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Role of Terrestrial Organic Matter in Food Webs of the Rocky Intertidal Zone

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ABSTRACT

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Terrestrial organic matter (TOM) constitutes an important source of energy in many aquatic environments (streams, lakes, wetlands). This is the first study to examine the role of TOM in food webs of the rocky intertidal zone. We compared the consumption of red alder leaves (*Alnus rubra*) to common marine sources of drifting detritus along the southern Oregon coast (*Nereocystis luetkeana*, *Phyllospadix* spp., and *Fucus gardneri*). We used short term (hours to days) and long term (months) feeding experiments to compare the rate of consumption among each plant species during the Spring and Fall of 2014 and 2015. In addition, we quantified the amount of TOM in beach wrack and in the drift of two streams that flowed directly to the rocky intertidal zone. We also measured the food quality of each plant species (C:N and polyphenolic concentrations). On average, the two small streams in this study transported 1,113.6 kg AFDM/m^3 of TOM per day during Fall leaf abscission to the rocky intertidal zone. Also, the biomass of terrestrial leaves in beach wrack varied from negligible (2.1 g AFDM) to the dominant source of detritus (60.7 g AFDM) depending on if it was the dominant riparian plant growing along the edges of the shore. Consistent with previous research, *N. luetkeana* was a high quality food (C:N = 15:1; polyphenolics = 418 mg/ml), whereas *F. gardneri* (C:N = 22:1; polyphenolics = 8098 mg/ml) was more recalcitrant. *Phyllospadix* spp. was puzzling because it had low concentrations of polyphenolics (800 mg/ml) but was not consumed. *Alnus rubra* had a high concentration of structural compounds (C:N = 33:1) and intermediate levels of polyphenolics (3,415 mg/ml after leaching). Both short term and long term experiments showed that the rates of consumption of Spring-shed, green leaves and freshly fallen brown leaves of *A. rubra* were intermediate between *N. luetkeana* and the less palatable marine species (*F. gardneri* and *Phyllospadix* spp.). Thus, *A. rubra* was eaten by common intertidal consumers and may constitute an important source of energy between brief inputs of more nutritious marine resources (e.g. *N. luetkeana*).

Keywords: energy flow from terrestrial to marine, terrestrial organic matter, rocky intertidal consumers

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INTRODUCTION

Research over the past several decades has shown that organic matter can readily flow across ecosystem boundaries having profound effects on ecosystem structure and function (e.g. Polis & Hurd 1996, Polis et al. 1997, Carpenter et al. 2005, Romero & Srivastava 2010, Richardson et al. 2009, Bartels et al. 2012). In particular, terrestrially-derived organic matter (TOM) can be an important food resource for aquatic consumers (Bärlocher 1985, Fisher & Likens 1973). For example, the energetic basis of some lotic ecosystems, especially small streams, is driven by inputs of terrestrially-derived primary production (e.g. Hall et al. 2000). Also, TOM can be an important source of nutrition in estuaries (Abrantes et al. 2013, Antonio et al. 2010) and in deep-sea ecosystems (Turner 1977, Rice et al. 2012, Voight 2007, 2008, 2009) where it provides both habitat (Rice et al. 2012, Young et al. 2013) and food (e.g. McLeod & Wing 2007).

Extensive research has shown the importance of phytoplankton, attached periphyton, and kelp as food for near-shore consumers in the marine environment (e.g. Kaehler et al. 2000, Simenstad & Wissmar 1985). More recently, research on intertidal detritivory has emphasized the importance of drift kelp, either produced locally or washed in from the subtidal zone. The availability of drift kelp can limit the growth and reproduction of near-shore consumers (e.g. Leighton & Boolootian 1963, Bustamante et al. 1995, Rodriguez 2003, Basch & Tegner 2007, Britton-Simmons et al. 2009). We were interested in investigating the role of TOM as a food resource in the rocky intertidal zone by comparing the rate of consumption of red alder leaves (*Alnus rubra*) to common species of drifting kelp and sea grass along the southern Oregon coast (*Nereocystis luetkeana*, *Fucus gardneri*, and *Phyllospadix* spp.).

Terrestrial organic matter may be transported directly to the intertidal zone by streams or it may blow in from riparian vegetation. Many small, first and second-order streams along the northwest coast of the United States drain directly to the sea. In southern Oregon, they often flow through dense forests into "pocket" bays with headlands to the north and south. Thus, the intertidal zone is the first marine habitat to receive terrestrial inputs if there are no estuaries. Estuaries generally occur at the mouth of large rivers, and they are a sink for organic matter including TOM (Ludwig et al. 1996, Nuwer and Keil 2005).

Waves mix the assortment of marine and terrestrial sources of detritus suspended in the water column while tides transport it up and down the intertidal zone (Kirkman and Kendrick 1997). Low wave action causes drifting detritus to accumulate in areas of lower hydrodynamic energy, whereas high wave action causes it to disperse throughout the near shore environment (Brown & McLachlan 1990, Krumhansl & Scheibling 2012, Lenanton et al. 1982). High tides, with low to moderate wave action, can cause detritus to accumulate in the upper intertidal zone, and as beach wrack on the shore (Baring et al. 2014). During low tides, longer strands of detritus can be trapped under rocks whereas, smaller drifting particles, depending on their buoyancy, will tend to settle in pools as these are habitats of lower hydrodynamic energy. Thus, detritus is vertically re-distributed twice a day throughout the rocky intertidal zone along the coastline of the Northeast Pacific Ocean.

Rocky intertidal consumers display a vast array of feeding modes (e.g. Kozloff 1993) potentially capable of exploiting terrestrial resources. Vascular leaves are an important component of TOM because they have greater potential as a food resource than woodier branches, cones, and needles. The quality of leaves as a food for either decomposers (bacteria and fungi) or detritivores (macro-consumers) is determined by the concentration of fibrous

material (cellulose and lignins) and polyphenolic compounds (Bärlocher 1985, Rosset et al. 1982, Suberkropp et al. 1976) both of which discourage consumption in freshwater (Irons et al. 1988, Newman 1991) and marine environments (e.g. Valiela et al. 1984; Hemminga et al. 1991; Paul & Van Alstyne 1992). Leaching and microbial conditioning decrease the concentration of polyphenolic compounds, soften the fibers, and can increase the nitrogen concentration of TOM (e.g. Rice 1982). Detritivore consumers in both freshwater and marine environments (e.g. gastropods and amphipods) attain carbon and nutrients (nitrogen) attributed to microbial conditioning of organic matter (Poovachiranon et al. 1986; Hall and Meyer 1998).

Compared to other species of kelp, *N. luetkeana* is one of the highest quality foods in coastal regions of the Northeast Pacific Ocean (Bedford & Moore 1985). It completely decomposes in as little as 6 days, and it has a high nutritional value without microbial conditioning (Smith & Foreman 1984). By contrast, surfgrass (*Phyllospadix* spp.) and bladderwrack (*F. gardneri*) are unpalatable, recalcitrant food resources, requiring > 70 days to decompose (Valentine & Heck 1999, Duarte 1990). Pocket bays along the Oregon coast are often surrounded by dense growths of red alder (*A. rubra*), which is one of the most common riparian species in the northwestern United States (e.g. Edmonds & Tuttle 2010, Hart et al. 2013). In streams, red alder leaves decompose in approximately 3 weeks making it one of the most labile terrestrial species in North America (Webster and Benfield 1986, Newman 1991). Conditioned leaves of red alder are also readily consumed by freshwater detritivores partly because it is able to fix nitrogen (Hart & Howmiller 1975; Sedell et al. 1975).

In temperate regions, large inputs of TOM to the rocky intertidal zone should be associated with autumn leaf abscission. However, inputs of TOM can take place throughout the growing season. In particular, storms can strip green leaves from plants during the Spring and

Summer (Norby et al. 2003, Williams & Whitham 1986, Valiela et al. 1998). Newly formed green leaves in the Spring have higher nutrient content and lower concentrations of polyphenolic and structural compounds (cellulose and lignin) than autumn-shed leaves (McArthur et al. 1986, Leff and McArthur 1990). Thus, Spring leaves of *A. rubra* may be a better source of nutrition for intertidal consumers than autumn-shed leaves of *A. rubra*. However, microbial conditioning can increase the value of autumn-shed leaves potentially narrowing the nutritional gap between them and Spring-shed leaves (Bärlocher 1985).

Overall, we are interested in understanding the value of TOM as a food resource in the rocky intertidal zone. In this initial investigation we tested 3 hypotheses: 1) small watersheds will transport a large standing stock of TOM to the marine environment, and large stocks will accumulate as beach wrack, 2) consumption of *A. rubra* will be faster than *Phyllospadix* spp. and *F. gardneri*, but slower than *N. luetkeana* in pools of the rocky intertidal zone, and 3) consumption rates of *A. rubra* in the rocky intertidal zone will be faster in the Spring (green leaves) than in the Fall (brown leaves).

METHODS

Site Descriptions

This study was conducted in two streams and a series of pocket bays consisting of short sandy beaches bordered by rocky headlands to the north and south at and near Cape Arago in southern Oregon (Figure 1). These streams are typical of the numerous small drainages that flow directly to the sea in this area. Both streams were small, shaded, cool, permanent reaches characterized by sandy substrate with small patches of cobble-sized particles (Table 1). In South Branch, conifers were the dominant riparian vegetation, primarily large Douglas Fir (*Pseudotsuga menziesii*), whereas a mixture of deciduous vegetation with abundant growths of red alder (*A. rubra*) were the dominant riparian vegetation in Norton Gulch. We measured depth

and velocity every 10 cm across the width of the stream to calculate flow (cross-sectional method) in the Fall of 2014. At the same time, we measured water temperature every hour in both streams (South Branch and Norton Gulch) using HOBO® data loggers (Onset Corporation, Pocasset MA, U.S.A.).

All beaches were either partially (South Cove) or completely protected by narrow openings and offshore rocky reefs (Sunset Bay, Drake's Cove, Norton Gulch, and Shore Acres). Norton Gulch and Sunset Bay were bordered by horizontal platforms supporting dense growths of surfgrass (*Phyllospadix* spp.) with channels and occasional pools running approximately north to south. However, rock pools were most abundant at South Cove and Drake's Cove, whereas Shore Acres had no channel or pool habitats. Beds of *N. luetkeana* were common in this area, and grew abundantly in and around each of these coves. Most beaches were surrounded by a mixture of *P. menziesii* and *A. rubra* except for Norton Gulch where *A. rubra* was the dominant riparian vegetation.

We measured the residual depth and surface area of 8 to 10 pools at 4 of the 5 sites (South Cove, Norton Gulch, Sunset Bay, Drake's Cove). Residual depth is the maximum water depth at low tide. These channels and pools showed a wide-range in size and were a good representation of all channels and pools in this area (Table 2). We measured temperature every hour for the duration of the study during the Spring of 2014 in 2 rock pools on each of the two surfgrass platforms (Sunset Bay and Norton Gulch), and in the Fall of 2014 in 2 rock pools at Drake's Cove and South Cove. Mean and minimum temperatures were very similar, whereas maximum temperatures were warmer in pools that occurred higher in the intertidal zone (Table 2).

We surveyed the population density of common invertebrates in 6 to 10 pools per site at 4 of our 5 sites (South Cove, Norton Gulch, Sunset Bay, Drake's Cove). Consistent with previous research, *Chlorostoma funebralis* (snails) and *Pagurus* spp. (hermit crabs) were common consumers in this area. On average, there were 19.6 snails and 5.8 hermit crabs/0.5 m^2 of pool surface area.

Abundance of TOM in Streams and in Beach Wrack (Hypothesis 1)

We were unable to quantify drift density of terrestrial inputs in the Spring of 2014 because of heavy rains and flooding. However, visual observations showed the obvious presence of green leaves of *A. rubra* in the stream and along the intertidal zone as a result of these storms. In the Fall of 2014 (Nov 5 – Dec 22), we collected 4 drift samples, one every 2 weeks, at the outflow of South Branch and Norton Gulch (Figure 1). A sample consisted of deploying a net (30 cm x 30 cm opening; 1.2 m long; 250 μm mesh) for 7 hrs during the day. On average, the net captured 54% and 40% of the flow at South Branch and Norton Gulch, respectively. The sides of the net were frequently swept by hand to prevent clogging. All samples were frozen until they were sorted into vascular leaves, red alder leaves, coarse particulate matter > 1 mm (CPOM = needles, cones, branches) and fine particulate organic matter (FPOM), 250 μm to 1 mm. All samples were dried (48 hours at 60° C), ashed (90 minutes at 550° C), and weighed to the nearest 0.01 of a gram to determine the ash-free dry mass (g AFDM) of each category (vascular leaves, *A. rubra* leaves, CPOM, and FPOM). We used AFDM to eliminate potential inaccuracies caused by small sand grains adhering to the leaf material. To estimate flow through the net, we measured depth and current velocity (Marsh-McBirney, Sigma, Flo-Mate 2; Hach Company, Loveland CO, USA) at three locations across the opening (left edge, middle, and right edge).

Flow-adjusted estimates (g AFDM/m^3·s^{-1}) based on the following formula, allowed us to compare the quantity of detrital inputs between streams (Allan and Russek 1985):

Drift Density = (g AFDM of sample · 100) / (T · W · V · 3600) where,

T = time the net was in the stream (hrs), W = width of the net (m), H = average height of water at the net opening (m), V = average velocity at the net opening (m/s), and 3600 is the number of seconds in an hour.

