2011

# VARIABILITY IN BIOMASS DECAY RATES AND NUTRIENT LOSS IN BLOOM-FORMING MACROALGAL SPECIES

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Recommended Citation

VARIABILITY IN BIOMASS DECAY RATES

AND NUTRIENT LOSS IN BLOOM-FORMING

MACROALGAL SPECIES

BY

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

BIOLOGICAL SCIENCES

UNIVERSITY OF RHODE ISLAND

2011

MASTER OF SCIENCE THESIS

OF

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UNIVERSITY OF RHODE ISLAND
2011

# ABSTRACT

This thesis is comprised of one manuscript. A summary of the manuscript follows:
Decaying macroalgae release nitrogen and other nutrients into the surrounding
marine environment, providing nutrients for future generations of primary
producers, as well as fueling a complex web of decomposer microorganisms.
There are relatively few studies that examine macroalgal decomposition rates in
areas impacted by macroalgal blooms, although fast-growing macroalgal bloom
species typically decay more quickly than slow-growing perennial species. We
studied whole tissue, organic content, and nutrient decay rates for five macroalgal
species in Narragansett Bay, RI in the summer of 2010 using an intertidal litterbag
design; four of these species are frequently present in macroalgal blooms in this
system. Our results, which we present as logistic decay rates (k), illustrate that the
red alga *Gracilaria vermiculophylla* decomposes most rapidly, followed by
ephemeral green algae (*Ulva rigida, Ulva compressa*) and the red alga *Agardhiella
subulata;* decay rates for these four species were significantly higher than that for
the perennial, non-bloom forming brown alga *Fucus vesiculosus*. We did not
observe refractory pools for any species, though we did not follow *F. vesiculosus*
through the end of its decay process. Decay rates were dependent upon water
temperature, with faster decomposition rates occurring during peak temperatures.
We speculate that the slow decomposition of *F. vesiculosus* may be attributable to
its relatively high cell wall phenolics, which have been shown in previous studies

to retard microorganismal decay. We observed nitrogen spikes during initial decay of *F. vesiculosus* due to chemical or biological immobilization of allochthonous nitrogen in the algal tissue. Nitrogen and organic material were lost from red species at a faster rate than green or brown species, likely due to faster leaching and/or greater decomposer action. Initial $\delta^{15}N$ values varied greatly among species, collection sites, and collection dates and generally did not exhibit predictable changes over the period of decay. Our results are of particular importance in eutrophied systems, where shifting productivity regimes may lead to changes in total nutrient cycling rates, and where changes in stable nitrogen isotopic values have been correlated with nitrogen released from sewage treatment plants.

One appendix of decay curves follows the manuscript.

# ACKNOWLEDGEMENTS

## PREFACE

This thesis is written in manuscript format. It is comprised of one manuscript

chapter with no appendices. I plan to submit this manuscript with Carol Thornber

to the journal Estuarine, Coastal, and Shelf Science.

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# Variability in biomass decay rates and nutrient loss in bloom-forming macroalgal species

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**Chapter 1**

Variability in biomass decay rates and nutrient loss in bloom-forming macroalgal species

**Abstract**

Decaying macroalgae release nitrogen and other nutrients into the surrounding marine environment, providing nutrients for future generations of primary producers, as well as fueling a complex web of decomposer microorganisms. There are relatively few studies that examine macroalgal decomposition rates in areas impacted by macroalgal blooms, although fast-growing macroalgal bloom species typically decay more quickly than slow-growing perennial species. We studied whole tissue, organic content, and nutrient decay rates for five macroalgal species in Narragansett Bay, RI in the summer of 2010 using an intertidal litterbag design; four of these species are frequently present in macroalgal blooms in this system. Our results, which we present as logistic decay rates ($-k$ d$^{-1}$), illustrate that the red alga *Gracilaria vermiculophylla* decomposes most rapidly, followed by green algae (*Ulva rigida, Ulva compressa*) and the red alga *Agardhiella subulata;* decay rates for these four species were significantly higher than that for the perennial, non-bloom forming brown alga *Fucus vesiculosus*. We did not observe refractory pools for any species, though we did not follow *F. vesiculosus* through the end of its decay process. Decay rates were dependent upon water temperature, with faster decomposition rates occurring during peak temperatures. We speculate that the slow decomposition of *F. vesiculosus* may be attributable to its relatively

high cell wall phenolics, which have been shown in previous studies to retard decay by microorganisms. We observed nitrogen spikes during initial decay of *F. vesiculosus* due to chemical or biological immobilization of allochthonous nitrogen in the algal tissue. Nitrogen and organic material were lost from red species at a faster rate than green or brown species, likely due to faster leaching and/or greater decomposer action. Initial $\delta^{15}N$ values varied greatly among species, collection sites, and collection dates and generally did not exhibit predictable changes over the period of decay. Our results are of particular importance in eutrophied systems, where shifting productivity regimes may lead to changes in total nutrient cycling rates, and where changes in stable nitrogen isotopic values have been correlated with nitrogen released from sewage treatment plants.

**Key Words (6)**

*Ulva*, nutrient cycling, stable isotope, macroalgae, litter bag, decay rates

**Regional Index**

USA, Rhode Island, Narragansett Bay

**Introduction**

     The availability of nitrogen in coastal systems is of critical importance for the ecological dynamics of primary producers and higher trophic levels (Hill and McQuaid 2009). Because nitrogen is frequently the limiting nutrient in estuarine

and marine systems, elevated levels of nitrogen are of particular importance in such areas (Howarth and Marino 2006). Nitrogen is absorbed by primary producers as dissolved inorganic nitrogen (DIN) and retained in their tissues until it is transferred to other trophic levels via leaching or decomposition (Brinson 1977, Banta et al. 2004), or via herbivory. The length of time that a producer retains nitrogen in its tissues, determined by its lifespan and its relative consumption by herbivores, as well as total producer biomass, is important to the total nitrogen cycling rate of an estuary (Banta et al. 2004, Holmer et al. 2004). Because different groups of primary producers (including phytoplankton, annual and perennial macroalgae, and seagrasses) vary in their nitrogen retention times (Twilley et al. 1986, Buchsbaum et al. 1991), the primary production regime in a system can strongly impact system-wide nutrient cycling rates.

