2008

Bottom-up and top-down controls on sedimentary ecosystem functioning in a seagrass habitat

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Recommended Citation

Spivak, Amanda C., "Bottom-up and top-down controls on sedimentary ecosystem functioning in a seagrass habitat" (2008). *Dissertations, Theses, and Masters Projects.* Paper 1539616861.
https://dx.doi.org/doi:10.25773/v5-5t5g-m947

Bottom-up and Top-down Controls on Sedimentary Ecosystem Functioning in a Seagrass Habitat.

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

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by
Amanda C. Spivak
2008

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

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ACKNOWLEDGEMENTS

The support and guidance provided by co-advisors, Drs. Elizabeth A. Canuel and J. Emmett Duffy, are gratefully acknowledged. Their willingness to bridge their disciplines of sediment organic geochemistry and community ecology, respectively, have made this project truly unique. I thank my advisory committee, Drs. Iris Anderson, Debbie Bronk, and John J. Stachowicz, for shaping the goals and design of this project and for constructive reviews of the manuscripts comprising this dissertation.

The setup, maintenance, and sampling of the three experiments could not have been accomplished without the help of J. Paul Richardson, Rachael Blake, James Douglass, Kristin France, and other members of the Duffy Lab. I also thank Lindsay Moore, Aaron Spivak, Tim Montgomery, Kristin France, Rachael Blake, Martin Wunderly, Michele Cochran, Beth Lerberg, and Gabby Blohn for help with measuring dissolved nutrient fluxes and for sampling sediments. In addition, Michele Cochran provided invaluable help with lab analyses while Hunter Walker and Betty Neikirk graciously analyzed water samples for nutrient concentrations. Mike Newman provided invaluable help with statistical analyses.

This project was supported through funding to J.E. Duffy (NSF OCE 0099226, NSF OCE 0352343), E.A. Canuel (DEB 0542645, DEB 0454736), and a VIMS graduate fellowship and a NCER EPA STAR grant (FP-91656901) to A.C. Spivak.

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ABSTRACT

Coastal seagrass ecosystems are complex habitats that are increasingly influenced by human perturbations. Disturbances that affect the strength of bottom-up (i.e. resource availability) and top-down (i.e. consumer) controls may also influence biomass distribution between trophic levels, sediment biogeochemistry, and seagrass ecosystem metabolism. Here, I experimentally tested how top-down and bottom-up perturbations interact with community structure (diversity, food chain length of epibenthic consumers) to alter sediment biogeochemistry and ecosystem metabolism in an experimental eelgrass (*Zostera marina*) system. My data indicated that resource availability influenced SOM composition and ecosystem metabolism. Light availability tended to be a stronger determinant of SOM composition while nutrient enrichment affected secondary production of invertebrate grazers more strongly than primary producers or SOM. Top-down predator effects on SOM composition and ecosystem flux rates tended to be weak. However, the strength of the trophic cascade may partly be a function of grazer community composition and grazer susceptibility to predation. Finally, my results indicated that grazer species identity and community composition strongly influenced SOM composition. In addition to the main effects of light, nutrients, predators, and grazers there were a variety of interactive effects between resources and food web composition. Consequently, the effects of resource availability and food web composition on seagrass ecosystem functioning should not be considered in isolation.

Top-down and bottom-up controls on seagrass ecosystem functioning.

Chapter 1. Introduction

Project Summary

Coastal seagrass ecosystems are complex habitats that are increasingly influenced by human perturbations. Disturbances that affect the strength of bottom-up (i.e. resource availability) and top-down (i.e. community structure) controls may also influence biomass distribution between trophic levels, sediment biogeochemistry, and seagrass ecosystem metabolism. Utilizing two mesocosm experiments and one field manipulation, I tested how top-down (food chain length) and bottom-up (light and nutrient) perturbations interact with benthic community structure (diversity, food chain length) to alter sediment biogeochemistry and ecosystem metabolism in an experimental eelgrass (*Zostera marina*) system. I estimated changes in sediment biogeochemistry by analyzing sediment organic carbon and nitrogen content as well as fatty acid biomarkers, which are functional proxies for organic matter. Ecosystem metabolism was estimated by measuring flux rates of dissolved oxygen and dissolved inorganic nitrogen and phosphate. Results from this study demonstrate that environmental perturbations are interactive and that results from single variable experiments cannot be used to predict the outcome of experiments with multiple variables and/or diverse species assemblages.

Introduction

Seagrass ecosystems provide habitat for economically and ecologically important organisms, transform nutrients through biogeochemical processes, and buffer anthropogenic sediment and nutrient inputs (Kemp et al. 2005; Orth et al. 2006). Despite their importance to human economies and populations, seagrass ecosystems are increasingly threatened by perturbations such as nutrient runoff, erosion due to land development, and over-fishing (Cloern 2001; Kemp et al. 2004; Orth et al. 2006). Alone and in combination, such anthropogenic disturbances can affect top-down (i.e. food chain length) and bottom-up (i.e. resource availability) controls in seagrass beds. Further, interactions between food web structure and abiotic processes have substantial consequences for ecosystem dynamics and function (McGrady-Steed et al. 1997; Tilman et al. 1997; Heck et al. 2000; Duffy et al. 2003; Hughes et al. 2004; Canuel et al. 2007). Thus, a goal of this project was to determine how top-down and bottom-up controls affect sediment biogeochemistry and ecosystem metabolism.

Perturbations that reduce predator abundance in seagrass ecosystems may precipitate changes in the biomass and diversity of neighboring trophic levels (Heck et al. 2000; Duffy et al. 2005; Heck and Valentine 2006; 2007). Eventually, such changes in food web structure and composition may cascade to affect ecosystem productivity and sediment biogeochemistry (Duffy et al. 2003; Canuel et al. 2007). For instance, predators such as fish and crabs consume grazing invertebrates, which feed on a variety of primary producers including epiphytes, macroalgae, benthic microalgae, and eelgrass blades (Valentine and Heck 1999; Duffy et al. 2001; Heck and Valentine 2006; Valentine and Duffy 2006). By altering primary producer community composition and biomass, grazers can affect primary productivity and organic matter (OM) cycling. Shifts in trophic structure and biodiversity that affect OM deposition may also influence nutrient cycling since OM quality is a partial determinant of sediment microbial activity and remineralization processes (Boschker and Cappenberg 1998) (Fig. 1). While the strength of this cascade is unknown, it has potentially important implications for carbon transfer to higher trophic levels, organic matter decomposition, nutrient recycling, and carbon sequestration in the sediments.

In addition to fluctuations in top-down controls (i.e. predator presence vs. absence), seagrass beds may be subjected to variations in bottom-up forcings (i.e. light and nutrient availability). For instance, the availability of excess nutrients in coastal waters is linked to increased surface water chlorophyll and seagrass loss (Cloern 2001; Kemp et al. 2005; Orth et al. 2006). While studies evaluating the effects of nutrient enrichment have focused on changes in water quality, dramatic alterations in sediment geochemistry can also occur. For example, in systems that have experienced prolonged eutrophication, such as the Chesapeake Bay, sediment organic matter accumulation has increased and its composition has been altered (Zimmerman and Canuel 2000; 2002). Fatty acids indicative of plankton (polyunsaturated fatty acids) and microbes (branched fatty acids) have increased since the early 1900's suggesting changes in microbial responses in the water column and sediments (Zimmerman and Canuel 2000; 2002). Thus, nutrient-mediated shifts in bottom-up forcings hold significant implications for ecosystem productivity, OM cycling, and sediment microbial activity.

Despite the importance of seagrass beds to human economies, health, and sustenance, carbon transformations are still ambiguous. A large body of research has examined the influence of allochthonous nutrients on water quality and seagrass production and density (Neckles et al. 1993; Moore et al. 1996; Orth et al. 2006; McGlathery et al. 2007). Other studies have described the characteristic species and their trophic interactions (Jernakoff et al. 1996; Duffy et al. 2001; Alfaro et al. 2006; Heck and Valentine 2006). Research emphasis has also been placed on microbial processes and decomposition of plant material (Cebrian and Duarte 2001; Holmer et al. 2004; Bouillon and Boschker 2006). Despite intensive research in these separate areas, little is understood about how biology and geochemistry interact to shape dynamic seagrass systems and the services they provide to society.

Experimental objectives.

The goal of this dissertation project was to experimentally test the interactive effects of eelgrass bed community structure (invertebrate grazer diversity and food chain length) and bottom up forcings (nutrient concentrations and light availability) on sediment organic matter (SOM) composition and whole ecosystem metabolism. This was accomplished using a suite of complementary studies, including two mesocosm experiments and one field experiment. The experiments were designed to test the effects of common anthropogenic disturbances: fishing-induced food web alteration, nutrient loading, and subsequent shading. Food web structure and composition were manipulated by varying predator presence and grazer biodiversity (species richness and identity), respectively. Bottom-up perturbations were simulated by varying light availability, an indirect effect of sediment loading and algal growth due to increased nutrient concentrations.

Experimental Hypotheses.

Research for this dissertation was structured around two overarching hypotheses:

Hypothesis 1: Above-ground benthic community composition (i.e. mesograzer identity and composition) and food chain length (i.e. predator presence) will alter the primary producer community resulting in changes in gross ecosystem production and sediment organic matter (SOM) composition.

Hypothesis 2: Bottom-up forcings (light availability and nutrient concentrations) will increase primary and secondary productivity thereby influencing SOM composition and quality.

Experimental Approach.

Experiment 1. The first mesocosm experiment examined top-down and bottom-up controls on SOM composition in an experimental seagrass ecosystem (Chapter 2). This experiment, conducted over 6 weeks in Summer 2003, was a factorial manipulation of grazer diversity (df = 2), predator presence (df = 1), and light intensity (df = 1). Grazer diversity treatments contained 0, 2, or 4 grazer species; grazers were chosen from a pool of six species, including three amphipods (*Gammarus mucronatus*, *Ampithoe longimana*, and *Caprella penantis*) two isopods (*Idotea balthica* and *Erichsonella attenuate*) and a gastropod (*Bittium varium*). Trophic structure was manipulated by exposing half of the grazer treatments to the generalist predator *Callinectes sapidus*. Light intensity was manipulated by shrouding half of the tanks with shade cloths, reducing natural light by 69%. There were 12 treatments replicated 5 times each. The experiment tested the following hypotheses:

H-1a: High light availability will increase biomass accumulation of above-ground and benthic algae, SOM lability, and sediment microbial activity.

H-1b: More species-rich grazer communities will reduce algal biomass but increase seagrass and benthic algal biomass, leading to changes in the composition and quality of algal material incorporated in the sediments.

H-1c: Predators will increase accumulation of algal biomass through a trophic cascade, thereby increasing SOM quantity, quality, and microbial activity.

Experiment 2. The second experiment was a field manipulation where I tested how community composition and nutrient availability alter SOM composition in a seagrass bed (Chapter 3). The field experiment, conducted over 4 weeks in Summer 2005, was a factorial manipulation of grazer presence (df = 1), predator presence (df = 1), and nutrient concentrations (df = 1). Because field cages were more likely to be contaminated by non-target grazer species than the mesocosm tanks, I manipulated grazers through the presence or absence of a multi-species community. Food chain length was manipulated through the presence or absence of blue crabs. Nutrient concentrations were varied over two levels: ambient and enriched (approximately 5x's ambient). There were eight treatments, replicated five times for a total of forty caged treatments. In addition to the caged treatments there were two uncaged treatments (with versus without nutrients). Grazer and predator presence were not manipulated in the uncaged treatments since it was impractical to maintain those treatments without cages. The two uncaged treatments were replicated five times each for a total of ten uncaged plots. The field experiment was conducted in the York River Estuary, VA and tested the following hypotheses:

H-2a: Nutrient enrichment will increase algal biomass and the deposition of algal-derived OM to the sediments. The increased lability of SOM will, in turn, stimulate sediment heterotrophic bacterial activity and the deposition of bacterial FA. Algae will indirectly decrease eelgrass abundance by increasing competition for light and nutrients.

H-2b: Grazers will reduce algae, as well as the abundance of the fatty acids characteristic of algae in the sediment, but will increase eelgrass.

H-2c: Predators will produce a trophic cascade in which grazer abundance is reduced and algal biomass and OM contributions to the sediment are increased.

Experiment 3. The third experiment was a mesocosm experiment where I tested how nutrient availability and food web composition affect ecosystem metabolism and SOM composition in an experimental seagrass habitat. (Chapters 4, 5). This experiment, conducted over five weeks in Summer 2006, was a factorial manipulation of grazer richness (df = 3), predator presence (df = 1), and nutrient enrichment (df = 1). Grazer richness was varied over four levels as treatments contained 0, 1, 3, or 5 species. The 1 species treatment was a monoculture of *G. mucronatus*, a perennially abundant amphipod. The 5 species treatment contained amphipod grazer species present in the York River at the time of the experiment: *G. mucronatus, Ampithoe valida*, *Elasmopus levis, Melita nitida,* and *Sympleustes* spp. The 3 species treatment contained grazers randomly drawn from the 5 grazer pool. Trophic structure was varied over two levels through the presence or absence of blue crabs. Water column nutrient availability was manipulated by adding fertilizer (5-30 x's ambient concentrations) to half of the tanks.

Thus, there were 16 treatments, each replicated 3 times for a total of 48 tanks. The goal of this experiment was to test the following hypotheses:

H-3a: Nutrient additions will increase algal biomass and, consequently, ecosystem productivity. Accumulation of algal biomass will, in turn, increase SOM quality, sediment microbial activity, and dissolved inorganic nitrogen (DIN) flux rates.

H-3b: Grazers will reduce algal biomass and algal contributions to SOM but will increase inorganic nitrogen flux by recycling consumed material back into the water column via excretion.

H-3c: Predator presence will initiate a trophic cascade whereby grazing activities are reduced but algal biomass, gross ecosystem productivity, and SOM quality are increased. DIN flux will be lower due to uptake by above-ground algae.

The results from the three experiments will be compared in detail in Chapter 6. This synthesis chapter will allow for a direct comparison of the effects of resource availability and top-down controls on SOM composition and ecosystem metabolism. In addition, this chapter will include an assessment of the relative importance of resource identity (i.e. nutrients vs. light) to ecosystem properties and functioning.

Significance.

A recent report by the National Academy of Sciences identified the first and second "grand challenges in environmental science" as understanding biogeochemical cycles and biological diversity and ecosystem functioning (NAS, 2000). While there are clear challenges in both of these areas, an even greater challenge is to address the linkages between them. This challenge was further highlighted in a recent NSF report noting the importance of studies identifying the role of functional diversity in geochemical transformations (Jumars and Hay 1999). This dissertation addresses gaps in our understanding of linkages between ecological and biogeochemical responses to human perturbations to coastal ecosystems. It is amongst the first studies to investigate the importance of food web composition and resource availability to both sediment biogeochemistry and seagrass ecosystem metabolism.

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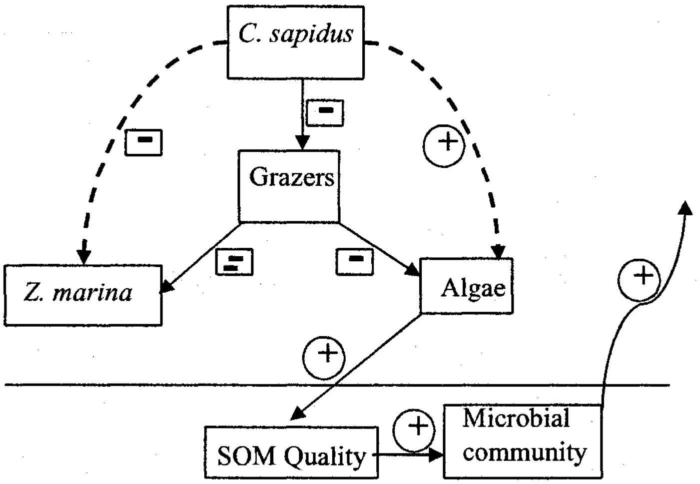
Spivak Fig. 1



C. sapidus
−
−
+
Grazers
Z. marina
−
−
Algae
+
+
SOM Quality
+
Microbial community

Chapter 2:

Top-down and bottom-up controls on sediment organic matter composition in an experimental seagrass ecosystem

Amanda C. Spivak[1], Elizabeth A. Canuel, J. Emmett Duffy, and J. Paul Richardson

Acknowledgements.

We thank J.G. Douglass, K.E. France, S. Grill, and M.A. Wunderly for assistance in setting up, maintaining, and sampling the experiments. We also thank M.A. Cochran, A.K. Hardison, and E.J. Waterson Lerberg for help with lab analyses. This work was improved by input from I.C. Anderson, D. Bronk, and J.J. Stachowicz. We also thank two anonymous reviewers and B. Thamdrup for constructive comments that improved the manuscript. This research was supported by NSF grants OCE 00-99226 and OCE 03-52343 to J.E. Duffy, NSF grants DEB 0542645 and DEB 0454736 to E. A. Canuel, and a NCER, STAR program, EPA grant FP-91656901 to A.C. Spivak. Although the research described in the article has been funded in part by the U.S. EPA's STAR program, it has not been subjected to any EPA review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred. Additional support was provided by Virginia Institute of Marine Science. This paper is contribution No. 2834 of the Virginia Institute of Marine Science, The College of William and Mary.

Abstract

Using an experimental mesocosm system, we tested the singular and interactive effects of resource availability (light) and community composition (food chain length and herbivore species richness) on eelgrass (*Zostera marina*) ecosystem properties and functioning. Food chain length was manipulated through the presence or absence of blue crab (*Callinectes sapidus*) predators, while grazer species richness varied across three levels (0, 2, or 4 crustacean species). We found important and interacting effects of bottom-up and top-down forcings on sediment organic matter (SOM) composition. Light increased eelgrass and algal biomass and sediment organic carbon and nitrogen content. Increasing grazer diversity generally decreased algal biomass and ecosystem production but interacted with food chain length (i.e., presence of predatory crabs) and light. Predators generally increased algal biomass and ecosystem production through a trophic cascade, which was stronger at high grazer diversity and under ambient light. SOM composition, determined using fatty acid biomarkers, was sensitive to all manipulated variables. Increasing grazer species richness often decreased the contributions of fatty acids derived from plant and algal sources, while increasing light had the opposite effect. Food chain length was generally a less important determinant of SOM composition than light, although predators did increase fatty acids representative of heterotrophic bacteria. Resource availability and epibenthic community composition strongly influence organic matter cycling, SOM composition, and the bacterial community in seagrass-bed sediments.

Introduction

Coastal ecosystems are often affected by multiple disturbances that alter both resource availability and community composition simultaneously. In the Chesapeake Bay, for example, seagrass beds are affected by commercial harvesting of the blue crab, *Callinectes sapidus* (Stephan et al. 2000), and by suspended sediment and nutrient loading that can lead to reduced light availability (Kemp et al. 2004). Changes in abundance of important predators, like striped bass or the blue crab, may precipitate changes in biomass of lower trophic levels (Hairston et al. 1960; Strong 1992; Pace et. al 1999). These shifting trophic interactions, along with reduced light availability, can affect primary producer abundance and productivity (Heck et al. 2000; Hughes et al. 2004; Borer et al. 2006) and, in turn, sediment organic matter (SOM) content (Canuel et al. 2007). Consequently, cascading changes in animal and plant biomass may alter the rates and pathways by which organic matter (OM) is cycled in an ecosystem (Schindler et al. 1997; Dangles and Malmqvist 2004).

Predicting how changing trophic structure affects OM cycling is complicated by the fact that predators induce shifts not only in prey biomass but also in prey community structure. In seagrass systems, for example, grazing invertebrates can consume epiphytic algae, macroalgae, benthic microalgae, and/or vascular plants (Valentine and Duffy 2006). Thus, shifts in grazer community composition may affect the abundance of different primary producers. Since seagrasses, macroalgae, and epiphytes differ in their biochemical composition and proportion of structural components, the food preferences of grazing invertebrates may, in turn, affect the quantity and lability of organic carbon delivered to the sediments and thus, the quantity and quality of sediment organic carbon

(Canuel et al. 2007). Such compositional changes need not be dramatic to affect ecosystem properties: small shifts in grazer richness and species composition can significantly affect plant and algal biomass and influence total sediment organic carbon (e.g., Duffy et al. 2003; Canuel et al. 2007).

Because sediment microbial communities are important mediators of carbon and other elemental cycles in coastal environments (Boschker et al. 1999; Holmer et al. 2001, 2004), changes in above-ground trophic structure and diversity that alter OM delivery to seagrass sediments may have important consequences for carbon cycling and storage. In terrestrial soils, by analogy, microbial community composition and activity are sensitive to changes in above-ground community structure (Setälä et al. 1998; Wardle et al. 2005). Though studies from marine habitats are fewer, microbial activity in sediments is strongly related to OM deposition (Canuel and Martens 1993; Boschker and Cappenberg 1998; Boschker et al. 2000). The potential cascade from consumer control of above-ground production to delivery and accumulation of below-ground OM may thus be important to carbon remineralization, recycling, and sequestration in the sediments.

Effective conservation and management of seagrass ecosystems requires a clear understanding of relationships between community ecology and biogeochemical cycling. A variety of studies have investigated coastal eutrophication (Cloern 2001; Duarte 2002 and references therein), trophic interactions in seagrass beds (Valentine and Duffy 2006; Heck and Valentine 2006 and references therein), and interactions between nutrient enrichment and food web ecology (McClelland and Valiela 1998; Deegan et al. 2002; Tewfik et al. 2005). Others have examined sediment nutrient and bacterial processes in seagrass beds (Holmer et al. 2001, 2004). Yet few studies have examined the relationships and feed-backs between above-ground ecology and below-ground geochemical cycling. Geochemical tools provide a way to detect and quantify such linkages between community structure and organic matter cycling. Specifically, lipid biomarkers are compounds reliably produced by a specific group of organisms that are sufficiently resistant to degradation to be preserved in sediments (Killops and Killops 1993). Diagnostic biomarkers often have site-specific methyl groups, double bonds, or cyclic side chains useful in tracing the sources of organic matter (Killops and Killops 1993). Bacteria, for example, synthesize iso- and anteiso- branched fatty acids while microalgae contain highly unsaturated long chain fatty acids (or alkanoic acids) (Volkman et al. 1998). One class of lipids, the fatty acids, is particularly useful because they have high source fidelity and exhibit a range of chemical reactivity (Canuel et al. 1995; Canuel and Martens 1996). Additionally, a sub-class of the fatty acids, the phospholipid-linked fatty acids (PLFA), are good indicators of recently viable cells since they are mainly derived from membrane lipids, which are rapidly hydrolyzed after cell death (White et al. 1979; Killops and Killops 1993). By quantifying both the total fatty acids and the PLFAs it is possible to compare OM contributions from detrital and viable or recently viable sources. Thus lipid biomarkers, and fatty acids in particular, provide a quantifiable link between the above-ground community and sediment geochemistry.

To assess the effects of changing community structure on carbon fate and storage in seagrass beds, we conducted an experimental manipulation of bottom-up forcing (light availability), community composition (grazer diversity), and food chain length (predator presence) and measured their interacting effects on ecosystem productivity, SOM quality, and sediment microbial activity. Specifically, we built on previous studies examining top-down effects on the above-ground community (Duffy et al. 2003) and on SOM (Canuel et al. 2007) to test several hypotheses. First, higher diversity of epibenthic grazers will reduce algal biomass but increase seagrass and benthic algal biomass, leading to changes in the composition and quality of algal material incorporated in sediments. Secondly, predators will increase accumulation of algal biomass through a trophic cascade, thereby increasing SOM quantity, quality, and sediment microbial activity. Finally, high light availability will increase biomass accumulation of above-ground and benthic algae, SOM lability, and sediment microbial activity.

Methods

Experimental design

We conducted a mesocosm experiment to examine the main and interactive effects of grazer species richness, food chain length, and light intensity on ecosystem properties including production, algal biomass accumulation, and sediment organic matter (SOM) content and composition. We established three grazer richness treatments containing no grazer species, random combinations of two grazer species, or four grazer species. Grazers were chosen from a pool of six species, including three amphipod crustacean species (*Ampithoe longimana*, *Gammarus mucronatus*, and *Caprella penantis*), two isopods (*Idotea baltica* and *Erichsonella attenuata*), and a gastropod (*Bittium varium*). These invertebrate grazers are common in the York River estuary during the spring and summer (Duffy et al. 2001, 2003). Food chain length was manipulated by exposing a parallel set of grazer treatments to a generalist predator common in the Chesapeake Bay, the blue crab, *Callinectes sapidus*. Light intensity was manipulated by covering half of the tanks with shade cloths (69% attenuation). There were a total of twelve treatments, each replicated five times. Due to extinctions and contaminations, however, six replicates were removed from the final analyses. Consequently, 54 replicates were used in statistical analyses; the zero grazer treatments had five replicates in ambient light and four replicates in low light, the two grazer treatments had four replicates, and the four grazer treatments had five replicates.

