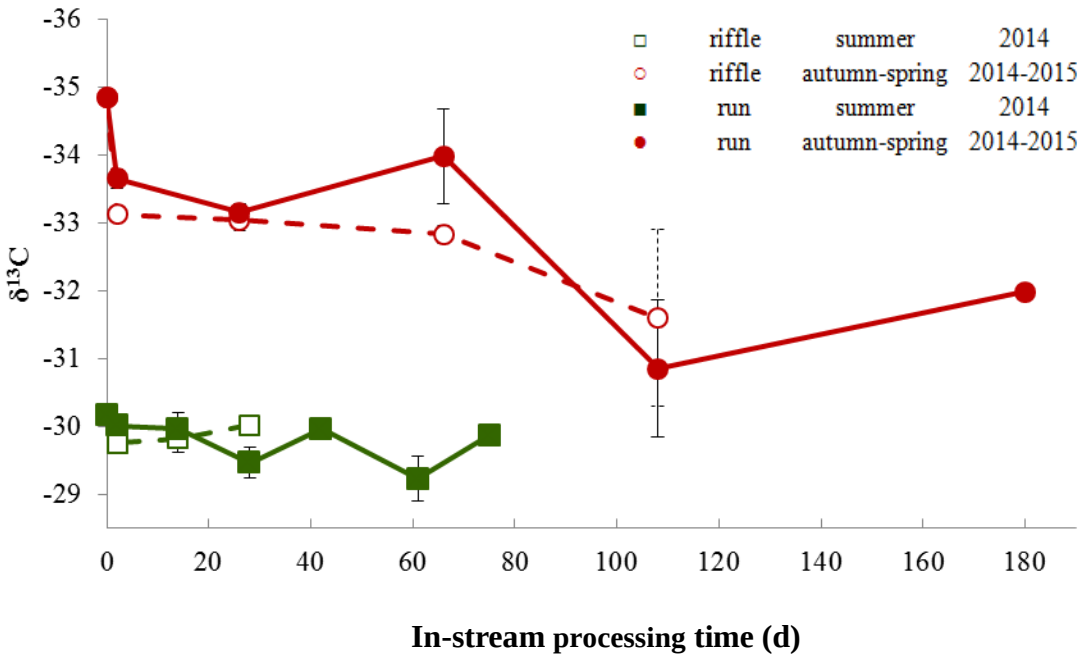


**Figure 20.** Comparison of mean $\delta^{13}C$ values for *Cladophora* throughout the study period.

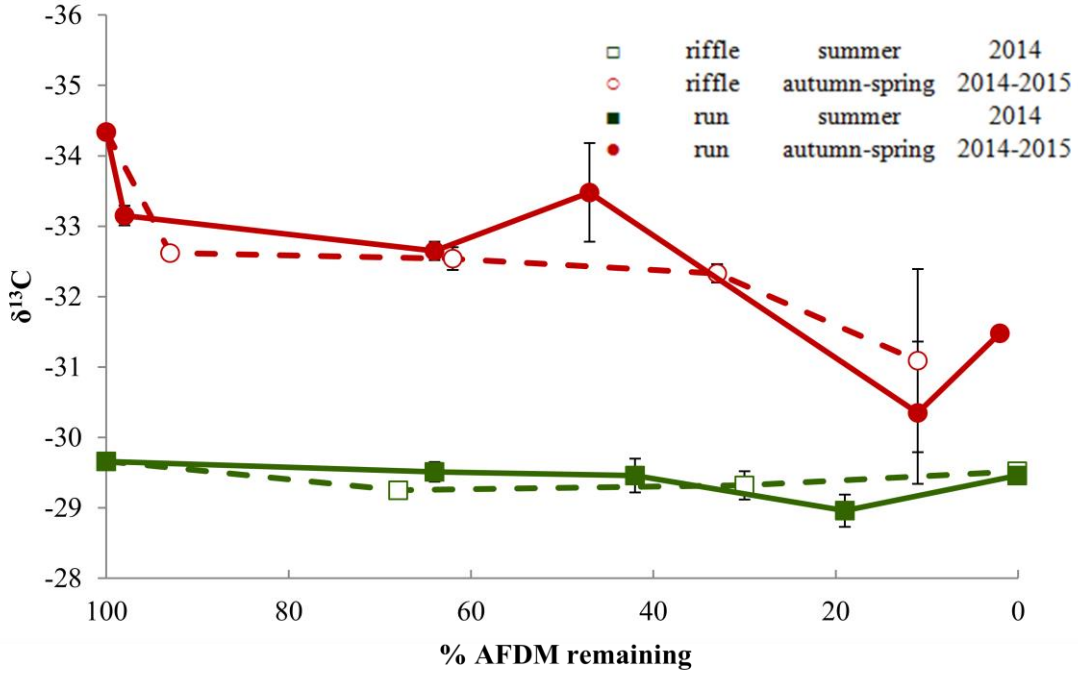


**Figure 21** Comparison of mean $\delta^{13}C$ values and AFDM for *Cladophora* throughout the study period.

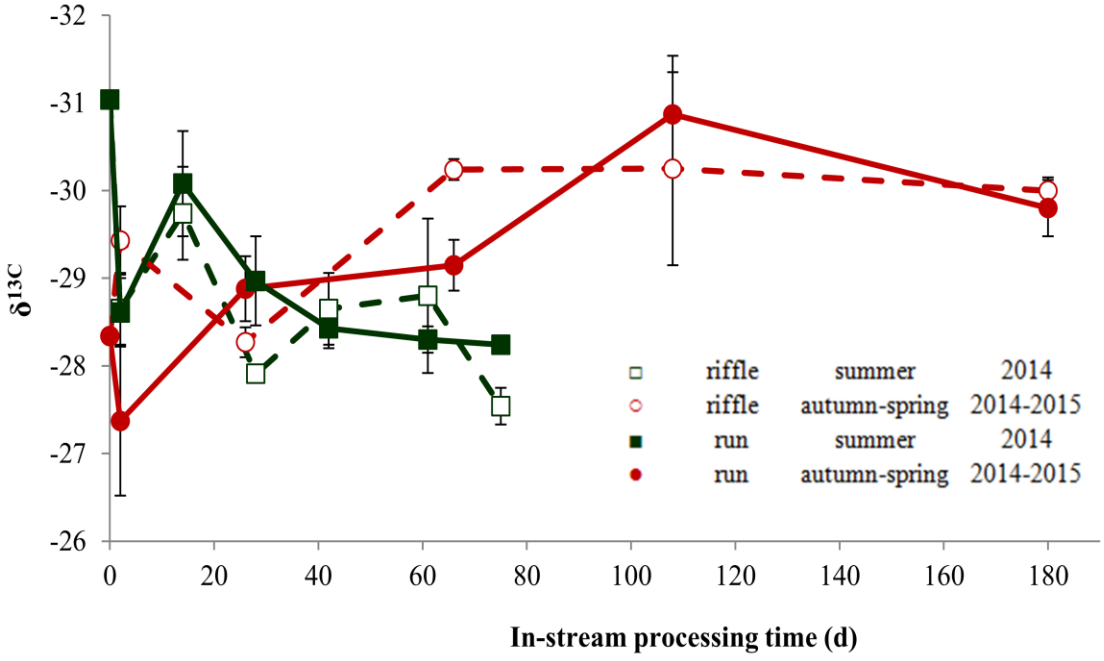


**Figure 22.** Comparison of mean $\delta^{13}C$ values for *Acer* throughout the study period.

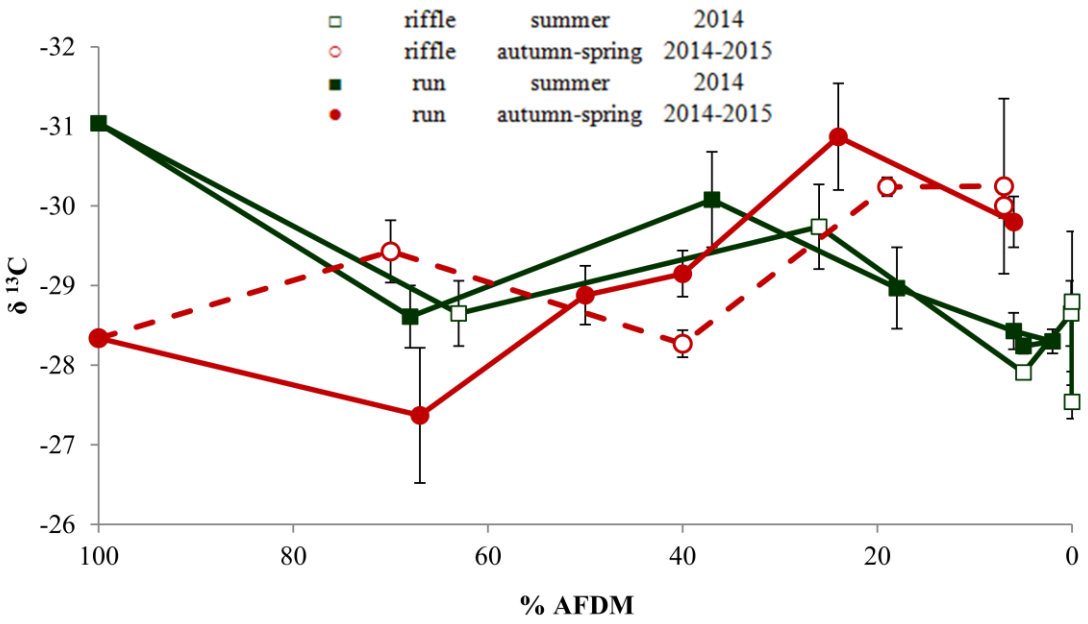


**Figure 23.** Comparison of mean δ $^{13}$C values and AFDM for *Acer* throughout the study period.

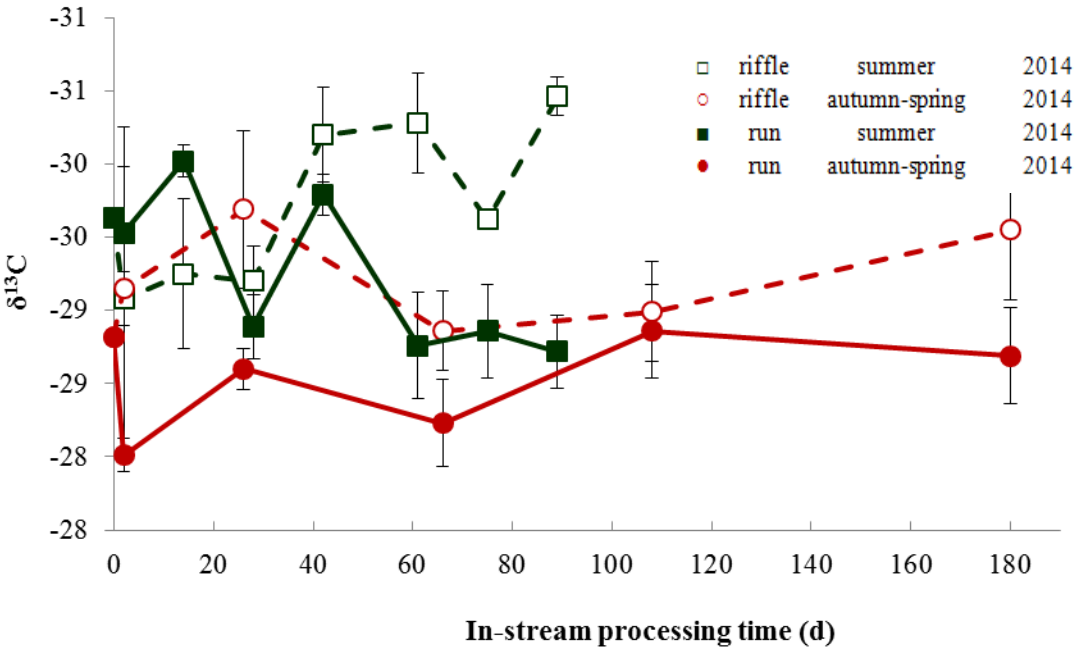


**Figure 24.** Comparison of mean $\delta^{13}C$ values for *Platanus* throughout the study period.

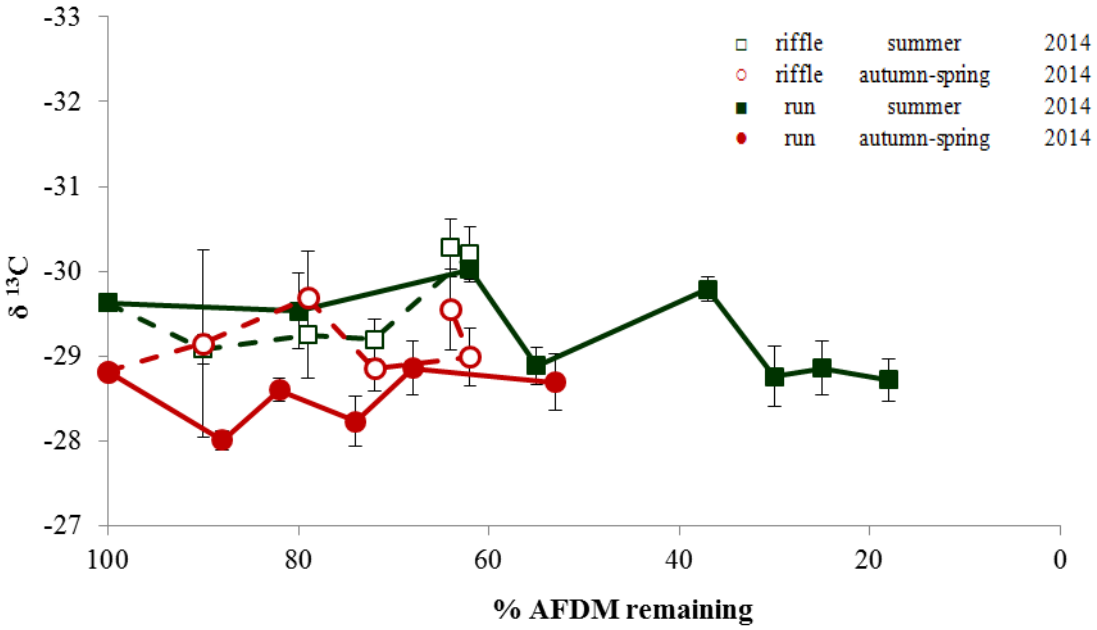