We used a 2-way ANOVA with "Sites" (Shore Acres and Norton Gulch) and "Detritus Categories" as main effects, and Tukey pairwise comparisons to test for differences in the drift density (DD) of each detritus category. In the initial analysis, "Sites" and the "Sites x Detritus Categories" interaction were not significant, thus, we re-ran the analysis using a 1-way ANOVA with "Detritus Categories" as the main effect (4 levels). This analysis required a Log$_e$ (DD+1) transformation to meet parametric assumptions.

We sampled beach wrack at the same two sites (Shore Acres and Norton Gulch), at the same times as stream drift in the Fall of 2014 (Nov 5 – Dec 21). That is, we collected four samples every two weeks at Shore Acres and on 2 of the 4 weeks at Norton Gulch. All beach wrack was removed by heavy wave action on 2 of the 4 weeks at Norton Gulch. Samples consisted of haphazardly tossing a PVC quadrant (50 cm x 50 cm) every 5 m along a 25 m transect at both beaches. All plant material within the quadrant was frozen before being separated into surfgrass (*Phyllospadix* spp.), kelp, terrestrial leaves (e.g. red alder), and other terrestrial material (e.g. needles, cones, branches, and bark). In the lab, all categories were dried (48 hours at 60° C), ashed (90 minutes at 550° C), and weighed to the nearest 0.01 of a gram (g AFDM).

We initially tried a 2-way ANOVA with "Sites" (Shore Acres and Norton Gulch) and "Detritus Categories" (4 levels) as main effects to test for differences in the abundance of *Phyllospadix* spp., kelp, terrestrial leaves, and "other terrestrial material". However, these data could not be transformed to meet parametric assumptions (equal variances). Thus, we used a Kruskal-Wallis non-parametric analysis to test for differences among detritus categories for both sites separately.

C:N and Polyphenolic Concentrations

We measured C:N and polyphenolic concentrations of each leaf species to determine their quality as a food resource. In the Fall of 2015, we compared the palatability (C:N and polyphenolic concentrations) of fresh, Fall-shed leaves of *A. rubra*, fresh fronds of *N. luetkeana* and fresh fronds of *F. gardneri* to samples of each species after 1 week of conditioning. That is, 8 fresh samples of *A. rubra*, *N. luetkeana*, and *F. gardneri* were compared to 8 extra packs of each species placed in litter bags (500 μm mesh) and deployed for 1 week in rock pools during the Fall 2015 feeding experiment. However, we did not compare fresh to conditioned *Phyllospadix* spp. leaves because of difficulties identifying dead and decomposing *Phyllospadix* spp. Thus, there was a total of 53 samples analyzed for C:N (BYU Environmental Analytical Laboratory) and polyphenolic compounds (BYU College of Life Sciences Chromatography Facility). Samples for polyphenolic analysis were: 1) freeze-dried, 2) ground to powder (500 mg dry weight), 3) submersed in 3 ml of 100% methanol, and 4) sonicated for 5 minutes and centrifuged for 10 minutes before the top layer (supernatant) was pipetted into a 10 ml bottle. Steps 3 and 4 were repeated to provide ~ 9 ml of extracted liquid, which was filtered (glass wool), and analyzed using High Performance Liquid Chromatography (HPLC).

We used a 1-way ANOVA with "conditioning" as a main effect (fresh vs conditioned) to determine if there was a significant decrease of C:N in *F. gardneri* and *A. rubra* after 1 week of conditioning in the marine environment. Only *A. rubra* required a transformation ($Log_e X$). However, we needed to used a Kruskal-Wallis analysis for *N. luetkeana* to compare C:N in fresh versus conditioned leaves because transformations did not produce equal variances. We also used a 1-way ANOVA ($Log_e X$) with "species" as a main effect (*A. rubra*, *F. gardneri*, *N. luetkeana*) and Tukey pair-wise comparisons to determine differences among species in C:N ratios of conditioned leaves. For polyphenolics, we again used a 1-way ANOVA with "conditioning" as the main effect (fresh vs conditioned) for *A. rubra* and *N. luetkeana*. *Nereocystis luetkeana* required a log transformation ($Log_e X$), whereas *F. gardneri* required a Kruskal-Wallis analysis. We also used a Kruskal-Wallis analysis and non-parametric, pair-wise comparisons (Ogle 2017) to determine differences among species in polyphenolic concentrations.

Feeding Experiments (Hypothesis 2)

Our feeding experiments consisted of two long-term experiments in the Spring and Fall of 2014 and two short-term experiments in the Spring and Fall of 2015. The long-term experiments provided an estimate of consumption as leaves change during conditioning whereas, short-term experiments show the immediate response of consumers to different leaf species without conditioning.

In both long-term experiments (2014), we used bags of different mesh sizes to parse detritivore consumption from microbial degradation. Fine-mesh bags (15 cm X 18 cm) were made of Nytex nylon (500 μm openings), sewn with 6 lb monofilament line, and sealed at the top

with a double layer of heavy duty velcro (Figure 2a). A 500-µm mesh is a good size to exclude

detritivores yet prevent hypoxia (Flores et al. 2013, Tolkkinen et al. 2015). Coarse containers

were constructed from rubber-coated wire (2.5 cm mesh), and leaves in open packs were sewn

together with 6 lb monofilament line (Figure 2a). Fine-mesh bags estimate microbial

decomposition in the absence of physical abrasion and detritivore consumption, coarse-mesh

bags show the effects of microbial degradation + detritivore consumption - abrasion, and open

packs show the effects of all three (abrasion + microbial degradation + consumption). Thus, we

can estimate the total rate of decay (open packs), the percentage of the total rate of decay

attributed to abrasion (open – coarse-mesh packs) and consumption (coarse-mesh – fine-mesh

packs). The leaf species showing the fastest rate of consumption will correspond to the largest

average difference between coarse-mesh bags and fine-mesh bags.

During the Spring of 2014 (May 12 – June 30) we deployed a total of 216 leaf packs of *A.

rubra*, *N. luetkeana* and *Phyllospadix* spp. over 51 days on two sandstone, surfgrass platforms

(*Phyllospadix* spp.) bordering Sunset Beach and Norton Gulch (Figure 1). We used a completely

random design, with three replicate leaf packs (~10 g wet weight) of each species randomly

assigned to one of the three treatments (fine-mesh, coarse-mesh, open), and randomly placed in a

channel or a pool on one of the 2 platforms. A completely random design was appropriate

because we knew little about the effects of potential extraneous variables (e.g. Ellison and

Gotelli 2004). We collected 3 packs of each species from each of the 3 treatments on both

platforms after 7, 20, 27, and 51 days.

Leaf packs were constructed using freshly removed green *A. rubra* leaves (~ 2 to 3 weeks

old), the distal and central portion of young *N. luetkeana* fronds, and whole blades of

Phyllospadix spp. each collected at or near our study sites. *Alnus rubra* leaves were refrigerated

and *N. luetkeana* and *Phyllospadix* spp. remained hydrated in a sea water table prior to pack construction.

Prior to deployment, each pack was fastened to a piece of PVC (30 cm) with a zip-tie. In the field, boulder-sized rocks were placed on the pipe to hold it in place. All packs (open, coarse, fine) were retrieved with a drift net (250 μm mesh), rinsed with a gentle stream of tap water over a sieve (75 μm mesh), dried (48 hours at 60° C), ashed (90 minutes at 550° C), and weighed to the nearest 0.01 of a gram to produce the final weight for each pack (g AFDM).

We estimated the total percent lost of the initial biomass (open packs), and the percent of the initial biomass lost to consumption (coarse-mesh % lost – fine-mesh % lost) and abrasion (open % lost – coarse-mesh % lost) for each leaf pack based on the following formula:

$$\text{Percent Lost} = 100 - ((F/I)*100) \text{ where,}$$

"F" and "I" are the final and initial pack weights (g AFDM), respectively. We calculated consumption as the percent lost of the initial pack biomass. We do not report the actual biomass lost to consumption because initial weights differed within and between species. That is, light packs that lost 90% of their biomass to consumption may have lost the same amount as heavy packs that lost 10% of their initial biomass to consumption. We estimated the initial weight of each pack (g AFDM) using a simple linear regression between wet weight biomass versus AFDM for each leaf species (Figure 3, Table 3). Before measuring initial wet weights, green leaves of *A. rubra* were gently washed with tap water and the outer surface of *N. luetkeana* fronds and *Phyllospadix* spp. blades were dabbed dry with paper towels for 30 s. Then all samples were ashed (550° C for 90 min), and weighed to the nearest 0.01 of a gram to determine AFDM for the regressions.

We took the average of all pair-wise differences among packs (e.g. consumption equal to each coarse-mesh pack – each fine-mesh pack) within each species (*A. rubra*, *N. luetkeana* and *Phyllospadix* spp.) on each date to estimate average consumption losses. We performed a 2-way ANOVA with "species" (3 levels) and "dates" (4 levels) as main effects, to test for differences in percent consumption between leaf species on each collection date. These data did not require a transformation.

During the Fall of 2014 (Nov 3 – Dec 22) we followed the same procedures used in the Spring of 2014 except we: 1) used brown, Fall-shed leaves of *A. rubra*, 2) used a randomized block design to reduce the effects of extraneous variables (e.g. sand accumulation), 3) excluded *Phyllospadix* spp. because it was not consumed in the Spring, and 4) eliminated the "open" treatment because after two weeks, it did not differ from the coarse-mesh treatment for any of the leaf species in the Spring. Thus, this design consisted of one fine-mesh pack (500 µm mesh) and one coarse-mesh pack (2.5 cm mesh) of both species (*A. rubra* and *N. luetkeana*) randomly positioned on bricks/blocks (Figure 2a) and randomly assigned to rock pools at 2 sites. That is, 16 bricks were deployed at Drake's Cove and 16 bricks at South Cove (Figure 2). Four bricks from both sites were randomly chosen and retrieved after 2 and 4 weeks, whereas 8 bricks were retrieved from both sites on week 6 for a total of 32 bricks and 128 leaf packs in this study. In the lab, all samples were ashed (550° C for 90 min), and weighed to the nearest 0.01 of a gram to determine the final pack weights.

Recently fallen leaves of *A. rubra* were air-dried at room temperature for 72 hours and bundled into packs ranging from 4.0 - 4.5 g dry weight whereas, fresh packs of *N. luetkeana* fronds ranged between 15 and 25 g wet weight. As in the Spring of 2014, we used linear regression (wet weight biomass vs AFDM) to estimate the initial g AFDM of both species (Table

3). However, Fall-shed leaves of *A. rubra* are more fragile than green leaves used in the Spring. Thus, we measured handling losses by weighing, deploying in rock pools, and immediately retrieving and re-weighing 5 extra packs of Fall-shed leaves of *A. rubra* at South Cove. Handling losses accounted for less than 1% of the initial pack dry weight, and was not included when calculating the percent lost for each pack.

The statistical procedures were the same as in the Spring. That is, we calculated the percent lost for each pack and subtracted coarse-mesh packs from fine-mesh packs to estimate average percent consumption of the initial pack biomass for each species on each date. However, instead of making all pair-wise comparisons between treatments we subtracted fine-mesh bags from coarse-mesh bags from the same block and averaged over all blocks for a species on a date. Preliminary analyses showed that "pools/blocks" and "sites" were not significant. Thus, we used a 2-way ANOVA with "species" (*A. rubra* and *N. luetkeana*) and "date" (3 levels) as main effects to compare percent consumption among leaf species on each date. These data did not require a transformation.

In the Spring of 2015 (May 14-19), we again used a randomized block design to examine the consumption of Spring-shed leaves of *A. rubra*, fronds of *N. luetkeana*, and blades of *Phyllospadix* spp, over 3 days without litter bags (Figure 2b). One pack of each species was randomly positioned on a wire-mesh block and randomly assigned to a pool at each of 4 sites (Norton Gulch, Drake's Cove, Sunset Bay, and South Cove). All blocks at each site were exposed to consumption for the same amount of time on each day (1.5 to 2 hrs) during the lowest, low tide. Before the next high tide, all blocks were removed to eliminate potential losses attributed to wave action, and covered with a moist cloth to prevent drying. We assumed that all losses would be attributed to consumption because losses attributed to microbial degradation

would be minimal over 3 days. Thus, we could measure consumption directly over the short term without bags of different mesh sizes. At the end of the third day, all packs were retrieved, dried (60° C for 48 hrs), and weighed. Again, we used regression to estimate the initial dry weight of each pack (Table 3). We did not ash these packs because they had little chance of accumulating sand while lying in a rock pool without waves.

We tested for independence among species on a block by comparing the consumption of *A. rubra* mixed with *N. luetkeana* and *Phyllospadix* spp. to the consumption of *A. rubra* in pools where it was the only species. That is, consumption of *A. rubra* may be greater on blocks with all three species if consumers were attracted by a high-quality food (*N. luetkeana*). We could verify independence if consumption rates were similar between single packs of *A. rubra* and *A. rubra* on blocks with all 3 species (mixed blocks). We used 50 mixed blocks and 54 blocks with a single pack of *A. rubra* for a total of 204 packs in this study.