Outdoor mesocosm experiments were conducted over six weeks during the summer of 2003 in an array of 113-liter, translucent fiberglass tanks that were continuously supplied with flowing estuarine water from the York River, Virginia (Duffy et al. 2003). Water passed first through a sand filter and then through 150 μm mesh. This eliminated larger invertebrates and minimized invasion by non-target animals while permitting passage of invertebrate larvae and algal spores, which often colonized the tanks. Water was supplied through "dump buckets" which regularly spilled the filtered water into the tanks, providing both turbulence and aeration. Tanks were stocked with clean sand to a depth of 10 cm; the percent total organic carbon (TOC) was below detection. Low OM content sand was used as a substrate in order to reduce initial heterogeneity between the tanks and to increase our ability to detect newly-deposited SOM (Canuel et al. 2007). Seventy-five pre-weighed eelgrass (*Zostera marina*) shoots, cleaned of grazers and epiphytes, were planted in the sand in each tank. This eelgrass density is within the range found in the York River estuary system (Orth and Moore 1986). One week after the grass was planted, invertebrate grazers were added to each grazer mesocosm (45 each for two-species treatments, 15 of each for four-species); these densities were near the low end of those found in the York River. Blue crabs (*C. sapidus*) were added two days after the grazers had acclimated. The six week experimental incubation time was chosen to minimize the risks of invasion by non-target grazer species and of complete consumption of the eelgrass, which increase at longer time intervals. This time period allows for major changes in animal (one to two grazer generations) and plant community development and in surface sediment characteristics (see Duffy et al. 2003, 2005; Canuel et al. 2007). Despite limitations, this experimental infrastructure simulates several aspects of the biotic and abiotic field situation well (Duffy et al. 2001). Results of the experiment for above-ground biomass and composition of seagrass and the associated community are reported elsewhere (Duffy et al. unpubl.). Here, we focus on patterns of SOM accumulation and composition.

Gross ecosystem production

As an estimate of whole-ecosystem metabolism, we measured gross ecosystem production (GEP; mmol L^{-1} O_2 d^{-1} m^{-2}) one week before the experiment was terminated. Due to time constraints and instrument availability these measurements were conducted only in ambient light treatments. Clear plastic wrap was placed on the water's surface of each tank to minimize oxygen exchange with the atmosphere and the water supply was shut off. Dissolved oxygen (DO) measurements were taken three to four times during each of two 4-hour incubations (10:00 – 14:00 h and 22:00 – 02:00 h) using a YSI Data Sonde to capture net daytime production and total respiration respectively (assuming that little to no production occurs at night). Tank water was stirred prior to each reading to disrupt any temperature or DO stratification that may have formed, while maintaining a closed system. If DO fell to hypoxic levels (2 mg L^{-1}) measurements ceased on that tank and the plastic cover was removed. We calculated the slope of changes in DO concentration versus the time elapsed and divided this by the area of the tank to obtain flux in O_2 mmol L^{-1} d^{-1} m^{-2}. Hourly light and dark rates were scaled to 14 hours of daylight and 10 hours of darkness to estimate net daily summer time GEP.

Bulk sediment organic matter

At the end of the experiment, three sediment cores (2.6 cm diameter) were collected from each mesocosm; and the upper 1 cm from each core was removed. Sub-samples from each core were combined into a composite sample in a pre-combusted (450 °C) jar. The sediment sample was homogenized and aliquots were removed to pre-combusted glass scintillation vials for analyses of benthic chlorophyll *a* (Chl *a*; a measure of microalgal biomass) and sediment TOC and total nitrogen (TN). All samples were stored at -20°C until analysis. Samples of benthic Chl *a* were analyzed within 6 weeks of collection according to Neubauer et al. (2000). Concentrations of TOC and TN were analyzed by standard methods using a Fisons CHN analyzer (Model EA1108) after removing inorganic carbon (Hedges and Stern 1984); acetanilide was used as the standard.

Lipid biomarker analyses

Lipid biomarker compounds were analyzed using a modified Bligh and Dyer (1959) method (Canuel and Martens 1993; Canuel et al. 2007). Briefly, sediment samples were extracted with methylene chloride:methanol (2:1, v:v) using an accelerated solvent extraction system (Dionex ASE 200). Following extraction, the samples were partitioned and the organic phase removed. Hexane was added to the aqueous phase and the samples were partitioned a second time; after which the hexane layer was added to the original organic phase. The combined organic phases sat over anhydrous Na_2SO_4 overnight to remove traces of water and were concentrated to 1 mL using turbo-evaporation (Zymark Turbo Vap 500). The total lipid extracts were separated into non-polar (F1/2) and polar (F3) fractions by eluting solvents of increasing polarity through silica gel columns (Guckert et al. 1985). F1/2 (neutral and glyco-lipids) and F3 (phospholipids) were each saponified, using procedures described in Canuel et al. (2007). Following saponification, the residue was extracted under basic (saponified-neutral; SAP-N) and acidic pH (saponified-acids; SAP-A). The SAP-A fractions were methylated using BF_3-CH_3OH and purified using silica gel chromatography. Just before GC injection, samples were evaporated to dryness under N_2 and a small volume of hexane (30 µL for the polar fraction and 100 µL for the non-polar) was added. The fatty acids (as methyl esters) were analyzed by gas chromatography following previously-published procedures (Canuel et al. 2007 and references therein). Peaks were quantified relative to an internal standard, methyl heneicosanoate, added just prior to GC analysis. Peak identities were verified using reference standards and by combined gas chromatography-mass spectrometry (GC-MS) using a Hewlett-Packard 6890 GC interfaced with a mass selective detector (MSD) operated in electron impact (EI) mode. Fatty acids are designated as A:BωC, where A is the total number of carbon atoms, B is the number of double bonds, and C is the position of the first double bond from the aliphatic "ω" end of the molecule. The prefixes "i" and "a" refer to *iso* and *anteiso* methyl branched fatty acids (see Canuel et al. 1995 and references therein). Results for two classes of fatty acids are presented: phospholipid-linked fatty acids (PLFA) which represent viable or recently viable biomass and total fatty acids which represent neutral, glyco-, and phospholipids and include the sum of the viable and detrital contributions.

Statistical analyses

The experiment was analyzed as a fully factorial 3-way analysis of variance (ANOVA), with grazer treatment (df=2), food chain length (i.e., predator presence or absence, df=1), and light availability (df=1) as fixed variables, using SAS version 9.0 for Windows. Analyses of fatty acid data were conducted on percent abundance. GEP data were subjected to a 2-way ANOVA since data were only available for ambient light treatments. From the ANOVAs we calculated the magnitude of main and interactive effects (ω^2, percentage of the variance explained). Due to contaminations and extinctions, two control and four 2-species mesocosms were removed from all statistical analyses; results presented here use the type III sum of squares (SS) from the ANOVA model. Included in the statistical analyses were five replicates in ambient light and four in low light of the zero grazer treatments, four replicates of the two grazer treatments, and five replicates of the four grazer treatments. There were two criteria for elimination: (1) grazer contamination totaled more than 500 mg AFDM and (2) failure of two grazer species (*Caprella* and *Bittium*) to establish necessitated elimination of mesocosms where this pair of species was initially stocked. To separate effects of grazer presence versus grazer species richness, we conducted a priori contrasts that partitioned the grazer SS from the ANOVA into two orthogonal components (see Duffy et al. 2005). The first contrast compared the two- and four-species treatments against the zero-species treatment (species presence contrast) and the second compared the two- vs. four-species treatments (species richness contrast).

To aid in interpreting the fatty acid data, we performed multiple regression analyses modeling the fatty acid groups as a function of biomass of the major primary producers, eelgrass, total algae, and benthic Chl *a*. The partial r^2 was calculated by dividing the type III SS for each response variable by the total SS. The analyses were performed on %TOC, individual fatty acids, and groups of fatty acids normalized to the sum of all fatty acids (% total FA or %PLFA). Additionally, we conducted principal components analysis (PCA; using Minitab 14) to better elucidate relationships between manipulated and response variables. We only performed PCA on SOM variables as these responded to primary producer abundance determined by grazers and crab predators. PCA loadings describe the relationships between the SOM response variables and the dominant principal components. PCA scores illustrate relationships between the observations and the dominant principal components. PCA loadings were also regressed against the major primary producer groups (*Z. marina*, total algal biomass, and benthic Chl *a*) to help interpret the non-dimensional results.

Results

Primary producer biomass and gross ecosystem production (GEP)

In general, primary producer biomass was enhanced by light and predator presence and decreased by grazers. Above-ground, light increased biomass of both *Z. marina* and algae (Table 1, Fig. 1A, B). Cascading predator effects resulted in grazers reducing primary producer biomass only in the absence of predators (grazer x predator interaction, Table 1). For example, grazer presence and richness decreased *Z. marina* biomass in the absence of predators (p=0.002, ω^2=0.28). Further, total algal biomass was reduced by grazer presence and richness, but increased when predators were present. Several other interactions between grazers, predators, and light were also significant (Table 1). In the sediments, benthic Chl *a* was increased by ambient light (p=0.023, ω^2=0.06, Fig. 1C), decreased by grazer presence (p=0.004, ω^2=0.01), and unaffected by crab predators.

Gross ecosystem production (GEP) in the ambient-light mesocosms was influenced by the interaction of predators and grazers (p=0.002, ω^2=0.19, Table 1, Fig. 2). Overall, blue crab predators increased GEP (p<0.001, ω^2=0.29), but only in the presence of grazers, reflecting a trophic cascade. Increasing grazer species richness reduced GEP, but only in the absence of predators (p=0.001, ω^2=0.39). Thus, grazer presence, richness, and predator presence are all important interacting determinants of GEP (Table 1).

Bulk sediment organic matter (SOM)

Over the course of the six-week experiment, measurable levels of TOC and TN accumulated in surface sediments (Table 1, Fig. 3). Sediment %TOC and %TN content were higher in ambient light than in shaded treatments (p=0.004, ω^2=0.12 and p<0.001, ω^2=0.18 respectively). Neither grazers nor predators significantly affected %TOC or %TN. Thus, bottom-up forcing had a stronger effect on TOC and TN accumulation than top-down processes.

Total fatty acids (total FA)

While bulk indicators of SOM were sensitive only to light availability, fatty acid composition was strongly influenced by both bottom-up and top-down forcing. On average, total fatty acid (total FA) abundance normalized to TOC ($\mu g\ mg^{-1}$) was significantly reduced by light but was unaffected by predators and grazers (Fig. 4A). For further analysis, both the total and phospholipid-linked fatty acids were categorized into sub-classes based on chain length, number of double bonds, and carbon branching patterns representing different sources of OM (Fig. 5).

Total FA composition was dominated (29 - 47% total FA) by even-numbered saturated compounds ($C_{12:0}$ - $C_{18:0}$), representing algal and bacterial sources. The relative abundance of short-chain fatty acids (SCFA; $\%(C_{12:0}+C_{14:0})$) was highest in ambient light in the presence of predators (Table 1, Fig. 5A). Grazer presence, however, decreased SCFA. SCFA were also positively related to benthic Chl *a* (Table 2). The contributions of $\%C_{16:0}$ and $\%C_{18:0}$ fatty acids were unaffected by any of the treatments and were unrelated to either eelgrass or benthic Chl *a* abundance (Table 1). The long-chain fatty acid $C_{24:0}$, comprising 3-16% of total FA, was increased by ambient light on average (Table 1, Fig. 5B), and decreased by grazers, but more so in ambient light and predator treatments. $C_{24:0}$ was also positively related to benthic Chl *a* (Table 2). Overall, light increased fatty acids that were positively associated with benthic microalgae (Chl *a*) while grazers, the dominant top-down control, generally, had the opposite effect.

Relative abundance of polyunsaturated fatty acids ($C_{18:4}$, $C_{20:4}$, $C_{20:5}$, $C_{22:5}$, $C_{22:6}$; grouped as polyunsaturated fatty acids, PUFA) was reduced by predators, but only in shaded treatments, reflecting an interaction between predators and light (Table 1, Fig. 5C). %PUFA abundance was not related to either eelgrass biomass or benthic Chl *a*

(Table 2). Linoleic ($C_{18:2\omega6}$) and linolenic ($C_{18:3\omega3}$) acids, were decreased when grazers were present ($p=0.035$, $\omega^2=0.07$; Table 1, Fig. 5D) but only in ambient light treatments (grazer by light interaction, $p=0.007$, $\omega^2=0.12$). *Z. marina* was positively related to $\%(C_{18:2\omega6} + \%C_{18:3\omega3})$ (Table 2). Overall top-down controls were important determinants of PUFA abundance, with predators decreasing %PUFA and grazers decreasing linoleic and linolenic acids.

Branched fatty acids (iso- and anteiso- $C_{13:0}$, $C_{15:0}$, $C_{17:0}$, $C_{19:0}$), representative of sediment heterotrophic bacteria, were sensitive to all three manipulated variables (Fig. 5E). Light generally decreased the relative abundance of branched fatty acids, though this effect was driven mainly by the two-grazer species treatment and translated into a grazer by light interaction effect (Table 1). Relative abundance of branched fatty acids was consistently higher in predator treatments ($p=0.013$, $\omega^2=0.07$). Branched fatty acids were positively related to benthic Chl *a* (Table 2). These results suggest that sediment heterotrophic bacteria are sensitive to both bottom-up and top-down controls.

Principal component analysis provided a summary of these changes in SOM with manipulation of light and epibenthic community composition. Principal components 1 (PC1) and 2 (PC2) explained 31.7% and 25.9% of the variance in total fatty acid composition, respectively (Fig. 6A, B). Percent TOC, $\%C_{24:0}$, and $\%(C_{12:0} + C_{14:0})$ had the most positive loadings on PC1 (Table 3) and also responded positively to ambient light (Figs. 3, 5). The association between PC1 and light is also supported by the positive relationship between benthic Chl *a* and PC1 loadings ($r^2=0.33$; $p<0.001$). In contrast, PC2 separated SOM variables according to crab predator or grazer effects. Variables with negative PC2 loadings (%PUFA and %BrFA) were affected by crab predators, albeit in opposite directions, while those with positive PC2 loadings (%($C_{12:0}$ + $C_{14:0}$), %($C_{18:2}$ + $C_{18:3}$), and %$C_{24:0}$ (ambient light only)) were decreased by grazers (Table 3). Bottom-up forcing interacted with top-down forcing of SOM composition as PC scores were influenced by crab predators and grazers differently depending on light availability (Fig. 6A, B). In ambient light (Fig. 6A), grazer-free treatments had positive PC1 and PC2 scores while the two- and four-grazer treatments were near zero or negative on PC2. In contrast, under low light (Fig. 6B), treatments with crabs had more positive PC2 scores while no-crab treatments were negative. Under both light regimes, the pattern is most evident for the zero- and four-grazer treatments (Fig. 6A, B). Thus, PCA results suggested that the dominant top-down control (grazers vs. crab predators) influenced total FA composition differently with light availability.

Phospholipid-linked fatty acids (PLFA)

Like total fatty acids, PLFA (µg PLFA mg^{-1} TOC; Fig. 4B), indicative of viable or recently viable OM sources, were also sensitive to top-down and bottom-up influences. None of the manipulated treatments affected total PLFA, %($C_{12:0}$+$C_{14:0}$), %$C_{16:0}$, or %$C_{18:0}$ PLFA (Table 1). The relative abundance of $C_{24:0}$ PLFA and linoleic and linolenic PLFA (%$C_{18:2\omega6}$ and %$C_{18:3\omega3}$) were higher under ambient light but only in the absence of grazers, which reduced linoleic and linolenic acid contributions (Fig. 5G, I). Predators increased linoleic and linolenic ($C_{18:2\omega6}$ and $C_{18:3\omega3}$) PLFA only under ambient light; this translated into a predator by light interaction (Table 1). Branched PLFA were lower in ambient light treatments (p=0.006, ω^2=0.08). In addition to main effects, there were a variety of interactive effects on PLFA composition and abundance (Table 1). Overall, the

PLFA results echo those for total FA, showing that community structure and light availability alter SOM deposition and probably sediment microbial response.

PC1 and PC2 explained 25.3% and 19.5% of the variance, respectively, in PLFA composition (Fig. 6C, D). Similar to the results for total FA, PC1 separated PLFA variables according to light availability. Percent TOC, $\%C_{24:0}$, and $\%(C_{18:2} + C_{18:3})$, which were increased by light (Figs. 3, 5) and correlated with primary producer biomass (Table 2), had more positive PC1 loadings (Table 3). PC1 was also positively related to total algal biomass, which increased in ambient light (r^2=0.10; p=0.018). In ambient light, PC2 separated response treatments by grazer presence (near zero) and absence (more negative) (Fig. 6C). The association of PC2 with grazers is supported by the negative relationship between PC2 and benthic Chl *a* (r^2=0.10; p= 0.017). In shaded treatments, neither PC1 nor PC2 clearly separated grazer and crab treatments (Fig. 6D).

Discussion

A realistic assessment of ecosystem functioning under changing conditions requires simultaneous consideration of top-down and bottom-up effects (Strong 1992; Hughes et al. 2004; Borer et al. 2006). In benthic, sedimentary systems, this should include effects on biomass and composition of above-ground primary producers and animals (Heck et al. 2000; Hughes et al. 2004; Borer et al. 2006), the below-ground community (Wardle et al. 2005), and organic matter composition in sediments (Holmer et al. 2004; Canuel et al. 2007). In this study, we showed experimentally that epibenthic food web structure and resource (light) availability strongly influenced the abundance and composition of SOM. Specifically, light increased and grazers decreased most measures of primary producer biomass and sediment organic matter. Grazer effects on primary producers and SOM composition were generally stronger in ambient light treatments, showing that animal communities and resource availability together shaped properties of this seagrass ecosystem. Perhaps surprisingly, given the strong effects of predators on above-ground algal biomass in this system (Duffy et al. 2005), effects of predators (food chain length) on SOM were less pervasive than those of light availability or grazers. Nevertheless, predators increased OM contributions from microbial sources generally (%SCFA, total FA), and from sediment heterotrophic bacteria specifically (%BrFA, total FA). This suggests that the previously demonstrated cascading effects of crab predators on primary producer biomass (Duffy et al. 2005; Canuel et al. 2007) also affect the accumulation of labile OM, eliciting a bacterial community response.

Bottom-up forcing

Many seagrass ecosystems suffer from suspended sediment and nutrient loading, both of which can reduce light availability (Duarte 2002; Kemp et al. 2004). Decreased water clarity negatively effects seagrass performance and has cascading effects on associated fauna, water quality, and sediment erosion (Orth and Moore 1983; Duarte 2002). With such wide-ranging effects it is likely that decreased water transparency would also affect SOM accumulation and biogeochemical processes in seagrass sediments (McGlathery et al. 1998; Holmer et al. 2004). Thus, a primary goal of our study was to elucidate how light availability, alone and in concert with changing food web structure, influences OM composition.

In our experimental system, light strongly increased above-ground plant and algal biomass (Table 1, Fig. 1), confirming that the level of shading we used limited primary production and accumulation of producer biomass. In the sediments, light increased benthic microalgal biomass and, presumably as a result, TN and TOC as well. These light effects translated into changing SOM composition by increasing the abundance of algal and microbial fatty acids (%($C_{12:0}$ + $C_{14:0}$); total FA), %$C_{24:0}$ (total FA, PLFA), and linoleic and linolenic acids (PLFA), and by decreasing heterotrophic bacterial fatty acids (%BrFA; total FA, PLFA) (Fig. 5). When expressed as a fraction of total FA, linoleic and linolenic acids were positively correlated with eelgrass biomass while %($C_{12:0}$ + $C_{14:0}$) (total FA), %$C_{24:0}$ (total FA), and branched fatty acids (total FA) were positively correlated with benthic microalgal biomass (Chl *a*). The positive relationship between benthic Chl *a* and heterotrophic bacterial fatty acids suggests that, in our system, microalgae served as a primary organic matter source for sediment bacteria. This is consistent with recent work showing that microalgae are often a major source of SOM and drive microbial degradation processes in seagrass beds (Boschker et al. 2000; Bouillon and Boschker 2006).

Although it is generally accepted that $C_{12:0}$ + $C_{14:0}$ derive from aquatic algal and microbial sources, the origin of $C_{24:0}$ is less clear. Vascular plants are typically considered the source of long chain fatty acids; however, diatoms have been reported to contribute as much as 30% of $C_{24:0}$ in some sediments (Volkman et al. 1980). Other studies have reported $C_{24:0}$ fatty acid in cyanobacterial mats (Edmunds and Eglinton 1984), diatoms (Viso and Marty 1993), and microalgae (Volkman et al. 1998 and references therein). These organisms are often associated with the community of organisms composing the microphytobenthos. In addition, %($C_{12:0} + C_{14:0}$) (aquatic algal and microbial OM) and %$C_{24:0}$ had similar PC1 and PC2 scores (Table 3). These FA classes responded similarly to light and food-web treatments, suggesting that they may share an organic matter source in our system.

Overall, light availability increased the abundance of above-ground primary producers, sediment TN and TOC content, and the relative contributions of FA typically considered to derive from aquatic sources such as algae and microbes. These results demonstrate that resource availability affects below-ground organic matter storage and cycling in this seagrass system in addition to the more obvious accumulation of plant biomass above-ground. Consequently, changes in water quality that result in reduced light availability may alter carbon cycling and storage in seagrass ecosystem sediments.

Community structure and top-down forcing

The community structure of seagrass ecosystems is rapidly changing as a result of reduced water quality, fishing pressure, and other human influences (Duarte 2002; Orth et al. 2006). The resulting shifts in community composition at multiple trophic levels may precipitate changes in ecosystem functioning (Heck et al. 2000; Duffy 2002). For example, loss of a top predator can indirectly reduce primary producer biomass via a trophic cascade (Hairston et al. 1960; Pace et al. 1999; Shurin et al. 2002). In seagrass systems specifically, shifts in species composition at intermediate trophic levels may also alter ecosystem properties and/or OM accumulation (Duffy et al. 2003; Canuel et al. 2007). A goal of this experiment was to determine how simultaneous changes in food web composition and resource availability influence ecosystem properties and functioning.

Food chain length (predator presence or absence) strongly influenced GEP, total algal biomass, and SOM composition (Table 1). This effect of crab predators was evidently mediated indirectly, as crabs inhibited or consumed grazing invertebrates, increasing algal biomass and, consequently, GEP. In the sediments, these effects of predators increased algal and microbial organic matter (%($C_{12:0}$ + $C_{14:0}$) total FA; Fig. 5A), presumably through the same trophic cascade mechanism. Interestingly, predators decreased the relative contribution of even-numbered polyunsaturated fatty acids (%PUFA Total FA; Fig. 5C), which are considered proxies for "fresh" algal material (Canuel and Martens 1993). This effect was strongest in shaded treatments where primary producer biomass was lower. Importantly, predators also increased OM contributions from sediment heterotrophic bacteria (%BrFA total FA; Fig. 5E), suggesting that trophic cascades can extend beyond animals and plants to OM and biogeochemical cycling. Consequently the removal of top predators may alter not only biomass and production of herbivores and plants, but also ecosystem processes mediated by sediment or soil communities (Setälä et al. 1998; Wardle et al. 2005). This has implications for seagrass ecosystems in Chesapeake Bay and elsewhere where blue crabs and predatory fishes are commercially harvested.

Overall, grazers strongly decreased ecosystem production, plant and algal biomass, and the contributions to the sediments of FA deriving from these sources (Table 1, Figs. 1, 2, 5). Above-ground, grazer presence decreased total algal and *Z. marina* biomass, resulting in reduced GEP; but only in the absence of predators, reflecting the strong trophic cascade demonstrated previously in the above-ground portion of this system (Duffy et al. 2005). Both grazer presence and richness were strong determinants of GEP, confirming that invertebrate species composition and diversity can influence ecosystem-level rate processes (Jonsson and Malmqvist 2003; Dangles and Malmqvist 2004). In the sediments, grazer presence decreased benthic microalgal biomass (Chl *a*), microbial fatty acids (%($C_{12:0}$ + $C_{14:0}$) total FA), linoleic and linolenic acids (total FA and PLFA), and %C_{24} (ambient light and with predators, total FA) (Fig. 5). Thus, grazing reduced the contribution of fatty acids characteristic of eelgrass and algae to SOM. Grazer richness only influenced heterotrophic bacterial fatty acid abundance (%BrFA total FA and PLFA; Fig. 5E), though this effect was mainly driven by the two species treatment. Overall, our results indicate that the presence of grazers is more important than the number of species in determining SOM composition and quality.