**Figure 25.** Comparison of mean $\delta^{13}C$ values vs. AFDM remaining for *Platanus* throughout the study period.

**Table 1.** ANCOVA results for macroinvertebrate data ($\alpha = 0.05$).

| Measure | Season, year(s) | df | F-crit | P-value | Pairwise differences | Significance |
|---|---|---|---|---|---|---|
| abundance | summer 2014 | 5 | 2.9 | 0.159 | | |
| | autumn–spring 2014–2015 | 5 | 1.5 | 0.207 | | |
| richness | summer 2014 | 5 | 7.09 | 0.001 | $C_{rif}\ C_{run} < A_{rif}\ A_{run} < P_{run}\ P_{rif}$ | A < B < C |
| | autumn–spring 2014–2015 | 5 | 6.6 | 0.001 | $C_{rif}\ C_{run} < A_{rif}\ A_{run}\ P_{run}\ P_{rif}$ | A < B |
| shredder | summer 2014 | 5 | 5.6 | 0.001 | $C_{rif}\ C_{run} < A_{rif}\ A_{run}\ P_{run}\ P_{rif}$ | A < B |
| | autumn–spring 2014–2015 | 5 | 7.6 | 0.001 | $C_{rif}\ C_{run} < A_{rif}\ A_{run}\ P_{run} < P_{rif}$ | A < AB < B |
| gathering-collector | summer 2014 | 5 | 4.4 | 0.008 | $C_{rif}\ A_{rif}\ A_{run}\ P_{run}\ P_{rif} < C_{run}$ | A < B |
| | autumn–spring 2014–2015 | 5 | 3.9 | 0.005 | $C_{rif}\ A_{rif}\ A_{run}\ P_{run}\ P_{rif} < C_{run}$ | A < B |
| clingers | summer 2014 | 5 | 3.7 | 0.038 | $C_{rif}\ A_{rif}\ A_{run}\ P_{run}\ P_{rif} < C_{run}$ | A < B |
| | autumn–spring 2014–2015 | 5 | 2.4 | 0.008 | $C_{rif}\ A_{rif}\ A_{run}\ P_{run}\ P_{rif} < C_{run}$ | A < B |
| sprawlers | summer 2014 | 5 | 5.0 | 0.003 | $C_{rif}\ C_{run} < A_{rif}\ A_{run}\ P_{run}\ P_{rif}$ | A < B |