We used a blocked ANOVA to compare rates of consumption among 3 species (green *A. rubra*, *N. luetkeana*, and *Phyllospadix* spp.) at 4 sites (Norton Gulch, Drake's Cove, Sunset Bay, and South Cove). The response variable was the pack percent lost (g dry weight) after 3 days. We blocked on the potential variation among pools and used "Species" (3 levels) and "Sites" (4 levels) as main effects. "Sites" and the blocking factor ("Pools") were not significant, so, the analysis was re-run as a 1-way ANOVA with "Species" as the main effect. These data required an arcsine, square-root transformation to meet parametric assumptions.

In the Fall of 2015 (November 24 - 30), we again used a randomized block design to conduct another short-term feeding experiment (7 days) using Fall-shed leaves of *A. rubra*, fronds of *N. luetkeana*, and *Fucus gardneri*. *Phyllospadix* spp. was replaced by *F. gardneri* because *F. gardneri* was the most abundant recalcitrant species at the sites in this study (South

Cove and Drake's Cove). A block consisted of randomly placing leaf packs in 6 sections of hard plastic drain pipe (Corex, 30 cm long, 20 cm diameter) fastened by zip ties to a wire frame coated with plastic (Figure 2c). The drain pipe eliminated the effects of wave action while allowing us to manipulate access by consumers with different mesh sizes. The ends of each canister were covered with either a fine mesh (500 µm) or a coarse mesh (2.25 cm) for each of the 3 species (*A. rubra*, *N. luetkeana*, and *F. gardneri*). Four blocks were placed in 4 pools randomly chosen at both sites. Boulder-sized rocks held the frame in place in each pool. All blocks were left in place for the full 7 days without removing them at high tide as was done in the Spring. Thus, we could not assume that microbial degradation was negligible. Consequently, we subtracted the percent lost in the fine-mesh canisters from the percent lost in the coarse-mesh canisters for each species to parse microbial degradation from consumption. We again used linear regression to estimate the initial dry weight of *N. luetkeana* and *F. gardneri* packs (Table 3). After 7 days, all packs were freeze-dried and weighed to provide final weights for calculating the average percent lost. We did not construct single packs of *A. rubra* because the Spring study showed that packs on a block were independent replicates.

We used a blocked ANOVA to compare rates of consumption among brown *A. rubra*, *N. luetkeana*, and *F. gardneri* after 1 week of exposure to consumers at South Cove and Drake's Cove. "Sites" and "Pools" were not significant, so the analysis was re-run as a 1-way ANOVA with "Species" as the main effect. These data did not require a transformation.

Consumption of Spring-shed versus Fall-shed leaves of *A. rubra* (Hypothesis 3)

We used data from the long-term studies during the Spring and Fall of 2014, to test the hypothesis that consumption would be greater on Spring-shed leaves than Fall-shed leaves of *A. rubra*. We used degree-days rather than Julian Days to eliminate the potential effects of

temperature differences between seasons on consumption rates. The number of degree-days are the average daily temperature summed from the start of the experiment to the final collection date. We used a 2-way ANOVA with "season" (Spring versus Fall) and "duration" of decomposition (early versus late) to determine if the percent of *A. rubra* consumed differed between the Spring and Fall. We made degree-days a categorical variable. That is, all leaf packs collected on various dates in the Spring and Fall between 0 and 350 degree days represented consumption during the early stages of decomposition (83 total consumption values), whereas, all packs collected between 351 to 615 degree days represented consumption during the late stages decomposition (43 total consumption values).

RESULTS

Abundance of TOM at Stream Inflows and in Beach Wrack

The average total inflow of TOM in the drift from South Branch and Norton Gulch during the Fall was 12.9 g AFDM/m^3·s^{-1}, which is equivalent to 33,438 kg AFDM/m^3·month^{-1} and 401,256 kg AFDM/m^3·year^{-1}. Most of this organic matter was CPOM and FPOM, which were not significantly different, but both were greater than vascular leaves and *A. rubra*, which were also not significantly different (Table 4 and Figure 4).

The average biomass of surfgrass (*Phyllospadix* spp.) in the wrack at Shore Acres Beach was 3x greater than kelp and "other" terrestrial matter (cones, needles, branches), with only a small biomass of terrestrial leaves (Figure 5a). However, the pattern was nearly reversed at Norton Gulch where dense growths of *A. rubra* surrounded the beach. That is, terrestrial leaves (mostly *A. rubra*) were the dominant source of organic matter at Norton Gulch (Figure 5b). Because of a high degree of variation between samples within categories, there were no significant differences at Shore Acres (Chi^2 = 3.92, d.f. = 3, p-value = 0.27), and only marginal

significance between terrestrial leaves (*A. rubra*) and "other terrestrial" matter at Norton Gulch (Chi^2 = 6.81, d.f. = 3, p-value = 0.08). Overall however, these data confirm our first hypothesis that small coastal watershed transport a large standing stock of TOM to the rocky intertidal zone, and that TOM can comprise the majority of organic matter in wrack on some beaches (e.g. Norton Gulch).

C:N and Polyphenolic Concentrations

The average C:N ratio and polyphenolic concentrations of conditioned leaves of *A. rubra* was significantly lower than freshly fallen leaves of *A. rubra* (Table 5). *Nereocystis luetkeana* followed the same pattern for polyphenolics (conditioned < fresh) but was reversed for C:N (conditioned > fresh). Also, C:N and polyphenolic concentrations were did not differ between conditioned and fresh leaves of *F. gardneri* (Table 5).

As expected, *N. luetkeana* was the highest quality food with the lowest average C:N ratio and lowest concentrations of polyphenolics after 1 week of conditioning (Table 5). Although *A. rubra* had the largest C:N ratio of conditioned leaves, it was intermediate in polyphenolic concentrations between *N. luetkeana* and *Phyllospadix* spp. with low concentrations and *F. gardneri* with high concentrations. That is, *F. gardneri* had 31.5x higher concentrations of polyphenolics than *N. luetkeana*, 11.5x higher concentrations than *Phyllospadix* spp., and 2.7x higher concentrations than *A. rubra*, which had 11.5x higher concentrations than *N. luetkeana* (Table 5).

Feeding Experiments

In the Spring (2014) long term experiment, the percent consumed of *N. luetkeana* was always significantly greater than *A. rubra* and *Phyllospadix* spp. until the last date when there was virtually no *N. luetkeana* remaining (Table 6 and Figure 6). Except for a small amount in a

few packs, all of the *N. luetkeana* was lost sometime between 7 and 20 days in both fine-mesh and coarse-mesh bags indicating a rapid rate of microbial degradation and probably also consumption. Consumption did not differ between *A. rubra* and *Phyllospadix* spp. until after 20 days when the percent consumed of *A. rubra* increased and was significantly greater than *Phyllospadix* spp. (Table 6 and Figure 6). The consumption of *Phyllospadix* spp. was never greater than 10% of the initial pack biomass showing that it was a poor food resource.

For *A. rubra* in the Spring (2014), losses in coarse-mesh packs (consumption + microbial decay) did not differ from "open" packs (consumption + microbial decay + abrasion) at the beginning and end of the experiment. However, losses in coarse-mesh packs exceeded losses in "open" packs in *A. rubra* towards the middle of the experiment (Table 7), which is opposite of expectations if abrasions losses were important. Also, losses in coarse-mesh packs and "open" packs did not differ at any time for *N. luetkeana* or *Phyllospadix* spp. (Table 7). Based on these results, we eliminated the "open" treatment from the Fall 2014, long-term experiment because abrasion losses appeared unimportant in the Spring.

In the Fall 2014 long-term experiment, all of the *N. luetkeana* packs were gone after the first 16 days compared to an average loss of 52 percent after 16 days in *A rubra* ($t_{24} = 5.76$; $P < 0.0001$). Figure 7 shows that losses attributed to consumption in *A. rubra* were greater than losses attributed to microbial decomposition early in the experiment, whereas this pattern was reversed at Julian Day 31 and 46 as the percent losses attributed to microbial decay steadily increased with time (Figure 7). Overall, both long term experiments support the second hypothesis that consumption of *A. rubra* would be slower than *N. luetkeana* but faster than *Phyllospadix* spp.

In the Spring 2015 short-term feeding experiment (3 days), there was no difference in the percent consumed of *A. rubra* alone versus *A. rubra* on a block with *N. luetkeana* and *Phyllospadix* spp. (Table 8 and Figure 8a). Thus, there was no evidence of a lack of independence between samples on the same block. After 3 days, *N. luetkeana* was consumed 1.75x faster than *A. rubra*, and 2x faster than *Phyllospadix* spp. (Table 8 and Figure 8a). That is, on average, consumers ate 52% of *N. luetkeana*, 16% of green *A. rubra*, and 1% of *Phyllospadix* spp. over a maximum of 6 hrs in the water (2 hrs/day).

In the Fall 2015 short-term feeding experiment (7 days), *N. luetkeana* was completely consumed in the coarse-mesh treatment, 40% degraded in the fine-mesh treatment for a difference of 60% consumed over the course of a week (Figure 8b). However, this calculation underestimates the rate of consumption, as i*n situ* observations showed that all *N. luetkeana* in coarse canisters was gone after the first day. Thus, consumption of *N. luetkeana* was significantly faster than *A. rubra* and *F. gardneri*, but there was no difference between *A. rubra* and *F. gardneri* (Table 9). Both short term experiments support the hypothesis that consumption of *A. rubra* would be slower than *N. luetkeana* but *A. rubra* was only faster than a poor quality marine food in the Spring (*Phyllospadix* spp.).

Consumption of Spring-shed versus Fall-shed leaves of *A. rubra*

Figure 9 shows that consumption of Fall-shed leaves was 3.6x faster than Spring-shed leaves ($F_{1,121}$ = 11.90; P = <0.001) during the early stages of decomposition (0 - 350° C), whereas seasonal differences were not significant ($F_{1,121}$ = 11.90; P = 0.66) in the later stages of decomposition (351 – 615° C). Thus, these results do not support our third hypothesis that Spring-shed leaves of *A. rubra* would be consumed faster than Fall-shed leaves.

DISCUSSION

For more than four decades, ecologists have investigated how the flow of energy from donor ecosystems can affect the productivity and food web dynamics of recipient ecosystems (e.g. Hynes 1975, Polis 1994). Recent reviews have concluded that most aquatic environments are heterotrophic partly because primary production is often limited by light availability and partly because large quantities of TOM flow through detrital pathways from the terrestrial environment (e.g. Sand-Jensen & Staehr 2009, Yvon-Durocher et al. 2012, Hoellein et al. 2013). We found that two small coastal streams in southern Oregon, on average, delivered 442.3 tons AFDM/m^3 on an annual basis to the sea. To our knowledge, this is the first calculation of the standing stock of terrestrial detritus for small coastal streams in the Northeast Pacific Ocean. This calculation is probably too high for an entire year because our samples were collected in the Fall during leaf abscission. Plus, we don't know the annual water yield of these streams to compare to previous estimates of terrestrial inflows to the sea from large rivers (1.65 x 10^8 tons of TOM/year; Hedges et al. 1997). Larger rivers certainly transport more TOM than small streams but large rivers also create large estuaries that process TOM *in situ* and thus, are sinks for TOM decreasing its transport to the sea (e.g. Sará et al. 2008). Clearly, small coastal streams in southern Oregon can deliver large standing stocks of TOM directly to the rocky intertidal zone each year.

We also found that terrestrial inputs of organic matter can constitute a large percentage of the beach wrack, but only where riparian vegetation grows close to the water's edge, as at Norton Gulch. Otherwise, the dominant type of organic matter on pocket beaches in Southern Oregon appears highly variable depending on several abiotic and biotic factors (e.g. type of near shore seaweeds, density and type of riparian vegetation, beach topography, and near shore currents).

Although primary production is approximately an order of magnitude less in the rocky intertidal zone than in adjacent coastal forests (Littler & Murray 1974, Van Tuyl et al. 2005), virtually all research on intertidal detritivory has emphasized drift kelp either produced locally or washed in from the subtidal (e.g. Duggins et al. 1989; Duggins & Eckman 1997). Drift kelp is an important source of energy for a variety of invertebrates in intertidal (e.g. Leighton & Boolotian 1963, Bustamante et al. 1995, Rodriguez 2003) and subtidal habitats (Vetter & Dayton 1998, Britton-Simmons et al. 2009). The availability of kelp can limit the growth and reproduction of intertidal consumers (e.g. Basch & Tegner 2007). In a recent review, Krumhansl & Scheibling (2012) estimated that > 80% of kelp productivity becomes part of the detrital pathway with somewhere between 10-50% being transferred out of the photic zone to the subtidal.

Are leaf-litter subsidies an important resource for marine macro-consumers between brief inputs of dislodged kelp? Our consumption experiments highlighted that *A. rubra* is both consumed over the short-term and the long-term, with the rate of consumption increasing as it becomes more palatable. Ultimately, it doesn't quite compare with the consumption of *N. luetkeana*, but when the resources of *N. luetkeana* are limited, it can certainly be consumed more readily than *Phyllospadix*. We found that *A. rubra* was not consumed any more readily than *F. gardneri*, but over the long-term, a bigger gap between the consumption of the two would be expected.

