REPORT

Role of first-order consumers in ecosystem carbon flow

Just Cebrian[1,2]

[1]Dauphin Island Sea Lab, 101 Bienville Blvd, Dauphin Island, Alabama, 36528, USA

[2]Department of Marine Sciences, University of South Alabama, Mobile, 36688, USA

E-mail: jcebrian@disl.org

Abstract

Herbivores and detritus consumers (i.e. microbial decomposers and invertebrate and vertebrate detritivores) are pivotal components of trophic food webs and thus play a paramount role in the trophic transference and turnover of producer-fixed carbon. Hence, elucidating patterns in carbon flux through these first-order consumers is important to understand the nature and controls of carbon flow in ecosystems. Here, using the largest literature compilation to date, I show that, in contrast with the current belief, aquatic herbivores accumulate on average three times as much biomass as do terrestrial herbivores for a given level of primary production and, as a consequence, turn over the ingested carbon only slightly faster than do terrestrial herbivores. Conversely, aquatic detritus consumers generally accumulate a much lower biomass (i.e. over ten times lower) than their terrestrial counterparts for a given level of primary production and, thus, they turn over the ingested carbon much more quickly (i.e. over ten times faster). Because the detrital pathway generally dominates the trophic flow of carbon in both aquatic and terrestrial ecosystems, carbon also tends to flow through the total compartment of first order-consumers (both herbivores and detritus consumers) at a much faster rate in aquatic than in terrestrial ecosystems. Thus, aquatic systems, because of faster carbon recycling rates through their basal and first-order levels of the food chain, appear to have a lower capacity than do terrestrial systems for retaining carbon under natural or anthropogenic increases in photosynthetic fixation.

Keywords

Carbon flow, decomposers, decomposition, detritivores, ecosystems, herbivores, herbivory.

INTRODUCTION

Herbivores and consumers of detritus (i.e. microbial decomposers and invertebrate and vertebrate detritivores) are key components of food webs and, thus, they are important determinants of carbon flow in ecosystems. This contention is based on a myriad of case studies in numerous types of aquatic and terrestrial ecosystems (see, for instance, reviews by Valiela 1995; Valentine & Heck 1999; Chapin *et al.* 2002). We know little, however, about how much and why the trophic transference and turnover of carbon through herbivores and detritus consumers differ between aquatic and terrestrial ecosystems. Elucidating the extent and causes of those differences would help improve our understanding of the nature and regulation of carbon flow in ecosystems.

One well-known contrast is that herbivory is generally more prevalent in aquatic than in terrestrial ecosystems (Petrusewicz & Grodzinski 1975; Cyr & Pace 1993; Cebrian & Duarte 1994). Although not extensive, the largest comparison to date has shown that, for a given value of primary production, aquatic herbivores consume on average three times more producer carbon than do terrestrial herbivores (Cyr & Pace 1993). Thus, because the efficiency of herbivore productivity (i.e. ratio of herbivore biomass produced per unit of producer biomass ingested) does not seem to vary systematically between aquatic and terrestrial herbivores (Schroeder 1981; Elser *et al.* 2000a), the production of herbivore biomass should be on average three times higher in aquatic than in terrestrial ecosystems for a given value of primary production. However, Cyr & Pace (1993) also documented that aquatic and terrestrial ecosystems with

similar levels of primary production tend to accumulate similar standing stocks of herbivore biomass.

These past results imply two important differences in the role of herbivores in carbon flow between aquatic and terrestrial ecosystems. First, for a given level of primary production aquatic herbivores should support on average three times higher predatory/non-predatory mortality losses per unit of biomass produced than do terrestrial herbivores because they produce three times more biomass, but accumulate similar standing stocks, in comparison with terrestrial herbivores. Thus, for a given level of primary production, aquatic herbivores appear to turn over and transfer carbon to higher trophic levels on average at a three times faster rate than their terrestrial counterparts. Secondly, for a given level of primary production aquatic and terrestrial herbivores seem to have a similar importance as carbon reservoirs because they tend to accumulate similar standing stocks. In view of their relevance for a complete understanding of carbon flow in ecosystems, these past results and corollaries need to be re-evaluated with extensive comparisons that cover a wider range of aquatic and terrestrial ecosystems.

To my knowledge, no patterns describing how aquatic and terrestrial ecosystems differ in carbon turnover through detritus consumers have been established yet. In part, this is probably because of the paucity of measurements of biomass of detritus consumers relative to measurements of herbivore biomass that has long pervaded in the ecological literature. However, in the last decade a significant number of reports of biomass of detritus consumers has appeared for both aquatic and terrestrial ecosystems and it is now possible to provide a first account of how the two types of ecosystems differ in the trophic transference and turnover of carbon through detritus consumers. This is of special relevance to understand carbon flow in ecosystems as in general most carbon fixed by producers enters the detrital compartment in both aquatic and terrestrial ecosystems (Cebrian & Duarte 1995; Schlesinger 1997; Cebrian 1999).