Macroalgal blooms are typically found in low wave-energy systems such as estuaries, and may persist for several days or weeks, depending on physical conditions and nutrient availability (Harlin 1995, Martins et al. 2007, Pedersen et al. 2010). Bloom dynamics in response to nitrogen inputs have been well studied, as they are frequently associated with eutrophic conditions (Peckol et al. 1994, Doering et al. 1995, Hauxwell et al. 1998, Raffaelli et al. 1998, Worm and Lotze 2006). Aside from washing up as wrack and entering terrestrial food webs (Mews et al. 2006, Spiller et al. 2010), bloom biomass typically is retained in marine food webs either through herbivore consumption (Valiela et al. 1997, Lotze et al. 2000) or microbial decay processes (Duarte and Cebrian 1996, Hardison et al. 2010).

Particularly in systems where herbivore consumption of blooms is limited, e.g. Guidone et al. (2010), understanding decay rates and processes is crucial.

Decomposing macroalgae can cause localized hypoxia and decreased benthic macrofaunal diversity (Viaroli et al. 1996, Flindt et al. 1997, Tagliapietra et al. 1998, Sfriso et al. 2001) and are frequently considered a public nuisance (Deacutis 2008, Liu et al. 2009). Because decaying macroalgae increase decomposer populations (Griffiths and Stenton-Dozey 1981, Inglis 1989) and release nitrogen and other nutrients into the surrounding marine environment, they fuel a complex web of decomposer microorganisms and provide nutrients for future generations of primary producers (Banta et al. 2004). Overall decay is characterized by microbial decomposition following an initial leaching of soluble compounds (Godshalk and Wetzel 1978, Valiela et al. 1985). Microbial decay may be selective (Rieper-Kirchner 1990); in other words, some types of molecules may be metabolized from algal tissues more quickly during the microbial phase depending upon decomposer communities and preferences, therefore changing the chemical makeup of the remaining biomass. Generally, tissue nitrogen concentration increases over the period of decay (see Odum et al. (1979) for a review) due to relatively slower loss of nitrogen-rich compounds or mobilization of surrounding nitrogen by microbes.

The rate at which macroalgae decompose and release their nutrients is a key component of their total nutrient recycling time. Although there are few studies that compare decay rates *among* bloom-forming macroalgal species (but see Banta et al 2004), in general, fast-growing drift macroalgae decay more

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quickly than perennial, k-selected macroalgal species such as *Fucus* (Schmidt 1980, Twilley et al. 1986, Buchsbaum et al. 1991, Mews et al. 2006). Slow decay of perennial species such as fucoids may be due to their high phenolic content (Targett et al. 1992, Zimmer et al. 2001, Mews et al. 2006). In addition, macroalgae with high nitrogen content should decompose quickly because decomposer fauna have increased demand for nutrients and bacterial growth efficiency increases when substrate nutrient content is high (Enriquez et al. 1993). Therefore, eutrophied systems may have an acceleration effect on the speed of nutrient turnover, because they are frequently characterized by an ephemeral, algal-dominated productivity regime, and second, they may facilitate faster bacterial decomposition if the nitrogen concentration of algal tissue is elevated compared to algae in non-eutrophied systems (Valiela et al. 1985).

Nitrogen exists in two stable isotopic forms: the lighter $^{14}$N isotope is much more abundant than the heavier $^{15}$N isotope. Secondary treated wastewater typically has a higher $^{15}$N:$^{14}$N ($\delta\,^{15}$N) isotope ratio than oceanic water because bacteria used in the wastewater-treatment process preferentially take up the lighter isotope (Heaton 1986). While macroalgae absorb and incorporate both nitrogen isotopes into their tissues (Runcie et al. 2003), they preferentially take up the lighter isotope (Fry 2006). By analyzing the $\delta\,^{15}$N in algal tissues, it may be possible in some cases to determine the source of the nitrogen used by macroalgae (DiMilla 2006, Thornber et al. 2008) and, as a result, macroalgae are commonly used in studies to track nitrogen flow in estuarine food webs (McClelland et al. 1997, Costanzo et al. 2003, Costanzo et al. 2005, Oczkowski et al. 2008).

However, comparatively little is known about the relative release of $^{15}N$ vs. $^{14}N$ in macroalgal decay processes. Because the microbial decomposer community takes up molecules and isotopes preferentially (mineralization; Banta et al. (2004), 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).

We studied the dynamics of macroalgal decay and nutrient release in Narragansett Bay, RI, a highly eutrophied estuarine system (Granger et al. 2000). The largest anthropogenic nutrient inputs are from sewage treatment plants located in the Providence River estuary, at the northern end of the Bay, while smaller treatment plants and other point-source anthropogenic nutrient inputs are distributed throughout the Bay (Pruell et al. 2006). As the human population increased in this region over the past 150 years, nitrogen inputs from sewage, manufacturing, and atmospheric deposition dramatically elevated nitrogen release from 35-50 million moles/year in the 1860's to 605 million moles/year in the 1980's (Nixon et al. 2008). Increased nutrient load has contributed to hypoxic events, particularly in the summer months and in geographically restricted areas such as Greenwich Bay (Bergondo et al. 2005). However, planned sewage treatment improvements project decreases in released N up to 30-50% from point sources during the summertime months by 2014 (Pryor et al. 2006).

In this study, we quantified biomass decay rates for four major bloom-forming species and one perennial species, expecting the perennial species (*Fucus*) to experience the slowest rate of decay, in Narragansett Bay's current (2011) early

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nutrient reduction regime. We quantified and compared rates of nitrogen and organic content loss in order to determine the chemical composition of the molecules consumed most readily by decomposers, expecting the most labile tissues to be consumed first, shown by an organic content decrease (as light sugars are released or metabolized) and a change in total N. The $\delta^{15}$N signature of the tissue was expected to increase over time as decomposer microorganisms preferentially mineralized the lighter N isotope. We interpret our data in the context of increasing anthropogenic stresses on coastal systems such as water warming from climate change and continued eutrophication.

**Methods**

*Study Site*

Narragansett Bay, Rhode Island, is a modest-sized, temperate coastal estuary (370 km$^2$) with several smaller embayments. The most frequently bloom-affected (Granger et al. 2000) of these embayments is Greenwich Bay, the site of a large fish kill in 2003 (Rhode Island Department of Environmental Management 2003). Primary producers in Narragansett Bay include seagrasses, phytoplankton, benthic microalgae, and macroalgae; typically, blooms of phytoplankton occur in the winter (Oviatt et al 2001) although recent years have seen a shift in maximum chlorophyll a to summer blooms (Nixon et al. 2009), while blooms of macroalgae are more common during the summer months (French et al. 1992, Granger et al.). Our field experiments were conducted from June to October 2010.

