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Biomass decay rates and tissue nutrient loss in bloom and non-bloom-forming macroalgal species

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ABSTRACT

Macroalgal blooms occur in shallow, low-wave energy environments and are generally dominated by fast-growing ephemeral macroalgae. When macroalgal mats undergo senescence and decompose they can cause oxygen depletion and release nutrients into the surrounding water. There are relatively few studies that examine macroalgal decomposition rates in areas impacted by macroalgal blooms. Understanding the rate of macroalgal bloom decomposition is essential to understanding the impacts of macroalgal blooms following senescence. Here, we examined the biomass, organic content, nitrogen decay rates and $\delta^{15}N$ values for five macroalgal species (the bloom-forming *Agardhiella subulata*, *Gracilaria vermiculophylla*, *Ulva compressa*, and *Ulva rigida* and the non-bloom-forming *Fucus vesiculosus*) in Narragansett Bay, Rhode Island, U.S.A. using a litterbag design. Bloom-forming macroalgae had similar biomass decay rates (0.34–0.51 k d^{-1}) and decayed significantly faster than non-bloom-forming macroalgae (0.09 k d^{-1}). Biomass decay rates also varied temporally, with a significant positive correlation between biomass decay rate and water temperature for *U. rigida*. Tissue organic content decreased over time in all species, although *A. subulata* and *G. vermiculophylla* displayed significantly higher rates of organic content decay than *U. compressa*, *U. rigida*, and *F. vesiculosus*. *Agardhiella subulata* had a significantly higher rate of tissue nitrogen decay (0.35 k d^{-1}) than all other species. By contrast, only the $\delta^{15}N$ of *F. vesiculosus* changed significantly over the decay period. Overall, our results indicate that bloom-forming macroalgal species decay more rapidly than non-bloom-forming species.

1. Introduction

Macroalgal blooms are typically found in shallow, low wave-energy systems such as estuaries that are influenced by nutrient loading (Guidone and Thornber, 2013). Macroalgal blooms may persist for several weeks when nutrients are available and physical conditions are calm (Harlin, 1995; Martins et al., 2007; Pedersen et al., 2010). Bloom biomass can wash up as wrack and enter terrestrial food webs (Mews et al., 2006; Spiller et al., 2010), or be retained in marine food webs either through herbivore consumption (Lotze et al., 2000; Valiela et al., 1997) or microbial decay processes (Duarte and Cebrian, 1996; Hardison et al., 2010). In systems where herbivore consumption of blooms is limited, such as Narragansett Bay, Rhode Island (Guidone et al., 2012, 2015), understanding macroalgal decomposition rates and processes is crucial to understanding overall nutrient cycling.

Decomposing macroalgae from blooms can cause localized hypoxia altering benthic macrofauna (Flindt et al., 1997; Ólafsson et al., 2013; Sfriso et al., 2001; Tagliapietra et al., 1998; Viaroli et al., 1996) and, subsequently, microbial decomposer communities (Godbold et al., 2009; Griffiths and Stenton-Dozey, 1981; Inglis, 1989). Algal decomposition also results in the release of nitrogen and other nutrients into the surrounding marine environment, which can fuel decomposer microorganisms and provide nutrients for future generations of primary producers (Banta et al., 2004; Gulbransen, 2013; Tyler et al., 2001; Williams, 1984). Nitrogen is frequently the limiting nutrient in coastal systems and elevated levels of nitrogen can have dramatic consequences for ecosystem structure and function (Howarth and Marino, 2006; Smith et al., 1999). The nitrogen retention time of a primary producer is important to the nutrient cycling rate of a system and is influenced by its longevity and biomass (Banta et al., 2004; Holmer et al., 2004). Primary producer diversity and productivity in a system can strongly impact system-wide nutrient cycling rates since primary producers vary in their nitrogen retention times

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(Buchsbaum et al., 1991; Twilley et al., 1986).

Few studies compare decomposition rates *among* bloom-forming macroalgal species (Banta et al., 2004; Hanisak, 1993; Paalme et al., 2002) but these have shown that fast-growing, opportunistic macroalgae decay more quickly than slow-growing, long-lived macroalgae such as *Fucus* (Buchsbaum et al., 1991; Mews et al., 2006; Schmidt, 1980; Twilley et al., 1986). Slow decay of long-lived species may be due to their high phenolic content (Mews et al., 2006; Targett et al., 1992; Zimmer et al., 2001). Macroalgal decay rates are also influenced by biochemical composition (i.e. structural and storage compounds or pigment composition) and morphological complexity (Buchsbaum et al., 1991; Hanisak, 1993). Eutrophic systems dominated by opportunistic bloom-forming macroalgae with rapid decay rates may have an acceleration effect on the speed of nutrient turnover.

Nitrogen exists in two stable isotopic forms; the lighter ^{14}N isotope is more abundant than the heavier ^{15}N isotope. Wastewater typically has a higher $^{15}N/^{14}N$ ratio ($\delta^{15}N$) than groundwater or oceanic water due to denitrification during the treatment process (Cole et al., 2004; Heaton, 1986). During denitrification, the main nitrogenous waste product of animals, urea, is hydrolyzed leading to an increase in the pH of the wastewater (Benson et al., 2008). This increase in pH favors the conversion of ammonium to ammonia gas, which is lost to the atmosphere through volatilization. Ammonia volatilization also increases with increasing temperatures (Ernst and Massey, 1960). When ammonia is volatilized the lighter isotope of nitrogen, ^{14}N, is preferentially lost resulting in ^{15}N enrichment of the remaining wastewater (Benson et al., 2008).