In a previous paper (Cebrian & Lartigue 2004), we examined how aquatic and terrestrial ecosystems differed in the extent of carbon consumption by herbivores and detritus consumers. The results showed that aquatic ecosystems tended to support larger levels of consumption by herbivores than did terrestrial ecosystems, but detritus consumption tended to remain similar in the two types of ecosystems. Here, I follow up on these previous results and investigate (i) the differences between aquatic and terrestrial ecosystems in the accumulation of biomass of herbivores and detritus consumers, and (ii) the implications on carbon turnover and trophic transference through these first-order consumers. The analysis presented here reveals new contrasts between aquatic and terrestrial ecosystems in

how carbon flows through the herbivore compartment. It also provides a first account of how carbon flux through detritus consumers differs between aquatic and terrestrial ecosystems. These new patterns contribute to a better understanding of the nature and regulation of carbon flow in ecosystems.

MATERIALS AND METHODS

Variables and characteristics of the data set

I surveyed the literature for data on net primary production and biomass of and carbon consumption by herbivores and detritus consumers in communities that represented a broad range of aquatic (streams, rivers, lakes, the open ocean, enclosed seas, estuaries, and shallow coastal ecosystems, such as sediment flats, seagrass beds, macroalgal beds and coral reefs) and terrestrial (tundra heathlands, taiga forests, temperate and tropical shrublands and forests, temperate and tropical grasslands, swamp forests and marshes, and desert shrublands) ecosystems. When compiling the data set, I made an effort to sample most ecological journals and as most 'grey' literature as possible. This approach, in combination with the large number of values gathered and wide range of systems encompassed, should guarantee that the data set is representative of the information available in the scientific record. That record is inevitably biased as a result of factors such as funding and research preferences, existence of in-site baseline information and explicit management needs. Indeed, the data set contains an unproportionally higher number of entries for well-studied community types such as oceanic and coastal phytoplankton communities, seagrass meadows, grasslands and forests, whereas the number is low for other much less explored types, such as freshwater benthic microalgal beds and tundra and desert shrublands. At any rate, even little-studied community types were searched extensively and thus, when values could be gathered for those community types, the range compiled was often large. As a consequence, the values obtained for little-studied community types, albeit few, nevertheless encompass a substantial fraction of the total range covered by the patterns obtained with the entire data set (see results). Therefore, the conclusions reached here should be indicative of what the current scientific record would allow to achieve and it also seems that the inclusion of more cases of little-studied community types would not change significantly the nature and strength of the patterns presented here.

I only considered community studies that met three criteria. First, the community had not been, nor was it during the duration of the study, deliberately impacted by human activities. Hence, the communities compiled had apparently been exposed to natural environmental conditions

and continued to be during the study. However, in some of the communities compiled, the effects of long-pervading human impacts, such as overfishing or overexploitation of top predators, may still have been present. Secondly, the studies encompassed at least 1 year of observations, with several measurements taken in each season, thereby allowing for an adequate integration of seasonal variability. In addition, reports of highly annual systems (i.e. where most biological activity occurs in late spring/summer) or systems with highly seasonal processes (e.g. fall detrital production in temperate communities of aquatic and terrestrial macrophytes, or fall detrital input in temperate streams, rivers and lakes) were considered only if they provided adequate sampling frequency during the important and other seasons for a correct weighting into yearly-integrated values. Thirdly, the reports included the most important types of producers, herbivores and/or detritus consumers in the community (i.e. accounting for most of the primary production and consumption of producer biomass or detritus in that community; values of detritus consumer biomass compiled for benthic communities were generally an exception, but see below). The data set, further explanations and list of references used are available in web Appendix S2–S4 (see Supplementary Material section at the end of this paper).

Most (>80%) of the values of net primary production, consumption by and biomass of herbivores and biomass of detritus consumers compiled in the data set were directly provided in the reports. In contrast, I found few reports with direct values of carbon consumption by detritus consumers. Indeed, only <30% of the values of consumption of detrital carbon compiled in the data set were directly provided in the reports. I used a variety of methods to estimate the rest of values of primary production and consumption by, and biomass of herbivores and detritus consumers gathered in the data set. As a result of space limitations, the derivation of those estimates is explained in web Appendix S1 (see section 'Estimate derivation'). The discussion of the error committed with those estimates and effects on the patterns obtained is also included in the web Appendix S1 (section 'Effects of the calculation error committed with my estimates on the patterns obtained'). In addition, the values of net primary production and/or detritus consumption compiled for most communities of rooted aquatic and terrestrial macrophytes referred only to the above-ground compartment, with only a few of those values including both the above- and below-ground compartments. The effects of this limitation on the patterns obtained are also discussed in web Appendix S1 (section 'Effects of comparing different system compartments on the patterns obtained'). Below, I briefly describe the variables studied and methods commonly used in the reports compiled.

Net primary production ($g\ C\ m^{-2}\ year^{-1}$) corresponds to the net incorporation of CO_2 into producer biomass through photosynthesis (i.e. gross primary production-producer respiration). It was often measured using methods of ^{14}C uptake or changes in oxygen concentration in field or lab incubations, leaf tagging and biomass accrual corrected for herbivory and natural mortality. Most authors estimated herbivore biomass ($g\ C\ m^{-2}$) as the product of natural herbivore abundance (which was measured with microscopy, capture/recapture methods or visual censuses) and mean herbivore individual weight. Methods to measure consumption by herbivores ($g\ C\ m^{-2}\ year^{-1}$) commonly included dilution or evacuation rate techniques (mostly in phytoplanktonic communities), exclosures/enclosures, models of herbivore metabolism and reconstruction techniques based on bite marks and leaf growth rates. Authors often derived mean consumption rates per herbivore individual or size class in lab or field experiments and extrapolated to a per m^2 basis using estimates of field densities of herbivore individuals or size classes.