*Species and Design*

We used five algal species, all of which are abundant in Narragansett Bay. Four were common bloom-forming species growing subtidally, the green algae *Ulva compressa* Linnaeus and *Ulva rigida* C. Agardh; the red algae *Agardhiella subulata* (C. Agardh) Kraft & M.J. Wynne and *Gracilaria vermiculophylla* (Ohmi) Papenfuss (a recent invader in this system); the fifth species was the perennial, brown alga *Fucus vesiculosus* Linnaeus. We collected fresh algae in Greenwich Bay with the exception of *F. vesiculosus*, which we collected from rocky shores in the lower Narragansett Bay, where it is more reliably found.

We cleaned fresh thalli in order to remove epiphytes and small animals. Then, the thalli were frozen in a -80ºC freezer for at least two days to induce tissue senescence (Buchsbaum et al. 1991). Thawed individuals were subsampled for determinations of wet:dry mass, initial organic content and nitrogen concentration and nitrogen isotopic ratio (see techniques below). We placed each individual pre-weighed algal thallus in a mesh litter bag measuring 20 x 20 cm, with a mesh size of 0.25 mm, and secured the bag with a cable tie for deployment in the field. This mesh size was designed to exclude meso- and micro-herbivore effects, and thus is a study of decay (not decomposition), as defined by Mews et al. (2006).

For each of seven experimental trials, we deployed 24 algal thalli of each of two species. Trials are referred to by their start date (6-14, 6-21, 7-12, 7-23, 7-26, 8-2, 8-17). To assess changes in decay rate, during the peak summer bloom-forming season, we used *Ulva rigida* in every trial and alternated the second species among the remaining four listed above. Each species was used in two

experimental trials, except for *G. vermiculophylla*. Litter bags for each species were randomly and evenly divided among four PVC stakes, with six litter bags per stake, for eight total stakes per trial. The stakes were then systematically interspersed at alternate 0.5 meter intervals along the mean low tide line of a protected sandy beach in Greenwich Cove [41.39'58.046 $^{\circ}$N, 71.26'27.65 $^{\circ}$W]. We secured the stakes in the sediment with metal sand anchors, and all litter bags rested on the sediment, to mimic the natural position of decaying macroalgae in these habitats (J. Conover, *pers. obs.*). We recorded water temperature with a TidBit v2 temperature logger (www.onsetcomp.com) and found no significant difference between our data and those from a nearby NOAA weather buoy (Conimicut Point Station ID# 8452944).

At regular intervals (Day 1, 2, 4, 8, 16, and 32), we removed one bag from each stake, weighed the remaining algal tissue inside, and took subsamples for dry mass, organic content and nitrogen isotope analysis. All sub samples (pre- and post-decay) were dried in a 30ºC oven for at least two days and then weighed. We used the wet and dry mass from the pre-decay samples to calculate a wet:dry mass ratio.

*Tissue Analyses*

Dry, weighed tissue samples from all thalli were placed in a 500°C muffle furnace for two hours; the remaining material was weighed and used to calculate the percent organic content (as ash-free dry mass).  For nitrogen isotope analyses, we ground additional dry tissue samples using a mortar and pestle and

encapsulated a small amount (2 - 3 mg) in duplicate, using 3.5 x 5 mm tin capsules

(Costech Analytical Technologies, Inc.). The samples were then analyzed using a

Carlo_Erba NA 1500 Series II Elemental Analyzer connected to a Micromass

Optima isotope mass spectrometer (Elementar Americas, Mt. Laurel NJ, USA) at

the US EPA Atlantic Ecology Division in Narragansett, Rhode Island. The mass

spectrometer provided a $\delta^{15}N$ value and total nitrogen concentration for each

sample. The $\delta^{15}N$ values of samples were calculated relative to a dogfish muscle

working standard (DORM-2; National Research Council of Canada, Ottawa,

Ontario, Canada), whose $\delta^{15}N$ value had been verified via analysis versus a

primary isotope standard (NIST RM 8549, IAEA-NO-3, potassium nitrate; NIST,

Gaithersburg, MD USA).  The nitrogen isotope composition of the tissue samples

was expressed as a part per thousand (per mil) difference from the composition of

$N_2$ in air (Mariotti 1983), as follows:

$$\delta^{15}N \text{ ‰} = [ (R\text{sample}/ R_{N2} ) - 1 ] \times 1000$$

where $R = {}^{15}N / {}^{14}N$.  Samples were analyzed in duplicate with a typical difference

of about 0.1 ‰.  Sample material reanalyzed periodically over a several month

period exhibited a precision of $\pm 0.30$ ‰, calculated as a single sigma standard

deviation of all replicate values.


*Statistical Analyses*

        We analyzed all data using JMP v 8.0 (SAS Institute, Inc., Cary, NC USA;

www.sas.com). To determine the rate of change in mass over time for each

experimental replicate (stake), we performed a log transformation on the

calculated % mass remaining data and fit a linear equation to the transformed data; all masses used were dry mass. Any increase in mass greater than 120% (n = ~20 of 327 total samples) was excluded from the analysis; these samples frequently had sediment indistinguishable from decaying tissue on them, which would bias our results. We determined the k (rate of change in mass over time) from the slope of the regression for each replicate stake, for each species during each trial. We calculated 'absolute' values for organic content and total nitrogen; these absolute values represent the amount of organic content or total nitrogen remaining in the tissue, expressed as a percentage of the initial amount (Buchsbaum et al. 1991). We determined k from these absolute values using the same regression process used for mass loss. We compared k values and initial values using one-way ANOVAs and post-hoc Tukey-Kramer HSD tests. Relative change in isotopic signature was calculated using the following equation:

$$[[\text{After } \delta^{15}N - \text{Before } \delta^{15}N] / \text{Before } \delta^{15}N] \times 100 = \text{relative change } \delta^{15}N$$

Total and isotopic nitrogen data are not available for *G. vermiculophylla* due to mass spectrometer equipment failure.

**Results**

*Biomass Decay*

All bloom-forming macroalgal species decayed three to five times faster than *Fucus*, the non-bloom forming species (Figure 1, Table 1). Decay rates varied significantly among species ($F_{4, 51} = 10.9645$, $p < 0.0001$). *U. rigida* and *U. compressa* had similar overall biomass decay rates (k = 0.44 ± 0.03, k = 0.43 ±

0.05, respectively). *A. subulata* had the slowest decay rate of the ephemeral

species (k = 0.34 ± 0.05), while *G. vermiculophylla* had the fastest (k = 0.51 ±

0.07). *F. vesiculosus* had a decay rate (k) of 0.09 ± 0.05 (Table 1).