The C:N ratios and polyphenolic concentrations that we obtained for *A. rubra* were expected, as there have been many studies in the freshwater environment which have already investigated this. However, the C:N ratios and polyphenolic concentrations that were obtained for *N. luetkeana* and *F. gardneri* were not expected. This is likely due to the difficulty of

characterizing food quality based on chemical analyses. For example, Nitrogen can be tied up in toxic compounds, or it can be tied up in proteins which are highly usable; Carbon can be something as simple and usable as a sugar, or something as recalcitrant as cellulose. Despite both having lower values than *A. rubra,* in terms of the chemical analyses, it doesn't parse out which ones are better food resources.

In our Spring 2014 experiment, the surfgrass samples grew, having an impact on our results. When a sample grows, we cannot accurately determine the true amount of consumption that occurs. None of our other experiments were impacted by samples growing, so this confounding variable was isolated to this first long-term experiment. Although this brings into question the results that were obtained for the Spring 2014 experiment, we are still able to speak to the consumption of surfgrass being quite minimal, as our Spring 2015 experiment did not encounter this issue. The issue of growth was eliminated from the Spring 2015 experiment, and it still highlighted the same conclusion: surfgrass is a poor resource.

Abrasion was a factor, which likely impacted the coarse-mesh packs in the applicable experiments, as a coarse mesh is not capable of mitigating mass loss from wave action. However, when we compared the mass loss from abrasion to the mass loss from consumption in the Spring 2014 experiment, the results indicated that there was no statistical difference between the mass loss of the two. This justification is a bit precarious, especially since leaves of *A. rubra* will be more brittle in the Fall. Using bags of different mesh sizes may not be the best way to manipulate abrasion losses; our long-term experiments may not have done the best job at parsing abrasion losses from consumption losses. Due to this, our short-term experiments were valuable, as they eliminated the abrasion losses. As the order of consumption between species was similar

between long-term and short-term experiments, we can safely assume that abrasion losses did not have a strong effect in the long-term experiments.

In the temperate zone, concentrations of phytoplankton in the marine environment reach their lowest levels during the Winter months because of short day lengths and a low angle of the sun (e.g. Lowe et al. 2014). Also, Winter storms increase vertical mixing and the transport of phytoplankton out of the photic zone (e.g. Kaiser et al. 2011, Miller & Wheeler 2012). Benthic seaweed productivity also declines in the Fall and Winter with the die-back of annual species and a decline in the growth of perennial species (e.g. Connell 1972, Steneck et al. 2002, Berglund et al. 2003). Kelp productivity in higher latitudes is largely governed by seasonal variations of abiotic conditions such as irradiance, photoperiod, and temperature (e.g., Bartsch et al. 2008). Productivity and standing stock of large canopy forming kelps in temperate waters is primarily driven by relative wave disturbance and secondarily by temperature (Cavanaugh et al. 2011). The abundance of drift kelp is generally linked seasonally to periods of both sustained high productivity and large wave or storm disturbances (reviewed in Krumhansl & Scheibling 2012). Winter storms export drift kelp to beach wrack and the intertidal zone where some can be trapped for consumption (Figurski 2010, Hagen et al. 2012). However, this ephemeral source of energy is rapidly exported or depleted (e.g. Hemminga et al. 1991). Can forest litter (e.g. leaves) "conditioned" by microbes constitute a valuable resource for detritivores in the rocky intertidal zone during the Fall and Winter when marine food resources decline?

Gonad growth and gametogenesis, including the investment of lipid-rich yolk (vitellogenesis) is known to peak during the Winter months when apparent food resources are low. This occurs in many temperate intertidal animals including mussels (e.g. Bayne 1976), sea urchins (Byrne 1990), barnacles (Crisp 1954) and amphipods (Sheader 1996). Amphipods,

which often have multiple short gametogenic cycles during the course of a year may paradoxically produce larger eggs in Winter than in times of greater apparent food availability (Sheader 1996). Does terrestrial input provide critically-timed energy for fueling vitellogenesis in intertidal animals?

Future research should investigate the flux of TOM as a proportion of the total energy in the rocky intertidal. Our research only looked at the flux of energy into this ecosystem (drift density); our measure of beach wrack was not a true measure of the flux of energy. Future research investigating the composition of the total energy that is TOM could lead to broader implications for the role of TOM in this ecosystem. Another future direction is to investigate the availability of TOM in the Fall and Winter, and the effect that this has on oogenesis. If TOM availability influences oogenesis, then this would also broaden the importance of TOM in this ecosystem.

LITERATURE CITED

Abrantes KG, Barnett A, Marwick TR, Bouillon S. 2013. Importance of terrestrial subsidies for estuarine food webs in contrasting East African catchments. *Ecosphere* 4(1): 14.

Allan JD, Russek E. 1985. The Quantification of Stream Drift. *Can. J. Fish. Aquat. Sci.* 42: 210-215.

Antonio ES, Kasai A, Ueno M, Kurikawa Y, Tsuchiya K, Toyohara H, Ishihi Y, Yokoyama H, Yamashita Y. 2010. Consumption of terrestrial organic matter by estuarine molluscs determined by analysis of their stable isotopes and cellulase activity. *Estuarine, Coastal and Shelf Science* 86: 401-407.

Baring RJ, Fairweather PG, Lester RE. 2014. Storm versus calm: Variation in fauna associated with drifting macrophytes in sandy beach surf zones. *Journal of Experimental Marine Biology and Ecology* 461: 397-406.

Bärlocher F. 1985. The role of fungi in the nutrition of stream invertebrates. *Botanical Journal of the Linnean Society* 91: 83-94.

Bartels P, Cucherousset J, Steger K, Eklöv P, Tranvik LJ, Hillebrand H. 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* 93(5): 1173-1182.

Bartsch I, Wiencke C, Bischof K, Buchholz CM, Buck BH, Eggert A, Feuerpfeil P, Hanelt D, Jacobsen S, Karez R, Karsten U, Molis M, Roleda MY, Schubert H, Schumann R, Valentin K, Weinberger F, Wiese J. 2008. The genus Laminaria sensu lato: recent insights and developments. *Europena Journal of Phycology* 43: 1-86.

Basch LV, Tegner MJ. 2007. Reproductive responses of purple sea urchin (*Strongylocentrotus purpuratus*) populations to environmental conditions across a coastal depth gradient. *Bull. Mar. Sci.* 81: 255-282.

Bayne BL. 1976. Marine mussels: their ecology and physiology. Cambridge University Press, 528 pp.

Bedford AP, Moore PG. 1985. Macrofaunal Involvement in the Sublittoral Decay of Kelp Debris: The Sea Urchin *Psammechinus miliaris* (Gmelin) (Echinodermata: Echinoidea). *Estuarine, Coastal and Shelf Science* 20: 19-40.

Berglund J, Mattila J, Rönnberg O, Heikkilä J, Bonsdorff E. 2003. Seasonal and inter-annual variation in occurrence and biomass of rooted macrophytes and drift algae in shallow bays. *Estuarine, Coastal and Shelf Science* 56: 1167-1175.

Britton-Simmons K, Foley G, Okamoto D. 2009. Spatial subsidy in the subtidal zone: utilization of drift algae by a deep subtidal sea urchin. *Aquatic Biology* 52: 233-243.

Brown AC, McLachlan A. 1990. *Ecology of sandy shores*. Amsterdam: Elsevier Science.

Bustamente RH, Branch GM, Eekhout S. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* 76: 2314–2329.

Byrne M. 1990. Annual reproductive cycles of the commercial sea urchin *Paracentrotus lividus* from an exposed intertidal and sheltered subtidal habitat on the west coast of Ireland. *Marine Biology* 104: 275-289.

Carpenter SR, Cole JJ, Pace ML, Van de Bogert M, Bade DL, Bastviken D, Gille CM, Hodgson JR, Kitchell JF, Kritzberg ES. 2005. Ecosystem Subsidies: Terrestrial Support of Aquatic Food Webs from ^{13}C Addition to Contrasting Lakes. *Ecology* 86(10): 2737-2750.

Cavanaugh KC, Siegel DA, Reed DC, Dennison PE. 2011. Environmental controls of giant-kelp

biomass in the Santa Barbara Channel, California. *Marine Ecology Progress Series* 429:

1-17.

Connell JH. 1972. Community interactions on the marine intertidal shores. *Annual review of*

Ecology and systematics 3: 169-192.

Crisp DJ. 1954. The breeding of *Balanus porcatus* (Da Costa) in the Irish Sea. *J. Marine*

Biological Association of the United Kingdom 33: 473-496.

Duarte CM. 1990. Seagrass nutrient content. *Mar. Ecol. Prog. Ser.* 67: 201-207.

Duggins DO, Eckman JE. 1997. Is kelp detritus a good food for suspension feeders? Effects of

kelp species, age and secondary metabolites. *Marine Biology* 128: 489-495.

Duggins DO, Simenstad CA, Estes JA. 1989. Magnification of Secondary Production by Kelp

Detritus in Coastal Marine Ecosystems. *Science* 245: 170-173.

Edmonds RL, Tuttle KM. 2010. Red alder leaf decomposition and nutrient release in

alder and conifer riparian patches in western Washington, USA. *Forest Ecology and*

Management 259: 2375-2381.

Ellison GN, Gotelli NJ. 2004. A primer of ecological statistics. Sinauer, Sunderland,

Massachusetts. 579 pages.

Figurski JD. 2010. Patterns and sources of variation in drift algae and the ecological

consequences for kelp forests. University of California, Santa Cruz.

Fisher SG, Likens GE. 1973. Energy flow in Bear Brook, New Hampshire: an integrate approach

to stream ecosystem metabolism. *Ecological monographs* 43: 421-439.

Flores L, Larranaga A, Pascoal C, Elosegi A. 2013. Effects of storage site on breakdown of

organic matter in a mountain stream. *Freshwater Biology* 58: 1267-1278.

Hagen EM, McCluney KE, Wyant KA, Soykan CU, Keller AC, Luttermoser KC, Holmes EJ,

    Moore JC, Sabo JL. 2012. A meta-analysis of the effects of detritus on primary producers

    and consumers in marine, freshwater, and terrestrial ecosystems. *Oikos* 121: 1507-1515.

Hall RO, Meyer JL. 1998. The trophic significance of bacteria in a detritus-based food web.

    Ecology 79: 1995-2012.

Hall RO Jr, Wallace JB, Eggert SL. 2000. Organic matter flow in stream food webs with reduced

    detrital resource base. *Ecology* 81: 3445-3463.

Hart SD, Howmiller RP. 1975. Studies on the decomposition of allochthonous detritus in two

    southern California streams. *Int. Ver. Theor. Angew. Limnol. Verh.* 19:1665-74.

Hart SK, Hibbs DE, Perakis SS. 2013. Riparian litter inputs to streams in the central Oregon

    Coast Range. *Freshwater Science* 32: 343-358.

Hedges JI, Keil RG, Benner R. 1997. What happens to terrestrial organic matter in the ocean?

    Org. Geochem. 27: 195-212.

Hemminga MA, Leeuw J de, Munck W de, Koutstaal BP. 1991. Decomposition in Estuarine Salt

    Marshes: The Effect of Soil Salinity and Soil Water Content. *Vegetatio* 94: 25-33.

Hoellein TJ, Bruesewitz DA, Richardson DC. 2013. Revisiting Odum (1956): A synthesis of

    aquatic ecosystem metabolism. *Limnol. Oceanogr.* 58(6): 2089-2100.

Hynes HBN. 1975. The stream and its valley. *Verhandlungen der Internationalen Vereinigung*

    fuer Theoretische und Angewandte Limnologie 19: 1-15.

Irons JG, Oswood MW, Bryant JP. 1988. Consumption of leaf detritus by a stream shredder:

    influence of tree species and nutrient status. *Hydrobiologia* 160(1): 53-61.

Kaehler S, Pakhomov EA, McQuaid CD. 2000. Trophic structure of the marine food web at the
Prince Edward Islands (Southern Ocean) determined by $\delta^{13}C$ and $\delta^{15}N$ analysis. *Mar Ecol Prog Ser* 208: 13-20.

Kaiser MJ, Attrill MJ, Jennings S, Thomas DN, Barnes DKA. 2011. *Marine ecology: processes, systems, and impacts* (2nd edition). Oxford University Press, New York, NY, USA.

Kirkman H, Kendrick GA. 1997. Ecological significance and commercial harvesting of drifting and beach-cast macro-algae and seagrasses in Australia: a review. *Journal of Applied Phycology* 9: 311-326.

Kozloff EN. 1993. *Seashore Life of the Northern Pacific Coast*. University of Washington Press, Seattle Washington. 373 pages.

Krumhansl KA, Scheibling RE. 2012. Production and fate of kelp detritus. *Mar Ecol Prog Ser* 467: 281-302.

Leff LG, McArthur JV. 1990. Effect of nutrient content on leaf decomposition in a coastal plain stream: a comparison of green and senescent leaves. *Journal of Freshwater Ecology* 5: 269-277.

Leighton D, Boolootian RA. 1963. Diet and growth in the black abalone, *Haliotis cracherodii*. *Ecology* 44: 227-238.

Lenanton RCJ, Robertson AI, Hansen JA. 1982. Nearshore accumulations of detached macrophytes as nursery areas for fish. *Marine Ecology Progress Series* 9: 51-57.

Littler MM, Murray SN. 1974. The primary productivity of marine macrophytes from a rocky intertidal community. *Marine Biology* 27: 131-135.