| | autumn–spring 2014–2015 | 5 | 6.0 | 0.001 | $C_{rif}\ C_{run} < P_{rif} < A_{rif}\ A_{run}\ P_{run}$ | A < AB < B |

$C_{run}$ = *Cladophora* run, $C_{rif}$ = *Cladophora* riffle, $A_{run}$ = *Acer* run, $A_{rif}$ = *Acer* riffle, $P_{run}$ = *Platanus* run, $P_{rif}$ = *Platanus* riffle

**Table 2.** Summary of mean richness (± 1 S.E.) and abundance (± 1 S.E.) of macroinvertebrates per pack.

| Macroproducer | Habitat | Season | Year(s) | richness/pack | no./pack |
|---|---|---|---|---|---|
| *Cladophora* | riffle | summer | 2014 | 3.1 ± 0.6 | 33.6 ± 16.3 |
| | | autumn–spring | 2014–2015 | 3.4 ± 0.4 | 10.3 ± 1.9 |
| | run | summer | 2014 | 4.3 ± 9.9 | 69.2 ± 19.1 |
| | | autumn-spring | 2014–2015 | 3.0 ± 9.4 | 19.4 ± 6.1 |
| *Acer* | riffle | summer | 2014 | 9.8 ± 0.9 | 40.0 ± 7.8 |
| | | autumn–spring | 2014–2015 | 6.0 ± 0.9 | 16.3 ± 3.3 |
| | run | summer | 2014 | 8.3 ± 0.8 | 38.5 ± 9.2 |
| | | autumn–spring | 2014–2015 | 6.1 ± 0.9 | 12.8 ± 3.1 |
| | riffle | summer | 2014 | 9.5 ± 0.8 | 44.9 ± 10.0 |
| | | autumn–spring | 2014–2015 | 4.9 ± 0.7 | 14.5 ± 1.9 |
| *Platanus* | run | summer | 2014 | 9.6 ± 0.7 | 46.8 ± 8.3 |
| | | autumn–spring | 2014–2015 | 5.8 ± 0.7 | 13.3 ± 2.3 |

**Table 3.** Mean abundance (± 1 S.E.) of each functional feeding group per pack (SHR = shredders, GC = gathering-collectors, FC = filtering-collectors, SCR = scrapers, PIE= piercers and PR = predators).