We found significant variation in *U. rigida* decay rates throughout the

summer months ($F_{6, 21}$ = 9.7547, *p* < 0.0001). The slowest decay rate occurred in

the June 14 trial (mean k = 0.21) and the fastest occurred during the July 23 trial

(mean k = 0.67). Rates of *U. rigida* biomass decay were positively correlated with

mean water temperature (*r* = 0.636, *p* = 0.0003). Mean trial period water

temperature ranged from 22.64°C to 24.48°C, with the highest mean temperature

occurring in late July (Figure 2).


*Organic Content*

Absolute organic content, expressed as a percentage of the original organic

content remaining in the tissue, decreased over the period of decay in all species,

though the loss rates (k) differed among species ($F_{4, 51}$ = 26.62, *p* < 0.0001, Table

1). Post-hoc analysis (Tukey HSD) revealed that red species (*A. subulata* and *G.

vermiculophylla*) lost absolute organic content significantly faster than *U. rigida*,

*U. compressa*, and *F. vesiculosus*. Initial tissue organic content was lowest in *A.

subulata* (60.06%) and highest in *U. compressa* (84.01%, Table 2); all species

were significantly different from each other except *F. vesiculosus* and *U. rigida*,

which had similar levels ($F_{4, 318}$ = 71.16, *p* < 0.0001). *U. rigida* initial organic

content was the same for all trials except the July 12 trial, where the initial organic

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content was 66.84%, significantly lower than all other trials ($F_{6, 155} = 18.26$, $p$ <0.0001).

*Total Nitrogen*

Absolute nitrogen (the percent of initial nitrogen remaining in the tissue) loss rates were nearly twice as high for *A. subulata* than for any other species ($F_{3, 17} = 13.92$, $p < 0.0001$, Table 1). The only species exhibiting absolute nitrogen values greater than 100% was *F. vesiculosus*, which had Day 1 values exceeding 150% and Day 2 values exceeding 100%, after which the values fell below the initial nitrogen values. Decaying *U. rigida* tissues were relatively enriched in nitrogen over the initial period of decay, from 2.0% to 3.2% (Day 0 to ~8; paired $t_{11} = 0.0003$).

Initial percent nitrogen levels varied among species, with *U. rigida* and *A. subulata* having nitrogen levels elevated slightly above *U. compressa* and *F. vesiculosus* ($F_{3, 88} = 2.97$, $p = 0.0361$, Table 2). Post-hoc analysis does not reveal significant differences among species. Similarly, we found significant variation in initial total nitrogen for *U. rigida* among starting dates; tissues collected at the end of the summer (Trial 8-2) had at least one and a half times as much nitrogen (3.3%) than earlier in the summer ($F_{3, 42} = 24.89$, $p < 0.0001$) and is significantly higher according to post-hoc analysis.

*Isotopic Nitrogen*

Changes in isotopic nitrogen ratios over the period of decay generally followed a trend of increasing variability; no consistent trends were observed except for *F. vesiculosus*, which was positively enriched in $^{15}$N over the decay period ($r = 0.63$, $p = 0.01$; Figure 3). *A. subulata* had a slight negative correlation ($r = 0.47$, $p = 0.04$), though late in the decay period samples sizes for this species were extremely low (n = 2). Initial $\delta^{15}$N values varied significantly among species ($F_{3, 95} = 6.41$, $p = 0.0005$; Table 2).

**Discussion**

The overall biomass and total nitrogen decay rates we recorded are near the maximum of those reported in a literature review by Banta et al. (2004), but do not exceed previously observed measurements. Water temperature was significantly positively correlated with *U. rigida* decay rates. Initial organic content and total nitrogen tissue values did not influence decay rate.

As we expected, fast-growing, bloom-forming ephemeral macroalgae are also fast-decaying. These findings are consistent with other studies comparing similar ephemeral and perennial species (Twilley et al. 1986, Buchsbaum et al. 1991, Kristensen 1994). Many morphological and chemical qualities differentiate ephemeral and perennial species, including but not limited to morphological complexity, nutrient content, and cell wall constituents. Ephemeral species tend to have simpler cell wall constituents and low phenolics (Siegel and Siegel 1973), both of which could potentially hasten the microbial decay process compared to perennial macroalgae.

Phenolic compounds such as those present in *Fucus* are known to impede decay of marine algae (Targett et al. 1992, Zimmer et al. 2001) and are likely responsible, in part, for the lower decay rate of *Fucus* compared with ephemeral species low in phenolics. Mews et al. (2006) found that decomposition (defined to include microbial decay and detritivore feeding) was more responsible for mass loss than was tissue leaching in *Ulva lactuca*; in *Fucus* the opposite was true, and leaching had a greater effect on mass loss. Antimicrobial compounds in *Fucus* may explain the lowered role of microbes in *Fucus* decomposition (Hornsey and Hide 1974).

We found no refractory pool in any of the ephemeral species, which is consist with other studies of macroalgae (Banta et al. 2004). While our experiments did not last long enough to test for a *Fucus* refractory pool, Buchsbaum et al. (1991) tested *Fucus* decay characteristics and did not find a refractory pool.

*Water temperature and decay*

Higher water temperatures frequently hasten bacterial metabolism in coastal waters (Pomeroy and Deibel 1986), increasing rates of colonization and decomposition (Paalme et al. 2002). Large temperature differences have been shown by Carpenter and Adam (1979) and by Birch et al. (1983) to strongly influence decomposition, however the relatively small temperature differences (~2°C) experienced in this study do not overcome the effect of species on decay rate. As water temperatures rise—as they have in Narragansett Bay (Nixon et al.

2008)—and decay rates experience a corresponding increase, there will likely be accelerated nutrient turnover from macroalgal detritus.

*Organic content changes during decay*

The change in organic content over the period of decay is consistent with the overall rate of biomass decay: species that decayed at a fast rate also lost organic content at a faster rate that slower-decaying species. All species except *A. subulata* lost organic content at a slower rate than they lost total biomass. By contrast, *A. subulata* lost organic content much faster relative to biomass, possibly indicating that the organic molecules in *A. subulata* are more available to bacterial colonizers than in other species, or that bacterial colonizers select organic molecules more aggressively on *A. subulata*.

Our findings indicate that for many species, the rate of biomass loss is underestimated when total carbon loss alone is used. Thus, data from studies in which C loss is treated as biomass loss (e.g. Banta et al. 2004) should be interpreted with caution.