Detritus consumers include microbial decomposers (i.e. bacteria and fungi) and detritivorous invertebrate and vertebrate organisms. The former metabolize dissolved and particulate detritus, whereas the latter feed on particulate detritus and attached bacteria and fungi. The values of detritus consumer biomass ($g\ C\ m^{-2}$) gathered for terrestrial communities included bacteria, fungi and invertebrate detritivores (micro-, meso- and macrofauna). No report accounted for vertebrate detritivores, but these organisms are generally rare in terrestrial habitats and contribute little to the total pool of detritus consumer biomass (Swift *et al.* 1979). For pelagic systems, the values compiled included bacteria, invertebrate detritivores (i.e. micro-, macro- and gelatinous zooplankton) and, when significant, vertebrate detritivores (i.e. some fish species). No report for pelagic communities accounted for fungi, but these decomposers are believed to be unimportant in most pelagic systems (Newell 1994, 1996). Despite the extensive literature search, I did not find any reports for benthic communities that met the three criteria for selection (see above) and provided values of biomass for both microbial decomposers and invertebrate and vertebrate detritivores. Most reports provided values of biomass only for invertebrate (micro-, meio- and macrofauna) and, when important, vertebrate (some fish species) detritivores. A few of them also included bacteria, but all of them disregarded fungi. The effects of this limitation are discussed in web Appendix S1 (section 'Effects of incomplete reports of detritus consumer biomass for benthic communities on the patterns obtained').

Detritus consumer biomass ($g\ C\ m^{-2}$) was often calculated as the product of field abundance (which was normally estimated with microscopy) and mean individual weight. Other methods included the use of ergosterol concentrations

as a proxy for fungal biomass and, for microbial decomposers in terrestrial systems, the fumigation/incubation technique. Authors often estimated carbon consumption by detritus consumers (g C m^{-2} year^{-1}) from measurements of mass loss for detritus enclosed in litter bags or incubation containers, measurements of oxygen consumption in incubations of detrital material, and models of community metabolism.

Finally, to also examine the differences in overall carbon flux through first-order consumers (i.e. both herbivores and detritus consumers) between aquatic and terrestrial systems, I calculated total consumption by first-order consumers (g C m^{-2} year^{-1}) as the sum of consumption by herbivores and detritus consumption whenever these two values were available for the same community. I also calculated total biomass of first-order consumers (g C m^{-2}) as the sum of the biomass of herbivores and detritus consumers whenever possible for the communities compiled.

Statistical methods

To examine how aquatic and terrestrial systems differ in carbon turnover through herbivores and detritus consumers, and whether those differences covary with the level of net primary production achieved, I analysed how the slope and elevation of the regression equations fitted between the biomass of and consumption by herbivores or detritus consumers, as dependent variables, and net primary production as the independent variable varied between the two types of ecosystems. The equations were adjusted with Model I least-square regression, which easily allows for comparisons of slopes (F-test) and elevations (ANCOVA) between relationships. Both the dependent and independent variables of the regression equations presented here bear measurement error, but there are two reasons that allow for the use of Model I regression in this case. First, it is well accepted that, when the measurement error committed with the dependent variable (Y-variate) largely exceeds the measurement error committed with the independent variable (X-variate), Model I regression yields robust results (Sokal & Rohlf 1995; Zar 1998). Here, the measurement error committed with the variable plotted as independent (primary production) is usually much smaller than the measurement error committed with the variables plotted as dependent (biomass of and consumption by herbivores, detritus consumers and total pool of first-order consumers). This can be clearly inferred from the description of methods provided above and in web Appendix S1 (see Supplementary Material); the techniques that have been used to derive the values of primary production gathered in the data set normally bear much less measurement error and are based on less assumptions than the techniques used to derive the values of biomass of and consumption by herbivores and detritus consumers.

The second reason stems from the fact that, when definite causality can be established between a pair of variables, Model I regression is the method of choice (Rayner 1985; Sokal & Rohlf 1995). At the scale covered in my comparisons, it is clear that the variability in primary production generates, at least partially, the differences observed in biomass of and consumption by herbivores and detritus consumers across ecosystems (see results), as the reverse situation (i.e. that the variability in biomass of and consumption by herbivores and detritus consumers generates the differences observed in primary production) is inconceivable. If that were the case, consumption by herbivores and detritus consumers should stimulate primary production to unrealistic levels. Therefore, Model I regression is an appropriate technique to assess the nature and strength of the dependence of biomass of and consumption by herbivores, detritus consumers and total pool of first-order consumers on primary production.