| | | | | Functional Feeding Group | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Macroproducer | Habitat | Season | Year(s) | SH | GC | FC | SCR | PI | PR |
| *Cladophora* | riffle | summer | 2014 | 0.2 ± 0.1 | 17.2 ± 11.0 | 0.25 ± 0.2 | 2.6 ± 1.0 | 0 | 0.6 ± 0.1 |
| | | autumn–spring | 2014–2015 | 3.0 ± 0.8 | 5.3 ± 1.9 | 0.1 ± 0.1 | 1.9 ± 0.2 | 0 | 0.1 ± 0.1 |
| | run | summer | 2014 | 0.4 ± 0.2 | 42.9 ± 14.0 | 0.8 ± 0.3 | 3.6 ± 0.7 | 0.1 ± 0.1 | 0.8 ± 0.2 |
| | | autumn–spring | 2014–2015 | 1.5 ± 0.6 | 10.6 ± 3.4 | 0 | 7.2 ± 3.1 | 0 | 0.1 ± 0.1 |
| *Acer* | riffle | summer | 2014 | 0.2 ± 0.1 | 11.1 ± 2.6 | 3.1 ± 1.7 | 10.0 ± 2.6 | 0 | 6.1 ± 2.1 |
| | | autumn–spring | 2014–2015 | 10.2 ± 2.4 | 3.6 ± 0.7 | 0.1 ± 0.1 | 0.8 ± 0.3 | 0.1 ± 0.1 | 1.3 ± 0.4 |
| | run | summer | 2014 | 0.9 ± 0.2 | 21.6 ± 5.9 | 0.4 ± 0.1 | 12.6 ± 1.9 | 0 | 6.9 ± 1.9 |
| | | autumn–spring | 2014–2015 | 7.8 ± 1.3 | 4.1 ± 1.0 | 0.1 ± 0.1 | 2.8 ± 1.1 | 0 | 1.7 ± 0.6 |
| *Platanus* | riffle | summer | 2014 | 1.4 ± 0.5 | 10.2 ± 2.0 | 4.1 ± 1.5 | 19.8 ± 3.9 | 0.1 ± 0.1 | 4.1 ± 0.9 |
| | | autumn–spring | 2014–2015 | 9.7 ± 1.4 | 2.4 ± 0.7 | 0 | 0.8 ± 0.4 | 0 | 1 ± 0.4 |
| | run | summer | 2014 | 1.5 ± 0.3 | 13.4 ± 3.6 | 0.8 ± 0.2 | 20.5 ± 2.8 | 0.2 ± 0.1 | 4.5 ± 1.1 |
| | | autumn–spring | 2014–2015 | 5.7 ± 1.3 | 2.6 ± 0.6 | 0.1 ± 0.1 | 3.9 ± 1.2 | 0 | 1.1 ± 0.3 |

**Table 4.** Mean abundance (± 1 S.E.) of each habit found per macroproducer.

| Macroproducer | Habitat | Season | Year(s) | Habit | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Clingers | Sprawlers | Burrowers | Climbers | Swimmers |
| *Cladophora* | riffle | summer | 2014 | 19.5 ± 11.6 | 0.7 ± 0.3 | 0 | 0.2 ± 0.1 | 0.1 ± 0.1 |
| | | autumn–spring | 2014–2015 | 7.5 ± 0.2 | 1.9 ± 0.7 | 0.2 ± 0.1 | 0 | 0.8 ± 0.4 |
| | run | summer | 2014 | 46.3 ± 14.0 | 0.7 ± 0.2 | 1.1 ± 0.3 | 0.2 ± 0.1 | 0.3 ± 0.1 |
| | | autumn–spring | 2014–2015 | 17.9 ± 6.1 | 1.0 ± 0.3 | 0.1 ± 0.1 | 0 | 0.5 ± 0.4 |
| *Acer* | riffle | summer | 2014 | 13.2 ± 3.6 | 8.1 ± 2.1 | 0.2 ± 0.1 | 4.0 ± 1.5 | 2.8 ± 1.2 |
| | | autumn–spring | 2014–2015 | 5.7 ± 1.2 | 5.8 ± 1.4 | 0.1 ± 0.1 | 0.3 ± 0.2 | 4.4 ± 1.6 |
| | run | summer | 2014 | 30.5 ± 6.7 | 10.0 ± 2.6 | 0.7 ± 0.2 | 0.5 ± 0.1 | 0.7 ± 0.2 |
| | | autumn–spring | 2014–2015 | 8.1 ± 2.2 | 6.1 ± 1.2 | 0.2 ± 0.0 | 0.5 ± 0.2 | 1.8 ± 0.6 |
| *Platanus* | riffle | summer | 2014 | 24.0 ± 5.0 | 5.5 ± 1.1 | 0.5 ± 0.2 | 1.8 ± 0.4 | 3.8 ± 1.2 |
| | | autumn–spring | 2014–2015 | 4.3 ± 1.2 | 6.6 ± 1.5 | 0.1 ± 0.1 | 0.4 ± 0.1 | 3.1 ± 0.9 |
| | run | summer | 2014 | 29.1 ± 4.5 | 8.8 ± 3.3 | 1.1 ± 0.4 | 0.9 ± 0.2 | 0.7 ± 0.2 |
| | | autumn–spring | 2014–2015 | 7.05 ± 1.5 | 4.1 ± 1.1 | 0.3 ± 0.2 | 0.4 ± 0.2 | 1.5 ± 0.6 |