Lowe AT, Galloway AWE, Yeung JS, Dethier MN, Duggins DO. 2014. Broad sampling and

    diverse biomarkers allow characterization of nearshore particulate organic matter. *Oikos*

    123: 1341-1354.

Ludwig W, Probst JL, Kempe S. 1996. Predicting the oceanic input of organic carbon

    by continental erosion. *Global Biogeochemical Cycles* 10: 23–41.

McArthur JV, Leff LG, Kovacic DA, Jaroscak J. 1986. Green Leaf Decomposition in Coastal

    Plain Streams. *Journal of Freshwater Ecology* 3: 553-558.

McLeod R, Wing SR. 2007. Hagfish in the New Zealand fjords are supported by

    chemoautotrophy of forest carbon. *Ecology* 88: 809-816.

Miller CB, Wheeler PA. 2012. *Biological Oceanography* (2nd edition). John Wiley & Sons, Ltd,

    Chichester, West Sussex, UK.

Newman RM. 1991. Herbivory and Detritivory on Freshwater Macrophytes by Invertebrates: A

    Review. *Journal of the North American Benthological Society* 10(2): 89-114.

Norby RJ, Sholtis JD, Gunderson CA, Jawdy SS. 2003. Leaf Dynamics of a Deciduous Forest

    Canopy: No Response to Elevated CO_2. *Oecologia* 136: 574-584.

Nuwer JM, Keil RG. 2005. Sedimentary organic matter geochemistry of Clayoquot

    Sound, Vancouver Island, British Columbia. *Limnology and Oceanography* 50: 1119–

    1128.

Ogle DH. 2017. FSA: Fisheries Stock Analysis. *R package version 0.8.13*.

Paul VJ, Van Alstyne KL. 1992. Activation of chemical defenses in the tropical green algae

    Halimeda spp. *Journal of Experimental Marine Biology and Ecology* 160: 191-203.

Polis GA. 1994. Food webs, trophic cascades and community structure. *Australian Journal of*

    Ecology 19: 121-136.

Polis GA, Anderson WB, Holt RD. 1997. Toward an Integration of Landscape and Food Web
    Ecology: The Dynamics of Spatially Subsidized Food Webs. *Annual Review of Ecology
    and Systematics* 28: 289-316.

Polis GA, Hurd SD. 1996. Linking Marine and Terrestrial Food Webs: Allochthonous Input from
    the Ocean Supports High Secondary Productivity on Small Islands and Coastal Land
    Communities. *The American Naturalist* 147(3): 396-423.

Poovachiranon S, Boto K, Duke N. 1986. Food preference studies and ingestion rate
    measurements of the mangrove amphipod *Parhyale hawaiensis* (Dana). *Journal of
    Experimental Marine Biology and Ecology* 98: 129-140.

Rice DL. 1982. The Detritus Nitrogen Problem: New Observations and Perspectives from
    Organic Geochemistry. *Marine Ecology Progress Series* 9: 153-162.

Rice ME, Reichardt HF, Piraino J, Young CM. 2012. Reproduction,
    development, growth, and the length of larval life of *Phascolosoma turnerae*, a wood-
    dwelling deep-sea sipunculan. *Invertebrate Biology* 131: 204-215.

Richardson JS, Zhang Y, Marczak LB. 2009. Resource Subsidies Across the Land-Freshwater
    Interface and Responses in Recipient Communities. *River. Res. Applic.* 26(1): 55-66.

Rodriguez SR. 2003. Consumption of drift kelp by intertidal populations of the sea
    urchin *Tetrapygus niger* on the central Chilean coast: possible consequences at different
    ecological levels. *Marine Ecology Progress Series* 251:141-151.

Romero GQ, Srivastava DS. 2010. Food-web composition affects cross-ecosystem interactions
    and subsidies. *Journal of Animal Ecology* 79: 1122-1131.

Rosset J, Bärlocher F, Oertli JJ. 1982. Decomposition of Conifer Needles and Deciduous Leaves in Two Black Forest and Two Swiss Jura Streams. *Int. Revue ges. Hydrobiol.* 67: 695-711.

Sand-Jensen K, Staehr PA. 2009. Net Heterotrophy in Small Danish Lakes: A Widespread Feature Over Gradients in Trophic Status and Land Cover. *Ecosystems* 12: 336-348.

Sarà G, Romano C, De Pirro M, Halldòrson PH, Sprovieri M, Rumolo P, Mazzola A. 2008. Role of peat organic matter on isotopic composition of most abundant benthic organisms in intertidal habitats of SW Iceland. *Mar Biol* 154: 191-198.

Sedell JR, Triska FJ, Triska NS. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. I. Weight loss and associated invertebrates. *Int. Ver. The or. Angew. Limnol. Verh.* 19:1617-27.

Sheader M. 1996. Factors influencing egg size in the gammarid amphipod *Gammarus insensibilis*. *Marine Biology* 124: 519-526.

Simenstad CA, Wissmar RC. 1985. δ^{13}C evidence of the origins and fates of organic carbon in estuarine and nearshore food webs. *Mar Ecol Prog Ser* 22: 141-152.

Smith BD, Foreman RE. 1984. An assessment of seaweed decomposition within a southern Strait of Georgia seaweed community. *Marine Biology* 84: 197-205.

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* 29(4): 436-459.

Suberkropp K, Godshalk GL, Klug MJ. 1976. Changes in the Chemical Composition of Leaves During Processing in a Woodland Stream. *Ecology* 57(4): 720-727.

Tolkkinen M, Mykrä H, Annala M, Markkola AM, Vuori KM, Muotka T. 2015. Multi-stressor impacts on fungal diversity and ecosystem functions in streams: natural vs. anthropogenic stress. *Ecology* 96: 672-683.

Turner RD. 1977. Wood, mollusks, and deep-sea food chains. *Bull. Am. Malacol. Union* 1976:13–19.

Valentine JF, Heck KL. 1999. Seagrass herbivory: evidence for the continued grazing of marine grasses. *Mar. Ecol. Prog. Ser.* 176: 291-302.

Valiela I, Wilson J, Buchsbaum R, Rietsma C, Bryant D, Foreman K, Teal J. 1984. Importance of Chemical Composition of Salt Marsh Litter on Decay Rates and Feeding by Detritivores. *Bulletin of Marine Science* 35(3): 261-269.

Valiela I, Peckol P, D'Avanzo C, Kremer J, Hersh D, Foreman K, Lajtha K, Seely B, Geyer WR, Isaji T, Crawford R. 1998. Ecological Effects of Major Storms on Coastal Watersheds and Coastal Waters: Hurricane Bob on Cape Cod. *Journal of Coastal Research* 14: 218-238.

Van Tuyl S, Law BE, Turner DP, Gitelman AI. 2005. Variability in net primary production and carbon storage in biomass across Oregon forests – an assessment integrating data from forest inventories, intensive sites, and remote sensing. *Forest Ecology and Management* 209: 273-295.

Vetter EW, Dayton PK. 1998. Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. *Deep-Sea Research* 45: 25-54.

Voight JR. 2007. Experimental deep-sea deployments reveal diverse Northeast Pacific wood-boring bivalves of Xylophagainae (Myoida: Pholadidae). *J Mollusc. Stud.* 73: 377–391.

Voight JR. 2008. Deep-sea wood-boring bivalves of Xylophaga (Myoida: Pholadidae) on the
Continental Shelf. *J. Mar. Biol. Assoc. U.K.* 88: 1467–1472.

Voight JR. 2009. Near-shore and offshore wood-boring bivalves (Myoida: Pholadidae:
Xylophagainae) of the deep Eastern Pacific Ocean: diversity and reproduction. *J.
Molluscan Stud.* 75: 167–174.

Webster JR, Benfield EF. 1986. Vascular Plant Breakdown in Freshwater Ecosystems. *Ann Rev
Ecol Syst* 17: 567-594.

Williams AG, Whitham TG. 1986. Premature Leaf Abscission: An Induced Plant Defense
Against Gall Aphids. *Ecology* 67: 1619-1627.

Young CM, Emson RH, Rice ME, Tyler PA. 2013. A paradoxical mismatch between fecundity
and recruitment in deep-sea opportunists: cocculinid and pseudococculinid limpets
colonizing vascular plant materials on the Bahamian Slope. *Deep-sea Research II* 92:36-
45.

Yvon-Durocher G, Caffrey JM, Cescatti A, Dossena M, Giorgio P del, Gasol JM, Montoya JM,
Pumpanen J, Staehr PA, Trimmer M, Woodward G, Allen AP. 2012. Reconciling the
temperature dependence of respiration across timescales and ecosystem types. *Nature*
487: 472-476.

TABLES

Table 1. Physical attributes of streams in this study during the Fall of 2014. Width, depth, and flow were the average of 4 measurements taken every 10 to 14 days from Nov 6, 2014 to Dec 22, 2014.

Site	Temperature (° C)			Width (m)	Depth (m)	Flow (m^3/s)
	Mean	Min	Max			
Norton Gulch Stream	10.7	8.30	12.51	1.15	0.16	0.05
South Branch	11.3	8.5	13.3	3.05	0.11	0.08

Table 2. Physical attributes of marine habitats (beaches, platforms, channels, pools). Beach length is the distance between rocky headlands to the north and south. Platform height is relative to the tidal mean lower, low water ("0"). The average and range (in parentheses) are shown for the width and depth of channels, and for pool temperatures, surface areas (S.A.), and depths. Temperature data for Norton Gulch and Sunset Bay were collected in the Spring of 2014, whereas temperatures for South Cove and Drake's Cove were collected in the Fall of 2014. Dashes indicate the absence of a habitat.

| Site | Beach | Platforms | | Channels | | Pools | | |
	Length (m)	Area (m^2)	Height (m)	Width (m)	Depth (cm)	Temp (° C)	S.A. (m^2)	Depth (cm)
South Cove	280	-	-	-	-	13.5 (12.0-15.1)	2.5 (0.3 – 4.8)	48 (22 - 87)
Shore Acres	100	-	-	-	-	-	-	-
Norton Gulch	80	1,610	0.4 – 1.0	0.85 (0.46 – 2.1)	43 (21 - 61)	12.1 (10.1- 16.5)	3.1 (0.7 – 12.2)	31 (25 - 37)
Drake's Cove	110	-	-	-	-	13.6 (12.6-15.1)	3.5 (0.8 – 9.2)	23 (21 - 24)
Sunset Bay	340	3,520	0.0 – 0.7	1.27 (0.49 – 2.56)	48 (22 - 78)	11.4 (10.0-15.1)	4.5 (1.3 – 8.8)	23 (10 - 42)

Table 3. Linear regressions used to estimate the initial biomass of leaf packs in this study.

Experiment/Species	Model	Adjusted R^2	P-value	Sample Size
Spring 2014				
A. rubra	Y = 0.342x + 0.179	0.99	<0.001	40
N. luetkeana	Y = 0.058x - 0.011	0.86	<0.001	50
Phyllospadix spp.	Y = 0.167x - 0.047	0.94	<0.001	51
Fall 2014				
A. rubra	Y = 0.971x – 0.005	0.99	<0.001	50
N. luetkeana	Y = 0.033x + 0.054	0.81	<0.001	50
Spring 2015				
A. rubra	Y = 0.412x + 0.164	0.80	<0.001	38
N. luetkeana	Y = 0.066x – 0.018	0.85	<0.001	40
Phyllospadix spp.	Y = 0.174x + 0.101	0.99	<0.001	40
Fall 2015				
A. rubra	Y = 0.901x + 0.016	0.99	<0.001	50
N. luetkeana	Y = 0.111x – 0.311	0.97	<0.001	30
F. gardneri	Y = 0.216x + 0.332	0.93	<0.001	60

Table 4. Tukey comparisons for drift density between the categories of organic matter averaged over the two streams in this study. Differences (g AFDM/m$^3 \cdot$s^{-1}) were back-calculated from a natural log (ln) transformation.

Category Comparisons	Difference	Statistics
CPOM > FPOM	0.91	$F_{3,32} = 16.93$; P = 0.22
CPOM > *A. rubra*	7.12*	$F_{3,32} = 16.93$; P = <0.001
CPOM > Vascular Leaves	4.25*	$F_{3,32} = 16.93$; P = <0.001
FPOM > *A. rubra*	3.25*	$F_{3,32} = 16.93$; P = <0.001
FPOM > Vascular Leaves	1.75*	$F_{3,32} = 16.93$; P = 0.02
Vascular Leaves > *A. rubra*	0.55	$F_{3,32} = 16.93$; P = 0.55

Table 5. The average total carbon and total nitrogen (C:N) and average polyphenolic concentrations of leaves from the Fall of 2015. "Fresh" are leaves prior to decomposition. "Conditioned" leaves are after a week of decomposition. We did not compare "fresh" versus "conditioned" for *Phyllospadix* spp. because of the difficulties of distinguishing these two states for this species. Pairwise comparisons of C:N and polyphenolics among leaf species was based on concentrations after one week of conditioning.