RESULTS

In a previous paper, we examined whether consumption by herbivores and net primary production were associated in aquatic and terrestrial ecosystems (Cebrian & Lartigue 2004; Fig. 5a). The results revealed a tendency for aquatic and terrestrial herbivores to consume greater amounts of carbon in ecosystems with a higher primary production, although the tendency was somewhat weak for the terrestrial data set. Here, I compare the slopes and elevations of the regression equations fitted for aquatic and terrestrial ecosystems, which are described in Table 1 in Cebrian & Lartigue (2004). The analysis shows that the rate of increase in consumption with higher primary production does not differ between aquatic and terrestrial ecosystems (H$_o$: equality between slopes, F-test, $P = 0.84$) but, for a given value of primary production, herbivores remove on average four times more carbon in aquatic than in terrestrial ecosystems (ANCOVA, $P < 0.001$).

Herbivore biomass also increases with higher primary production in aquatic and terrestrial ecosystems (Fig. 1). The rate of increase in herbivore biomass with higher production is similar between the two types of ecosystems (F-test, $P = 0.35$) but, for a given level of primary production, aquatic ecosystems support on average three times more herbivore biomass than do terrestrial ecosystems (ANCOVA, $P < 0.001$).

We also examined previously whether larger detritus consumption was associated with higher primary production in aquatic and terrestrial ecosystems and found strong associations for the two types of systems (Cebrian & Lartigue 2004; Fig. 11a, Table 1). Here, I compare the slope and intercept of the regression equations fitted to the two types of systems. The analysis shows that the rate of increase
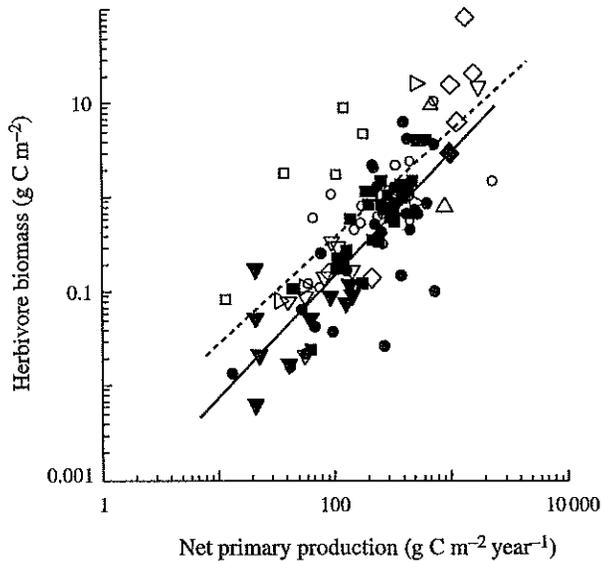
Figure 1 The relationships between herbivore biomass and net primary production for aquatic (log biomass = −2.67 (±0.36) + 1.12 (±0.15) log production; $n = 48$, $R^2 = 0.54$, $P < 0.001$) and terrestrial ecosystems (log biomass = −3.43 (±0.28) + 1.30 (±0.12) log production; $n = 65$, $R^2 = 0.63$, $P < 0.001$). Symbols denote the following aquatic communities: communities of freshwater phytoplankton (open circles), communities of marine phytoplankton (open squares), freshwater benthic microalgal beds (open left-tilted triangles), marine benthic microalgal beds (open right-tilted triangles), marine macroalgal beds (open diamonds), meadows of freshwater submerged macrophytes (open upside-down triangles) and seagrass meadows (open triangles); and the following terrestrial communities: communities of tundra shrubs and grasses (closed upside-down triangles), freshwater and marine marshes − emergent macrophytes (closed diamonds), temperate and tropical shrublands and forests (closed circles), temperate and tropical grasslands (closed squares) and mangroves (closed triangles). Dashed (aquatic ecosystems) and continuous (terrestrial ecosystems) lines depict the regression equations. Data have been log-transformed to comply with the assumptions of least-square regression analysis.

in detritus consumption with higher production is similar between the two types of systems (F-test, $P = 0.29$) but, unlike herbivores, detritus consumers tend to consume a similar amount of carbon in aquatic and terrestrial ecosystems that have a similar primary production (ANCOVA, $P = 0.20$).