Overall, food chain length and grazers strongly affected GEP, primary producer biomass, and SOM composition. Predators mediated carbon flow and accumulation between lower trophic levels while grazers altered the composition of OM delivered to the sediment. Further, our results suggest that above-ground communities may influence sediment heterotrophic bacteria. Consequently, human-induced shifts in the abundance or composition of above-ground communities can indirectly affect sediment biogeochemistry by influencing the pathways (invertebrate grazers vs. bacteria) through which OM is cycled.

Interactions between bottom-up and top-down forcings

Since seagrass habitats are perturbed by multiple stressors, developing a comprehensive understanding of ecosystem responses is imperative for conservation and restoration (Duarte 2002; Orth et al. 2006). However, most studies have investigated the effects of human stressors, such as eutrophication (see Cloern 2001) or changing biodiversity (see Duffy 2006), on seagrass systems singularly (but see Heck et al. 2000 and Hughes et al. 2004). Thus a major goal of this work was to investigate how interactions between decreased resource (light) availability and altered food web structure (grazer community and predator presence) affect ecosystem properties. Interactions between the three manipulated variables had pervasive effects on the abundances of above-ground eelgrass and algal biomass and SOM composition. While the majority of interactions were between grazers and light or predators, there were also several three-way interactions.

Overall, most interactive effects of the treatments on SOM largely stemmed from light or predators mediating grazer effects on primary producer biomass and organic matter. Generally, grazer effects were stronger in ambient light while predator controls were more prevalent in shaded treatments (Table 1), suggesting that the strength of trophic cascades may depend on the availability of light or other resources, as in some freshwater systems (Chase 2003). The results of the PCA analyses best summarize the interactive effects of light, grazers, and predators on SOM (Table 3, Fig. 6), suggesting that grazers can strongly determine SOM composition, that their effects are damped by predators, and that changing light intensity affects the relative strength of this trophic cascade.

Our results largely confirm our original hypotheses. Grazers decreased total algal biomass and altered SOM composition. Predator inclusion resulted in a trophic cascade whereby total algal biomass, algal and microbial organic matter (%($C_{12:0}$+$C_{14:0}$) Total FA), and bacterial fatty acid abundance (%BrFA of Total FA) in the sediments were increased. Ambient light increased above-ground and sediment primary producer abundance, sediment total nitrogen and organic carbon, and algal and microbial organic matter (%($C_{12:0}$+$C_{14:0}$) total FA, %$C_{24:0}$ total FA and PLFA). Contrary to our predictions, grazers decreased *Z. marina* biomass, benthic Chl *a,* and fatty acids derived from algal and microbial organic matter (%($C_{12:0}$+$C_{14:0}$) total FA) while reduced light availability increased bacterial organic matter (%BrFA total FA). This latter result was largely driven by the treatment with two grazer species. The complex interactive effects among resources, predators, and grazers suggest that above-ground and sediment properties are unlikely to respond in simple, predictive ways to multiple disturbances. Further, our results demonstrated that resource availability and food web structure strongly influence ecosystem properties and that synergism between bottom-up and top-down controls may affect sediment carbon composition and storage in natural seagrass beds. This underscores the need for additional multi-factorial experimental and field approaches to understanding the cycling of organic matter in estuarine systems. Realistic mesocosm experiments are initially helpful in identifying subtle changes in SOM and focusing research questions and methods. However, field experiments will clearly be necessary to explore how linkages between above-ground processes and SOM are related in the more complex natural environment. Combined, results from both approaches should be useful in designing more effective management strategies for the preservation of productive seagrass ecosystems.

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Table 1. Tests of significance, estimated magnitudes of effect (ω^2), and contrasts of grazer richness vs. presence for light availability, food chain length, grazer species richness, and their interactions on ecosystem production, plant biomass, sediment total nitrogen, sediment organic carbon, and sediment fatty acid abundance. When an interaction between grazers and light or predators was significant, the data set was divided according to the interaction (i.e., low light vs. ambient light or no predators vs. predators) and an ANOVA was performed again. For interactive effects, G refers to grazers, C to crab predators, and L to light. For contrast analyses, P indicates where grazer presence affected the response variable and R refers to a richness effect. Significant *p* values are in bold.

Response	Light			Crab predators			Grazers			Interactions				Error		Contrast
	MS	*p*	ω^2	MS	*p*	ω^2	MS	*p*	ω^2		MS	*p*	ω^2	MS	ω^2	
Gross ecosystem production	NA			23.38	**<0.001**	0.29	5.42	**0.014**	0.12	GxC	8.33	**0.002**	0.19	1.03	0.40	PR
No predators							13.26	**0.001**	0.39					0.59	0.61	PR
Predators							0.49	0.661	0.00					1.14	1.03	
Z. marina (AFDW)	80.95	**0.027**	0.06	28.50	0.180	0.01	37.11	0.101	0.04	GxC	61.94	**0.025**	0.09	15.31	0.61	P
No predators	78.71	**0.005**	0.17				67.22	**0.002**	0.28					7.87	0.57	PR
Predators	14.84	0.428	0.00				31.82	0.269	0.03					22.75	1.04	
Total algae (log AFDW + 0.001)	6.79	**0.005**	0.04	35.46	**<0.001**	0.25	16.69	**<0.001**	0.23	GxC	12.52	**<0.001**		0.76	0.33	PR
No predators	0.65	0.473	0.00				56.83	**<0.001**	0.77					1.22	0.25	PR
Predators	1.46	**0.019**	0.15				0.35	0.230	0.03					0.23	0.87	
Benthic Chl *a* (μg cm^{-2})	352.73	**0.023**	0.06	100.12	0.217	0.00	408.49	**0.004**	0.01					63.60	0.8	P
%TOC	0.06	**0.004**	0.12	0.01	0.669	0.00	0.01	0.398	0.00					0.01	0.90	
%TN	0.01	**<0.001**	0.18	0.00	0.955	0.00	0.00	0.294	0.00					0.00	0.89	
Total fatty acids (TFA)*																
TFA:OC (μg mg$_{TOC}^{-1}$)	193.25	**0.016**	0.08	1.18	0.846	0.00	32.46	0.359	0.00					30.87	0.89	
%SCFA (C_{12}+C_{14}) of TFA	95.18	**<0.001**	0.30	20.06	**0.014**	0.06	15.70	**0.010**	0.08					3.02	0.59	P
%$C_{16:0}$ of TFA	3.43	0.851	0.00	61.69	0.427	0.00	206.40	0.129	0.04					95.84	1.00	
%$C_{18:0}$ of TFA	0.44	0.826	0.00	9.25	0.319	0.00	1.01	0.895	0.00							
%C_{24} of TFA	13.64	**0.003**	0.11	0.00	0.983	0.00	1.85	0.277	0.01	GxL	6.98	**0.011**	0.10	1.40	0.72	
										GxC	6.58	**0.014**	0.09			
Low light				0.15	0.636	0.00	0.88	0.290	0.02	GxC	2.37	**0.047**	0.15	0.67	0.86	
Ambient light				0.14	0.799	0.00	8.48	**0.030**	0.16					2.06	0.76	P
No predators	4.97	**0.045**	0.09				0.75	0.516	0.00					1.09	0.80	
Predators	8.95	**0.032**	0.10				7.67	**0.023**	0.16					1.70	0.67	P
%PUFA of TFA	0.20	0.927	0.00	104.82	**0.042**	0.05	9.18	0.682	0.00	GxL	100.43	**0.021**	0.10	23.77	0.89	
										LxC	100.01	**0.047**	0.05			
Low light				197.48	**0.002**	0.27	23.42	0.259	0.02					16.21	0.73	
Ambient light				0.03	0.976	0.00	91.26	0.072	0.13					30.63	0.97	P
%($C_{18:2}$ + $C_{18:3}$) of TFA	44.80	0.061	0.04	4.75	0.534	0.00	43.86	**0.035**	0.07	GxL	67.44	**0.007**	0.12	12.10	0.77	P
Low light				5.33	0.398	0.00	2.34	0.725	0.00					7.16	1.09	
Ambient light				30.67	0.188	0.02	116.77	**0.004**	0.28					16.59	0.69	P
%BrFA (i,a C_{13}-C_{19}) of TFA	47.83	**0.023**	0.06	57.81	**0.013**	0.07	46.15	**0.008**	0.11	GxL	47.37	**0.007**	0.11	8.57	0.72	R

Low light				23.75	**0.005**	0.24	3.86	0.215	0.03					2.32	0.78	
Ambient light				34.81	0.132	0.04	89.57	**0.007**	0.26					14.25	0.74	R
Phospholipid linked fatty acids (PLFA)*																
PLFA:OC (μg mg_{TOC}^{-1})	0.35	0.399	0.00	0.39	0.375	0.00	0.45	0.407	0.00					0.485	1.04	
%SCFA (C_{12}+C_{14}) of PLFA	1.39	0.587	0.00	7.11	0.223	0.01	10.19	0.125	0.03	GxCxL	21.20	**0.016**	0.10	4.66	0.85	
%$C_{16:0}$ of PLFA	38.88	0.536	0.00	36.72	0.548	0.00	246.27	0.097	0.04	GxCxL	469.76	**0.014**	0.10	99.90	0.84	
%$C_{18:0}$ of PLFA	148.45	0.188	0.01	162.97	0.168	0.02	105.10	0.291	0.01					82.74	1.00	
%$C_{24:0}$ of PLFA	9.98	**<0.001**	0.17	0.44	0.425	0.00	0.46	0.516	0.00					0.68	0.76	
%PUFA of PLFA	19.39	0.221	0.01	37.30	0.092	0.03	56.42	**0.017**	0.10					12.57	0.83	P
%($C_{18:2}$ + $C_{18:3}$) of PLFA	587.83	**0.005**	0.08	223.76	0.074	0.02	377.71	**0.007**	0.09	LxC	303.22	**0.039**	0.03	66.52	0.57	P
										GxL	499.44	**0.002**	0.12			
										GxCxL	253.48	**0.030**	0.05			
Low light				2.90	0.319	0.00	4.34	0.235	0.03	GxC	10.14	**0.045**	0.15	2.79	0.82	
Ambient light				544.12	**0.048**	0.07	940.86	**0.003**	0.25	GxC	463.56	**0.04**	0.11	124.46	0.58	P
%BrFA (i,a C_{13}-C_{19}) of PLFA	60.24	**0.006**	0.08	1.68	0.629	0.00	60.19	**<0.001**	0.15	GxL	51.29	**0.002**	0.12	66.52	0.60	R
										GxCxL	27.38	**0.029**	0.06			
Low light				5.29	0.394	0.00	18.22	0.098	0.10					6.97	0.88	P
Ambient light				18.09	0.126	0.03	91.99	**<0.001**	0.40					7.15	0.51	R

* Biomarker response variables are expressed either as % of total fatty acids or as % of phospholipid-linked fatty acids. Data were analyzed by 3-factor Model III ANOVA. p values <0.05 are in bold.

P and R indicate whether grazer presence or richness effects, respectively, were significant as determined through contrast analysis.

Table 2. Regression analyses of *Z. marina* biomass (AFDW, g) and benthic Chl *a* (μg cm^{-2}) against the major fatty acids groups. Significant relationships (p <0.05) are noted in bold.

Response	*Z. marina*			Benthic Chl *a*			Total
	Coefficient	Partial r^{2*}	p	Coefficient	Partial r^{2*}	p	Model r^2
Total fatty acids (TFA)							
%SCFA ($C_{12:0} + C_{14:0}$) of TFA	0.09	0.03	0.171	0.12	0.22	**<0.001**	0.25
%$C_{24:0}$ of TFA	0.00	0.00	0.968	0.07	0.22	**<0.001**	0.22
%PUFA of TFA	-0.13	0.01	0.428	0.03	0.00	0.718	—
%($C_{18:2} + C_{18:3}$) of TFA	0.26	0.08	**0.041**	0.05	0.01	0.439	0.09
%BrFA (i,a C_{13}-C_{19}) of TFA	-0.20	0.06	0.066	0.11	0.08	**0.034**	0.14
Phospholipid linked fatty acids (PLFA)							
%SCFA ($C_{12:0} + C_{14:0}$) of PLFA	0.06	0.02	0.285	0.00	0.00	0.897	—
%$C_{24:0}$ of PLFA	0.05	0.07	0.052	0.00	0.00	0.813	—
%PUFA of PLFA	-0.07	0.01	0.588	-0.05	0.01	0.449	—
%($C_{18:2} + C_{18:3}$) of PLFA	0.32	0.04	0.121	0.20	0.08	**0.037**	0.12
%BrFA (i,a C_{13}-C_{19}) of PLFA	-0.16	0.04	0.137	-0.03	0.00	0.509	—

*Partial r^2 were calculated by dividing the Type III SS by the Total SS.

Table 3. Loadings from principal components analysis of sediment organic matter composition and content for total fatty acids (total FA) and phospholipid linked fatty acids (PLFA). Polyunsaturated fatty acids (PUFA) are comprised of: $C_{18:4}$, $C_{20:4}$, $C_{20:5}$, $C_{22:5}$, $C_{22:6}$.

	Total FA		PLFA	
Variable	PC1	PC2	PC1	PC2
TOC (mg g^{-1})	0.494	-0.221	0.324	-0.148
%($C_{12:0}$ + $C_{14:0}$)	0.512	0.169	0.526	0.140
%$C_{16:0}$	-0.229	0.527	-0.536	-0.168
%($C_{18:2}$ + $C_{18:3}$)	0.222	0.453	0.137	-0.662
%$C_{24:0}$	0.583	0.118	0.216	-0.557
%PUFA	-0.018	-0.632	0.492	0.290
%BrFA (i,a $C_{13:0}$-$C_{19:0}$)	0.228	-0.160	-0.152	0.312

Figure Captions.

Fig. 1. Effects of grazers, predators, and light availability on above ground primary producers (*Z. marina* and total algae) and benthic Chl *a*. Light, generally, increased primary producer biomass. Grazers decreased *Z. marina* biomass (in the absence of predators) and total algal biomass. Predators decreased both *Z. marina* and total algal biomass but the magnitude of this effect varied with grazer richness, resulting in grazer by predator interactive effects. Error bars represent standard error. There were four replicates of each zero grazer treatment in low light and five in high light; four replicates of each two grazer treatment and five replicates of each four grazer treatment. Statistical results are reported in Table 1.

Fig. 2. Effects of grazers and predatory crabs on summer gross ecosystem production, measured as dissolved oxygen (DO) flux. Predators (crabs) mediated a negative grazer effect on gross ecosystem production through a trophic mechanism. The magnitude of the predator effect increases with grazer richness. Data are only from ambient light treatments. Error bars represent standard error. Statistical results are reported in Table 1.

Fig. 3. Effects of light, grazers, and predators on sediment carbon and nitrogen. (A) Light increased sediment total nitrogen (%TN) and (B) total organic carbon content (%TOC). Neither grazer richness nor food chain length affected %TN or %TOC. Error bars represent standard error. Statistical results are reported in Table 1.

Fig. 4. (A) Abundance of total fatty acids (Total FA) and (B) phospholipid linked fatty acids (PLFA) normalized to total sediment organic carbon content (μg $mg_{TOC}{}^{-1}$). Light decreased total FA (μg $mg_{TOC}{}^{-1}$ (A)) but had no effect on PLFA (μg $mg_{TOC}{}^{-1}$ (B)). Error bars represent standard error. Statistical results are reported in Table 1.

Fig. 5. (A-J) Effects of light, grazers, and predators on total fatty acids (Total FA) and phospholipid linked fatty acids (PLFA) sub-classes. Light, predators, and grazers had strong singular and interactive effects on total fatty acids and phospholipid linked fatty acids. The polyunsaturated fatty acid (%PUFA) sub-class, representing fresh algal material, is comprised of: $C_{18:4}$, $C_{20:4}$, $C_{20:5}$, $C_{22:5}$, $C_{22:6}$. The branched fatty acid (%BrFA) sub-class, representing heterotrophic bacteria, includes iso- and anteiso $C_{13:0}$, $C_{15:0}$, $C_{17:0}$, $C_{19:0}$. Error bars represent standard error. See text for biomarker sources and Table 1 for statistical results.

Fig. 6. Score plots from principal component analysis for total fatty acids (Total FA) and phospholipid linked fatty acids (PLFA) in ambient light and shaded treatments. Error bars represent standard error. G denotes grazers and C refers to crab predators.

Fig. 1. Spivak et al.

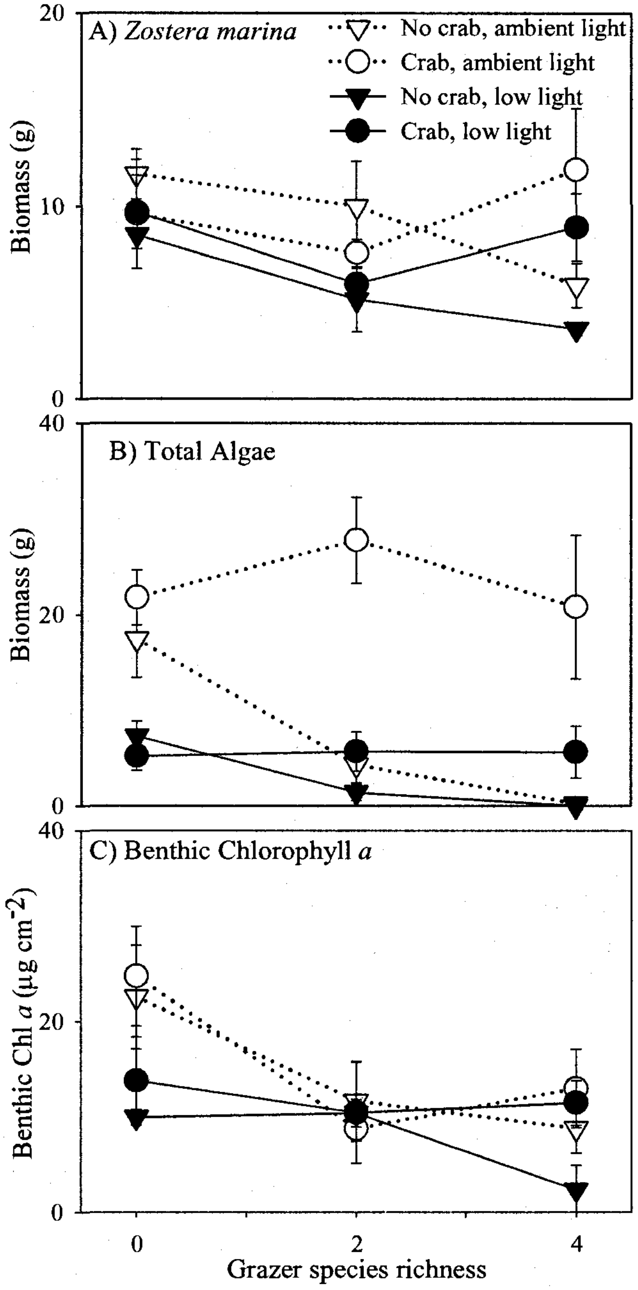


Fig. 2. Spivak et al.

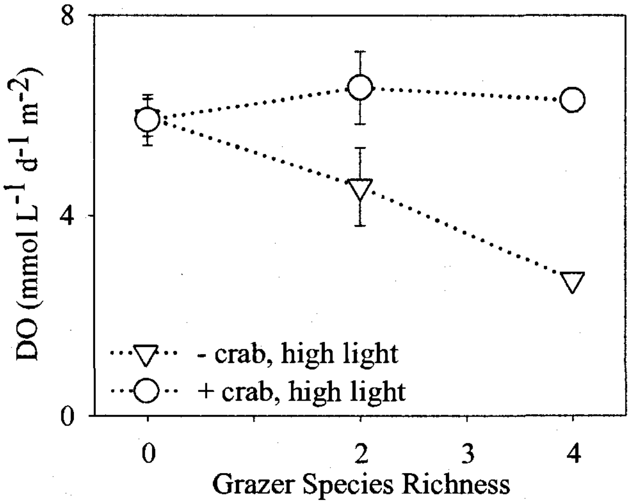


Fig. 3. Spivak et al.

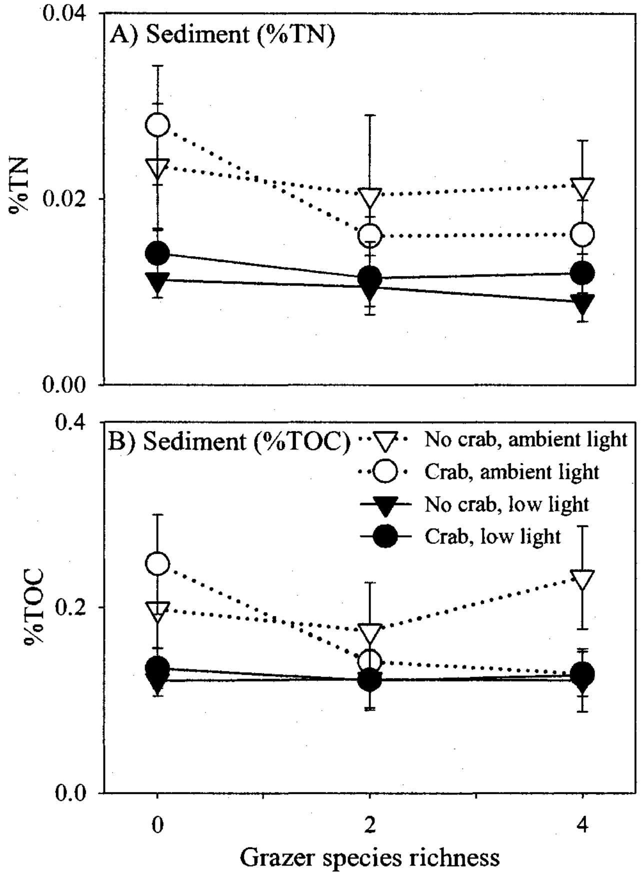


Fig. 4. Spivak et al.

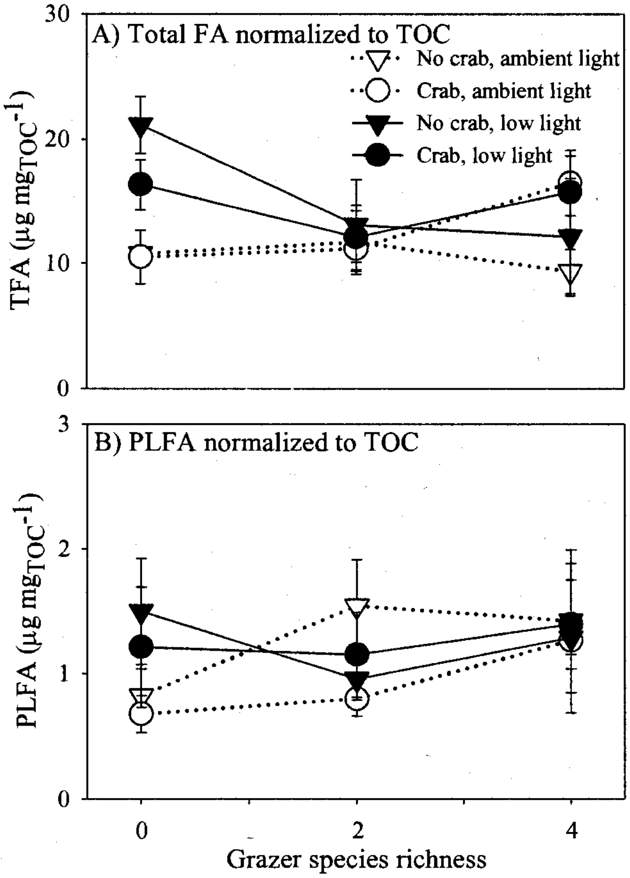


Fig. 5. Spivak et al.