**Table 5.** ANCOVA results for AFDM remaining ($\alpha = 0.05$).

| Season, year(s) | df | F-crit | P-value | Pairwise differences | Significance |
|---|---|---|---|---|---|
| summer 2014 | 5 | 2.9 | 0.004 | $C_{rif}$ $C_{run}$ > $A_{riffle}$ $A_{run}$ > $P_{run}$ $P_{rif}$ | A > AB > B |
| fall–spring 2014–2015 | 5 | 22.2 | 0.001 | $C_{rif}$ $C_{run}$ $A_{riffle}$ $A_{run}$ > $P_{run}$ $P_{rif}$ | A > B |

$C_{run}$ = *Cladophora* run, $C_{rif}$ = *Cladophora* riffle, $A_{run}$ = *Acer* run, $A_{rif}$ = *Acer* riffle, $P_{run}$ = *Platanus* run, $P_{rif}$ = *Platanus* riffle

**Table 6.** Summary of k-values, R-squared, p-values, and F-critical value of each decaying macroproducer.

| Macroproducer | Habitat | Season | Year(s) | $-k$ ($d^{-1}$) | $R^2$ | P-value | F-crit |
|---|---|---|---|---|---|---|---|
| *Cladophora* | riffle | summer | 2014 | 0.235 | 0.60 | 0.020 | 9.2 |
| | | autumn–spring | 2014–2015 | 0.036 | 0.88 | 0.005 | 29.8 |
| | run | summer | 2014 | 0.142 | 0.72 | 0.008 | 15.2 |
| | | autumn-spring | 2014–2015 | 0.022 | 0.90 | 0.003 | 37.0 |
| *Acer* | riffle | summer | 2014 | 0.152 | 0.60 | 0.023 | 9.2 |
| | | autumn–spring | 2014–2015 | 0.015 | 0.81 | 0.013 | 17.9 |
| | run | summer | 2014 | 0.047 | 0.70 | 0.009 | 14.5 |
| | | autumn–spring | 2014–2015 | 0.014 | 0.69 | 0.040 | 8.9 |
| *Platanus* | riffle | summer | 2014 | 0.019 | 0.84 | 0.001 | 32.9 |
| | | autumn–spring | 2014–2015 | 0.002 | 0.84 | 0.028 | 15.8 |
| | run | summer | 2014 | 0.018 | 0.89 | <0.001 | 49.6 |
| | | autumn–spring | 2014–2015 | 0.003 | 0.74 | 0.027 | 11.4 |

**Table 7.** ANCOVA results for isotopic values ($\alpha = 0.05$).

| Season, year(s) | df | F-crit | P-value | Pairwise differences | Significance |
|---|---|---|---|---|---|
| summer 2014 | 7 | 6.4 | 0.001 | $BOM_{rif}$ $BOM_{run}$ < $C_{rif}$ $C_{run}$ $A_{rif}$ $A_{run}$ $P_{run}$ $P_{rif}$ | A < B |
| autumn–spring 2014–2015 | 7 | 50.6 | 0.001 | $C_{rif}$ $C_{run}$ < $A_{rif}$ $A_{run}$ $P_{run}$ $P_{rif}$ $BOM_{rif}$ $BOM_{run}$ | A < B |