The biomass of detritus consumers also increases with higher primary production in aquatic and terrestrial ecosystems (Fig. 2). The rate of increase in biomass with higher production does not differ significantly between the two types of ecosystems (F-test, $P = 0.10$) but, interestingly, terrestrial detritus consumers accumulate a much higher biomass (i. e. over ten times higher) than do aquatic detritus
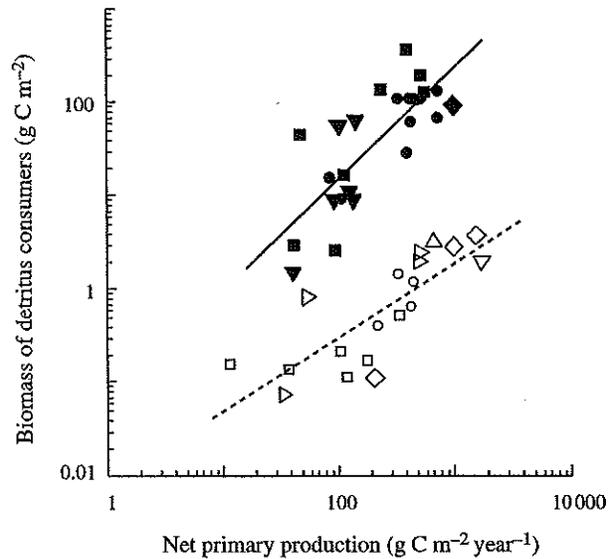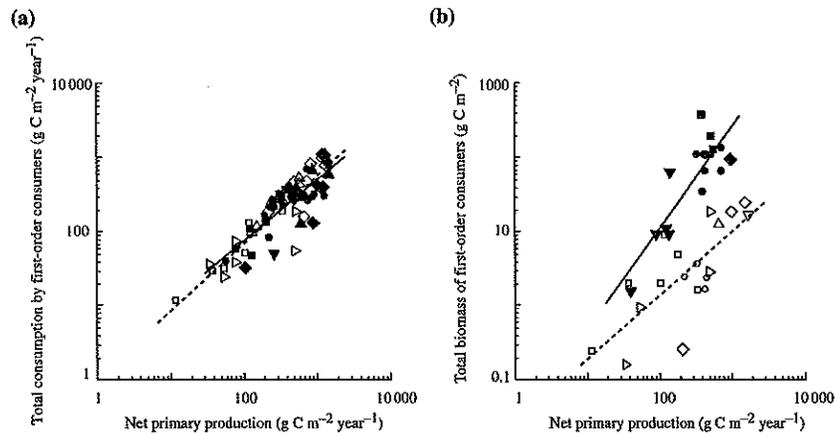

Figure 2 The relationships between detritus consumer biomass and net primary production for aquatic (log biomass = −2.10 (±0.35) + 0.79 (±0.14) log production; $n = 19$, $R^2 = 0.62$, $P < 0.001$) and terrestrial ecosystems (log biomass = −1.21 (±0.44) + 1.19 (±0.19) log production; $n = 27$, $R^2 = 0.61$, $P < 0.001$). Symbols and lines as in Fig. 1. Data have been log-transformed to comply with the assumptions of least-square regression analysis.

consumers for a given value of primary production (ANCOVA, $P < 0.001$).

Total consumption by first-order consumers (i.e. both herbivores and detritus consumers) increases with higher primary production at a similar rate in aquatic and terrestrial ecosystems (Fig. 3a, F-test, $P = 0.48$) and, for a given level of primary production, first-order consumers consume a similar amount of carbon in the two types of ecosystems (ANCOVA, $P = 0.87$). Total biomass of first-order consumers also increases with higher primary production in aquatic and terrestrial ecosystems (Fig. 3b). The rate of increase does not differ significantly between the two types of ecosystems (F-test, $P = 0.10$) but, for a given level of primary production, terrestrial ecosystems support on average a much higher (i. e. over ten times higher) total biomass of first-order consumers than do aquatic ecosystems (ANCOVA, $P < 0.001$).

DISCUSSION

The results presented here show that in general herbivory is more prominent in aquatic than in terrestrial ecosystems; for a given level of primary production, herbivores consume on average four times more producer biomass in aquatic ecosystems. That consumption by herbivores tends to be greater in aquatic than in terrestrial ecosystems has also been

Figure 3 (a) The relationships between total consumption by first-order consumers and net primary production for aquatic (log consumption $= 0.03$ (± 0.20) $+ 0.91(\pm 0.08)$ log production; $n = 26$, $R^2 = 0.82$, $P < 0.001$) and terrestrial ecosystems (log consumption $= 0.24$ (± 0.24) $+ 0.82$ (± 0.09) log production; $n = 46$, $R^2 = 0.64$, $P < 0.001$). (b) The relationships between first-order consumer biomass and net primary production for aquatic (log biomass $= -1.59$ (± 0.43) $+ 0.86$ (± 0.18) log production; $n = 19$, $R^2 = 0.56$, $P < 0.001$) and terrestrial ecosystems (log biomass $= -1.68$ (± 0.54) $+ 1.36$ (± 0.21) log production; $n = 18$, $R^2 = 0.70$, $P < 0.001$). Symbols and lines as in Fig. 1. Data have been log-transformed to comply with the assumptions of least-square regression analysis.

found in past comparisons (Petrusewicz & Grodzinski 1975; Whittaker 1975; Cyr & Pace 1993; Cebrian & Duarte 1994; Cebrian *et al.* 1998; Griffin *et al.* 1998; Cebrian 1999). To date, however, only one report (Cyr & Pace 1993) has examined whether herbivore biomass also tends to be larger in aquatic ecosystems. Compiling data from the literature, Cyr & Pace (1993) documented that aquatic and terrestrial ecosystems with a similar primary production tended to maintain a similar herbivore biomass. This contrasts with the finding reported here that, for a given level of primary production, aquatic ecosystems tend to support three times more herbivore biomass than do terrestrial ecosystems. This controversy probably stems from the fact that my analysis includes a wider range of ecosystem types and more values of herbivore biomass (i.e. 28 and 50 values for aquatic and terrestrial systems in Cyr & Pace (1993) vs. 48 and 65 values here).