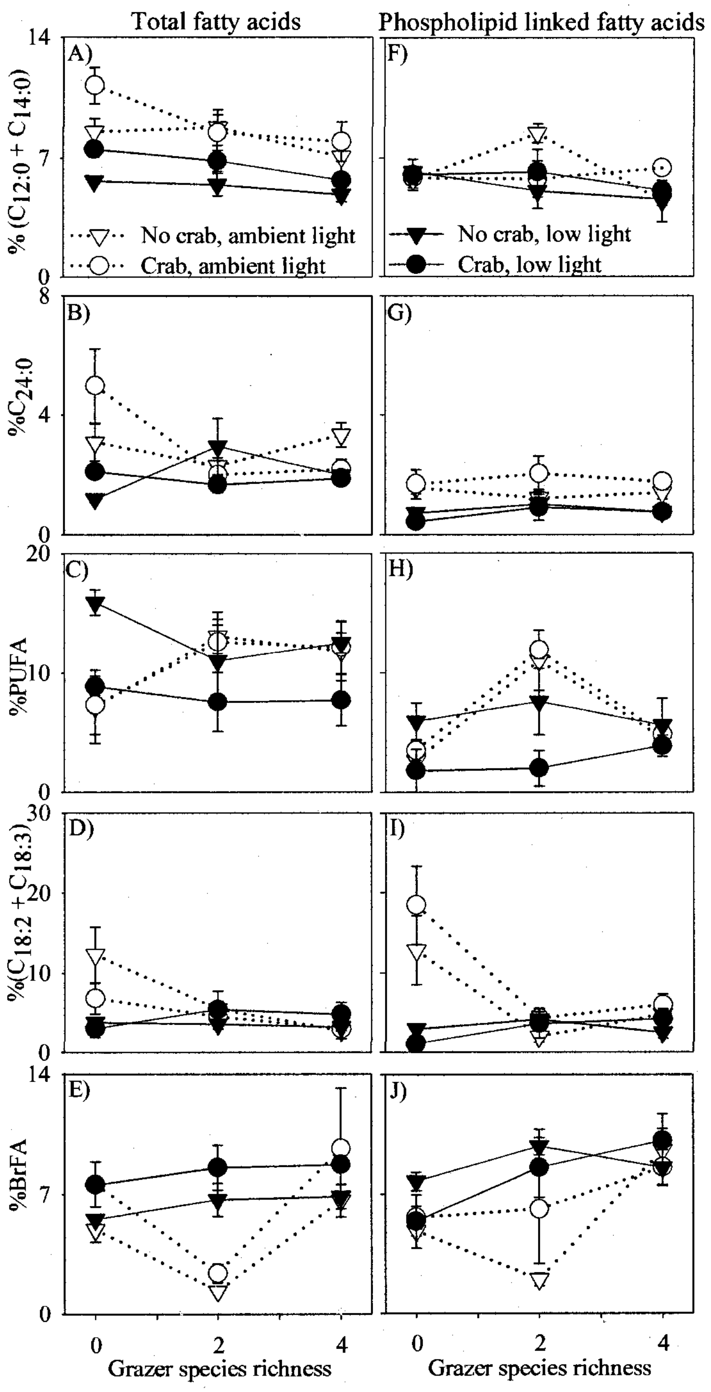
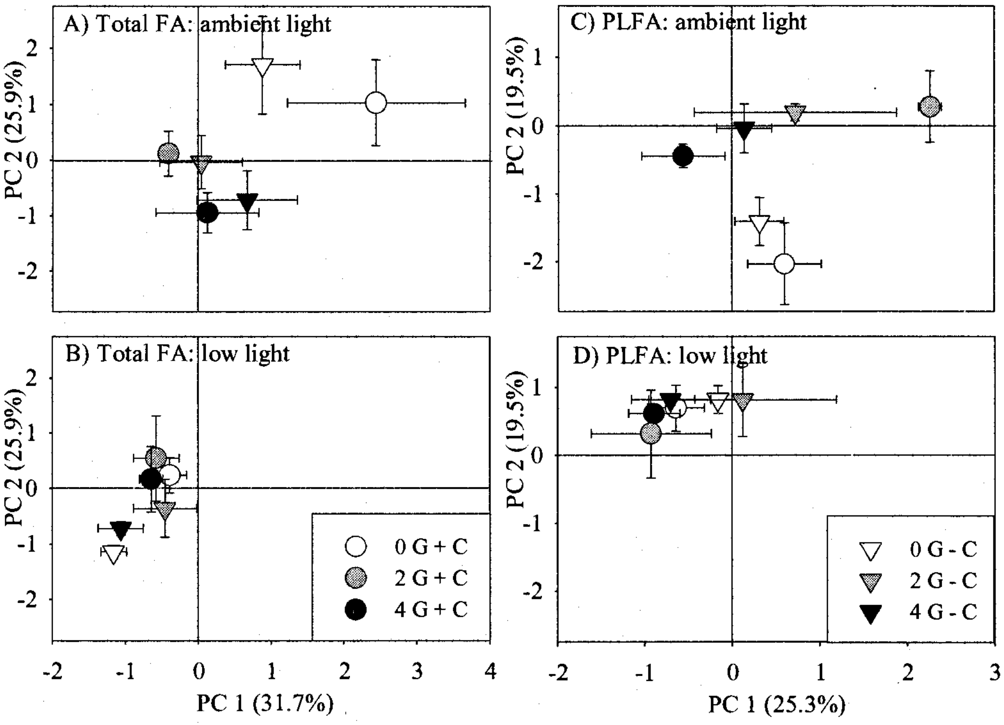


Fig. 6. Spivak et al.



Chapter 3:

Community composition and nutrient availability alter sediment organic matter composition in a seagrass bed: a field experiment.

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Acknowledgements.

We would like to thank R.E. Blake, K.E. France, L.A. Moore, and N. Yavit for help maintaining and sampling the field cages; H. Walker and B.B. Neikirk for analyzing water samples for nutrient concentrations; and M.A. Cochran and M.A. Wunderly for assistance in the lab. I.C. Anderson, D. Bronk, and J.J. Stachowicz provided valuable input on experimental goals and design. This work was made possible through a NSF grant (OCE 03-52343) to J.E. Duffy and a NCER, STAR program, EPA grant (FP-91656901) to A.C. Spivak. E.A. Canuel was supported by NSF awards DEB-0542645 and DEB-0454736 during the study period. Although the research described in the article has been funded in part by the U.S. EPA's STAR program, it has not been subjected to any EPA review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred. Additional support was provided by Virginia Institute of Marine Science. This article is contribution XXXX of the Virginia Institute of Marine Science, The College of William and Mary.

ABSTRACT

Eutrophication and fishing are common perturbations in aquatic ecosystems with pervasive impacts on community structure, including species diversity and abundance, that may cascade to sediment biogeochemistry. While changes in sediment processes in response to these stressors are likely important to ecosystem functioning, they are poorly understood. To address this issue, we experimentally manipulated water column nutrient levels and food web composition (i.e. predator and grazer presence and absence) in a factorial design using field enclosures situated in a *Zostera marina* bed. After 28 days, we quantified sediment organic matter (SOM) accumulation and composition using measures of total organic carbon and nitrogen as well as fatty acid (FA) biomarkers. Nutrient enrichment led to a rapid increase of epiphytes and a decline in *Z. marina* biomass. Responding to the available algae, grazers reduced epiphytes and FAs derived from microalgae. Predators reduced *Z. marina* abundance and possibly its ability to trap particulate OM, leading to lower sediment organic carbon content and total FA abundance. There was evidence of a trophic cascade as FA contributions from epiphytes and diatoms were higher in treatments with both grazers and predators than in treatments with grazers only. Predators increased labile diatom-derived OM, which likely resulted in the higher proportions of bacterial FA measured in predator treatments. Interactions between nutrient availability and food web composition indicated that SOM responses were complex and not predictable from single variables. Changes in SOM accumulation and composition, combined with a rapid heterotrophic bacterial response, suggest that resource availability and community structure are important to sediment biogeochemistry.

INTRODUCTION

Bottom-up (i.e. resource availability) and top-down (i.e. food chain length) controls act in concert across multi-level food webs (Carpenter et al. 1985, Hunter and Price 1992, Power 1992, Borer et al. 2006) in freshwater (Elser & Goldman 1991, Brett & Goldman 1997, Forrester et al. 1999, Chase 2003) and marine systems (Micheli 1999, Hughes et al. 2004, Burkepile & Hay 2006) to affect patterns of biomass distribution and biogeochemical cycles. Elevated resource availability and changes in top predator abundance may increase plant biomass and the delivery of plant-derived organic matter (OM) to the sediments in tri-trophic seagrass systems (Canuel et al. 2007, Spivak et al. 2007). The quality and rate of OM deposition can have large effects on bacterial decomposition and carbon burial in sediments (Hansen & Blackburn 1992, Cebrian & Duarte 2001). Consequently, resource availability and community composition may synergistically alter sediment biogeochemistry and ecosystem functioning. Here, we experimentally tested how food web structure and nutrient enrichment alter sediment organic matter (SOM) quality and content in a natural seagrass (*Zostera marina*) ecosystem.

In vegetated coastal habitats, photosynthetic carbon is channeled through grazers, exported to neighboring ecosystems, or buried in the sediments (Pergent et al. 1994, Duarte & Cebrian 1996, Cebrian & Duarte 2001, Duarte et al. 2005). Small, invertebrate grazers mainly consume nutrient-rich algae and epiphytes, leaving senesced seagrass blades as the main source of buried OM (Pergent et al. 1994, Duarte & Cebrian 1996, Cebrian 1999, Cebrian & Duarte 2001). Eutrophication may alter the proportion of algal and epiphytic carbon that is exported or buried by stimulating higher rates of production and changing the composition of primary producer assemblages (Cloern 2001, Duarte 2002). Deposition of higher quality OM derived from labile algae can stimulate bacterial decomposition (Hansen & Blackburn 1992, Boschker and Cappenberg 1998) and, hence, the depletion of oxygen in the sediments. As anaerobic conditions develop, sulfate reduction may become a dominant pathway for OM decomposition. Thus, eutrophication may dually impact seagrass by increasing algal-mediated shading (Cloern 2001, Duarte 2002, Orth et al. 2006) and sediment dissolved sulfide concentrations (Hemminga 1998, Calleja et al. 2007, Pérez et al. 2007).

The symptoms of eutrophication may be diminished or exacerbated by food web composition and structure (Carpenter et al. 1985, Pace et al.1999). In a two level trophic system, strong grazing controls reduced the negative effects of nutrient loading by transforming algae into animal biomass (Williams & Ruckelshaus 1993, Hughes et al. 2004, Burkepile & Hay 2006, Heck & Valentine 2007). Further, grazer species identity and feeding preferences may influence the composition of the primary producer community (Duffy & Hay 2000, Duffy 2002). In a three-level trophic system, predators may exaggerate the effects of nutrient enrichment by inhibiting grazers and releasing algae and epiphytes from grazing pressures via a trophic cascade (Oksanen et al. 1981, Carpenter et al. 1985, Forrester et al. 1999, Pace et al. 1999). Therefore, the effects of nutrient enrichment in seagrass beds may, in part, be determined by trophic structure and community composition.

Despite potentially strong bottom-up and top-down effects on OM deposition and the importance of SOM quality to sediment biogeochemistry (Duffy et al. 2003, Canuel et al. 2007, Spivak et al. 2007), the synergistic effects of nutrient enrichment and community composition on SOM are poorly understood. This is likely due to the difficulty in identifying and manipulating links between above-ground ecology and sediment processes under realistic conditions. Lipid biomarkers are a functional proxy for linking OM to its potential sources (Canuel et al. 1995, Canuel & Martens 1996), since these compounds are reliably produced by specific groups of organisms (Killops & Killops 1993). Diagnostic biomarkers often have site-specific methyl groups, double bonds, or cyclic side chains useful for tracing sources of OM (Killops & Killops 1993). Bacteria, for example, synthesize iso- and anteiso- branched fatty acids while microalgae contain highly unsaturated long chain fatty acids (Volkman et al. 1998). In addition, lipid biomarkers are sufficiently resistant to degradation to be preserved in sediments, allowing for the identification of OM that has been deposited on ecological and historical timescales (Meyers 1997, Zimmerman & Canuel 2002). Here, we used fatty acids, a class of lipid biomarkers with high source fidelity and a range of chemical reactivity (Canuel et al. 1995, Canuel & Martens 1996), to experimentally quantify links between the above-ground community and SOM content and composition.

To assess the effects of changing resource availability and food web structure on carbon fate and storage in a natural seagrass bed, we conducted an experimental manipulation of bottom-up forcing (water column nutrient availability) and community composition (grazer and predator presence) and measured their interacting effects on SOM quantity and quality. Specifically, we built on previous mesocosm studies examining the effects of community diversity (Canuel et al. 2007) and light availability (Spivak et al. 2007) on SOM composition to test several hypotheses in a field experiment. First, we predicted that nutrient enrichment will increase algal biomass and the deposition of algal-derived OM to the sediments. The increased lability of SOM will, in turn, stimulate sediment heterotrophic bacterial activity and the deposition of bacterial FA. Second, algae will indirectly decrease *Zostera marina* abundance by increasing competition for light and nutrients. The presence of a grazer community will reduce algae and the abundance of their characteristic FA in the sediment but will increase *Z. marina*. Finally, the presence of predators will result in a trophic cascade in which grazer abundance is reduced and algal biomass and OM contributions to the sediments are increased.

METHODS

Experimental design

We conducted a field experiment to examine the main and interactive effects of food web structure (i.e. grazer and predator presence) and water column nutrient availability on SOM content and composition. Grazer treatments had two levels, either zero grazers or an assemblage of three species. Predator presence was manipulated by exposing parallel sets of these two grazer treatments to a generalist predator, the blue crab, *Callinectes sapidus*. Nutrient availability was controlled through Osmocote™ fertilizer additions to half of the cages. In total, there were eight treatments, each replicated five times for a total of forty experimental field cages. To control for caging effects, we established no-cage control plots which only received nutrient treatments, since it was impractical to maintain grazer and predator treatments without cages. There were two no-cage treatments (with nutrients versus without nutrients), each replicated five times for a total of ten no-cage control plots.

Treatments were applied to caged enclosures (51 cm^2 x 81 cm) and no-cage control plots (51 cm^2) situated in a *Zostera marina* bed adjacent to Goodwin Islands, an archipelago in the York River estuary, VA. The cages were covered with 250 μm Nitex mesh which permitted water circulation and passage of propagules but prevented predator and grazer immigration and emigration. Before experimental treatments were applied, caged enclosures and no-cage control plots were defaunated with a liquid insecticide, Sevin™. Douglass et al. (2007) described cage design and the defaunation process in greater detail. The experiment ran for 28 days during Summer 2005. This time period was chosen to minimize the risk of invasion by non-target grazer species and to permit development of the animal and plant community and of surface sediment characteristics. During this time temperature and salinity ranged from 23.76 °C – 27.00 °C and 15.67-19.51 psu, respectively (K.A. Moore *unpubl.*).

Four days after defaunation, grazer, predator, and nutrient treatments were applied to the caged enclosures. Grazer treatments consisted of an assemblage of three species, including an amphipod crustacean (*Gammarus mucronatus*, 40 individuals) and two isopods (*Idotea balthica*, 40 individuals, and *Erichsonella attenuata*, 20 individuals). Predator treatments were stocked with two blue crabs (*Callinectes sapidus*), with carapace widths of 20 – 40 mm. Grazers and blue crabs were collected from the surrounding *Zostera marina* bed immediately before addition to the cages and were stocked in proportions and abundances that reflected those in the field at the time of the experiment. Nutrient treatments were applied by suspending two perforated PVC tubes containing Osmocote™ slow release fertilizer (N:P = 3:1) above the sediments. We added 200 g of Osmocote™ during the first week and 400 g thereafter to achieve the desired and sustained level of enrichment. Weekly, and immediately before the fertilizer was refreshed, 25 mL of water from three replicates of each treatment were filtered through a pre-combusted (450° C) glass fiber filter. Water samples were initially chilled and later frozen (-20 °C) until analysis for NH_4^+, $NO_2^- + NO_3^-$, and PO_4^{-3} concentrations by standard methods with a Lachat auto-analyzer (Smith & Bogren 2001, Knepel & Bogren 2002, Liao 2002).

Bulk sediment organic matter (SOM)

At the end of the experiment, three sediment cores each of 2.6 cm diameter and 2.1 cm diameter were collected from every caged enclosure and no-cage control plot. Larger cores were analyzed for sediment total organic carbon (TOC), total nitrogen (TN), and fatty acid content (FA) while smaller cores were used to determine benthic chlorophyll *a* concentration (Chl *a*; a measure of microalgal biomass). The upper 1 cm from each core was removed; sub-samples from each core were combined into a composite sample in a pre-combusted (450 °C) jar (bulk SOM and FAs) or scintillation vial (benthic Chl *a*). Samples were stored at -80 °C (bulk SOM and FAs) or at -20 °C (benthic Chl *a*) until analysis. Samples of benthic Chl *a* were analyzed within six weeks of collection according to Neubauer et al. (2000). TOC and TN were analyzed by standard methods using a Fisons Flash EA (Model 1112) after removing inorganic carbon (Hedges & Stern 1984); acetanilide was used as the standard.

Fatty acid analyses

Fatty acids (FA) were analyzed using a Bligh & Dyer (1959) method revised according to Macnaughton et al. (1997). Briefly, sediment samples were extracted with methanol : chloroform : K_2HPO_4 50 mM buffer (2:1:0.8, v:v:v) using an accelerated solvent extraction system (Dionex ASE 200). Following extraction, the samples were partitioned and the organic phase removed. Anhydrous Na_2SO_4 was added to the sample to remove water overnight. The samples were concentrated to 1 mL (Zymark Turbo Vap 500) and then saponified using procedures described in Arzayus & Canuel (2004). Following saponification, the residue was extracted under basic (saponified-neutral) and acidic pH (saponified-acid). The saponified acid fraction was methylated using BF_3-CH_3OH and purified using silica gel chromatography. Before analysis by gas chromatography (GC), samples were evaporated to dryness under N_2 and a small volume of hexane was added. The FAs, as methyl esters, were analyzed by gas chromatography following previously-published methods (Canuel & Martens 1993, Zimmerman & Canuel 2001). Peaks were quantified relative to an internal standard, methyl heneicosanoate, added just prior to GC analysis. Peak identities were verified using reference standards and by combined gas chromatography-mass spectrometry using a Hewlett-Packard 6890 GC interfaced with a mass selective detector operated in electron impact mode. FAs are designated as A:BωC, where A is the total number of carbon atoms, B is the number of the double bonds, and C is the position of the first double bond from the aliphatic "ω" end of the molecule. The prefixes "i" and "a" refer to *iso* and *anteiso* methyl branched FAs (see Canuel et al. 1995 and references therein).

Statistical analyses

The experiment was analyzed as a fully factorial three-way analysis of variance (ANOVA), with grazer treatment (df = 1), predator treatment (df = 1), and nutrient availability (df = 1) as fixed variables using SAS version 9.1 for Windows. Analyses of FA were conducted on percent of total FA abundance. Data were transformed by log or arcsine square root functions as necessary to maintain homogeneity of variance as determined by the Cochran's C test. From the ANOVAs we calculated the magnitude of main and interactive effects (ω^2, percentage of variance explained). Due to failure of caged enclosures (e.g., tears or holes in Nitex mesh) seven replicates were removed from the final statistical analyses. No-cage control plots were also excluded from the final ANOVA since their inclusion would have resulted in an unbalanced statistical design. However, contrasts were performed to determine the effect of cage presence on primary producer biomass and sediment organic matter (SOM) content and composition. Thus, 33 replicates were used in statistical analyses; caged control treatments had four replicates in each nutrient condition, grazer treatments had four replicates with nutrients and five without, crab treatments had three replicates with nutrients and four without, combined grazer and predator treatments had five replicates with nutrients and four without. Results presented use the type III sum of squares (SS) from the ANOVA models.

To interpret the bulk SOM and fatty acid data, we performed multiple regression and principal components analyses (PCA; Minitab 14). Multiple regression tests modeled %TOC, %TN, and the FA groups as functions of *Zostera marina* biomass, epiphytic Chl *a*, and benthic Chl *a*. The partial r^2 was calculated by dividing the type III SS for each response variable by the total SS. In the PCA, we included *Z. marina* biomass, epiphytic Chl *a*, benthic Chl *a*, %TOC, %TN, and FA groups. PCA yielded loadings and scores, which described correlations between dominant principal components and response variables (loadings) and observations (scores). PCA loadings were regressed against *Z. marina* biomass, epiphytic Chl *a*, and benthic Chl *a* to help interpret the non-dimensional results.

RESULTS

Cage effects

Field cages reduced photosynthetically active radiation by 66% relative to ambient, to an average of 262 μE s^{-1} m^{-2}, which is within the range of saturating irradiance for *Zostera marina* (see Douglass et al. 2007). Contrast analyses showed that field cages reduced *Z. marina* biomass ($p < 0.001$), epiphytic Chl *a* ($p = 0.006$), benthic Chl *a* ($p = 0.013$), total FA abundance ($p = 0.002$), and OM contributions from diatoms ($C_{20:5\omega3}$: $C_{22:6\omega3}$, $p = 0.001$) (Figs. 1-3) but increased abundances of %($C_{22:5} + C_{22:6}$) ($p = 0.022$), %BrFA ($p = 0.015$), and %10Me17 ($p = 0.001$) (Figs. 3, 4). Overall, caged enclosures reduced primary producer biomass and OM contributions to the sediment but increased FA from sediment heterotrophic bacteria.

Nutrient concentrations

During the first week of the experiment, nutrient treatments received 200 g of Osmocote™ which increased the concentration of ($NO_2^- + NO_3^-$) ($p < 0.001$) but not of NH_4^+ or of PO_4^{-3}. For the remainder of the experiment, Osmocote™ additions were increased to 400 g, thereby raising the concentrations of ($NO_2^- + NO_3^-$), NH_4^+, and PO_4 (all $p < 0.001$; Table 1).

Primary producers

Nutrients, predators, and grazers altered final above-ground primary producer abundances (Fig. 1, Table 2). Nutrients and predators each decreased *Zostera marina* biomass while grazers decreased epiphytes. In contrast, benthic Chl *a* was insensitive to all three treatments.

Bulk sediment organic matter (SOM)

Measurable levels of TOC and TN accumulated in the surface sediments during the experiment (Fig. 2A, B, Table 2). Predators decreased %TOC while grazers increased %TN. Neither %TOC nor %TN was influenced by nutrients nor was either variable correlated to the final biomass of any primary producer group (Table 3).

Total fatty acids (total FA)

Within caged enclosures, predators decreased total FA abundance ($\mu g\ g^{-1}$ sediment; Fig. 2C, Table 2), which was positively correlated to *Zostera marina* biomass (Table 3). Although predators had the only significant effect on total FA concentration, all three treatment variables influenced FA composition. To analyze composition, total FA was divided into sub-classes based on chain length, degree of saturation, and carbon branching patterns as these groups represent different OM sources.

The proportion of short chain saturated FA (SCFA; $\%(C_{12:0} + C_{14:0})$), representing algal and microbial sources, in the sediment was decreased by nutrients (Fig. 3A, Table 2). Grazers increased $\%(C_{12:0} + C_{14:0})$ in the absence of predators, resulting in a significant interaction between grazer and predator effects (Table 2). Overall, bottom-up and top-down controls were both important determinants of algal and microbial contributions to the sediment.

The proportion of long chain saturated FA (LCFA; %($C_{24:0}$ + $C_{26:0}$+ $C_{28:0}$)), comprising 3-7% of total FA, was consistently increased by grazers (Fig. 3B, Table 2). Nutrients increased %LCFA in the presence of predators but tended to decrease %LCFA in the absence of predators, creating a nutrient by predator interaction effect. %LCFA correlated positively with benthic Chl *a* and negatively with epiphytic Chl *a* (Table 3), suggesting that benthic microalgae became a proportionately greater source of LCFA as grazers consumed epiphytes. %LCFA was positively correlated with abundances of two grazer species, *Gammarus mucronatus*, an amphipod, and *Erichsonella attenuata*, an isopod ($p = 0.004$, $r^2 = 0.21$ and $p = 0.031$, $r^2 = 0.11$, respectively; data not shown). Thus, food web composition and nutrient availability interactively altered LCFA contributions from epiphytic and benthic algae.