The $\delta^{15}N$ of primary producers has been shown to reliably reflect the source of N (e.g. atmospheric or wastewater derived; Cole et al., 2004; DiMilla, 2006; Thornber et al., 2008). As a result, macroalgae are commonly used in studies to track nitrogen flow in estuarine food webs (Costanzo et al., 2003, 2005; McClelland et al., 1997; Oczkowski et al., 2008). However, comparatively little is known about the relative release of ^{15}N and ^{14}N during the macroalgal decay process. Because the microbial decomposer community takes up molecules and isotopes preferentially (Banta et al., 2004; Buchsbaum et al., 1991), the $\delta^{15}N$ signature of a decaying alga may change over time depending on the rates of nitrogen mineralization and incorporation (Fellerhoff et al., 2003; Rossi et al., 2010).

In this study, we quantified biomass decay rates, organic and nitrogen content loss, and the nitrogen isotopic signatures for four major bloom-forming and one non-bloom-forming macroalgal species as they decayed. We interpret our data in the context of increasing anthropogenic stresses on coastal systems, particularly increasing sea surface temperature from climate change.

2. Methods

2.1. Study site

Narragansett Bay, Rhode Island, U.S.A. is a temperate, highly eutrophic coastal estuary (370 km^2) with several smaller embayments. Greenwich Bay is the most frequently bloom-affected of these embayments, likely due to its hydrodynamic characteristics (Deacutis, 2008; Granger et al., 2000). Abdelrhman (2005) determined that the circulation in Greenwich Bay is counterclockwise with an estimated flushing time of 9.21 days. However, the local water retention time was predicted to be up to 21.38 days (Abdelrhman, 2005), indicating that nutrient loading in Greenwich Bay may be amplified by the long water retention time (Deacutis, 2008). In 2003, Greenwich Bay was the site of a large fish kill caused by an anoxic event following the decay of an algal bloom that was fueled by rainfall-driven eutrophication (Rhode Island Department of Environmental Management, 2003).

2.2. Species and design

We determined the decay rates of four common bloom-forming species in Greenwich Bay: the green algae *Ulva compressa* Linnaeus and *Ulva rigida* C. Agardh and the red algae *Agardhiella subulata* (C. Agardh) Kraft & M. J. Wynne and *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Guidone and Thornber, 2013), and a long-lived, non-bloom-forming brown alga *Fucus vesiculosus* Linnaeus. *Gracilaria vermiculophylla* is a recent invader in this system (Nettleton et al., 2013). All algae were collected in Greenwich Bay with the exception of *F. vesiculosus*, which was collected from rocky shores in lower Narragansett Bay, at various sites based on availability (Supplementary Table 1).

After collection, thalli were cleaned in order to remove epiphytes and epifauna. The thalli were then frozen at −80 °C for at least 2 days to induce tissue senescence (Buchsbaum et al., 1991; Castaldelli et al., 2003). Although frozen material may have a high rate of leaching immediately following rehydration due to cellular damage from freezing, the initial rate of leaching in frozen samples is similar to the natural rate of leaching that occurs during cell lysis in non-frozen detritus (Castaldelli et al., 2003).

Thawed individuals were subsampled to determine the wet: dry mass ratio, initial organic and nitrogen content, and initial nitrogen isotopic ratio. Individual pre-weighed thalli of similar sizes (n = 1 thallus per litterbag) were then placed in a litterbag (200 × 200 mm) with a mesh size of 250 μM to exclude detritivores (Mews et al., 2006). The average starting wet mass of each algae was: *A. subulata:* 6.2 ± 0.7 g, *G. vermiculophylla* 8.9 ± 1 g, *U. compressa* 6.1 ± 0.8 g, *U. rigida* 4.9 ± 0.4 g, and *F. vesiculosus* 19.8 ± 1.9 g (mean ± 1 SE).

For each trial (n = 7), we deployed 24 litterbags (e.g. thalli) of each of two species. Trials are referred to by their start date: June 14th (6–14), June 21st (6–21), July 12th (7–12), July 23rd (7–23), July 26th (7–26), August 2nd (8–2), and August 17th (8–17); all trials were conducted between June and September 2010. To assess changes in decay rate during the peak summer bloom-forming season, *U. rigida* was included in every trial and the second species was *F. vesiculosus* (7–12 & 8–17), *G. vermiculophylla* (7–23), *U. compressa* (6–14 & 7–26), or *A. subulata* (6–21 & 8–2). Each species was used in two experimental trials, except for *G. vermiculophylla*. Litterbags were randomly divided among 8 PVC stakes (n = 6 litterbags per stake), secured with metal sand anchors, and interspersed at alternate 0.5 m intervals below the mean low tide line of a protected sandy beach in Greenwich Cove (41°39′55.8″N, 71°26′29.1″W) following the contour of the shoreline. Litterbags were always water covered and rested on the sediment to mimic the natural position of decaying macroalgae in an area that did not have a macroalgal mat present. Litterbags were not under or within a macroalgal canopy, although it was common to find small clumps of drift macroalgae decaying in the study area.

At regular intervals (Day 1, 2, 4, 8, 16, and 32), one bag was removed from each stake, the remaining algal tissue was weighed, and subsamples were taken for dry mass, organic and nitrogen content, and $\delta^{15}N$ analyses. Instead of Day 32, macroalgae in the 6–14 trial were collected on Day 35 and macroalgae from the 8–17 trial were collected on Day 34. All samples (pre- and post-decay) were dried at 30 °C until they had a constant weight (i.e. >48 h) and then weighed to determine the dry mass.

2.3. Biomass decomposition

To determine the biomass decomposition rate (i.e. the decay constant k) for each experimental replicate (i.e. stake), we