My results suggest a new portrait of how carbon turnover through herbivores differs between aquatic and terrestrial ecosystems. For a given level of primary production, aquatic herbivores appear to turn over and transfer carbon to higher trophic levels only slightly faster (1.3 times on average) than do terrestrial herbivores, but not three times faster as found by Cyr & Pace (1993). Aquatic herbivores consume on average four times more carbon than do terrestrial herbivores for a given level of primary production and, because the efficiency of herbivore productivity (i.e. ratio of herbivore biomass produced per unit of producer carbon ingested) does not vary systematically between the two types of herbivores (Schroeder 1981; Elser *et al.* 2000a), they should also produce four times more biomass. The data compiled here also shows that aquatic herbivores tend to

accumulate three times more biomass than do terrestrial herbivores for a given level of primary production and, thus, they should turn over the ingested carbon only 1.3 times faster (the ratio of a four-fold greater production to a three-fold greater accumulation). These results suggest that, for a given level of primary production, aquatic herbivores should tend to support 1.3 times, but not three times as previously proposed (Cyr & Pace 1993), greater predatory/non-predatory mortality losses per unit of produced biomass than do terrestrial herbivores.

There is now ample evidence that higher nutrient concentrations in producers stimulate the synthesis of RNA and enzymes in aquatic and terrestrial herbivores, thereby increasing their metabolical and mass-specific growth rates (Mattson 1980; Sterner & Hessen 1994; Hartley & Jones 1997; Elser *et al.* 1996, 2000a,b, 2003; Stelzer & Lamberti 2002; Sterner & Elser 2002). Higher mass-specific growth rates, in turn, may be conducive to a larger accumulation of herbivore biomass and higher areal rates of consumption of producer carbon (Cebrian 1999; Cebrian & Lartigue 2004; Sterner & Elser 2002; Schade *et al.* 2003). Therefore, the differences in biomass and consumption observed between aquatic and terrestrial herbivores for a given level of primary production may partially result from differences in internal nutrient concentrations between aquatic and terrestrial producers. Indeed, in a previous paper (Cebrian & Lartigue 2004; Fig. 2), we compiled values of producer internal nitrogen and phosphorus concentrations (as % of dry weight) and net primary production for a wide range of aquatic and terrestrial ecosystems and showed that, for a given level of primary production, aquatic producers tended to have larger internal nitrogen and

phosphorus concentrations than did terrestrial producers. These differences may have been partly responsible for the higher levels of biomass and consumption found for aquatic herbivores.

In contrast, aquatic and terrestrial detritus consumers tend to consume a similar amount of carbon for a given level of primary production. This tendency may partially result from the interaction between the quantity and quality of producer detritus generated in aquatic and terrestrial ecosystems. For a given level of primary production, aquatic herbivores remove on average four times more biomass than do terrestrial herbivores. Hence, assuming steady-state of producer biomass over the study period (which was seemingly the case in most of the studies compiled), aquatic systems should generate on average four times less producer detritus than terrestrial systems for a given level of primary production. Detritus of aquatic producers, however, tends to have higher internal nutrient concentrations than does detritus of terrestrial producers (Tenore *et al.* 1982; Enriquez *et al.* 1993; Cebrian 1999; Cebrian & Lartigue 2004) and it has been well established that higher nutrient concentrations in aquatic and terrestrial producer detritus stimulate the rate of consumption by decomposers and detritivores per unit of detritus mass (Iversen 1974; Melillo *et al.* 1982; Goldman *et al.* 1987; Enriquez *et al.* 1993; Cebrian 1999; Sterner & Elser 2002). Therefore, for a given level of primary production, aquatic ecosystems tend to generate less producer detritus, but the detritus tends to support greater consumption rates per unit of detritus mass. As producer detritus generally accounts for a significant fraction, albeit variable, of the total detrital pool in ecosystems, this interaction may partially explain why aquatic and terrestrial ecosystems tend to support similar areal rates of detritus consumption for a given level of primary production.

The results present a first account of how carbon turnover through detritus consumers varies between aquatic and terrestrial ecosystems. For a given level of primary production, aquatic and terrestrial detritus consumers tend to consume a similar amount of carbon and, because the efficiency of secondary production (i.e. ratio of consumer biomass produced per unit of detritus carbon consumed) does not seem to vary systematically between them (Schroeder 1981), they should also tend to produce a similar amount of biomass. Yet, my comparison shows that aquatic detritus consumers tend to accumulate a much lower biomass (i.e. over ten times lower) than their terrestrial counterparts for a given level of primary production. It thus follows that, for a given level of primary production, aquatic detritus consumers should turn over and transfer carbon to higher trophic levels at a much faster rate (i.e. over ten times faster) than do terrestrial detritus consumers. This strongly suggests that detritus consumers generally support much

higher predatory/non-predatory mortality rates per unit of produced biomass in aquatic than in terrestrial ecosystems.