Polyunsaturated FA (PUFA; %($C_{20:4}$+ $C_{20:5}$) and %($C_{22:5}$+ $C_{22:6}$)), indicative of labile algal OM, were affected by nutrient and food web manipulations (Fig. 3C, D, Table 2). Grazers decreased %($C_{20:4}$+ $C_{20:5}$) but the grazing effect was eliminated in the presence of predators, resulting in a grazer by predator interaction. Predators increased %($C_{20:4}$+ $C_{20:5}$) in non-nutrient treatments only, creating a predator by nutrient interaction. %($C_{20:4}$+ $C_{20:5}$) was correlated negatively with benthic Chl *a* and positively to epiphytic Chl *a* (Table 3). Biomasses of the grazers *Gammarus mucronatus* and *Erichsonella attenuata* were negatively correlated with %($C_{20:4}$+ $C_{20:5}$) ($p = 0.008$, $r^2 = 0.18$ and $p = 0.012$, $r^2 = 0.16$, respectively; data not shown). Predators decreased

%($C_{22:5}$+ $C_{22:6}$) in the absence of grazers, resulting in a grazer by predator interaction. Overall, the main and interactive effects of community composition and resource availability were important determinants of labile algal OM deposition and accumulation.

We used two ratios ($C_{16:1\omega7}$: $C_{16:0}$ and $C_{20:5\omega3}$: $C_{22:6\omega3}$) to determine the relative contributions of diatom-derived OM to the sediments (Budge & Parrish 1998, Shin et al. 2000). Grazers decreased both ratios and hence the abundance of diatom-derived FA relative to contributions from other microalgae (Fig. 3E, F, Table 2). Predators increased diatom:dinoflagellate FA ($C_{20:5\omega3}$: $C_{22:6\omega3}$), but the magnitude was weaker in the presence of grazers and resulted in a grazer by predator interaction. Epiphytic Chl *a* was positively correlated to both ratios while benthic Chl *a* was negatively correlated to $C_{20:5\omega3}$: $C_{22:6\omega3}$ (Table 3). Biomass of the grazing isopod *Idotea balthica* was positively related to $C_{20:5\omega3}$: $C_{22:6\omega3}$ ($p = 0.019$, $r^2 = 0.12$; data not shown). Combined, these data suggest that epiphytes were a major source of diatom OM in the sediments and that above-ground animal activities altered SOM supply and composition.

FAs representative of sediment microbial and bacterial OM (10Me17:0, and iso- and anteiso- $C_{13:0}$, $C_{15:0}$, $C_{17:0}$, $C_{19:0}$) comprised 10% - 14% of total FA (Fig. 4). Branched odd-numbered FAs (%BrFA; iso- and anteiso- $C_{13:0}$, $C_{15:0}$, $C_{17:0}$, $C_{19:0}$), representative of sediment heterotrophic bacteria (Volkman & Johns 1977, Perry et al. 1979), were increased by predators (Fig. 4A, Table 2) and negatively correlated to *Zostera marina* biomass and to epiphytic Chl *a* (Table 3). 10Me17:0, indicative of sulfate reducing bacteria, comprised 1% - 2% of total FA. Nutrients and predators increased %10Me17:0 (Fig. 4B, Table 2), which was correlated negatively to *Z. marina* and positively to benthic Chl *a* (Table 3). These data suggest that food web structure, particularly predator presence, and resource availability influenced the sediment heterotrophic bacterial and microbial community.

Using PCA, we evaluated the effects of nutrients, grazers, and predators on primary producer abundance, bulk SOM, and FA groups. Principal components 1 (PC1) and 2 (PC2) explained 26.0% and 21.8%, respectively, of the variance in the data. PC1 tended to separate treatments according to grazer effect; variables increased by grazers (%TN, %($C_{12:0} + C_{14:0}$), %($C_{24:0} - C_{28:0}$), and %$C_{16:0}$) had negative loadings while those decreased by grazers (epiphytic Chl *a*, %($C_{20:4}$+ $C_{20:5}$), and %$C_{16:1\omega7}$) had positive loadings (Fig. 5A). PC1 was correlated positively to epiphytic Chl *a* and negatively to *Zostera marina* (Table 4). PC2 tended to separate variables according to predator effect; *Z. marina* biomass, total FA, %TOC, and %($C_{22:5} + C_{22:6}$) were decreased by predators and had positive PC2 loadings while %BrFA and %10me17:0br were increased by predators and had negative PC2 loadings (Fig. 5A). PC2 was positively correlated to *Z. marina* biomass and epiphytic Chl *a* (Table 4). Similar to PC loading results, PC scores separated treatments according to grazer and predator presence (Fig. 5B). Treatments with only grazers were generally negative on PC1 while those with only predators had more positive scores. Along PC2, caged control treatments had positive scores while grazer and predator treatments were more negative. The combined grazer and predator treatment was near zero on PC1 and PC2 in the absence of nutrients and negative on PC2 in the presence of nutrients. Since the scores of the grazer and predator treatment and the predator-only treatment were similar in the presence of nutrients it is likely that under eutrophic conditions predators were stronger determinants of SOM composition than grazers. Combined, our PCA results suggest that food web composition strongly influences FA contributions from primary producers and that nutrient additions tended to shift the composition of the primary producer community towards a dominance of epiphytes and a loss of *Z. marina*.

DISCUSSION

Patterns of biomass distribution and accumulation in marine systems are well known to be influenced by both top-down and bottom-up forcing (Paine 1980, Menge 2000 and references therein, Borer et al. 2006). Since carbon storage, export, and deposition are related to biomass production (Duarte & Cebrian 1996, Cebrian 1999, Cebrian & Duarte 2001), top-down and bottom-up controls may extensively influence ecosystem properties and biogeochemical cycling. For example, increased deposition of plant-derived OM can stimulate sediment bacterial decomposition and, in turn, can affect dissolved inorganic nutrient pools and fluxes (Hansen & Blackburn 1992). The importance of understanding such feedbacks is necessary for effective conservation and management of sensitive coastal habitats (Cloern 2001, Duarte 2002). This experiment is one of the first to identify and quantify the effects of epibenthic community structure and nutrient availability on SOM composition in a natural seagrass bed.

Nutrient enrichment and SOM composition

Eutrophication is a central cause of many coastal ills including algal blooms and seagrass decline (Cloern 2001, Duarte 2002, Orth et al. 2006). Nutrient enrichment stimulates rapid growth of algae which may, in turn, increase light attenuation and shade seagrass (Short et al. 1995, Hughes et al. 2004 and references therein). Increased algal biomass has the potential to translate into higher rates of labile OM deposition to the sediments, if grazer controls are not sufficiently strong. Under low nutrient conditions most algal and epiphytic carbon is consumed or exported, leaving vascular plant material as a main constituent of SOM (Duarte & Cebrian 1996, Cebrian 1999). Since the availability of labile OM is an important determinant of decomposition rates, shifts in the proportion of algal versus vascular plant OM in the sediments may affect bacterial activity and remineralization processes (Hansen & Blackburn 1992, Boschker & Cappenberg 1998, Holmer et al. 2004). A goal of this experiment was to determine whether water column nutrient enrichment could precipitate changes in SOM composition and if these shifts were related to primary producer abundance and species composition.

In our experiment, nutrient enrichment stimulated an early increase in epiphytes ($p < 0.05$, $\omega^2 = 0.41$, Douglass et al. 2007) which likely reduced light availability to *Zostera marina*, leading to a decline in its abundance (Fig. 1A, Table 2). By the end of the experiment, there was no evidence of a nutrient effect on epiphytes suggesting that grazer population growth and consumption effectively controlled the initial pulse (Douglass et al. 2007; Fig. 1B, Table 2). Strong grazing pressure on epiphytes may have resulted in a compensatory increase in *Z. marina* biomass had the experiment lasted more than four weeks. An alternative hypothesis, that nutrient enrichment increased the palatability of seagrass and, consequently, its susceptibility to grazing (McGlathery 1995), seems unlikely since we did not detect a statistical interaction between nutrients and grazers.

In the sediment, nutrient enrichment singularly and interactively affected OM contributions from benthic algae, epiphytes, and heterotrophic bacteria. Surprisingly, nutrients decreased SCFA (%($C_{12:0}$ + $C_{14:0}$)), proxies for algal and microbial biomass (Fig. 3A, Table 2). OM contributions from benthic algae and epiphytes were influenced by interactions between nutrients and predators. Nutrient enrichment increased the abundance of LCFA (%($C_{24:0}$ – $C_{28:0}$)), which correlated positively with benthic Chl *a* (Table 3), when predators were present (Fig. 3B, Table 2). In contrast, when predators were absent, nutrients increased %($C_{20:4}$ + $C_{20:5}$) (Fig. 3C; Table 2), which was positively correlated with epiphytic Chl *a* (Table 3). Thus, strong nutrient and nutrient by predator interactions influenced the relative dominance of primary producer groups and, hence, their FA contributions to SOM.

Changes in OM delivery and composition stimulated responses by two functionally distinct groups of heterotrophic bacteria. Nutrient enrichment increased %10Me17:0, a FA in sulfate reducing bacteria (Dowling et al. 1986), but had no effect on %BrFA, biomarkers for heterotrophic bacteria (Fig. 4, Table 2). It is curious that nutrients did not elicit similar responses in both bacterial FA groups, however, BrFA and 10Me17:0 may reflect different communities of organisms. For instance, %BrFA was negatively related to epiphytic Chl *a* while %10Me17:0 correlated positively with benthic Chl *a* (Table 3). This suggests that bacteria represented by BrFA responded to early epiphytic OM deposition, which gradually decreased as grazer populations grew. As benthic Chl *a* became a proportionately greater source of labile SOM, sulfate reducing bacterial metabolism and production of 10Me17:0 likely increased. Higher rates of heterotrophic bacterial activity may have reduced sediment oxygen availability and increased sulfide production, creating conditions which can be toxic to seagrass (Hemminga 1998, Calleja et al. 2007, Pérez et al. 2007). This is supported by the negative correlations between *Zostera marina* and both bacterial FA groups (Table 3). Consequently, nutrient availability may have indirectly affected seagrass survival by altering SOM composition, heterotrophic bacterial activity, and thus sediment oxidizing conditions.

In summary, our data suggest that increased nutrient availability altered the composition of above-ground primary producer communities, SOM composition, and sediment microbial communities (Canuel et al. 2007, Spivak et al. 2007). The rapid sediment heterotrophic community response to OM inputs may have implications for nutrient recycling and seagrass survivability.

Above-ground community structure and SOM composition

The ongoing depletion of commercially valuable predators from coastal habitats has broad implications for ecosystem functioning and nutrient cycling (Jackson et al. 2001, Scheffer et al. 2005, Halpern et al. 2006). Predator loss can lead to increased grazer biomass as well as more intense intraspecific competition which could affect grazer community composition (Shurin & Allen 2001, Duffy 2006). Subsequent shifts in grazer species richness and, hence, grazer food preferences may then cascade to alter plant species abundance and identity (Lubchenco 1978, Schmitz 2004). The deposition of plant and algal biomass to the sediments may alter SOM lability, which is a determinant of bacterial activity and an important food source for benthic communities (Boschker & Cappenberg 1998, Hansen & Blackburn 1992, Danovaro et al. 1999). A goal of this experiment was to determine whether changes in food web structure indirectly affect SOM composition by altering primary producer biomass and its deposition to the sediments.

By the end of the experiment, predators decreased *Zostera marina* biomass, sediment TOC, and total FA abundance (Figs. 1, 2, Table 2). Unnatural confinement of predators may have contributed to *Z. marina* decline through crab destruction of the grass blades (Douglass et al. 2007). Loss of *Z. marina* corresponded with lower %TOC and total FA abundance, possibly due to lower effectiveness of the grass in trapping fine sediment and particulate OM (Fig. 2, Table 2). This is consistent with the positive correlation between *Z. marina* and total FA abundances (Table 3). In addition to decreasing *Z. marina* biomass and bulk SOM content, predators influenced SOM composition by decreasing labile OM from algal and microbial sources (%($C_{12:0}$ + $C_{14:0}$) and %($C_{22:5}$ + $C_{22:6}$)) and %($C_{24:0}$ – $C_{28:0}$) (non-nutrient treatments only; Fig. 3, Table 2). This was opposite to previous findings demonstrating the role of blue crabs in reducing grazers and increasing algal biomass in similar experiments (Duffy et al. 2005, Canuel et al. 2007, Spivak et al. 2007). Benthic microalgae were the likely source of LCFA ($C_{24:0}$ – $C_{28:0}$), as suggested by positive correlations with benthic Chl *a*; LCFA were negatively correlated with epiphytic Chl *a* (Table 3). LCFA are the dominant FA in vascular plants but may also occur in microalgae at trace levels and have been identified in benthic diatoms (Volkman et al. 1980, Viso & Marty 1993), cyanobacterial mats (Edmunds & Eglinton 1984), and microalgae (Volkman et al. 1998 and references therein). Although predators decreased FAs representing algae and microbes in general, they increased FA specifically deriving from diatoms (e.g., higher ratio of $C_{20:5\omega3}$: $C_{22:6\omega3}$; Fig. 3, Table 2) and, perhaps as a result, sediment heterotrophic bacterial FAs (%BrFA and %10Me17:0; Fig. 4, Table 2). The positive predator effect on %BrFA is consistent with previous seagrass mesocosm experiments (Canuel et al. 2007, Spivak et al. 2007) and suggests that the above-ground community's effects on primary producers can penetrate to influence sediment bacteria. Thus, food chain length could have important indirect effects on sediment bacterial processes such as OM decomposition and remineralization.

The grazer community influenced primary producer abundance and SOM content and composition. Grazers consumed epiphytes, reducing epiphytic Chl *a* and the abundance of FAs positively correlated to epiphytic Chl *a* (%($C_{20:4}$ + $C_{20:5}$), $C_{16:1\omega7}$: $C_{16:0}$, and $C_{20:5\omega3}$: $C_{22:6\omega3}$) (Fig. 1, 3, Tables 2, 3). "Fresh" algae are generally the source of ($C_{20:4}$ + $C_{20:5}$) (Canuel & Martens 1993) while diatom prevalence, relative to the microalgal community, is expressed by ratios of $C_{16:1\omega7}$: $C_{16:0}$ and $C_{20:5\omega3}$: $C_{22:6\omega3}$ (Budge & Parrish 1998, Shin et al. 2000). Although algal and microbial OM, sources of %($C_{12:0}$ + $C_{14:0}$), and benthic algae, a source of %($C_{24:0}$ – $C_{28:0}$) (Table 3), were potential food sources, abundances of these FA groups increased in grazer-only treatments. This suggests that grazers selectively consumed other food sources, likely epiphytes, allowing OM sources of %($C_{12:0}$ + $C_{14:0}$) and %($C_{24:0}$ – $C_{28:0}$) to accumulate. Thus, grazers likely reduced the relative contributions of epiphytic FAs to the sediments but increased the relative OM contributions from the microphytobenthos. The importance of grazers in mediating seagrass ecosystem properties is well recognized (reviewed by Valentine & Duffy 2006). Our field results confirm previous findings from mesocosm experiments (Canuel et al. 2007, Spivak et al. 2007) that grazers influence SOM quality and lability and that these impacts indirectly influence bacterial community composition and activity.

The importance of the above-ground animal community in determining primary producer biomass and SOM content and composition is summarized by the PCA results (Fig. 5). In the absence of nutrients, PC1 separated treatments according to predator or grazer presence, as treatments with crabs only had positive scores while those with grazers only had negative scores (Fig. 5B). Thus, response variables that grazers increased (%TN, %($C_{12:0}$ + $C_{14:0}$), and %($C_{24:0}$ – $C_{28:0}$)) and predators decreased (*Z. marina* biomass, total FA, %TOC, %($C_{22:5}$ + $C_{22:6}$)) had negative PC1 loadings (Fig. 5A). The addition of nutrients shifted grazer, predator, and control treatment scores to more positive values for PC1, which appeared to be related to increased abundance of epiphytes as epiphytic Chl *a* and PC1 were positively correlated (Table 4).

PC2 separated the scores of caged control treatments from those of grazers and/or predators. Consequently variables that were higher in the absence of grazers and predators (epiphytic Chl *a*, total FA, %($C_{22:5}$ + $C_{22:6}$), and %($C_{20:4}$ + $C_{20:5}$)) had positive PC2 loadings. PC1 and PC2 regressed positively with epiphytic Chl *a* (Table 4), indicating that epiphytes were most abundant in the absence of animals or when predators controlled grazing effects. This is supported by the positive loadings of epiphytic Chl *a* and %($C_{20:4}$ + $C_{20:5}$) on PC1 and PC2 (Fig. 5). *Z. marina* regressed negatively with PC1 and positively with PC2, likely because of the strong negative effects of predators on plant biomass (Table 4). These results confirm the patterns shown by the individual FA classes that the presence and composition of above-ground communities were strong determinants of SOM content.

Interactive effects of nutrients and trophic structure on SOM composition

Coastal habitats are often impacted by multiple stressors, including commercial fishing and nutrient pollution, that alter seagrass food web structure and nutrient cycling (Cloern 2001, Duarte 2002, Orth et al. 2006). Previous studies have addressed top-down and bottom-up controls on biomass accumulation and seagrass productivity (Hughes et al. 2004, reviewed by Valentine and Duffy 2006). Our study is novel in addressing the potential impacts of these interactions on sediment biogeochemistry, as detected in SOM accumulation and composition.

Interactions between grazers and predators altered abundances of FAs derived from epiphytic and benthic microalgae. In the absence of predators, grazers consumed epiphytes and reduced accumulation of FA from epiphytic diatoms (%($C_{20:4}$ + $C_{20:5}$) and $C_{20:5\omega3}$: $C_{22:6\omega3}$; Fig. 3, Table 3), while increasing the abundance of %SCFA (%($C_{12:0}$ + $C_{14:0}$); Fig. 3). Accumulation of FA from epiphytic diatoms in predator treatments is consistent with crabs suppressing or inhibiting grazers, creating a trophic cascade (Douglass et al. 2007). In contrast, predators reduced %($C_{22:5}$ + $C_{22:6}$); these FA are dominant in dinoflagellates and microalgae other than diatoms (Budge & Parrish 1998 and references therein). Interactions between nutrients and predators also affected OM contributions from epiphytes and benthic microalgae. Nutrient enrichment increased FAs associated with epiphytes (%($C_{20:4}$ + $C_{20:5}$)) in the absence of predators and increased FAs from benthic microalgae (%($C_{24:0}$ – $C_{28:0}$)) in the presence of predators (Fig. 3, Table 3). Combined, these data suggest that interactions between grazers, predators, and basal resources influenced algae differentially with subsequent effects on SOM composition.

Largely, our results support the premise that grazer communities benefit seagrass by reducing algal biomass and that epiphytes and *Zostera marina* are equally important in a tri-trophic system. Nutrient enrichment shifted the PC1 scores indicating that nutrients increase epiphytes and decrease *Z. marina* biomass despite the presence of a grazer assemblage (Fig. 5, Table 4). Since the PC scores of the predator only and the combined grazer and predator treatments were similar, predators may more strongly influence SOM composition than grazers under elevated nutrient conditions and the short timescale of our experiments. Overall, our data demonstrate that interactions between grazers, predators, and nutrients strongly influence the primary producer community, its contributions to the sediments and the sediment microbial responses.

Inter-experimental comparisons

Previous experiments in this system have varied food web composition and light levels using mesocosms (Canuel et al. 2007, Spivak et al. 2007). The value of results from these experiments depends in part on how accurately the system mimics the natural environment. Here, we briefly compare the results from this field experiment with the mesocosms. In both the present field experiment and a previous mesocosm experiment (Canuel et al. 2007), grazer presence and richness, respectively, increased algal and microbial contributions to SOM. Predators decreased "fresh" OM, represented by polyunsaturated FA (e.g., %($C_{18:4} + C_{20:4} + C_{20:5} + C_{22:5} + C_{22:6}$) in Spivak et al. (2007) and by %($C_{22:5} + C_{22:6}$) here). Shading (Spivak et al. 2007) and nutrients (this study) decreased *Zostera marina* biomass and SOM deriving from algae and microbes ($C_{12:0}$ + $C_{14:0}$). Finally, in all three experiments, predators increased the abundance of sediment heterotrophic bacteria (%BrFA). The general similarities between this and previous experiments are encouraging and suggest that conditions in the mesocosms reflected the natural environment in important ways.

Overall, our results demonstrate that SOM composition reflected changes in the abundance and composition of the primary producer community precipitated by shifts in trophic structure and resource availability. Nutrients increased epiphytes early in the experiment leading to a decline in *Zostera marina* (Fig. 1). Grazer populations responded rapidly to the available algae, decreasing epiphytes (Fig. 1) and their contribution of representative FAs in the sediments ($\%(C_{20:4} + C_{20:5})$, $C_{20:5\omega3} : C_{22:6\omega3}$, $C_{16:1\omega7} : C_{16:0}$; Fig. 3).Grazer control of algae did not increase *Z. marina* abundance, however, perhaps due to the short timeframe of the experiments. Predators reduced *Z. marina* and evidently its ability to trap particulate OM, leading to lower sediment organic carbon content and total FA abundance (Figs. 1, 2). There was some evidence of a trophic cascade as FA contributions from epiphytes ($\%(C_{20:4} + C_{20:5})$) and diatoms ($C_{20:5\omega3} : C_{22:6\omega3}$) were higher in treatments with both grazers and predators than in treatments with grazers only (Fig. 3). In addition, predators increased diatom derived OM which may have stimulated sediment heterotrophic bacteria (%BrFA) in general and sulfate reducing bacteria (%10Me17:0) in particular (Fig. 4). The sensitivity of SOM composition to nutrient availability and food web structure suggest that sediment biogeochemistry is strongly influenced by both top-down and bottom-up controls. Further, the changes in SOM composition demonstrate that episodic shifts in community composition and resource availability can rapidly influence sediment processes and ecosystem functioning.

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Table 1. Average concentration (µM) of water column nutrients sampled on days 14 and 23 of the experiment when Osmocote™ additions were 400 g per treatment. Concentrations were higher in nutrient vs. non-nutrient treatments ($p < 0.001$).

Response	Nutrients		No Nutrients	
	Day 14	Day 23	Day 14	Day 23
$NO_2^- + NO_3^-$	5.55	6.31	0.11	0.29
NH_4^+	4.98	8.45	0.69	2.28
PO_4^{-3}	0.27	0.57	0.01	0.09

Table 2. Tests of significance and estimated magnitudes of effect (ω^2) for nutrient availability, predator presence, grazer presence, and their interactions on plant biomass, sediment total nitrogen, sediment organic carbon, and sediment fatty acid abundance. Except where noted, analyses were performed on un-transformed data. When an interaction between nutrients and predators or grazers was significant, the data set was divided according to the interaction (i.e., nutrients vs. no nutrients), and an analysis of variance was performed again. For interactive effects: G, grazers; P, predators; N, nutrients. MS refers to the mean squared. Signficant relationships ($p < 0.05$) are in bold.