$C_{run}$ = *Cladophora* run, $C_{rif}$ = *Cladophora* riffle, $A_{run}$ = *Acer* run, $A_{rif}$ = *Acer* riffle, $P_{run}$ = *Platanus* run, $P_{rif}$ = *Platanus* riffle, $BOM_{run}$ = benthic organic matter run, $BOM_{rif}$ = benthic organic matter riffle

**Table 8.** Summary of mean $\delta^{13}C$ values (± 1 S.E.) per pack.

| Macroproducer | Habitat | Season | Year(s) | $\delta^{13}C$ |
|---|---|---|---|---|
| *Cladophora* | riffle | summer | 2014 | -29.44 ± 0.09 |
| | | autumn–spring | 2014–2015 | -32.58 ± 0.52 |
| | run | summer | 2014 | -29.40 ± 0.15 |
| | | autumn–spring | 2014–2015 | -32.58 ± 0.59 |
| *Acer* | riffle | summer | 2014 | -28.90 ± 0.44 |
| | | autumn–spring | 2014–2015 | -29.42 ± 0.37 |
| | run | summer | 2014 | -29.10 ± 0.40 |
| | | autumn–spring | 2014–2015 | -29.07 ± 0.49 |
| *Platanus* | riffle | summer | 2014 | -29.72 ± 0.19 |
| | | autumn–spring | 2014–2015 | -29.18 ± 0.15 |
| | run | summer | 2014 | -29.28 ± 0.18 |
| | | autumn–spring | 2014–2015 | -28.54 ± 0.14 |

**Table 9.** Comparison between the (*k*) values of study leaves and known literature**.**

| Species | Habitat | Season(s) | *k* ($d^{-1}$) | Order | Citation |
|---|---|---|---|---|---|
| *Acer* Mix | run | autumn–spring | 0.014 | 7 | 2014–2015 |
| | riffle | autumn–spring | 0.015 | 7 | 2014–2015 |
| | run | summer | 0.047 | 7 | 2014 |
| | riffle | summer | 0.152 | 7 | 2014 |
| *A. saccharinum* | riffle/run | autumn | 0.023 | 2 | Swan and Palmer 2004 |
| | riffle/run | summer | 0.070 | 2 | Swan and Palmer 2004 |
| | run | autumn | 0.017 | n.a. | Herbst 1980 |
| | run | autumn | 0.013 | n.a. | Herbst 1980 |
| | riffle/run | autumn | 0.007 | 2 | Swan and Palmer 2006 |
| | riffle/run | autumn | 0.014 | 2 | Swan and Palmer 2004 |
| *A. negundo* | run | autumn–spring | 0.018 | 2 | Hill et al. 1988 |
| | run | autumn–spring | 0.017 | 4 | Hill et al. 1988 |
| | n.a. | autumn | 0.023 | 3 | McArthur et al. 1988 |
| | n.a. | summer | 0.032 | 3 | McArthur et al. 1988 |
| *P. occidentalis* | riffle | autumn–spring | 0.002 | 7 | 2014–2015 |
| | run | autumn–spring | 0.003 | 7 | 2014–2015 |
| | riffle | summer | 0.019 | 7 | 2014 |
| | run | summer | 0.018 | 7 | 2014 |
| | riffle/run | autumn | 0.002 | 2 | Swan and Palmer 2006 |
| | riffle/run | summer | 0.050 | 2 | Swan and Palmer 2004 |
| | riffle/run | autumn | 0.016 | 2 | Swan and Palmer 2004 |
| | riffle/run | summer | 0.004 | 2 | Swan and Palmer 2004 |
| | run | autumn–winter | 0.003 | n.a. | Bauers 2004 |
| | riffle | winter-spring | 0.005 | 2 | Sponseller and Benfield |
| | riffle | autumn | 0.071 | 3 | Jacobs 1998 |
| | riffle | autumn | 0.009 | 2 | Jacobs 1999 |
| | riffle | n.a. | 0.013 | 2 | Edinger et al. 2008 |
| | riffle/run | autumn | 0.004 | n.a. | Benfield et al. 1977 |

n.a. = information not available in text

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