When herbivores and detritus consumers are lumped into a common trophic pool (i.e. first-order consumers), the patterns observed in total consumption by herbivores and detritus consumers parallel those found in detritus consumption alone; the rate of increase in consumption with higher primary production is similar in aquatic and terrestrial ecosystems and, for a given level of production, the two types of systems tend to support a similar consumption. This parallelism is a consequence of the fact that in general the detrital pathway dominates the trophic transference of carbon in both aquatic and terrestrial systems. To document this, I have compared the extent of consumption by herbivores (Fig. 5a in Cebrian & Lartigue 2004) with that of detritus consumption (Fig. 11a in Cebrian & Lartigue 2004) at a number of levels of primary production in aquatic and terrestrial ecosystems. In aquatic ecosystems, decomposers and detritivores consume roughly the same amount of carbon as do herbivores at a production level of 10 g C m^{-2} year^{-1}, but they consume on average 1.5 and 3 times more carbon at production levels of 100 and 1000 g C m^{-2} year^{-1} respectively. In terrestrial ecosystems, decomposers and detritivores consume five times more carbon than do herbivores at a production level of 10 g C m^{-2} year^{-1}, eight times at a production level of 100 g C m^{-2} year^{-1} and 12 times at a production level of 1000 g C m^{-2} year^{-1}. In view of these differences, and as primary production exceeds 100 g C m^{-2} year^{-1} for most of the systems compared, it is easy to see why the patterns found in total consumption by herbivores and detritus consumers parallel those found in detritus consumption alone.

Likewise, the patterns found in total biomass of first-order consumers parallel those found in the biomass of detritus consumers alone; the rate of increase in biomass with higher primary production does not differ significantly between aquatic and terrestrial ecosystems but, for a given level of production, terrestrial ecosystems accumulate a much higher biomass than aquatic ecosystems. This results from the fact that, for a given level of primary production, the biomass of terrestrial detritus consumers tends to be much larger (i.e. over ten times larger) than the biomass of aquatic detritus consumers and the biomass of aquatic and terrestrial herbivores. Thus, the differences found between aquatic and terrestrial ecosystems in the biomass of detritus consumers alone drive the differences observed in the sum of herbivore and detritus consumer biomass. Considered together, these patterns imply that in general, carbon is turned over and transferred through the pool of first-order consumers to higher trophic levels at a much faster rate in aquatic than in terrestrial systems. For a given level of primary production, the analysis presented here suggests that the rate of carbon turnover through first-order

consumers tends to be more than ten times faster in aquatic systems.

CONCLUSIONS

This report shows substantial differences between aquatic and terrestrial ecosystems in the rate of carbon flow through herbivores and detritus consumers. The exercises presented in the web Appendix S1 demonstrate that, despite some limitations of the data set (i.e. indirect estimates, different system compartments compared, incomplete values of detritus consumer biomass in benthic systems), those differences are robust. The results first confirm previous observations that herbivores tend to consume more producer biomass in aquatic than in terrestrial ecosystems. However, contrary to the current belief, herbivores also tend to accumulate a larger biomass in aquatic ecosystems, thereby turning over and transferring carbon to higher trophic levels only slightly faster than they do in terrestrial ecosystems. The differences in the rate of carbon turnover through detritus consumers are much larger. Decomposers and detritivores tend to consume a similar amount of carbon in aquatic and terrestrial ecosystems, but tend to accumulate a much lower biomass in aquatic ecosystems. As a consequence, carbon is turned over and transferred through detritus consumers to higher trophic levels at a much faster rate in aquatic than in terrestrial ecosystems. The analysis suggests that, for a given level of primary production, the extent of these differences exceeds one order of magnitude.

Because in general most primary production in both aquatic and terrestrial systems enters the detrital pathway, the differences in carbon turnover through the total pool of first-order consumers (both herbivores and consumers of detritus) between the two types of systems parallel the differences found in carbon turnover through detritus consumers alone. It has been shown that in general carbon turns over much faster through the pools of producer biomass and detritus in aquatic than in terrestrial ecosystems (Enriquez *et al.* 1993; Cebrian & Duarte1995; Schlesinger 1997; Cebrian *et al.* 1998; Cebrian 1999). This report documents that this is also the case for the pool of detritus consumers and total pool of first-order consumers. Thus, it may be expected that upon increases in net primary production as a result of anthropogenic or natural impacts, and provided the patterns obtained here hold under those impacts, the extra carbon fixed by producers will remain as producer biomass, detritus or biomass of detritus/first-order consumers for a much shorter time span in aquatic than in terrestrial ecosystems before being released back into the atmosphere or transferred to higher trophic levels in the food web. Thus, aquatic systems, because of faster carbon

recycling rates through their basal and first-order levels of the food chain, appear to have a lower capacity than do terrestrial systems for retaining carbon under increases in photosynthetic fixation.

ACKNOWLEDGEMENTS

SUPPLEMENTARY MATERIAL

The following information is available from http://www.blackwellpublishing.com/journals/products/suppmat/ELE/ELE574/ELE574.html

Appendix S1 Estimate derivation and effect on patterns obtained

Appendix S2 Notes for using the data set

Appendix S3 Data set

Appendix S4 Literature used for the compilation of the data set

REFERENCES

Cebrian, J. (1999). Patterns in the fate of production in plant communities. *Am. Nat.*, 154, 449–468.

Cebrian, J. & Duarte, C.M. (1994). The dependence of herbivory on growth rate in natural plant communities. *Funct. Ecol.*, 8, 518–525.

Cebrian, J. & Duarte, C.M. (1995). Plant growth-rate dependence of detrital carbon storage in ecosystems. *Science*, 268, 1606–1608.

Cebrian, J. & Lartigue, J. (2004). Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecol. Monogr.*, 74(2), in press.