Leaf Species/Comparison	C:N	C:N Statistics	Polyphenolics (mg/ml)	Polyphenolics Statistics
Fresh *A. rubra*	35:1*	$F_{1,14} = 19.6$; $P = 0.001$	18,106*	$F_{1,14} = 73.2$; $P = < 0.001$
Conditioned *A. rubra*	32:1		3,415	
Fresh *N. luetkeana*	14:1*	$Chi^2 = 7.4$; $P = 0.007$	541*	$F_{1,9} = 9.1$; $P = 0.01$
Conditioned *N. luetkeana*	17:1		295	
Fresh *F. gardneri*	22:1	$F_{1,14} = 2.8$; $P = 0.12$	6,918	$Chi^2 = 0.01$; $P = 0.92$
Conditioned *F. gardneri*	23:1		9,278	
Fresh *Phyllospadix* spp.	26:1	n.a.	800	n.a.
A. rubra > *N. luetkeana*	-	$F_{2,17} = 150$; $P = < 0.001$*	-	$Z = 2.40$; $P = 0.02$*
F. gardneri > *N. luetkeana*	-	$F_{2,17} = 150$; $P = < 0.001$*	-	$Z = 3.22$; $P = 0.004$*
A. rubra > *F. gardneri*	-	$F_{2,17} = 150$; $P = < 0.001$*	-	$Z = -1.10$; $P = 0.27$

Table 6. Tukey comparisons of average differences in the percent consumed of the initial pack biomass between 3 leaf species over 51 days in the Spring of 2014. "Julian Day" was a categorical variable.

Treatment Comparisons	Julian Day	Difference (%)	Statistics
A. rubra > *Phyllospadix* spp.	7	6.73	$t_{161} = -0.67; P = 0.50$
	20	23.62*	$t_{161} = 3.73; P = <0.001$
	27	16.02*	$t_{161} = 2.17; P = 0.04$
	51	19.93*	$t_{161} = 3.40; P = <0.001$
N. luetkeana > *A. rubra*	7	42.36*	$t_{161} = -3.73; P = <0.001$
	20	50.90*	$t_{161} = -4.53; P = <0.001$
	27	44.62*	$t_{161} = -5.27; P = <0.001$
	51	17.13*	$t_{161} = 3.20; P = 0.002$
N. luetkeana > *Phyllospadix* spp.	7	35.63*	$t_{161} = -2.52; P = 0.01$
	20	74.52*	$t_{161} = -6.23; P = <0.001$
	27	60.64*	$t_{161} = -4.01; P = <0.001$
	51	2.80	$t_{161} = -0.44; P = 0.66$

Table 7. Tukey comparisons of average differences in the percent of the initial pack biomass lost to consumption versus abrasion for 3 leaf species over 51 days in the Spring of 2014. "Julian Day" was a categorical variable.

Treatment Comparisons	Julian Day	Difference (%)	Statistics
A. rubra	7	8.99	$F_{3,204} = 11.45$; $P = 0.14$
	20	11.23*	$F_{3,204} = 11.45$; $P = 0.02$
	27	21.71*	$F_{3,204} = 11.45$; $P = <0.001$
	51	9.41	$F_{3,204} = 11.45$; $P = 0.22$
N. luetkeana	7	17.24	$F_{3,75} = 0.97$; $P = 0.99$
	20	3.00	$F_{3,75} = 0.97$; $P = 0.99$
	27	18.32	$F_{3,75} = 0.97$; $P = 0.93$
	51	9.17	$F_{3,75} = 0.97$; $P = 0.97$
Phyllospadix spp.	7	13.68	$F_{3,53} = 4.66$; $P = 0.35$
	20	11.38	$F_{3,53} = 4.66$; $P = 0.06$
	27	7.08	$F_{3,53} = 4.66$; $P = 0.99$
	51	1.15	$F_{3,53} = 4.66$; $P = 0.99$

Table 8. Tukey comparisons of average differences in the percent consumed of the initial pack biomass between 3 leaf species over 3 days in the Spring of 2015. "m" designates the mixed leaf treatment and "a" are *A. rubra* leaves alone in a rock pool. Differences were back-calculated from an arcsin square-root transformation.

Treatment Comparisons	Difference (%)	Statistics
A. rubra (a) = *A. rubra* (m)	0.14	$F_{3,160} = 93.44$; $P = 0.82$
A. rubra (m) < *N. luetkeana* (m)	16.97*	$F_{3,160} = 93.44$; $P < 0.001$
A. rubra (m) > *Phyllospadix* (m)	7.85*	$F_{3,160} = 93.44$; $P < 0.001$
N. luetkeana (m) > *Phyllospadix* (m)	42.33*	$F_{3,160} = 93.44$; $P < 0.001$

Table 9. Tukey comparisons of average differences in the percent consumed of the initial pack biomass for the Fall

2015 short term feeding experiment (7 days).