Response	Nutrients			Predators			Grazers			Interactions				Error	
	MS	p	ω^2	MS	p	ω^2	MS	p	ω^2		MS	p	ω^2	MS	ω^2
Zostera marina (AFDM)	3.76	**0.001**	0.21	1.79	**0.017**	0.09	0.68	0.128	0.02					0.27	0.65
ln Epiphytic Chl *a*	0.10	0.468	0.00	0.48	0.119	0.02	5.93	**<0.001**	0.43					0.18	0.55
Benthic Chl *a*	0.06	0.380	0.00	0.17	0.152	0.03	0.00	0.987	0.00					0.08	1.08
%TN	0.00	0.628	0.00	0.00	0.279	0.01	0.00	**0.022**	0.12					0.00	0.95
%TOC	0.00	0.875	0.00	0.11	**0.032**	0.10	0.05	0.152	0.03					0.02	0.94
Total FA (μg g^{-1})	1.62	0.898	0.00	664.03	**0.014**	0.14	12.91	0.717	0.00					96.10	0.92
%($C_{12:0}+C_{14:0}$)	1.81	**0.014**	0.11	1.52	**0.024**	0.09	1.45	**0.026**	0.08	G*P	2.38	0.006	0.15	0.26	0.72
%$C_{16:0}$	0.03	0.909	0.00	0.74	0.569	0.00	20.81	**0.005**	0.17					2.22	0.80
%$C_{18:0}$	1.07	0.164	0.03	2.45	**0.040**	0.09	0.42	0.380	0.00					0.52	0.96
%($C_{24:0}$-$C_{28:0}$)	1.00	0.454	0.00	3.33	0.177	0.02	14.04	**0.009**	0.13	N*P	9.76	0.025	0.09	1.72	0.75
No Nutrients				12.78	**0.014**	0.20	12.32	**0.015**	0.19					1.58	0.56
Nutrients				0.81	0.523	0.00	3.33	0.207	0.04					1.87	1.02
%($C_{18:2}+C_{18:3}$)	0.01	0.901	0.00	0.04	0.738	0.00	0.49	0.267	0.01					0.68	1.04
%($C_{20:4}+C_{20:5}$)	0.22	0.713	0.00	0.77	0.494	0.00	10.58	**0.017**	0.09	N*P	22.14	0.001	0.21	1.60	0.64
										G*P	11.81	0.012	0.10		
No Nutrients				16.27	**0.002**	0.31	4.70	0.064	0.07	G*P	8.02	0.020	0.14	1.15	0.47
Nutrients				7.03	0.092	0.09	5.89	0.120	0.07					2.10	0.80
%($C_{22:5}+C_{22:6}$)	0.00	0.970	0.00	2.88	**0.010**	0.14	0.14	0.542	0.00	G*P	1.90	0.032	0.08	0.37	0.81
%($C_{16:1\omega7}$)	3.92	0.608	0.00	0.51	0.852	0.00	126.60	**0.007**	0.18					14.50	0.91
$C_{16:1\omega7} : C_{16:0}$	0.02	0.526	0.00	0.01	0.756	0.00	0.65	**0.002**	0.23					0.05	0.85
$C_{20:5\omega3} : C_{22:6\omega3}$	4.41	0.291	0.00	96.83	**<0.001**	0.26	78.98	**<0.001**	0.21	G*P	43.23	0.002	0.11	3.78	0.42
arcsine (sqrt(%BrFA))*	0.00	0.323	0.01	0.01	**0.043**	0.09	0.00	0.343	0.00					0.00	0.97
%10me17:0	0.31	**0.007**	0.17	0.30	**0.008**	0.16	0.01	0.698	0.00					0.04	0.90

* %BrFA (Σ iso-, anteiso- $C_{13:0}$, $C_{15:0}$, $C_{17:0}$, $C_{19:0}$)

Table 3. Regression analyses of *Zostera marina* (ash-free dry mass, g), benthic Chl *a* ($\mu g\ cm^{-2}$), and epiphytic Chl *a* ($\mu g\ cm^{-2}$ blade area) against bulk SOM and the fatty acid groups (expressed as % of total FA). Signifcant relationships ($p < 0.05$) are in bold.

Response	*Zostera marina*			Benthic Chl *a*			Epiphytic Chl *a*			Total
	Coefficient	Partial r^2*	p	Coefficient	Partial r^2*	p	Coefficient	Partial r^2*	p	Model r^2
%TN	0.01	0.09	0.106	-0.01	0.01	0.691	0.00	0.01	0.515	0.11
%TOC	0.07	0.08	0.128	0.04	0.00	0.720	0.01	0.00	0.810	0.08
Total FA ($\mu g\ g^{-1}$)	6.09	0.15	**0.027**	-1.02	0.00	0.886	4.34	0.06	0.145	0.21
%($C_{12:0}$+$C_{14:0}$)	0.23	0.05	0.209	0.29	0.01	0.552	-0.37	0.10	0.072	0.15
%$C_{16:0}$	0.40	0.02	0.376	-0.18	0.00	0.879	-0.96	0.11	0.060	0.13
%$C_{18:0}$	0.37	0.09	0.092	0.18	0.00	0.750	0.01	0.00	0.962	0.10
%($C_{24:0}$-$C_{28:0}$)	0.29	0.01	0.444	2.81	0.17	**0.010**	-1.18	0.18	**0.009**	0.36
%($C_{20:4}$+$C_{20:5}$)	-0.29	0.01	0.486	-2.59	0.13	**0.027**	1.18	0.16	**0.015**	0.31
%($C_{22:5}$+$C_{22:6}$)	0.26	0.06	0.173	-0.18	0.00	0.726	0.14	0.02	0.495	0.08
arcsine (sqrt(%BrFA))†	-0.03	0.22	**0.003**	0.04	0.05	0.135	-0.04	0.25	**0.002**	0.52
%10me17:0br	-0.22	0.40	**<0.001**	0.28	0.08	**0.048**	-0.11	0.07	0.063	0.56
%($C_{16:1\omega7}$)	-0.43	0.00	0.669	-3.32	0.04	0.225	3.38	0.24	**0.005**	0.28
$C_{16:1\omega7}$: $C_{16:0}$	-0.05	0.02	0.385	-0.15	0.02	0.383	0.22	0.24	**0.004**	0.28
$C_{20:5\omega3}$: $C_{22:6\omega3}$	-0.44	0.01	0.600	-5.24	0.14	**0.025**	2.05	0.13	**0.032**	0.28

*Partial r^2 values were calculated by dividing the type III SS by the total SS.

† %BrFA (Σ iso-, anteiso- $C_{13:0}$, $C_{15:0}$, $C_{17:0}$, $C_{19:0}$)

Table 4. Regression analyses of *Zostera marina* (ash-free dry mass, g), benthic Chl *a* ($\mu g\ cm^{-2}$), and epiphytic Chl *a* ($\mu g\ cm^{-2}$ blade area) against principal components 1 and 2. Significant values ($p < 0.05$) are in bold.

Response	*Zostera marina*			Benthic Chl *a*			Epiphytic Chl *a*			Total
	Coefficient	Partial r^2*	p	Coefficient	Partial r^2*	p	Coefficient	Partial r^2*	p	Model r^2
PC 1	-1.30	0.17	**0.004**	-1.38	0.03	0.225	1.49	0.19	**0.003**	0.39
PC 2	1.65	0.34	**<0.001**	-1.67	0.05	0.086	1.77	0.32	**<0.001**	0.70

* Partial r^2 values were caculated by dividing the type III SS by the total SS.

FIGURE CAPTIONS

Figure 1. Effects of nutrients, predators, and grazers on *Zostera marina* (A), epiphytic Chl *a* (B), and benthic Chl *a* (C). The presence of cages reduced the abundances of all three primary producers. Nutrients and predators reduced *Z. marina* abundance while grazers reduced epiphytic Chl *a*. For Figures 1-4, statistical results are reported in Table 2, error bars represent standard error, and a letter in upper right hand corner designates which treatment significantly affected the response variable.

Figure 2. Effects of nutrients, predators, and grazers on sediment organic carbon (%TOC; A), sediment nitrogen (%TN; B), and sediment total fatty acid (FA) abundance (C). Predators decreased %TOC and total FA while grazers increased %TN. Nutrient enrichment did not affect %TOC, %TN, nor Total FA.

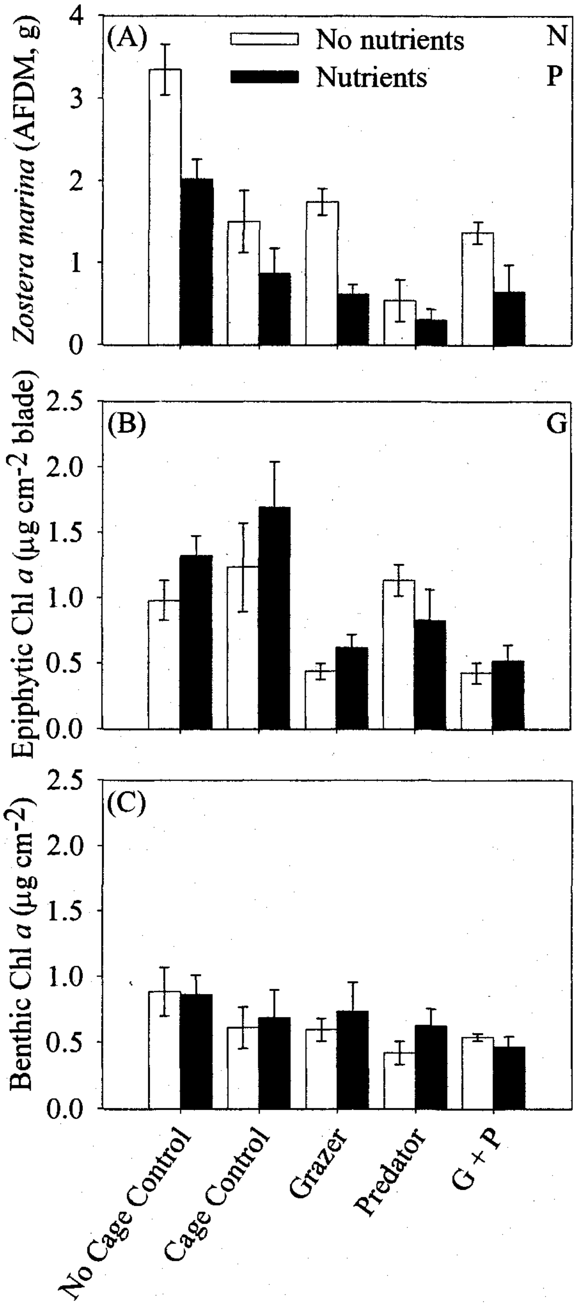
Figure 3. (A-D) Effects of nutrients, predators, and grazers on fatty acid subclasses (expressed as % of total FA) representing algal and microbial sources of organic matter (OM). Nutrients, predators, and grazers had strong singular and interactive effects on algal and microbial contributions to the sediments. (E-F) The prevalence of OM deriving from diatoms, relative to other microalgae, was influenced by grazers and predators only. See text for biomarker sources.

Figure 4. Effects of nutrients, predators, and grazers on the abundance of sediment heterotrophic bacterial fatty acids (expressed as % of total FA). The presence of cages increased abundances of %BrFA (A; Σ (iso-, anteiso- $C_{13:0} + C_{15:0} + C_{17:0} + C_{19:0}$)) and

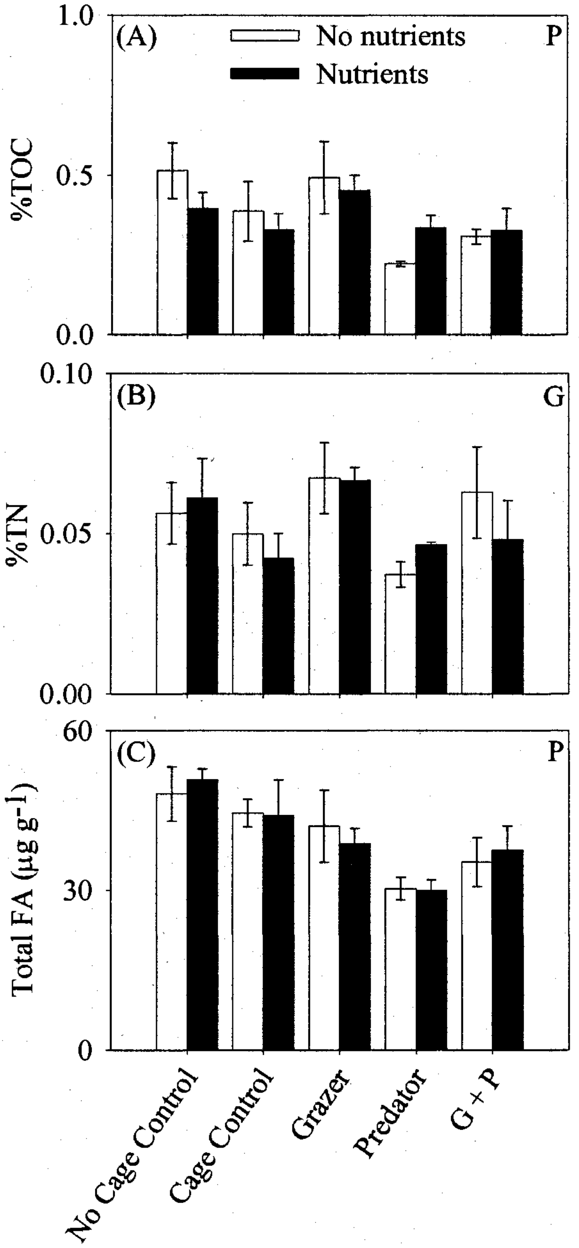
%10Me17:0 (B). Both %BrFA and %10Me17:0 were increased by predators but only %10Me17:0 was increased by nutrients.

Figure. 5. Loadings (A) and score plots (B) from principal component analysis (PCA) for primary producers, sediment organic carbon, sediment nitrogen, and sediment fatty acid (FA) groups. In (A), the following abbreviations were used: TFA for total FA, E Chl a for epiphytic Chl *a*, and B Chl a for benthic Chl *a*. In (B), treatments are indicated as follows: nutrients by +N, no nutrients by –N, caged control by CC, grazers by G, predators by P, and combined grazers and predators by GP. Table 4 lists correlations between PC1, PC2, and the primary producers. Error bars represent standard error.

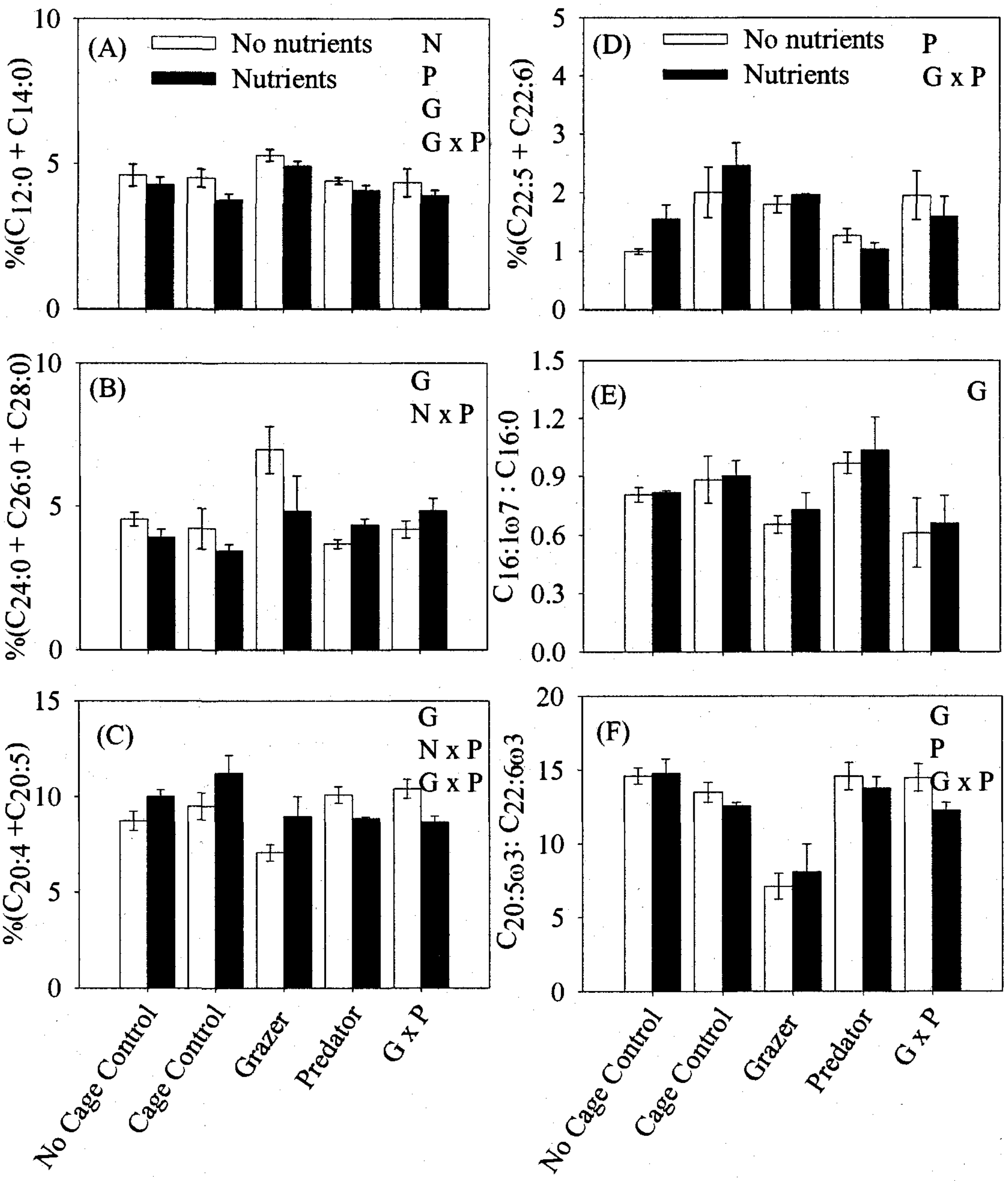
Spivak et al . Fig. 1



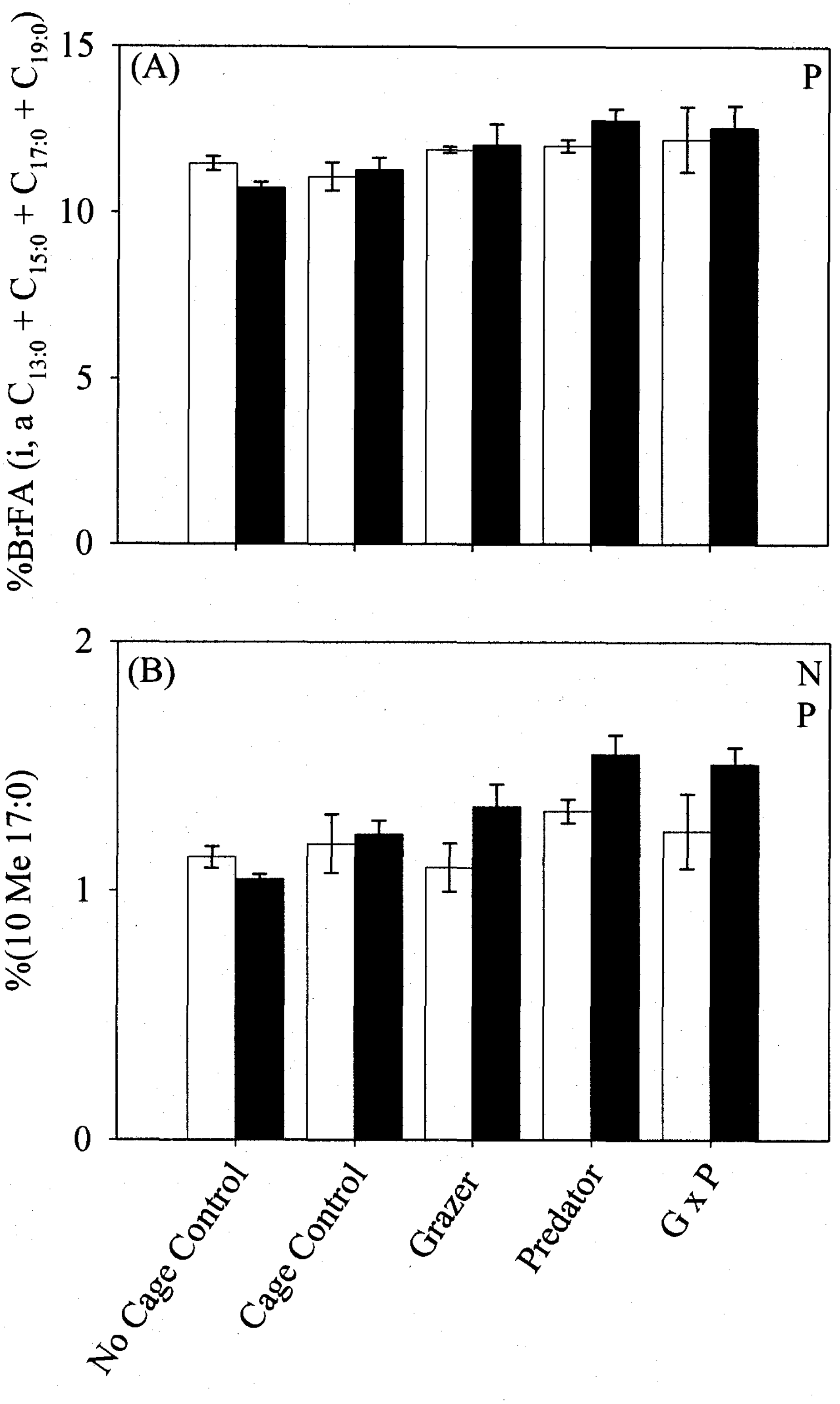
Spivak et al. Fig. 2



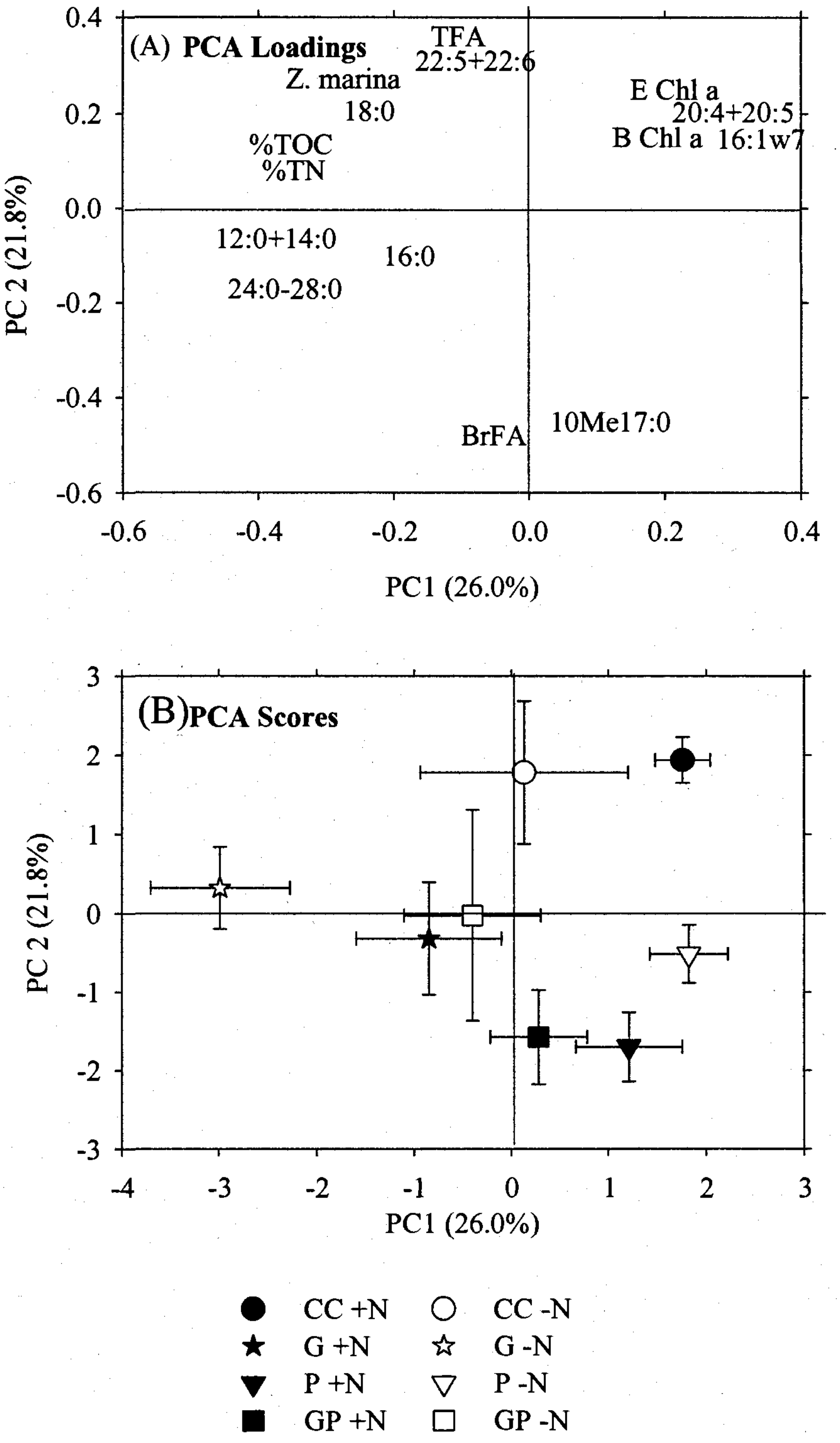
Spivak et al. Fig. 3



Spivak et al. Fig. 4



Spivak et al. Fig. 5



Chapter 4:

Nutrient enrichment and food web composition affect ecosystem metabolism in an experimental seagrass habitat.

Amanda C. Spivak, Elizabeth A. Canuel, J. Emmett Duffy, and J. Paul Richardson

Abstract.