Cebrian, J., Williams, M., McClelland, J. & Valiela, I. (1998). The dependence of heterotrophic consumption and C accumulation on autotrophic nutrient content in ecosystems. *Ecol. Lett.*, 1, 165–170.

Chapin, III, F.S., Matson, P.A. & Mooney, H.A. (2002). *Principles of Terrestrial Ecosystem Ecology*. Springer Verlag, New York, USA.

Cyr, H. & Pace, M.L. (1993). Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature*, 361, 148–150.

Elser, J.J., Dobberfuhl, D.R., MacKay, N.A. & Schampel, J.H. (1996). Organism size, life history, and N:P stoichiometry. *Bioscience*, 46, 674–684.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A. *et al.* (2000a). Nutritional constraints in terrestrial and freshwater food webs. *Nature*, 408, 578–580.

Elser, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B. *et al.* (2000b). Biological stoichiometry from genes to ecosystems. *Ecol. Lett.*, 3, 540–550.

Elser, J.J., Acharya, K., Kyle, M., Cotner, J. Makino, W., Markow, T. *et al.* (2003). Growth rate-stoichiometry couplings in diverse biota. *Ecol. Lett.*, 6, 936–943.

Enriquez, S., Duarte, C.M. & Sand-Jensen, K. (1993). Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia*, 94, 457–471.

Goldman, J.C., Caron, D.A. & Dennett, M.R. (1987). Regulation of gross growth efficiency and ammonium regeneration in bacteria by substrate C:N ratio. *Limnol. Oceanogr.*, 32, 1239–1252.

Griffin, M.P.A., Cole, M.L., Kroeger, K.D. & Cebrian, J. (1998). Dependence of herbivory on autotrophic content and net primary production across ecosystems. *Biol. Bull.*, 195, 233–234.

Hartley, S.E. & Jones, C.G. (1997). Plant chemistry and herbivory, or why the world is green. In: *Plant Ecology* (ed. Crawley, M.J.). Blackwell Science Ltd, Oxford, U.K., pp. 284–324.

Iversen, T.M. (1974). Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to nitrogen content of ingested leaves. *Oikos*, 25, 278–282.

Mattson, W.J. (1980). Herbivory in relation to plant nitrogen content. *Annu. Rev. Ecol. Syst.*, 11, 119–161.

Melillo, J.M., Aber, J.D. & Muratore, J.M. (1982). Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, 63, 621–626.

Newell, S.Y. (1994). Ecomethodology for organoosmotrophs: prokaryotic unicellular versus eukaryotic mycelial. *Microb. Ecol.*, 28, 151–157.

Newell, S.Y. (1996). Established and potential impacts of eukaryotic mycelial decomposers in marine/terrestrial ecotones. *J. Exp. Mar. Biol. Ecol.*, 200, 187–206.

Petrusewicz, K. & Grodzinski, W. (1975). The role of herbivore consumers in various ecosystems. In: *Productivity of World Ecosystems* (eds Reichle, D.E., Franklin, J.F. & Goodwall, D.W.). National Academy of Science, Warsaw, Poland, pp. 64–70.

Rayner, J.M.V. (1985). Linear relations in biomechanics: the statistics of scaling functions. *J. Zool. Ser. A*, 206, 415–439.

Schade, J.D., Kyle, M., Hobbie, S.E., Fagan, W.F. & Elser, J.J. (2003). Stoichiometric tracking of soil nutrients by a desert insect herbivore. *Ecol. Lett.*, 6, 96–101.

Schlesinger, W.H. (1997). *Biogeochemistry: An Analysis of Global Change*, 2nd edn. Academic, San Diego, USA.

Schroeder, L.A. (1981). Consumer growth efficiencies: their limits and relationships to ecological energetics. *J. Theor. Biol.*, 93, 805–828.

Sokal, R.R. & Rohlf, F.J. (1995). *Biometry*, 3rd edn. W. H. Freeman and Company, New York, USA.

Stelzer, R.S. & Lamberti, G.A. (2002). Ecological stoichiometry in running waters: periphyton chemical composition and snail growth. *Ecology*, 83, 1039–1051.

Sterner, R.W. & Hessen, D.O. (1994). Algal nutrient limitation and the nutrition of aquatic herbivores. *Annu. Rev. Ecol. Syst.*, 25, 1–29.

Sterner, R.W. & Elser, J.J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, USA.

Swift, M.J., Heal, O.W. & Anderson, J.M. (1979). *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific, Oxford, USA.

Tenore, K.R., Cammen, L., Findlay, S.E.G. & Phillips, N. (1982). Perspectives of research on detritus: do factors controlling the availability of detritus to macroconsumers depend on its source? *J. Mar. Res.*, 40, 473–490.

Valentine, J.F. & Heck, K.L. (1999). Seagrass herbivory: evidence for the continued grazing of marine grasses. *Mar. Ecol. Progr. Ser.*, 176, 291–302.

Valiela, I. (1995). *Marine Ecological Processes*, 2nd edn. Springer-Verlag, New York, USA.

Whittaker, R.H. (1975). *Communities and Ecosystems*, 2nd edn. Macmillan, New York, USA.

Zar, J.H. (1998). *Biostatistical Analyses*, 4th edn. Prentice Hall, New Jersey, USA.