Treatment Comparisons	Difference (%)	Statistics
A. rubra = F. gardneri	1.73	$F_{2,21} = 32.95$; $P = 0.96$
N. luetkeana > A. rubra	49.04*	$F_{2,21} = 32.95$; $P < 0.001$
N. luetkeana > F. gardneri	47.31*	$F_{2,21} = 32.95$; $P < 0.001$
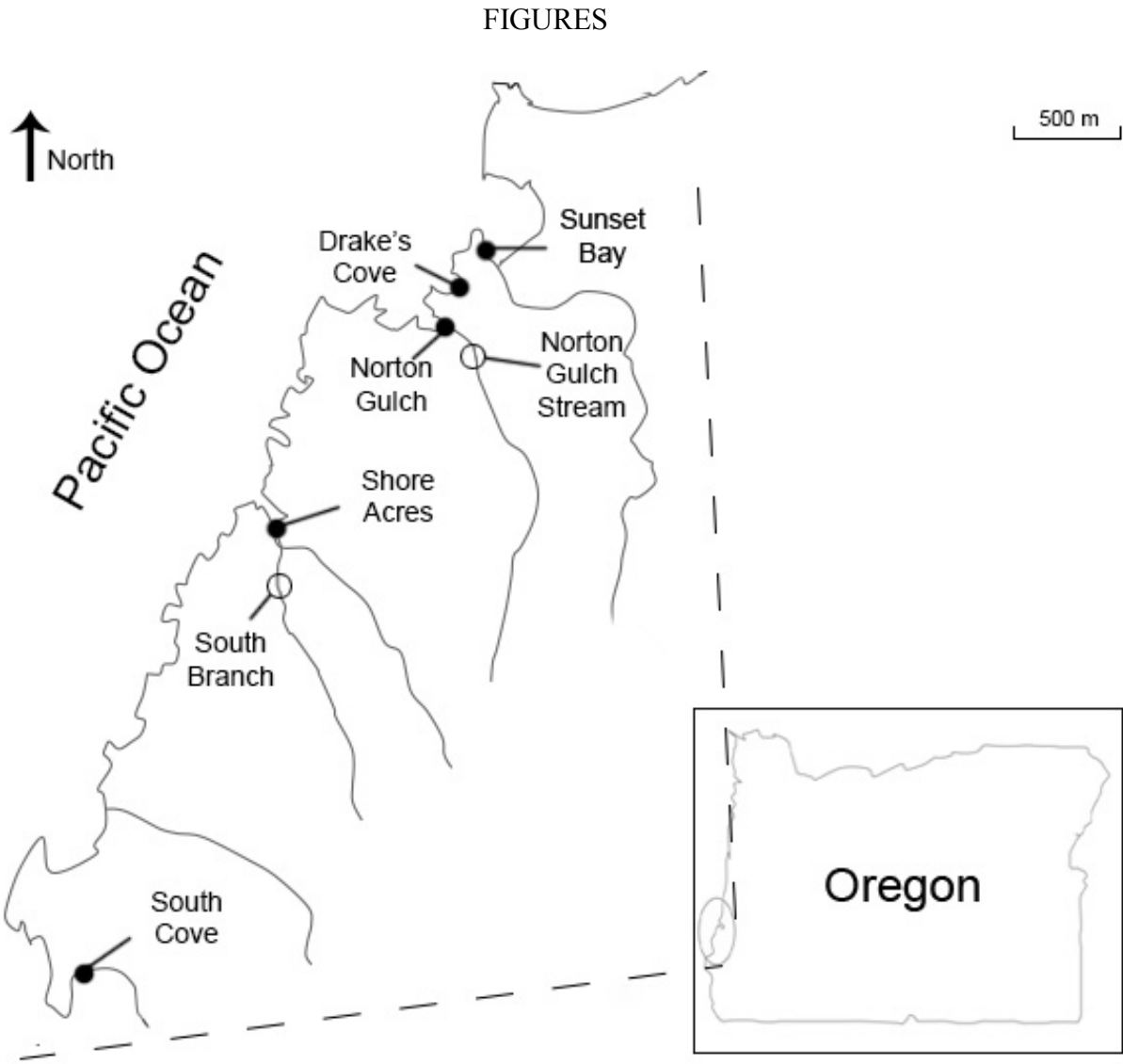
Figure 1. Map of sites near Coos Bay in southern Oregon (U.S.A.) showing the streams used to quantify TOM in the drift (open circles) and the pocket bays where beach wrack was sampled and where our feeding experiments were conducted (closed circles).
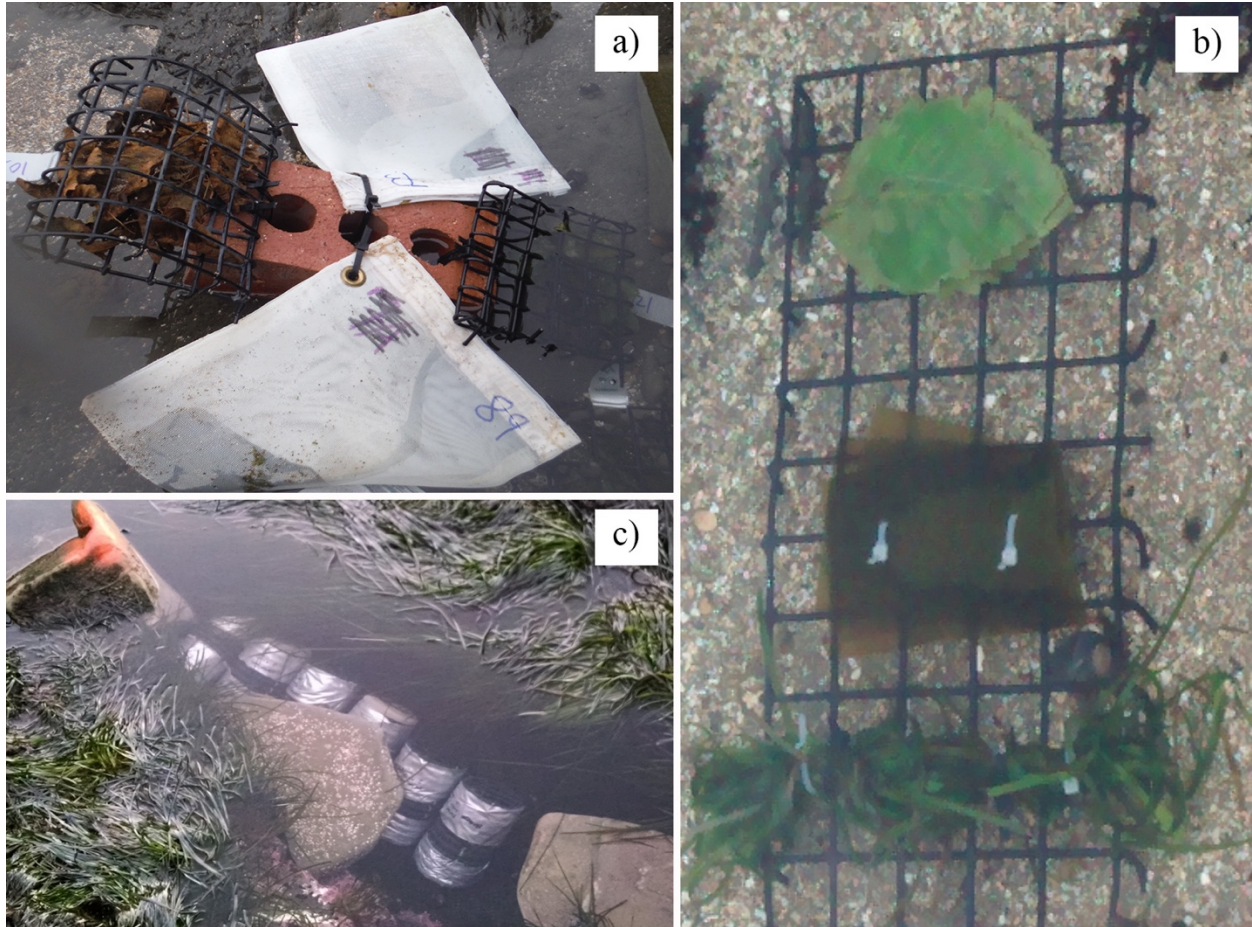
Figure 2. A "block" used in the long-term feeding experiment in the Fall of 2014 showing coarse-mesh (2.5 cm) and fine-mesh (500 μm) treatments of *Alnus rubra* and *Nereocystis luetkeana* (a), a "mixed pack" block from the short-term feeding experiment in the Spring of 2015 showing green *A. rubra*, young fronds of *N. luetkeana*, and *Phyllospadix* spp. (b), and a block from the short-term feeding experiment in the Fall of 2015 with *A. rubra*, *N. luetkeana*, and *Fucus gardneri* in canisters (c).
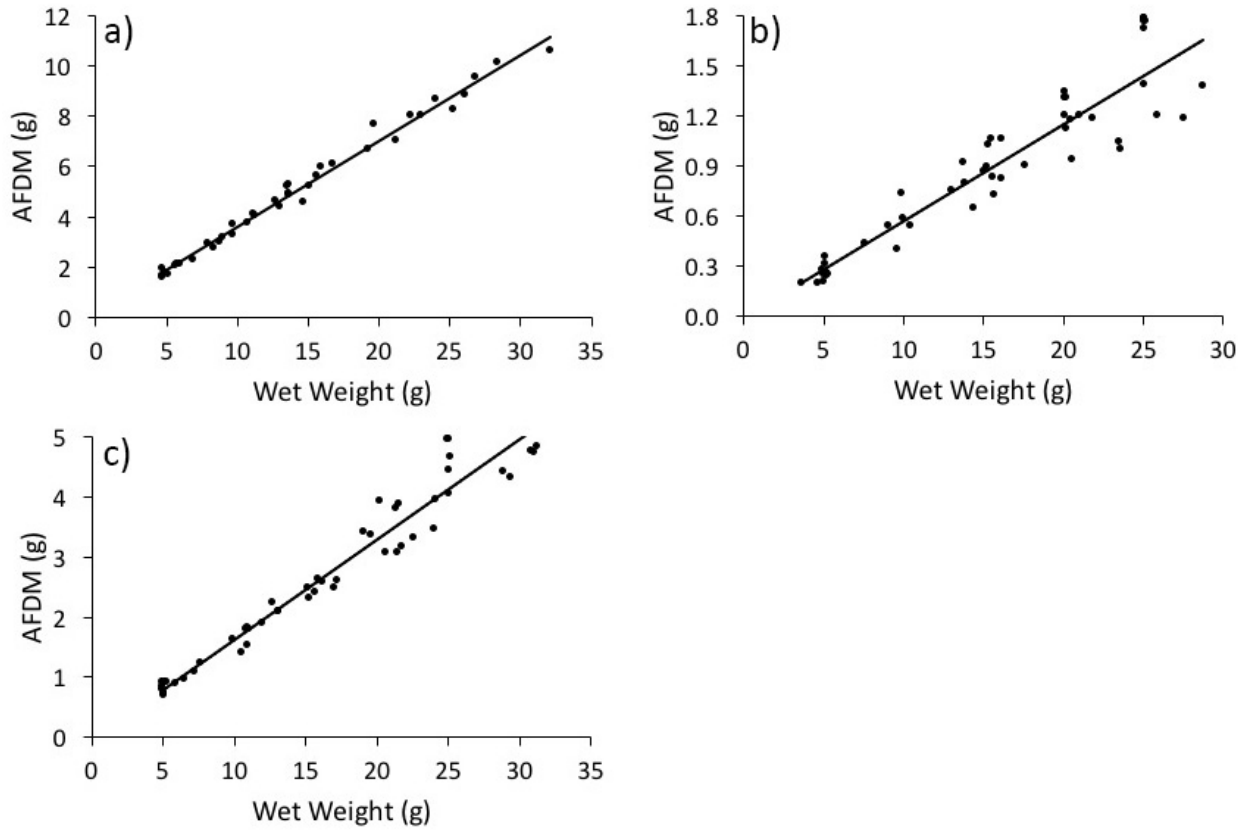
Figure 3. Linear regression showing the relationship between wet weight biomass and ash-free dry mass (AFDM) for *A. rubra* (a), *N. luetkeana* (b), and *Phyllospadix* spp. (c) from the Spring of 2014.
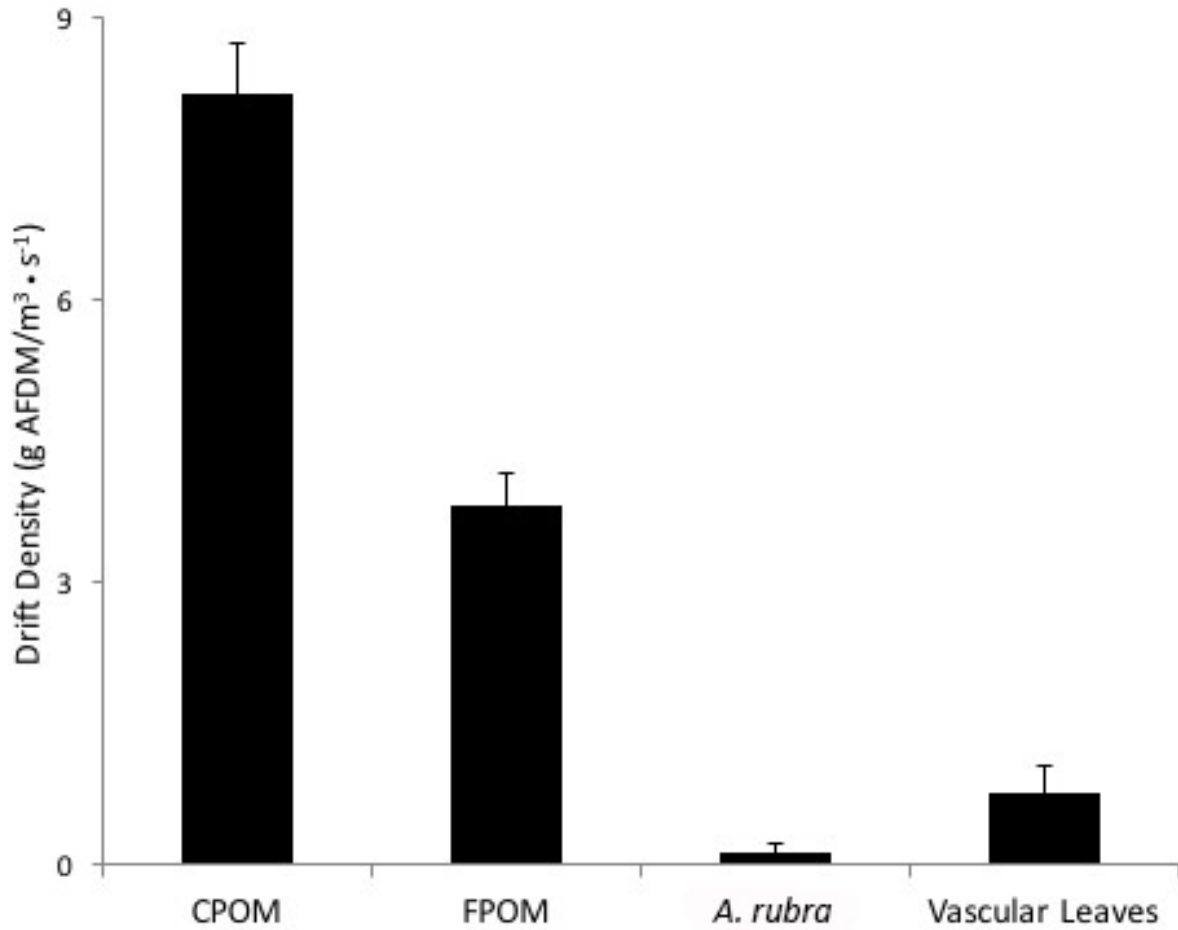
Figure 4. Average drift density of terrestrial organic matter from Shore Acres and Norton Gulch during the Fall of 2014. Coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) represent particles > 1 mm in size and between 250 μm – 1 mm, respectively. *Alnus rubra* leaves and other vascular leaves and were separated from the CPOM. Means and standard errors were back-calculated from a natural log transformation.
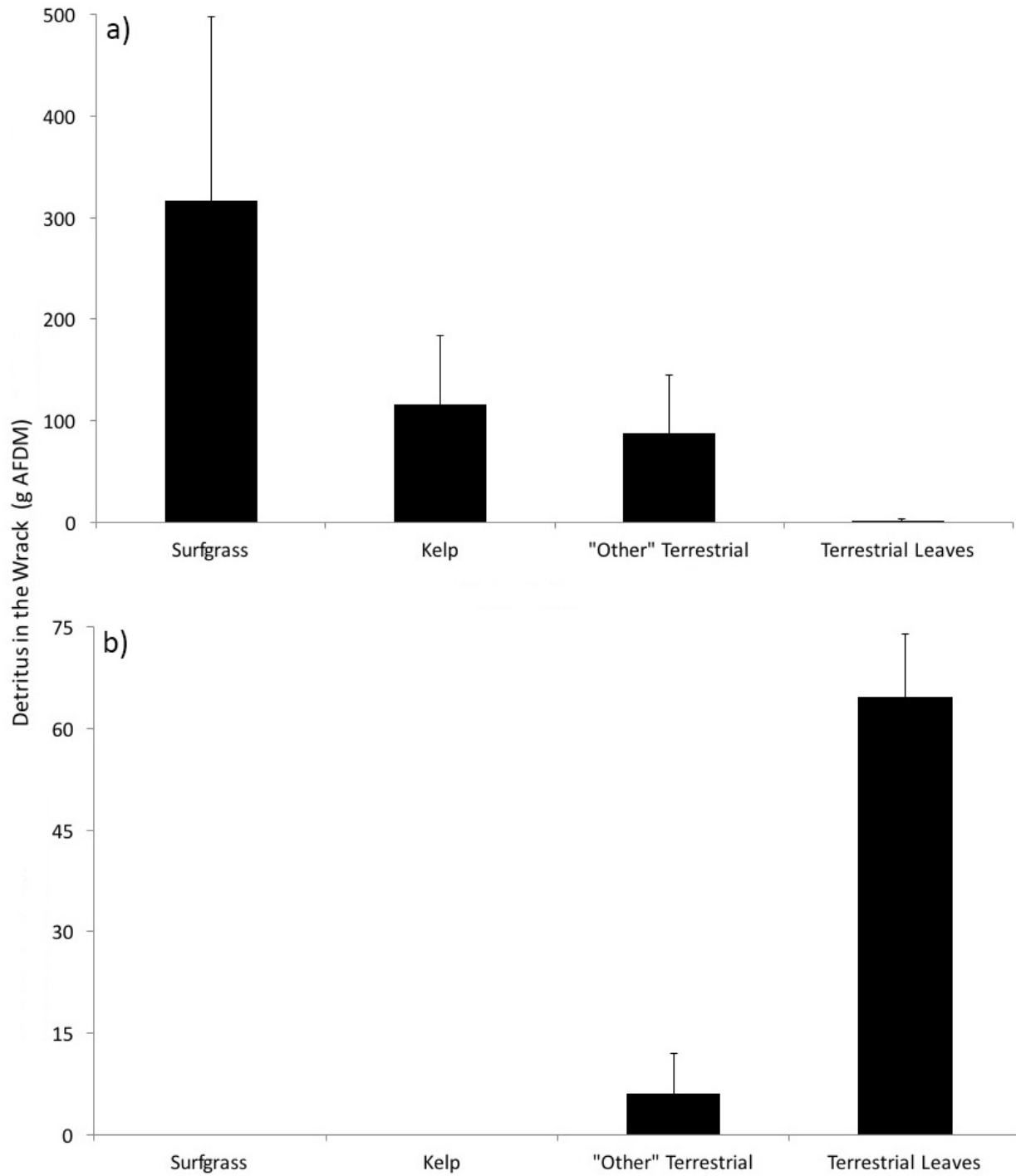
Figure 5. Average AFDM of organic matter in beach wrack sampled on four dates (every 2 weeks) from Nov 5 to Dec 21 at Shore Acres (a) and on two dates at Norton Gulch (b) during the Fall of 2014. Terrestrial leaves were separated from other terrestrial matter (cones, needles, bark, branches). Vertical bars represent one standard error around the mean.
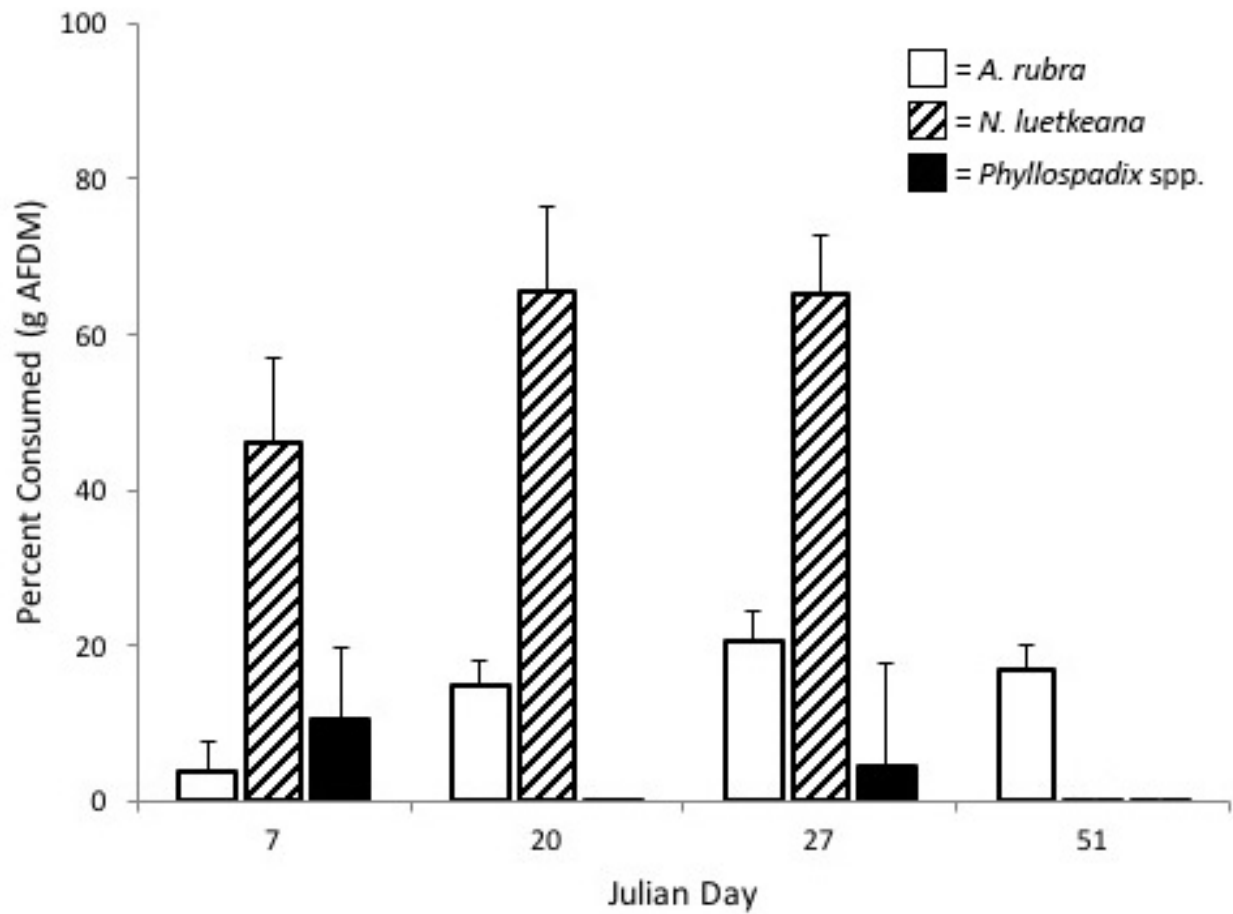
Figure 6. Average percent consumed of the initial pack biomass on each date for 3 leaf species over 51 days in the