In seagrass habitats, both bottom-up and top-down controls can influence biomass accumulation within the food web, sediment biogeochemistry, and ecosystem productivity. However it is unclear how changes in above-ground biomass and sediment organic matter quality precipitated by such shifts in bottom-up and top-down forcings also translate to changes in basic elemental cycles and fluxes. Using an experimental seagrass mesocosm system, we manipulated water column nutrient concentrations, food chain length (i.e. predator presence vs. absence), and grazer species richness (0, 1, 3, or 5 species) in a factorial design to address two main questions: (1) how do nutrient availability and food web composition affect the biomasses and stoichiometry of primary producers and grazers; (2) to what extent does ecosystem metabolism (productivity and nutrient fluxes) reflect above-ground plant and animal abundances vs. bulk sediment organic matter quality? Surprisingly, by the conclusion of the five week experiment, nutrient enrichment strongly increased secondary production but had little effect on primary production. Although the biomass of the dominant amphipod grazer, *Gammarus mucronatus*, was higher in nutrient enriched treatments it was not clear whether this effect was due to higher food availability or quality. Changes in above-ground primary producer biomass mediated by nutrient enrichment and grazer presence showed similar patterns to those of gross ecosystem production (mmol O_2 m^{-2} d^{-1}). Conversely, daily inorganic nutrient flux rates were unrelated to the biomasses of primary producers or grazers, suggesting that microbial processes in the sediments may have contributed to the observed fluxes. Combined, our data suggest that complex interactions between bottom-up and top-down controls governed patterns of nutrient storage and cycling.

Acknowledgements.

We would like to thank R.E. Blake, G. Blohm, M.A. Cochran, J.G. Douglass, B.W. Lerberg, and M.A. Wunderly for assistance in setting up, maintaining, and sampling the mesocosm tanks; M.A. Whalen for sorting plant, algae, and grazer samples; and H. Walker and B.B. Neikirk for analyzing water samples for nutrient concentrations. I.C. Anderson, D. Bronk, and J.J. Stachowicz provided valuable input on experimental goals and design and comments on the manuscript. This work was supported by a NCER, STAR program, EPA grant (FP – 91656901) to A.C. Spivak, NSF OCE-0352343 to J.E. Duffy, and NSF DEB-0542645 to E.A. Canuel. Although the research described was partly funded by the US EPA's STAR program, it has not been subjected to EPA review and therefore does not necessarily reflect the views of the Agency. No official endorsement should be inferred. Additional support was provided by Virginia Institute of Marine Science. This is contribution XXXX of the Virginia Institute of Marine Science, College of William and Mary.

Introduction.

Interactions between bottom-up influences of resource availability and top-down influences of trophic structure have important impacts on community dynamics and ecosystem functioning. For instance, nutrient enrichment of coastal waters often leads to higher abundances of algae, reduced water clarity, and, potentially, seagrass loss (McGlathery 1995; Cloern 2001; Orth et al. 2006). Conversely, top-down controls in a three-level food chain (i.e. predators – grazers – autotrophs) may moderate the effects of nutrient enrichment. For example, in seagrass systems, nutrient impacts may be exacerbated by predator inhibition of grazers or alleviated by strong grazing controls on algae (Hughes et al. 2004; Duffy et al. 2005; Heck and Valentine 2006). By extension, shifts in the relative importance of bottom-up and top-down forcings that influence the standing stocks and elemental content of primary producers and animals may also alter nutrient dynamics and, hence, energy availability to the food web (Vanni and Layne 1997; Elser and Urabe 1999). Here, we tested experimentally whether nutrient availability (i.e. bottom-up control) and food web composition (i.e. top-down control) interactively influenced plant and animal biomass and stoichiometric ratios and whether these changes were reflected by changes in ecosystem metabolism in an experimental seagrass habitat.

In seagrass beds, invertebrate grazers serve as the key intermediate trophic link between primary producers and higher levels of the food web (Klumpp et al. 1989). Consequently, the abundance and efficacy of invertebrate grazers may be affected by changes in either bottom-up or top-down controls. For instance, higher rates of primary production and, hence food availability, may lead to increased grazer biomass or grazer-mediated nutrient recycling. In turn, grazers may fuel primary production by regenerating dissolved inorganic nutrients (Urabe 1993; Elser and Urabe 1999; Liess and Hillebrand 2006; Vanni et al. 2006). Whereas bottom-up controls tend to be strengthened by excess nutrients, trophic cascades are weakened by predator removal. For example fishing of predators may reduce predation pressure on grazers and increase grazer population growth. At high abundances or densities, grazers may be able to control algal growth stimulated by bottom-up controls (Hughes et al. 2004; Armitage et al. 2005; Heck and Valentine 2007). By reducing algal biomass, grazers can indirectly benefit seagrasses which are competitively inferior to fast-growing algae. Thus, interactions between changing bottom-up and top-down trophic controls may strongly affect community composition and ecosystem properties.

Resource availability and consumption (bottom-up and top-down controls, respectively) not only affect biomass distribution across trophic levels but also the stoichiometry of primary producers and rates of nutrient cycling. For instance, increased supply of nitrogen and phosphorous can increase the internal elemental content of primary producers, especially algae (Sterner and Elser 2002). When grazers consume the nutritionally rich algae they incorporate nutrients needed for growth and metabolism and excrete the unused elements (Elser and Urabe 1999; Sterner and Elser 2002; Anderson et al. 2005). Consuming food of higher quality may increase grazer fitness and population growth (Elser et al. 1996; Mackay and Elser 1998). By excreting the excess nutrients back into the water column, grazers can influence algal production and community composition (Sterner and Elser 2002; Vanni et al. 2002). Top-down controls, while less straightforward than bottom-up effects, can strongly alter community composition via stoichiometric shifts (Vanni et al. 1997; Elser et al. 1998; Frost et al. 2002) as well as the more obvious effects of changing prey abundance. Thus, changing bottom-up and top-down controls can affect both plant and animal abundance and elemental cycling.

While nutrient cycling within the water column can be affected by stoichiometric imbalances between primary producers and grazers, sediment nutrient fluxes can also be strongly influenced by the stoichiometry of deposited organic matter. For example, increased resource availability may increase the abundance and nutrient content of primary producers which may then be deposited to the sediments. Since sediment organic matter (SOM) quality and lability are partial determinants of sediment microbial activity, increased algal contributions may result in higher rates of sediment remineralization. However, not all of the remineralized nutrients will be returned to the water column as sediment bacteria may retain nutrients to maintain optimum stoichiometric balance (Elser et al. 1995). Alternatively, high rates of organic matter deposition may stimulate microbial activity leading to sediment anoxia and, consequently, nitrate influx (denitrification) and carbon burial (Hessen et al. 2004; Dahllof and Karle 2005). Further, when sediments are aerobic, phosphate is chemically bound and biologically unavailable but as anoxic conditions develop phosphate is desorbed and may by released to the overlying water column (Valiela 1995). Thus, depending on the quantity and quality of organic matter delivered to the benthos, sediments may be a source or a sink of inorganic nutrients.

Previous seagrass experiments demonstrated that resource availability and food chain length can influence above-ground biomass distribution between trophic levels (Duffy et al. 2001; Duffy et al. 2003; Douglass et al. 2007), SOM composition and quality (Canuel et al. 2007), and gross ecosystem productivity (Spivak et al. 2007). But it remains unclear how these effects translate into changed ecosystem process rates. To assess the effects of resource availability and food web structure on seagrass ecosystem properties and fluxes, we conducted an experimental manipulation of water column nutrient enrichment and food web composition (i.e. food chain length and herbivore species richness) and measured their effects on above-ground biomass, stoichiometric ratios, and ecosystem metabolism. We predicted that nutrient enrichment would increase plant and algal biomass and this would lead to higher rates of gross ecosystem production. In turn, nutrient enrichment would increase the quality of plant and algal derived organic matter deposited to the sediments, thereby increasing sediment microbial activity, leading to higher rates of sediment dissolved inorganic nitrogen (DIN) flux. Secondly, we expected that grazers would reduce algal abundance and recycle the consumed biomass back into the water column as DIN. Finally, we predicted that predators would initiate a trophic cascade by reducing grazers and indirectly increasing primary producer abundance. The increased plant and algal biomass would, in turn, increase gross ecosystem production, sediment organic matter quality, and sediment DIN flux.

Methods

Experimental Design.

We conducted a mesocosm experiment to determine the main and interactive effects of nutrient availability, grazer species richness, and food chain length on the accumulation of primary producer and grazer biomass, flux rates of dissolved oxygen and inorganic nutrients, and the elemental ratios of seagrass, algae, and invertebrate grazers. Water column nutrient availability was manipulated by adding Osmocote™ (N:P:K 3:1:2) fertilizer to half of the tanks. Grazer species richness varied across four levels (0, 1, 3, or 5 species); the highest richness level contained five amphipod species present in the York River, Virginia, at the time of the experiment, each replicate of the intermediate level contained random a combination of three species, and the lowest richness level only had the most abundant species, *Gammarus mucronatus*. The remaining four grazer taxa were: *Elasmopus levis*, *Melita nitida*, *Ampithoe valida*, and *Sympleustes* spp. Food chain length was manipulated by exposing parallel sets of grazer treatments to a generalist predator, the blue crab, *Callinectes sapidus*. The 16 treatments were replicated 3 times each for a total of 48 mesocosm tanks.

The outdoor mesocosm experiment was conducted over five weeks during summer 2006 in 120-liter translucent fiberglass tanks that were continuously supplied with water from the York River estuary, Virginia, USA. Water passed through a sand filter and then through 150 μm mesh before filling 'dump buckets' which regularly spilled into the tanks, providing turbulence and aeration. The filtering process eliminated larger animals and debris and minimized invasion by non-target animals while permitting passage of invertebrate larvae and algal spores, which often colonized the tanks. The tanks were filled with a sand – mud mixture (9:2), averaging 0.80% (± 0.18 SE) organic matter content, to a depth of 10 cm. In contrast with previous experiments (Canuel et al. 2007; Spivak et al. 2007), we chose to use a sediment substrate with approximately 1% OM to facilitate *Zostera marina* transplant success and growth (Koch 2001). One hundred pre-weighed eelgrass (*Zostera marina*) shoots, cleaned of grazers and epiphytes were planted in each tank. Sixteen days later, grazing invertebrates were added to each grazer mesocosm. The five-species treatment received 18 individuals of each species, the three-species treatment had 30 individuals of each species, and the one-species treatment had 90 individuals of *G. mucronatus*. Eleven days later, two juvenile blue crabs were added to each predator treatment. Each nutrient treatment received 200 g of Osmocote™ slow release fertilizer in the first two weeks of the experiment and 100 g every week thereafter. Preliminary experiments revealed that Osmocote™ additions resulted in a peak in dissolved inorganic nitrogen (DIN) concentrations within 24 h. After this, DIN levels declined and remained constant for the next four days before dropping again. Thus, we refreshed half the fertilizer additions twice weekly to maintain elevated and constant nutrient levels.

Nutrients were delivered through two perforated PVC tubes that were suspended from the top of the tanks. Twice a week, one nutrient PVC tube from each nutrient treatment was refreshed with new fertilizer. Water column nutrient concentrations were monitored each week by measuring NH_4^+ concentrations from five randomly chosen tanks of each nutrient treatment using the Koroleff colorimetric method. The five week experimental incubation time was chosen to minimize the risk of invasion by non-target animals and to prevent the complete consumption of eelgrass by the grazers. This time period permitted major changes in animal (one to two grazer generations) and plant community development and in surface sediment characteristics (Duffy et al. 2003; Canuel et al. 2007; Spivak et al. 2007). Despite limitations, this experimental infrastructure simulated several aspects of the biotic and abiotic field conditions well (Duffy et al. 2001). For instance, tank water averaged 25°C while water temperatures at

Goodwin Island archipelago, the system upon which this experiment was based, averaged 23°C (Moore unpubl. data). At the end of the five week experiment we measured whole ecosystem fluxes of dissolved oxygen (DO), NH_4^+, NO_x, and PO_4^{-3}, as well as primary producer biomass and the carbon and nitrogen ratios of sediments, primary producers, and invertebrate grazers (see below). Results for the aboveground plant and animal community and for SOM accumulation and composition are reported elsewhere (Duffy et al. in prep; Spivak et al. in prep).

Primary producers.

At the end of the experiment we collected above-ground seagrass blades, macroalgae, artificial seagrass blades for epiphytic chlorophyll *a* (Chl *a*), and sediments for benthic Chl *a* to determine primary producer biomasses. Because the tanks were a flow-through system, we did not measure phytoplankton abundance. Seagrass and algae were frozen (-20 °C) until analysis when they were dried (60 °C) and then combusted (400 °C) to determine ash-free dry mass (AFDM). Epiphytic chlorophyll *a* was extracted from the artificial seagrass blades in a 90:10 (v:v) acetone : methanol solution for 24 h at -20 °C. Samples were processed according to Douglass et al. (2007). For benthic Chl *a,* three sediment cores (1.5 cm diameter) were collected from each tank and the upper 1 cm was removed. The surface sediments from the three cores were combined in a pre-combusted (450 °C) scintillation vial. Sediment samples were frozen (-20 °C) and analyzed within six weeks of collection according to (Neubauer et al. 2000). Since benthic microalgal distribution can be patchy, we used composite samples to increase the likelihood that the benthic Chl *a* concentrations represented the entire surface sediments in the mesocosm tanks.

Grazers.

Invertebrate grazers were collected at the end of the experiment and stored in ethanol. Sub-samples were analyzed for grazer species identity, abundance, and size class. Grazer ash-free dry mass (AFDM) was determined using previously established calculations (Edgar 1990).

Ecosystem metabolism.

We measured fluxes of dissolved oxygen (DO), NH_4^+, NO_x, and PO_4^{-3} to characterize whole-ecosystem metabolism. Four days before the end of the experiment, we measured DO and sampled water (25 mL) for dissolved inorganic nutrient concentrations approximately every hour over two four-hour incubation periods, one during the day (10:00 – 14:00 h) and another at night (22:00 – 02:00 h). Flux rates were estimated by regressing dissolved nutrient concentration against elapsed time (see below).

Half of the Osmocote™ fertilizer in the nutrient treatments was refreshed three days (50 g) and half was refreshed one week (50 g) prior to measuring water column flux rates. We estimated that the NH_4^+ loading rate from the fertilizer at the time of the flux measurement incubations was 0.24 $\mu M\ h^{-1}$. Immediately prior to the incubation period, the water supply was shut off and clear plastic sheeting (2 mm thickness) was placed on the water's surface to minimize oxygen exchange with the atmosphere. Before each measurement, the water was stirred to disrupt any stratification that may have formed. DO concentrations were measured using a YSI datasonde. Water samples were filtered through a pre-combusted (450 °C) glass fiber filter and frozen (-20° C) until analysis for NH_4^+, NO_x, and PO_4^{-3} concentrations by standard methods using a Lachat auto-analyzer (Smith and Bogren 2001; Knepel and Bogren 2002; Liao 2002).

We calculated the slope of change in concentration versus the time elapsed and divided this by the area of the tank to obtain flux. Because the measured DIN and PO_4^{-3} flux rates were much higher than the dissolution rate of Osmocote™, we are confident that our flux rates reflect biological processes within the experimental tanks. Hourly day and night rates were scaled to the volume of the mesocosm tanks (120 l) and to 14 h of light and 10 h of darkness to estimate daily summertime gross ecosystem production (GEP) of dissolved oxygen and daily net flux rates of inorganic nitrogen and phosphorus. DIN concentrations were calculated by summing NH_4^+ and NO_x. To calculate respiration, hourly nighttime oxygen consumption were scaled to 24 h and converted to carbon units using an assumed respiratory coefficient (RQ) of 1.0 (Hopkinson and Smith 2005; Middelburg et al. 2005). The production to respiration (P:R) was calculated by dividing estimated gross ecosystem production by respiration.

Elemental composition of primary producers, grazers, and sediments.

At the end of the experiment we collected seagrass blades, macroalgae, grazers, and sediments from each mesocosm to assess the effects of water column nutrient enrichment on their elemental composition. Twenty individuals each of the amphipods *G. mucronatus* and *A. valida* were collected from the treatments in which they were originally stocked. Three sediment cores (2.6 cm diameter) were collected from each tank and the top 1 cm was removed. The surface sediments from each core were combined into a composite sample. All samples were stored in separate pre-combusted (450 °C) vials and stored at -20 °C until analysis for total organic carbon (TOC) and total nitrogen (TN) content by standard methods with a Fisons Flash Elemental Analyzer (Model 1112) after removing inorganic carbon (Hedges and Stern 1984). We used acetanilide as the standard. Molar elemental ratios were calculated by first normalizing TOC and TN to the molar weight of carbon and nitrogen, respectively, and then dividing molar TOC by molar TN. We did not measure the phosphorus content of the sediments.

Statistical analyses.

The results were analyzed as a fully factorial three-way analysis of variance (ANOVA, SAS version 9.1 for Windows), with grazer treatment (df = 3), food chain length (i.e. predator presence or absence, df = 1) and nutrient availability (df = 1) as fixed factors. Data were logarithmically transformed as necessary to maintain homogeneity of variance as determined by the Cochran's C test. From the ANOVAs, we calculated the magnitude of main and interactive effects (ω^2, estimated proportion of variance explained by the experimental variable). The analyses included three replicates of every treatment except for the no nutrient, no crab, one grazer species treatment. One replicate of this treatment was excluded because it was contaminated by more than 500 mg of ash-free dry mass of non-target grazers. One additional sample was excluded from analyses of *Z. marina* and macroalgal biomass (nutrient, no crab, five grazers) while four samples were excluded from analysis of grazer biomass (no nutrients, no crabs, five grazers; nutrients, no crabs, five grazers; nutrients, crabs, one grazer; nutrients, crabs, three grazers) due to sample loss. Thus, we report the type III sum of squares (SS) results from the ANOVA model.

To help interpret the drivers of ecosystem flux rates, we performed multiple linear regressions of daily GEP, daily respiration, and daily fluxes of DIN and PO_4^{-3} against the abundances of the major primary producers. To detect correlations between the flux rates, we performed a multiple linear regression of daily GEP against daily DIN and PO_4^{-3}. Simple linear regressions of daily GEP, daily respiration, and daily flux rates of DIN and PO_4^{-3} against sediment C:N were also performed. In addition, to understand whether respiration was related to autochthonous organic matter production or bulk sediment organic matter quality, we regressed respiration against net ecosystem production and sediment C:N.

Results

Nutrient concentrations.

During the first two weeks 200 g of Osmocote™ fertilizer were added to each nutrient treatment, resulting in an average NH_4^+concentration of 29.23 μM (± 5.45 SE). Osmocote™ additions were reduced to 100 g per nutrient treatment for the remaining three weeks and the average NH_4^+concentration fell to 14.37 μM (± 1.32 SE). Concentrations of NH_4^+ were 0.95 μM (± 0.25 SE) and 2.58 μM (± 0.57 SE) in the non-nutrient treatments during weeks 1-2 and 3-5, respectively. Thus, the NH_4^+ concentration of nutrient treatments was approximately 30 times ambient during the first two weeks and 5 times ambient during the remaining three weeks. The NH_4^+ concentrations we observed in the no-nutrient treatments were typical of late spring and summer conditions in the York River estuary while the concentrations in the nutrient amended treatments were similar to or higher than late fall conditions (K. Moore *unpubl. data*).

Primary producer biomass.

Primary producer biomass was generally reduced by grazers and increased by nutrient additions. Relative to the grazer-free controls, grazers reduced epiphytic Chl *a* and nearly eliminated macroalgae (Fig. 1; Table 1). Grazers decreased *Z. marina* biomass in the three and five species treatments, but not in the one grazer species treatment which suggested that *G. mucronatus* was not responsible for eelgrass loss. Nutrient additions uniformly increased epiphytic Chl *a* but increased macroalgae only in the absence of grazers, resulting in a nutrient by grazer interaction. Overall, grazers were stronger determinants of plant and algal biomass than were predators or nutrient enrichment, as indicated by the estimated magnitudes of effect (Table 1). Benthic Chl *a* was insensitive to food chain length, grazer richness, and nutrient availability.

Grazer biomass.

In the treatments with multiple grazer species, *G. mucronatus* was the most abundant grazer and the largest contributor to total grazer biomass in both the presence (75 - 85% of total grazer biomass) and absence (66 - 68%) of predators (Fig. 2; Table 1). Because *G. mucronatus* was so abundant we divided the grazer response into two categories: *G. mucronatus* only and minor grazers (i.e. grazers other than *G. mucronatus*). Predator presence reduced minor grazer biomass but had no effect on *G.*

mucronatus, suggesting that *G. mucronatus* may was susceptible than other grazers to predation by blue crabs. Nutrient enrichment increased *G. mucronatus* biomass but had no effect on the minor grazers.

Elemental ratios.

Nutrient enrichment increased the nitrogen content of eelgrass as reflected in higher %TN and lower C:N of *Z. marina* blades (Fig. 3; Table 1). Grazers decreased *Z. marina* %TN in nutrient treatments and increased %TOC in non-nutrient treatments; resulting in grazer by nutrient interaction effects for both variables. Under ambient nutrients, predators decreased %TN which resulted in higher C:N and created predator by nutrient interaction effects. Heavy grazing prevented us from obtaining macroalgal samples for nutrient analysis from every tank. However, there was evidence of a positive nutrient effect on macroalgal quality as the C:N was 26.92 (± 2.02 S.E.; n = 8) in non-nutrient treatments and 14.77 (± 1.17 S.E.; n = 12) in nutrient treatments.

Elemental content of SOM was less sensitive than that of primary producers to changes in nutrient concentration, predator presence, and grazer richness (Fig. 4; Table 1). Predators generally increased %TOC of bulk SOM and, consequently, C:N. Grazer richness had an idiosyncratic influence on SOM %TN and %TOC, both being maximized in the three-grazer treatment under nutrient enrichment, but had no effect on the molar C:N.

At the end of the five-week experiment, there were measureable differences in the total nitrogen (%TN) and organic carbon (%TOC) content of both grazer species measured: *G. mucronatus* and *A. valida* (Fig. 5, Table 1). Elevated nutrient concentrations increased %TN and %TOC of *G. mucronatus* but reduced the %TOC content of *A. valida*. Surprisingly, predator presence increased the %TOC content of *A. valida*. While TOC and TN content of the varied somewhat, the molar C:N ratio did not change in response to our experimental manipulations. Thus, the stoichiometric ratio of grazers was more conservative than that of their primary producer food sources.

Ecosystem fluxes.

Gross ecosystem production (GEP) and respiration were both increased by nutrient enrichment and reduced by grazers (Fig. 6; Table 1). Predators decreased GEP and respiration only at the zero and one species richness levels, resulting in a predator by grazer richness interaction. The ratio of production to respiration (P:R) was generally lower in grazer treatments compared with grazer-free controls. Predators influenced P:R in an idiosyncratic way resulting in a predator by grazer interaction effect. Daily GEP was positively correlated to the daily flux rate of DIN ($p = 0.013$; $r^2 = 0.13$) but was not related to PO_4^{-3} (data not shown). Net daily fluxes of DIN and PO_4^{-3} increased with nutrient enrichment but were unaffected by food web manipulations (Fig. 7; Table 1). The slope of the ratio of the fluxes of DIN:PO_4^{-3} was 15.4, which was similar to Redfield values.

Discussion.

Surprisingly, the strongest effect of nutrient enrichment in our experiment was increased accumulation of grazer, not plant, biomass. Nutrients efficiently passed through the food chain, increasing the biomass of the grazing amphipod, *Gammarus mucronatus,* which was able to regulate primary producer abundance. Grazer consumption of plants and algae translated into lower rates of ecosystem production. While top-down (i.e. grazing) controls governed primary producer biomass and production, nutrient enrichment dominated effects on the stoichiometry of *Z. marina* and on DIN and PO_4^{-3} flux rates. Although we do not have data for carbon and nitrogen composition of macroalgae it seems likely that nutrient enrichment may have increased *G. mucronatus* biomass by increasing primary producer quality, rather than or in addition to increasing primary production per se. Our results also indicated that DIN and PO_4^{-3} were recycled at roughly Redfield proportions. Overall, grazing determined the productivity and abundance of plants and algae while nutrient enrichment influenced the storage and cycling of inorganic nitrogen and phosphorous.