*Total nitrogen*

Out of all five species examined, *U. rigida* and *U. compressa* had the highest and lowest initial total nitrogen values, respectively. These species were collected from the same location in each trial and are morphologically identical in the field and had similar natural biomass abundance, however, in this study *U. rigida* lost its nitrogen twice as fast as *U. compressa*, perhaps because it had a

higher initial N content and thus had more nitrogen available in its tissues for removal by leaching or microbial colonizers. Tissue enriched with nitrogen has accelerated biomass decay rates (Valiela et al. 1985); here it also may affect nitrogen loss rates. Buchsbaum et al. (1991) found that *Ulva lactuca* and *Gracilaria tikvahiae* decay rapidly and speculate that this may be due to low cell wall phenolics and large nitrogen pools. They found that *F. vesiculosus* decayed at half the rate of *U. lactuca* and *G. tikvahiae* and speculate that its slower decay rate was a result of a smaller total nitrogen pool and high initial phlorotannin levels that reduce activities of microbial cellulases (Swain 1979, Horner et al. 1988).

All species experienced a net loss of nitrogen as they decayed; this was expected because as tissue degrades and disperses, so will the nitrogen-containing molecules. The proportion of nitrogen in the remaining tissue, however, increased during the decay process. This increase has been observed previously and consistently in vascular plants in estuarine systems (de la Cruz 1965, Odum et al. 1979). Odum et al. (1979) attribute the nitrogenous compound increase not to an accumulation of soluble proteins, but instead to nitrogen-structural complexes (phenol-proteins), resistant amino groups, and nitrogenous humic acids. Rice (1982) observed increased reactive phenols and humic material for the nonliving macroalgal detritus complex over the decay period. The high phenolic levels of *Fucus* (the most structurally and chemically similar to vascular plants of the species studied) may be partially responsible for the very high early-decay nitrogen levels it experiences.

As tissues decay, they may experience net nutrient mineralization or net immobilization (Banta et al. 2004). We observed immobilization only in one species, *F. vesiculosus*, when absolute nitrogen values exceed 100% of the original tissue nitrogen on Day 1 and 2, indicating that early in the decay process *F. vesiculosus* incorporates more nitrogen into its tissues than it loses to the surrounding environment. Buchsbaum et al. (1991) attribute this immobilization effect to phenolic compounds that slow nitrogen loss by either binding directly to proteins in the water column (Rice 1982) or by slowing decay by inhibiting bacterial enzymes (Swain 1979), though they observed immobilization only in marsh grasses. We examined total nitrogen on a much finer time scale to find the immobilization effect.

*Stable isotopic nitrogen findings*

Initial stable isotope values were extremely variable across time and between collection sites. This is consistent with previous studies that have documented differences in stable isotope values in biota in estuaries exposed to varying amounts of nitrogen from different sources (e.g., atmospheric nitrogen versus human wastewater (McClelland and Valiela 1998, McKinney et al. 2001, Cole et al. 2004). The results of our study suggest that even in a given location, a single experimental sample would not be adequate to characterize the isotopic signature of an algal population as it can change significantly in as little as two weeks within a single species.

Stable isotopic nitrogen values did not follow a consistent pattern over the period of decay in any species except *F. vesiculosus*, which experienced an increase in $\delta^{15}N$ over time. The signal increase was likely due to experimental conditions: the *F. vesiculosus* was collected near the south end of Narragansett Bay, where macroalgae are less affected by nitrogen effluent and have a lower $\delta^{15}N$ (Oczkowski et al. 2008). As the *F. vesiculosus* tissue decayed in our experiment, it may have incorporated allochthonous nitrogen with higher $\delta^{15}N$ values, either by chemical immobilization by cell wall phenolics or biological immobilization of microorganisms.

Previous studies on stable isotopic nitrogen found slight decreases in $\delta^{15}N$ during decay and attributed the change to bacterial immobilization (Lehmann et al. 2002, Fourqurean and Schrlau 2003, Hill and McQuaid 2009). It is possible that bacterial immobilization was occurring in our study, but only *F. vesiculosus* had an initial signal discernibly different from the (higher) allochthonous nitrogen value, though this difference is not significant. Fourqurean and Schrlau's (2003) mechanism for nitrogen accumulation suggests that the allochthonous nitrogen originates from microbial exoenzymes whose nitrogen binds to reactive carbohydrates and phenols in the detritus, thus raising the isotopic nitrogen signature of *Fucus* spp. detritus. The high variability in the isotopic nitrogen signal over time and among species is consistent with Fogel and Tuross (1999) and Fellerhoff et al. (2003), who found significant fluctuations in signal change directionality in decomposing plants. The prevalence of these fluctuations in

decaying plants and algae underscores the importance of large sample sizes in isotopic sampling.

An awareness of the nitrogen signal in decaying macroalgae is important because the signal is not static, and a single measurement cannot capture the isotopic signature of the entire process. Also, decaying algae should not be treated as if they have a $\delta^{15}N$ consistent with living tissue because of bacterial processes and immobilization. To test the mechanism of bacterial incorporation of isotopic nitrogen by phenolic binding, a low $\delta^{15}N$ alga with low phenolic constituents should be observed over the course of decay in high $\delta^{15}N$ waters.

*Comparison with perennial algae and vascular plant decay*

Seagrass beds have declined worldwide and have frequently been accompanied by an increase in macroalgal blooms (Hauxwell et al. 2001, Hauxwell et al. 2003). This regime shift may have also impacted nutrient cycling dynamics associated with decay. Of the major estuarine primary producers, phytoplankton decay most quickly, followed by macroalgae, then seagrasses and finally marsh grasses, the order of which is primarily determined by the size of the initial tissue nitrogen pool (Valiela et al. 1985). The cell walls of algae do not accumulate nitrogen like vascular plants do and, in addition, lose their initial cell wall nitrogen very quickly. Green and red algal detritus have faster rates of nutrient mineralization and are more nutrient-rich than detritus from brown algae or sea- and marsh grasses (Buchsbaum et al. 1991). A second important determinant of algal decay rates is their less complex cell wall polysaccharide

structures compared with vascular plants (Hunter et al. 1974, Godshalk and Wetzel 1978, Tenore 1983). A byproduct of this fast decay is that macroalgal regimes lead to less producer-derived organic matter accumulation (see Banta et al. 2004 for a review).