Spring of 2014. Vertical bars represent one standard error around the mean. "Julian Day" was a categorical variable.
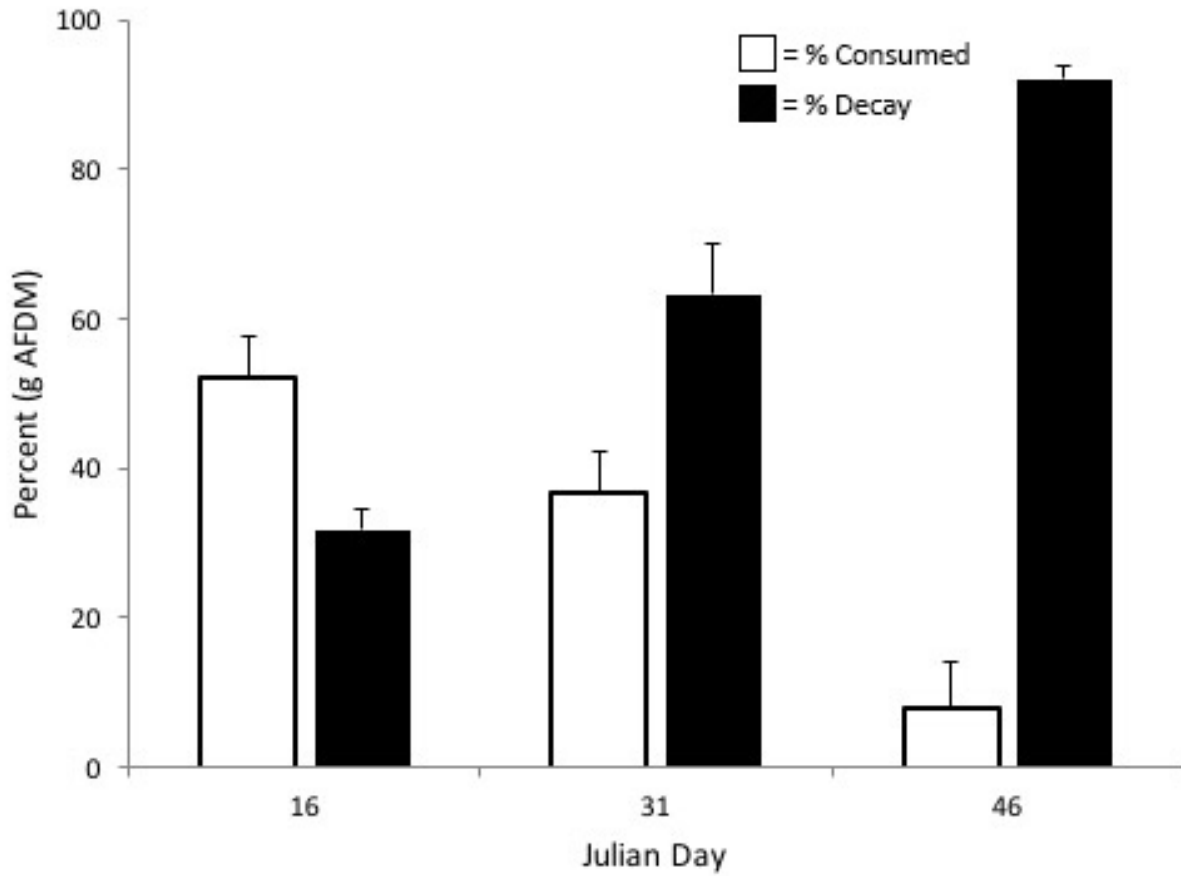
Figure 7. Average percent losses of the initial pack biomass attributed to consumption and microbial decay for *A. rubra* over 46 days in the Fall of 2014. Vertical bars represent one standard error around the mean. "Julian Day" was a categorical variable.
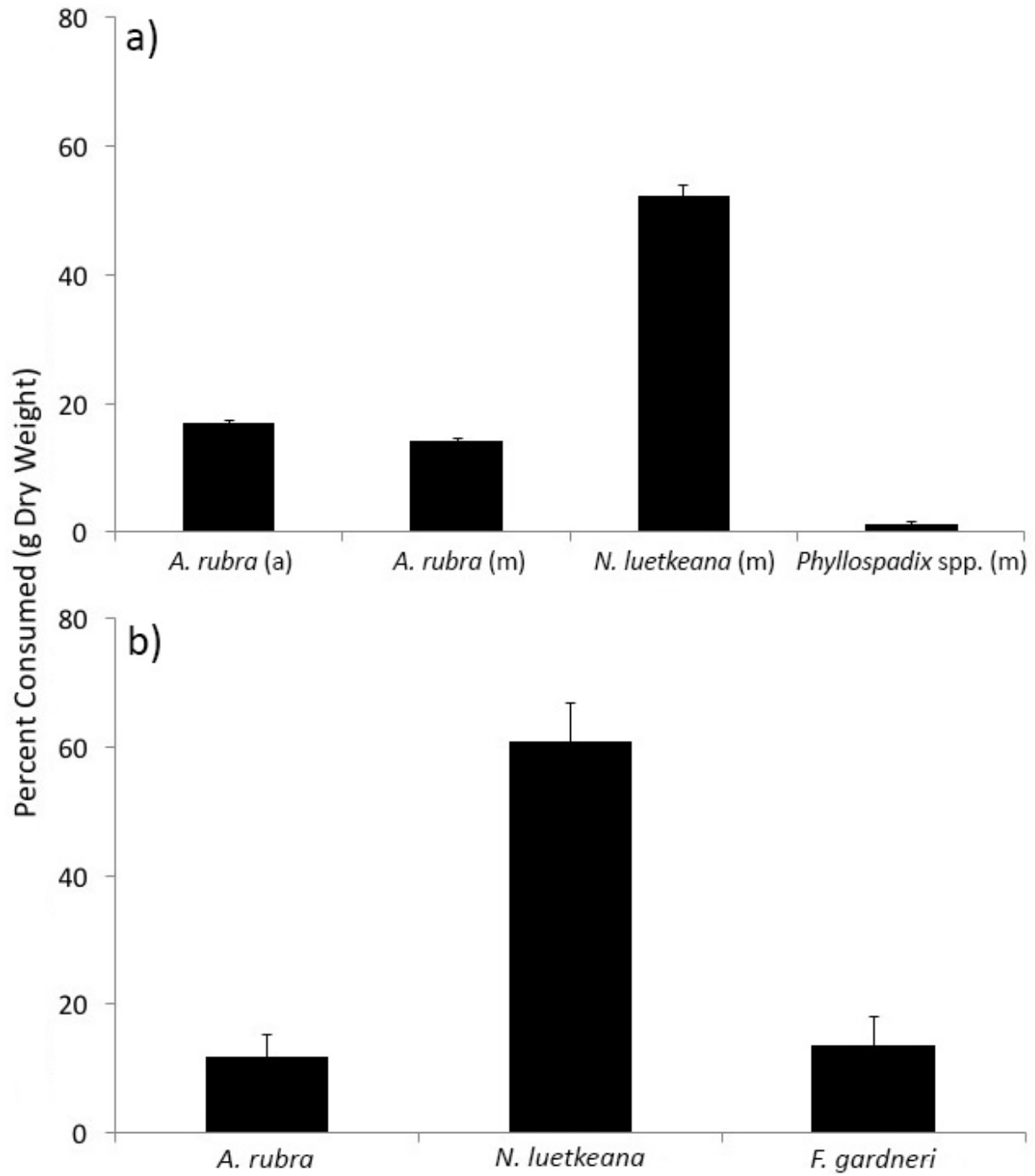
Figure 8. Average percent consumed of the initial pack biomass for 3 leaf species over 3 days in the Spring of 2015 (a). "m" are mixed blocks with all three species whereas, "a" are blocks with only *A. rubra* packs. Also, the average percent consumed for 3 leaf species over 7 days in the Fall of 2015 (b).   Vertical bars represent one standard error around the mean.
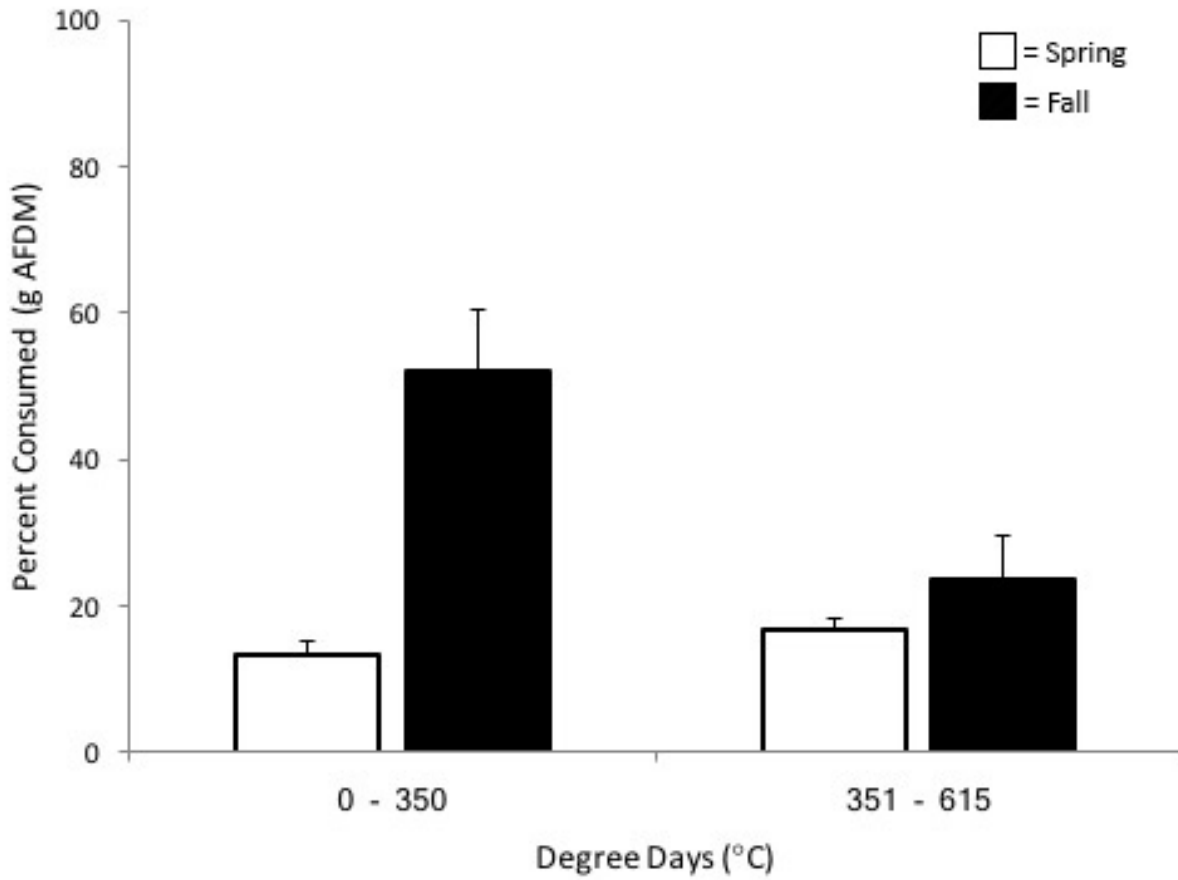
Figure 9. Average percent of the initial pack biomass attributed to consumption of *A. rubra* over 615 degree days in the Spring and Fall (2014). Vertical bars represent one standard error around the mean. Degree days were a categorical variable.