As a result of their rapid and complete decay, macroalgae transfer important quantities of nutrients to the surrounding water, which has important implications for the sediment and water column microphytobenthos that utilize those nutrients in the estuarine regime (Sassi et al. 1988). In oligotrophic conditions such as reefs, the rapid turnover supplies nutrients necessary for production (Sassi et al. 1988), but in eutrophied waters, nutrients are made rapidly available to an already nutrient-rich environment characterized by nutritional dynamism and trophic instability caused by macroalgal dominance (Flindt et al. 1997). Duarte and Cebrian (1996) observe greater herbivory in systems dominated by macroalgae. The balance between decay and herbivory in these systems may influence the transfer of nutrients from macroalgae to other trophic levels via different pathways. Understanding the coupled effects of faster nutrient turnover through rapid decay and greater rates of herbivory is crucial to understanding system-wide shifts in nutrient cycling brought about by macroalgal productivity regimes in eutrophied coastal systems.

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**Table and Figures**

Table 1. Mean decay rates for total biomass, absolute organic content, and absolute total nitrogen for each species studied. Decay rates are presented as k values, determined from regression analysis of log-transformed data. Letters represent significant differences determined by Tukey-Kramer post-hoc tests.

| | Biomass -k $\pm$ 1 SE | | Absolute organic content -k $\pm$ 1 SE | | Absolute total nitrogen -k $\pm$ 1 SE | |
|---|---|---|---|---|---|---|
| *Ulva rigida* | 0.44 ± 0.03 | A | 0.26 ± 0.02 | B | 0.18 ± 0.02 | B |
| *Ulva compressa* | 0.43 ± 0.05 | A | 0.15 ± 0.02 | BC | 0.08 ± 0.004 | B |
| *Agardhiella subulata* | 0.35 ± 0.05 | A | 0.59 ± 0.08 | A | 0.35 ± 0.10 | A |
| *Gracilaria vermiculophylla* | 0.51 ± 0.07 | A | 0.36 ± 0.004 | A | - | |
| *Fucus vesiculosus* | 0.09 ± 0.05 | B | 0.06 ± 0.02 | C | 0.12 ± 0.05 | B |

Table 2. Mean initial tissue measurements of organic content, total nitrogen, and isotopic nitrogen for each macroalgal species. Letters in isotopic N column represent significant differences determined by a Tukey-Kramer post hoc test.

| | Organic content (% ± 1 SE) | Total nitrogen (% ± 1 SE) | $\delta^{15}$N (per mil ± 1 SE) | |
|---|---|---|---|---|
| *Ulva rigida* | 78.84 ± 0.62 | 2.26 ± 0.14 | 9.86 ± 0.29 | B |
| *Ulva compressa* | 84.01 ± 1.39 | 1.70 ± 0.10 | 9.91 ± 0.42 | AB |
| *Agardhiella subulata* | 60.06 ± 1.33 | 2.23 ± 0.09 | 11.29 ± 0.13 | A |
| *Gracilaria vermiculophylla* | 72.89 ± 1.52 | - | - | |
| *Fucus vesiculosus* | 79.50 ± 0.37 | 1.79 ± 0.11 | 8.95 ± 0.38 | B |
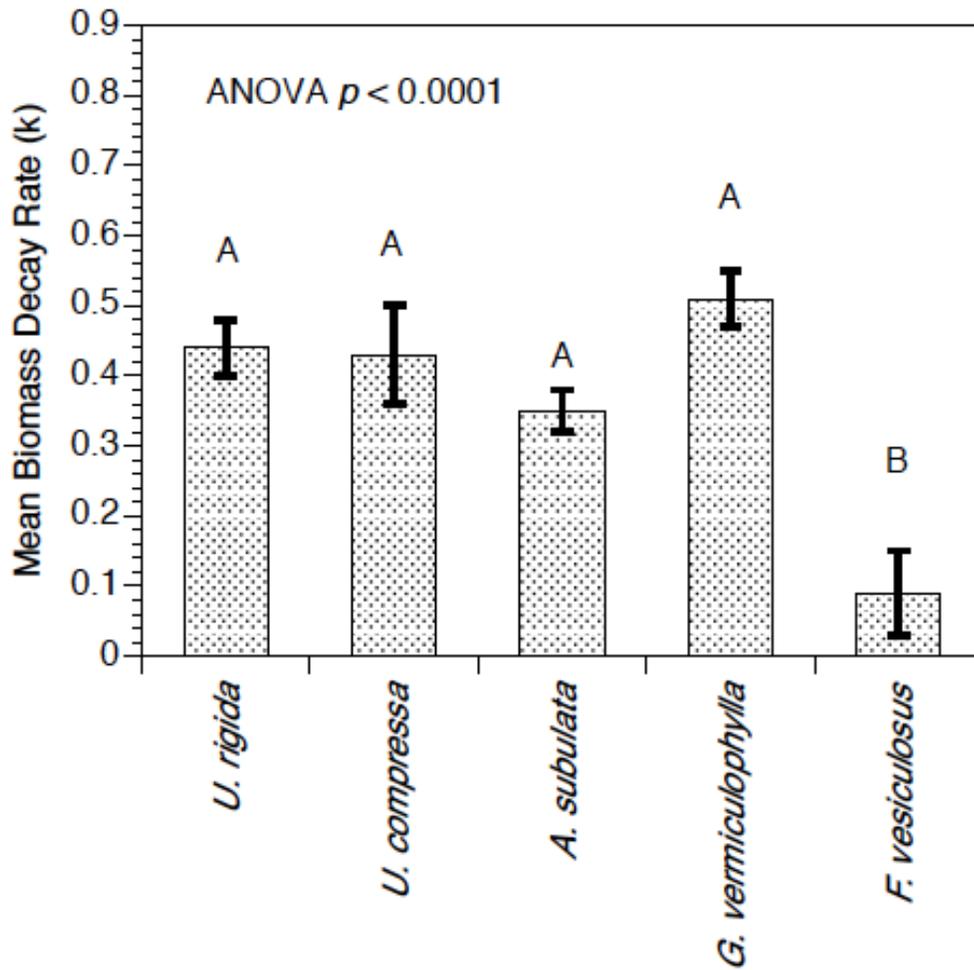
Figure 1. Mean biomass decay rate (-k) for each species. Letters indicate
   significant differences determined by Tukey-Kramer post hoc tests.
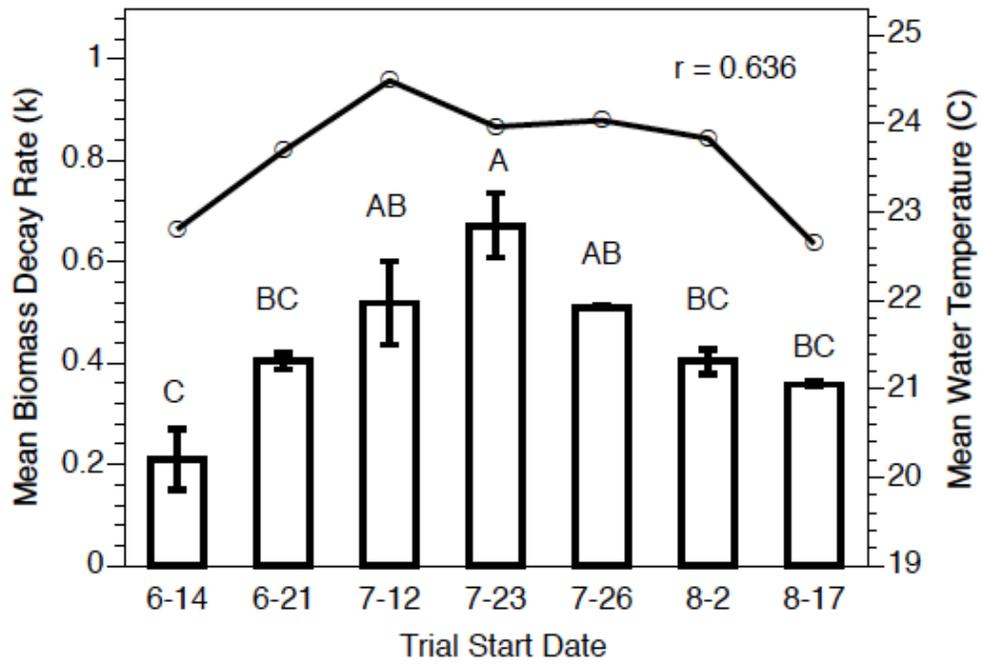
Figure 2. Mean *Ulva rigida* biomass decay rates (-k) with mean water temperature overlay. There is a significant correlation between *U. rigida* biomass decay rate and mean water temperature (r = .636, *p* = 0.0003).
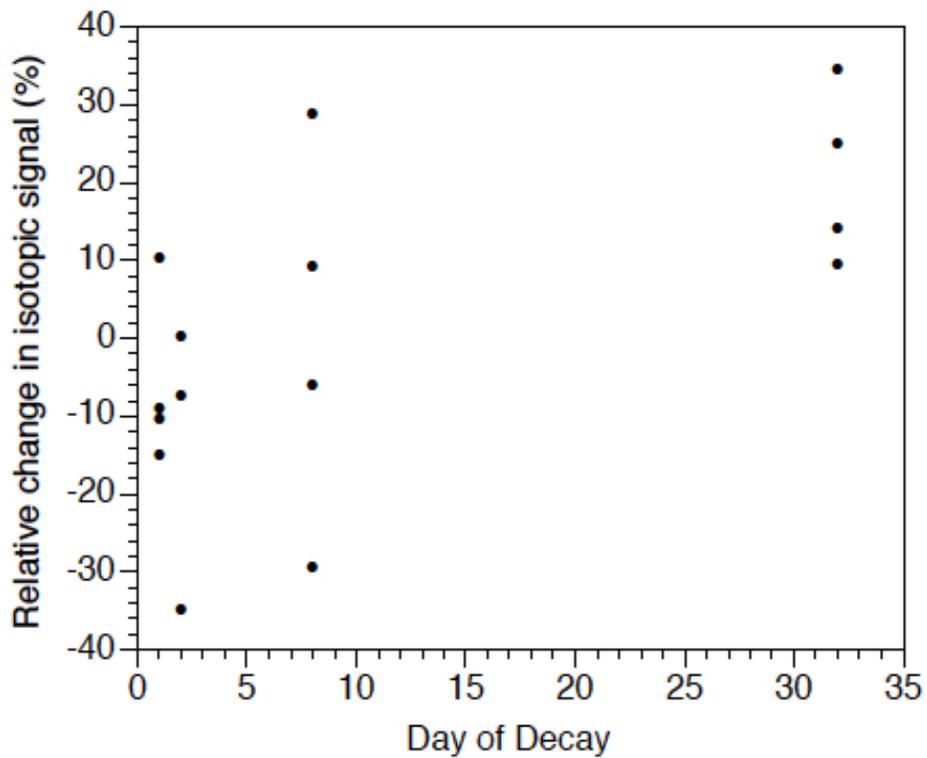
Figure 3. Change in isotopic signal over the period of decay for *Fucus vesiculosus*. The relative change in signal is expressed as a percent change from the initial $\delta^{15}N$ value measured in *F. vesiculosus* tissue before decay. There is a significant positive correlation between the change in isotopic signature and decay time ($r = 0.63$, $p = 0.01$).

# Appendix 1

Biomass decay graphs follow. The percent dry biomass remaining (y axis) per day of decay (x axis) is displayed for each macroalgal species.

*Agardhiella subulata*
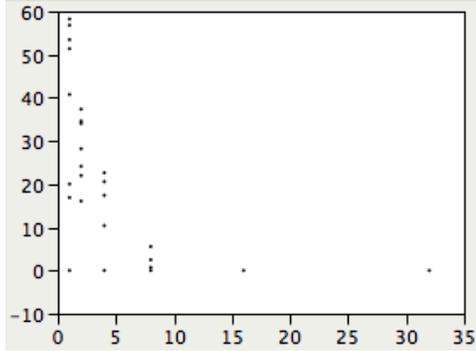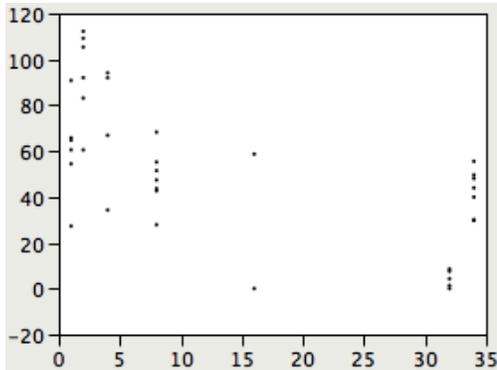


*Gracilaria vermiculophylla*
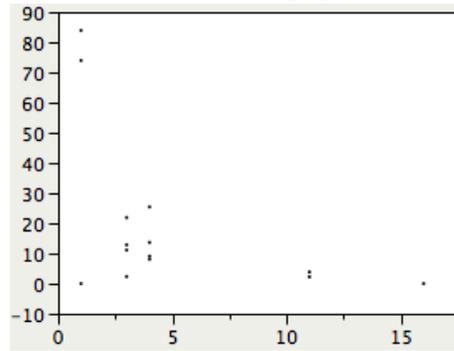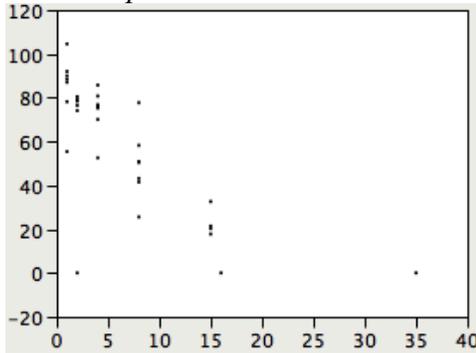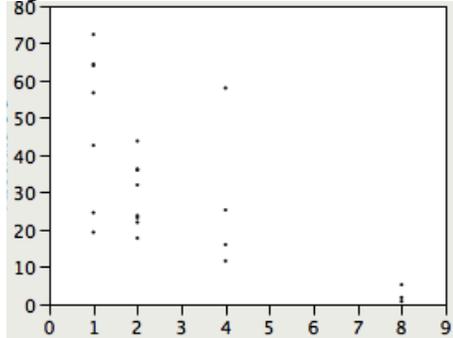


*Ulva compressa*
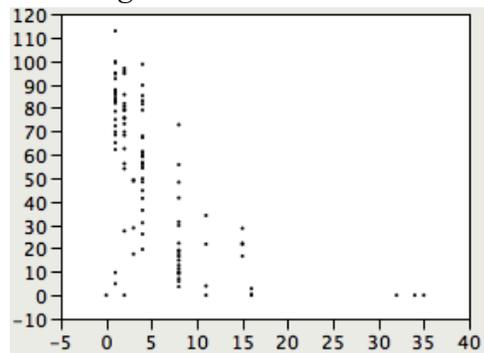
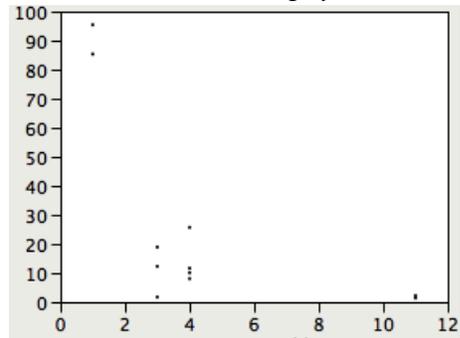

*Ulva rigida*



*Fucus vesiculosus*

Organic content decay graphs follow. The absolute organic content (y axis) per day of decay (x axis) is displayed for each macroalgal species.
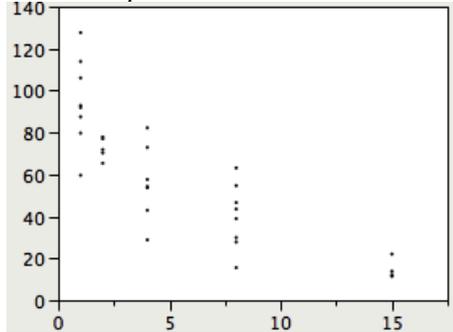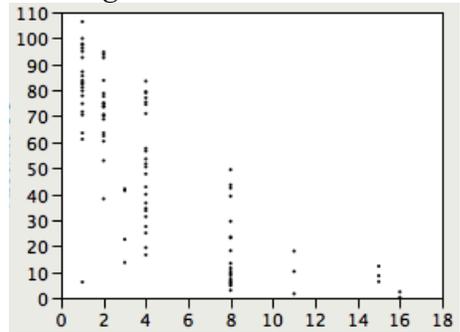
*Agardhiella subulata*



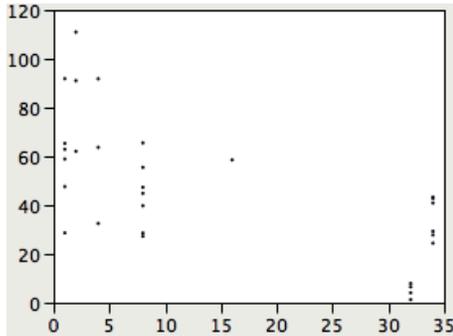*Graciliaria vermiculophylla*



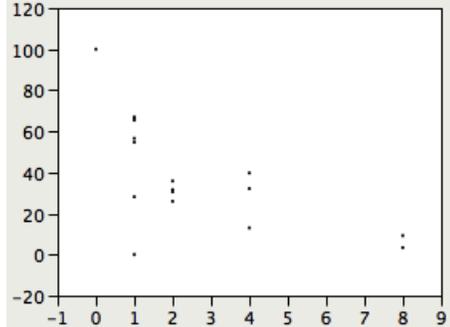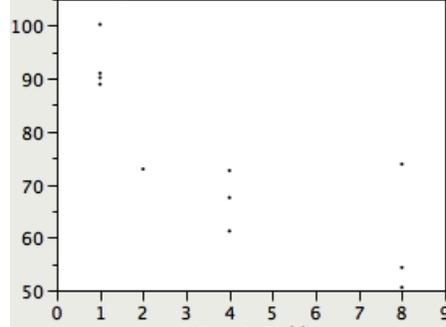*Ulva compressa*



*Ulva rigida*



*Fucus vesiculosus*

Total nitrogen decay curves follow. The absolute total nitrogen (y axis) per day of decay (x axis) is displayed for each macroalgal species.
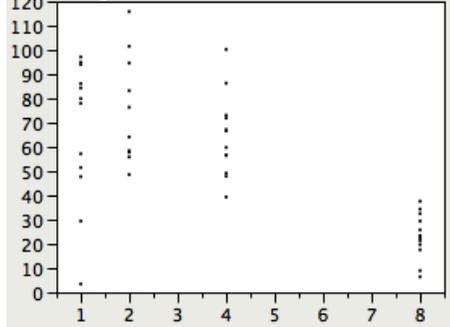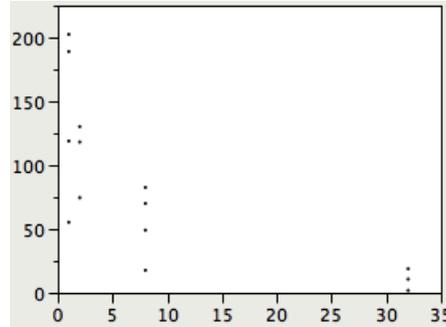
*Agardhiella subulata*



*Ulva compressa*



*Ulva rigida*



*Fucus vesiculosus*

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