Effects of nutrient enrichment and food web composition on plant and animal biomass

The nutrient enhancement of macroalgae and epiphytic algae was absent in grazer treatments, showing that grazing was a stronger determinant of algal biomass than bottom-up forcing. Grazers also decreased eelgrass biomass, but only in the three and five species treatments, which included *Ampithoe valida* a member of a family known to graze heavily on macroalgae and seagrass (Duffy and Hay 2000; Valentine and Duffy 2006). Since *Z. marina* abundance was similar in the grazer-free controls and in the monocultures, *G. mucronatus* likely had little effect on eelgrass biomass, which is consistent with previous experiments in this system (Duffy and Harvilicz 2001; Duffy et al. 2001). It is perhaps surprising that *G. mucronatus* did not indirectly increase *Z. marina* biomass by reducing competitive macroalgae and epiphytes. The minor grazers likely reduced *Z. marina* biomass directly by grazing on leaves or indirectly by damaging the leaves while consuming attached algae. Overall these data corroborate previous studies showing that the individual grazer species filled different functional roles which, in turn, affected primary producer community composition.

The positive effect of nutrient enrichment on *G. mucronatus* biomass indicated that primary production stimulated by nutrient enrichment was rapidly channeled to grazing invertebrates and, by extension, higher trophic levels. Unlike *G. mucronatus*, minor grazer biomass was not elevated in nutrient enriched treatments. Minor grazers may have consumed primary producers that were unresponsive to nutrient amendments or, more likely, that they were outcompeted by *G. mucronatus*. It is also possible that the changes in grazer abundance reflected an early successional sequence; a different pattern might have emerged had the experiment run longer (Cardinale et al. 2007). However, it is likely that differences in grazer biomass were due to species-specific variations in life history and sensitivity to environmental conditions (i.e. temperature, salinity, DO, etc.) (Procaccini and Scipione 1992; Attrill et al. 1999). Since the experimental duration permitted the production of at least two amphipod generations (Duffy 2003) our results should reflect interactions between the grazer species.

Predators reduced minor grazer biomass but did not affect *G. mucronatus*, suggesting that the minor grazers, either as individuals or as a population, were more susceptible to predation by crabs. Despite the negative predator effect on minor grazer biomass, there was no evidence of a trophic cascade suggesting that the primary producer community reflected the dynamics of the most abundant grazer species. This finding is in contrast to previous experiments in which crab predators initiated a trophic cascade, increasing biomasses of macroalgae and sediment microalgae (Duffy et al. 2005; Canuel et al. 2007; Spivak et al. 2007). It is possible that the low vulnerability of *G. mucronatus* to predation prevented a trophic cascade. The absence of predator effects underscores the importance of understanding how system productivity and community composition can affect interactions between successive trophic levels (Chase 2003; Borer et al. 2005).

Overall, both bottom-up and top-down controls regulated biomass in this system, but affected different components. Grazing tended to be a stronger determinant of primary producer abundance even under nutrient addition. This result corroborates previous studies demonstrating that grazing controls can overwhelm nutrient effects because grazer consumption of algae is immediate whereas nutrient stimulation of algal growth has a time lag (Hillebrand 2002). The relative importance of bottom-up versus top-down controls on grazers also depended on grazer identity. For instance, *G. mucronatus* was more abundant in nutrient-enriched treatments and was unaffected by predation. Whereas minor grazers did not respond to nutrient enrichment but were decreased by predators. These results confirm that grazer community composition can, in part, determine whether bottom-up controls ascend or top-down controls cascade through a food web (Chase 2003; Borer et al. 2006).

Effects of nutrient enrichment and food web composition on plant and animal stoichiometry

While grazers were the main determinant of primary producer abundance, nutrient enrichment strongly influenced the quality of producer tissues. Nutrient enrichment decreased the C:N of *Z. marina* and macroalgal tissues, thereby increasing their nutritional value to grazing invertebrates. Conversely, there was no difference in grazer C:N in the nutrient vs. non-nutrient treatments. The less plastic stoichiometry of invertebrate grazer vs. primary producer tissues is typical (Sterner and Elser 2002).

There were two possible explanations for the lower C:N of *Z. marina* blades in the nutrient vs. non-nutrient treatments (Fig. 3C; Table 1). First, *Z. marina* was nutrient limited in the non-nutrient treatments and absorbed the nitrogen from the water column to relieve nutrient stress. Second, *Z. marina* might have exhibited 'luxury consumption' by absorbing more nitrogen than needed for immediate growth and metabolism (Sterner and Elser 2002). However, since C:N values of *Z. marina* leaves have been reported between 7.2 – 17.8 (Atkinson and Smith 1983), 'luxury consumption' seems unlikely. The lowered seagrass C:N may not have increased grazing, as observed in other systems (McGlathery 1995; Goecker et al. 2005), since *Z. marina* biomass was decreased in both the non-nutrient and nutrient treatments at higher levels of species richness (Fig. 1B). However, grazers reduced *Z. marina* %TN in nutrient-enriched treatments (Fig. 3A; Table 1). Thus, it is possible that grazers either consumed nitrogen-rich seagrass tissues or that they damaged the seagrass blades and this led to nitrogen leaching. In non-nutrient treatments, *Z. marina* %TOC was increased by grazers while C:N was increased by predators (Figs. 3B-C; Table 1). Mechanical damage to the plant blades caused by grazers and predators might have induced a plant physiological response, such as production of carbon-rich secondary metabolites including phenolics (Hay et al. 1994; Arnold and Targett 2002) or increased storage of carbohydrates (Alcoverro et al. 2001). Accumulation of these carbon-rich moieties, could reduce *Z. marina* quality as inferred by the C:N ratios. The negative effect of grazers and predators on *Z. marina* quality (non-nutrient treatments) is consistent with the hypothesis that plants increase carbon-based defenses and / or store carbohydrates when resource availability is low (Bryant et al. 1983; Alcoverro et al. 2001; Massey et al. 2005). However, there is little research on seagrass physiological responses to grazing damage and more evidence is needed to support the mechanism put forth here (Heck and Valentine 2006). Nutrient effects on eelgrass and macroalgal tissues did not translate into alter SOM quality as indicated by the C:N. However, sediment C:N is a poor indicator of OM sources since SOM reflects contributions from primary producers, animals, and sediment microbes as well as the products of OM decomposition by sediment bacteria. Thus, sediment C:N likely reflected a mixture of OM sources (Elser and Foster 1998).

Due to stricter biochemical constraints, elemental ratios of animals are generally less flexible than vascular plants and algae (Elser et al. 2000; Sterner and Elser 2002; Vrede et al. 2004). As such, we expected the C:N of grazers to remain constant despite changes in plant and algal quality. Nutrient enrichment slightly but significantly increased %TN and %TOC of *G. mucronatus* but decreased %TOC of *A. valida*. Predators, however, increased the %TOC of *A. valida*. Although the nitrogen and carbon content of grazers changed in response to nutrients and food chain length, the C:N of both grazers was insensitive to our experimental manipulations. This supported our prediction that grazer stoichiometry would be less plastic than *Z. marina* and algae. Since the C:N of grazers was lower than the C:N of potential food sources (i.e. primary producers and sediments), it is likely that grazers preferentially retained nutrients to maintain an optimal stoichiometric balance. Previous studies demonstrated that C:N ratios of invertebrates (insects and crustacea) are relatively constrained, likely reflecting their body structure and life history (Sterner and Elser 2002). Similarly, zooplankton have a narrow variation in N but are more variable in P content, which is likely due to changes in growth rate and biochemical requirements (Sterner and Elser 2002).

Ecosystem metabolism was a function of plant biomass and sediment dynamics

A final goal of this experiment was to determine whether ecosystem productivity and fluxes of inorganic nutrients reflected changes in above-ground biomass or in SOM quality. Although our measured flux rates reflected combined water column and sediment dynamics we acknowledge that sediment microbial processes are important to biogeochemical cycles and should be considered in greater detail. GEP and ecosystem respiration were increased by nutrient additions and decreased by grazers, reflecting similar changes in primary producers While GEP was correlated to above-ground primary producer biomass, ecosystem respiration appeared to be driven by benthic processes. Respiration was negatively related to surface sediment C:N but was not correlated to net ecosystem production ($r^2 = 0.03, p = 0.195$; data not shown). This suggests that sediment microbes, including benthic microalgae, rather than above-ground biomass, dominated ecosystem respiration. However, sediment C:N only explained 17% of the variation in ecosystem respiration flux. It is possible that water column processes or processes in the deeper sediments (i.e., below 0-1 cm) may explain more of the variation, but we do not have information to support or refute this hypothesis. Grazers also decreased the ratio of GEP to respiration (P:R), which is indicative of the balance between autotrophy and heterotrophy (Fig. 6C; Table 1). Combined, these data indicate that grazers were the strongest determinant of ecosystem metabolism but that nutrient effects on SOM quality likely had indirect effects on respiration rates.

Since patterns of GEP mirrored above-ground plant and algal biomass, we expected daily flux rates of DIN to reflect uptake by plants (Hansen et al. 2000), release by grazers (Vanni 2002), and removal by sediment microbial processes (Dahllof and Karle 2005). Thus, we predicted that DIN flux rates would be low when plant biomass was high and that flux rates would be high when grazers were abundant. Instead, DIN flux rates were increased by nutrients at all levels of grazer species richness (Fig 7A; Table 1) and were not correlated to the abundances of any of the primary producers or grazers (Table 2; grazer data not shown) nor sediment C:N (Table 3). In non-nutrient treatments, DIN fluxes were negative indicating that inorganic nitrogen was being removed, likely by sediment microbial processes. However, in the presence of nutrient enrichment, DIN fluxes were consistently positive suggesting high rates of regeneration. It is possible that the short experimental duration combined with the high abundances of macroalgae and grazers prevented or reduced benthic microalgal productivity in nutrient-enriched treatments. This community is particularly important to sediment redox conditions and oxygen sensitive processes that mediate in nitrogen transformations and cycling (McGlathery et al. 2007).

In this system, the most likely contributors to PO_4^{-3} flux were grazers and sediments. Grazers recycle PO_4^{-3}, from ingested plants and algae, back into the water column while PO_4^{-3} is effluxed from sediments under anaerobic conditions (Nixon et al. 1980; Valiela 1995). Consequently, we predicted that PO_4^{-3} flux rates would increase with grazer abundance and the availability of labile SOM. At the end of the five week experiment, daily flux rates of PO_4^{-3} were increased by nutrients but were unaffected by predator presence or grazer species richness (Fig. 7B; Table 1). This indicates that grazer recycling of PO_4^{-3} was not a large contribution to the daily flux rate. PO_4^{-3} flux correlated positively to epiphytic Chl *a* and negatively to surface sediment C:N (Tables 2, 3). It is possible that nutrient enrichment increased epiphytic biomass, which contributed labile OM to the sediments and increased SOM quality. Sediment microbial activity likely increased in response to higher quality OM, potentially leading to lower sediment oxygen concentrations and increased efflux of PO_4^{-3}. Sediment release may be a more likely source of inorganic phosphorous than bacterial remineralization as microbes might retain some of the recycled nutrient to maintain internal stoichiometric balance (Elser et al. 1995). Since epiphytic Chl *a* and surface sediment C:N only cumulatively explain 20% of the variation in PO_4^{-3} other processes must also be important determinants of PO_4^{-3} flux. Another possibility is that the C:N ratio of surface sediments (0-1 cm) was not representative of the entire sediment pool (10 cm depth). If oxygen concentrations decreased with increasing depth, as is typical of coastal sediments, release of PO_4^{-3} from the deeper anoxic sediments would be likely. Combined, these data suggest SOM quality and likely, sediment reducing conditions, were likely stronger determinants of daily PO_4^{-3} flux than grazer richness or predator presence.

In coastal areas, relative fluxes of inorganic nitrogen and phosphorus are generally lower than the Redfield ratio of 16:1, possibly due to the removal of nitrogen by denitrifying bacteria (Nixon et al. 1980; Valiela 1995). In this experiment, daily fluxes of DIN and PO_4^{-3} were being regenerated at roughly the Redfield ratio, suggesting that algal organic matter is being recycled and that denitrification may not be an important process in this system (McGlathery et al. 2007). Nutrient enrichment increased the relative flux of DIN to PO_4^{-3}, from 16.06 (± 3.38 S.E.) to 28.83 (± 3.29 S.E.) in non-nutrient and nutrient treatments, respectively. The higher DIN flux in nutrient enriched treatments suggest that fertilizer additions may have fueled the microbial community and increased recycling. In addition, there was no correlation between the ratio of DIN:PO_4^{-3} fluxes and grazer species richness nor predator presence (data not shown). Combined, these data suggest that both water column and sediment processes contributed to fluxes of inorganic nutrients and that DIN and PO_4^{-3} were regenerated at rates in ratios consistent with Redfield organic matter.

Our results largely supported our initial hypotheses and demonstrated that bottom-up and top-down controls affected where biomass accumulates within the food web, the stoichiometric ratios of primary producers, and ecosystem metabolism. Nutrient enrichment increased_macroalgae and epiphytic Chl *a* which, in turn, increased GEP and *G. mucronatus* biomass. The grazing community effectively controlled algal and epiphytic production stimulated by nutrient enrichment, lending support to the hypothesis that invertebrate grazers can alleviate negative effects of eutrophication (Armitage et al. 2005; Burkepile and Hay 2006; Heck and Valentine 2007). Surprisingly, predators did not initiate a trophic cascade. Although there were few main predator effects, predator interactions with grazers and nutrient enrichment underscore the complexity of the system. However, the absence of strong predator effects may lend support to the notion that community composition can, in part, determine the strength of trophic cascades. Combined, our results indicate that shifts in resource availability and food web composition influence nutrient storage (as biomass) and cycling in seagrass habitats.

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Table 1. Tests of significance and estimated magnitude of effects (ω^2) of nutrient enrichment, food chain length, and grazer species richness and their interactions on biomass, elemental ratios, and daily flux rates. When an interaction was significant the dataset was divided according to the interaction (i.e. predators vs. no predators and nutrients vs. no nutrients) and single factor ANOVAs were run. For interactions, P refers to predators, G to grazers, and N to nutrients. Significant *p* values are listed in bold.

Response	Nutrient enrichment			Food chain length			Grazer community			Interactions	Model error	
	p	MS	ω^2	*p*	MS	ω^2	*p*	MS	ω^2		MS	ω^2
Plant biomass												
Zostera marina (AFDM, g)	0.086	29.62	0.01	0.086	29.71	0.02	**<0.001**	184.00	0.38	PxG 0.023 (34.51)	9.39	0.54
Predators	0.260	16.11	0.01				**0.012**	59.31	0.29		11.82	0.64
No predators	0.173	16.65	0.02				**<0.001**	149.59	0.70		6.61	0.29
Macroalgae (AFDM, g)	**0.018**	116.88	0.02	0.472	9.95	0.00	**<0.001**	846.81	0.53	NxG <0.001 (194.85) NxPxG 0.041 (58.15)	18.71	0.32
Nutrients				0.286	26.79	0.00	**<0.001**	918.32	0.81		21.87	0.18
No nutrients				0.859	0.51	0.00	**0.002**	125.56	0.42		15.55	0.54
Epiphytic Chl *a* ($\mu g\ cm^{-2}$)	**0.003**	54.88	0.09	0.279	6.50	0.00	**0.006**	27.21	0.12		5.36	0.81
log Benthic Chl *a* ($\mu g\ cm^{-2}$)	0.297	0.20	0.00	0.121	0.45	0.02	0.912	0.03	0.00		0.18	1.12
Grazer Biomass												
log *Gammarus mucronatus*	**0.034**	2.16	0.05	0.419	0.28	0.00	0.219	0.68	0.02		0.41	0.99
log Minor Grazers	0.799	0.01	0.00	**<0.001**	3.10	0.20	0.205	0.28	0.03		0.16	0.87
Stoichiometry												
Z. marina %TN	**<0.001**	12.37	0.53	0.154	0.21	0.01	**0.019**	0.37	0.04	NxP 0.024 (0.55) NxG 0.007 (0.47) PxG 0.038 (0.31)	0.10	0.33
Nutrients				0.574	0.04	0.00	**0.008**	0.71	0.31		0.13	0.60
No nutrients				**0.006**	0.69	0.31	0.147	0.14	0.07		0.07	0.58
Predators	**<0.001**	9.34	0.83				0.950	0.01	0.00		0.11	0.19
No predators	**<0.001**	3.75	0.52				**0.002**	0.65	0.16	NxG 0.005 (0.51)	0.08	0.20
Z. marina %TOC	0.471	5.08	0.00	0.777	0.78	0.00	**0.012**	41.02	0.10	NxP 0.036 (45.95) NxG 0.013 (39.93)	9.53	0.80
Nutrients				0.203	17.92	0.03	0.053	32.26	0.19		10.15	0.78
No nutrients				0.093	28.50	0.08	**0.009**	49.10	0.33		8.87	0.65
Predators	0.095	42.06	0.10				0.212	22.34	0.06		13.33	0.85
No predators	0.198	9.94	0.02				**0.022**	23.77	0.19	NxG 0.006 (34.14)	5.48	0.50
Z. marina C:N (molar)	**<0.001**	1374.60	0.57	0.058	46.13	0.01	0.315	14.64	0.00	NxP 0.042 (53.29)	11.88	0.40
Nutrients				0.847	0.13	0.00	**0.045**	11.71	0.20		3.47	0.76
No nutrients				**0.048**	96.37	0.18	0.813	6.17	0.00		20.81	0.89
Predators	**<0.001**	1015.37	0.83				0.903	2.69	0.00		14.34	0.21
No predators	**<0.001**	430.26	0.67				0.059	28.50	0.06		9.24	0.26
SOM %TN	0.834	0.00	0.00	0.148	0.00	0.01	**0.040**	0.00	0.07		0.00	0.93
SOM %TOC	0.925	0.00	0.00	**0.035**	0.15	0.05	**0.045**	0.09	0.07		0.03	0.93

SOM C:N (molar)	0.051	4.92	0.03	**<0.001**	18.86	0.15	0.404	1.20	0.00		1.19	0.83
G. mucronatus %TN	**0.043**	12.50	0.04	0.676	0.49	0.00	0.274	3.74	0.01		2.73	0.99
G. mucronatus %TOC	**0.028**	189.32	0.05	0.818	1.86	0.00	0.153	69.66	0.04		34.20	0.96
G. mucronatus C:N (molar)	0.151	2.25	0.02	0.834	0.05	0.00	0.102	2.58	0.06		1.02	0.98
A. valida %TN	0.421	3.93	0.00	0.766	0.53	0.00	0.958	0.02	0.00	NxPxG 0.045 (27.15)	5.76	0.97
log *Ampithoe valida* %TOC	**0.027**	0.01	0.05	**0.002**	0.02	0.12	0.092	0.00	0.06		0.00	0.71
A. valida C:N (molar)	0.299	0.06	0.00	0.905	0.00	0.00	0.477	0.03	0.00		0.05	1.03
Daily Flux rates												
GEP (mmol O_2 m^{-2} d^{-1})	**<0.001**	9.70E+04	0.09	0.084	1.83E+04	0.01	**<0.001**	1.58E+05	0.44	PxG 0.0318 (1.91E+04)	5727.31	0.44
Predators	**0.002**	6.40E+04	0.21				**<0.001**	7.56E+04	0.47		4480.88	0.28
No predators	**0.040**	3.55E+04	0.09				**<0.001**	1.03E+05	0.57		7056.85	0.38
Respiration (mmol C m^{-2} d^{-1})	**<0.001**	6.48E+04	0.28	**0.024**	8.70E+03	0.03	**0.001**	1.01E+04	0.11	PxG 0.017 (6069.89)	1534.90	0.54
Predators	**<0.001**	3.95E+04	0.51				0.784	843.09	0.00		2352.66	0.58
No predators	**<0.001**	2.61E+04	0.38				**<0.001**	1.54E+04	0.44		662.61	0.18
Production : Respiration (P:R)	0.098	0.26	0.02	0.408	0.06	0.00	**<0.001**	1.01	0.27	PxG 0.044 (0.266)	0.09	0.69
Predators	0.182	0.18	0.02				**<0.001**	1.04	0.52		0.09	0.45
No predators	0.326	0.09	0.00				0.064	0.25	0.19		0.08	0.87
DIN (mmol m^{-2} d^{-1})	**<0.001**	5.26E+04	0.48	0.352	538.21	0.00	0.145	116.26	0.02		602.95	0.45
PO_4^{-3} (mmol m^{-2} d^{-1})	**<0.001**	109.82	0.38	0.517	0.91	0.00	0.060	5.83	0.04		2.13	0.61
DIN : PO_4^{-3}	**0.002**	4171.45	0.12	0.400	275.86	0.00	0.537	279.04	0.00		377.93	0.94

Table 2. Regression of daily ecosystem flux rates against biomass of the major primary producer groups. The coefficient indicates the directionality of the relationship while the partial r^2 indicates the goodness of fit. Significant *p* values are in bold.

Ecosystem function	*Zostera marina*			Epiphytic Chl *a*			Macroalgae			Benthic Chl *a*			Total Model
	Coefficient	Partial r^2*	*p*	Coefficient	Partial r^2*	*p*	Coefficient	Partial r^2*	*p*	Coefficient	Partial r^2*	*p*	r^2
GEP (mmol O_2 m^{-2} d^{-1})	9.17	0.09	**<0.001**	5.15	0.01	0.310	9.35	0.26	**<0.001**	32.36	0.01	0.327	0.36
Respiration (mmol C m^{-2} d^{-1})	3.34	0.06	0.054	6.32	0.05	0.064	1.75	0.05	0.086	0.96	0.00	0.965	0.16
DIN (mmol m^{-2} d^{-1})	-2.21	0.06	0.083	3.00	0.03	0.229	0.23	0.00	0.754	7.35	0.00	0.649	0.10
PO_4^{-3} (mmol m^{-2} d^{-1})	-0.11	0.06	0.090	0.30	0.10	**0.025**	-0.05	0.03	0.191	-0.37	0.00	0.662	0.20

* partial r^2 was calculated by dividing the type III SS by the corrected total SS.

Table 3. Regressions of daily ecosytem flux rates against sediment organic matter quality (C:N). The coefficient indicates the directionality of the relationship while r^2 indicates the goodness of fit. Significant *p* values are in bold.

Ecosystem function	Sediment C:N (mol:mol)		
	Coefficient	r^2	*p*
GEP (mmol O_2 m^{-2} d^{-1})	-34.06	0.10	**0.029**
Respiration (mmol C m^{-2} d^{-1})	-21.82	0.21	**0.001**
DIN (mmol m^{-2} d^{-1})	-6.62	0.04	0.153
PO_4^{-3} (mmol m^{-2} d^{-1})	-0.53	0.10	**0.026**

Table 4. Ecosystem respiration as a function of sediment organic matter quality and gross ecosystem production (i.e. autochthonous organic matter). The coefficient indicates the directionality of the relationship while the partial r^2 indicates the goodness of fit. Significant p values are in bold.

Flux	Sediment C:N (molar)			GEP (mmol O_2 m^{-2} d^{-1})			Total Model
	Coefficient	Partial r^2*	*p*	Coefficient	Partial r^2*	*p*	r^2
Respiration (mmol C m^{-2} d^{-1})	-20.09	0.17	**0.003**	34.64	0.03	0.195	0.20

* partial r^2 was calculated by dividing the type III SS by the corrected total SS.

Figure Captions.

Figure 1. The effects of nutrients (N), predators (P), and grazer richness (G) on primary producer biomass. Nutrient enrichment increased macroalgae (A) and epiphytic Chl *a* (C). Grazers reduced abundances of macroalgae (A), *Z. marina* (B), and epiphytic Chl *a* (C). Benthic Chl *a* (D) was unaffected by the experimental manipulations. For this and the following figures, all error bars are standard error and the statistical results are reported in Table 2.

Figure 2. The effects of nutrients (N) and predators (P) on grazer biomass. Nutrients increased the biomass of *G. mucronatus* (B) while predators reduced the abundance of minor grazers (C).

Figure 3. The effects of nutrients (N), predators (P), and grazer richness (G) on *Z. marina* elemental content. (A) %TN was increased by nutrients and decreased by grazers. (B) %TOC was increased by grazers but only in non-nutrient treatments, resulting in a grazer by nutrient interaction. (C) Nutrients decreased C:N (mol:mol) and, hence, increased the nutritional quality of *Z. marina*.

Figure 4. The effects of nutrients (N), predators (P), and grazer richness (G) on sediment organic matter (SOM) elemental content. (A) %TN was influenced by grazer richness but was unaffected by nutrients and predators. (B) %TOC was increased by predators and influenced by grazers but unaffected by nutrients. (C) C:N was increased by predators.

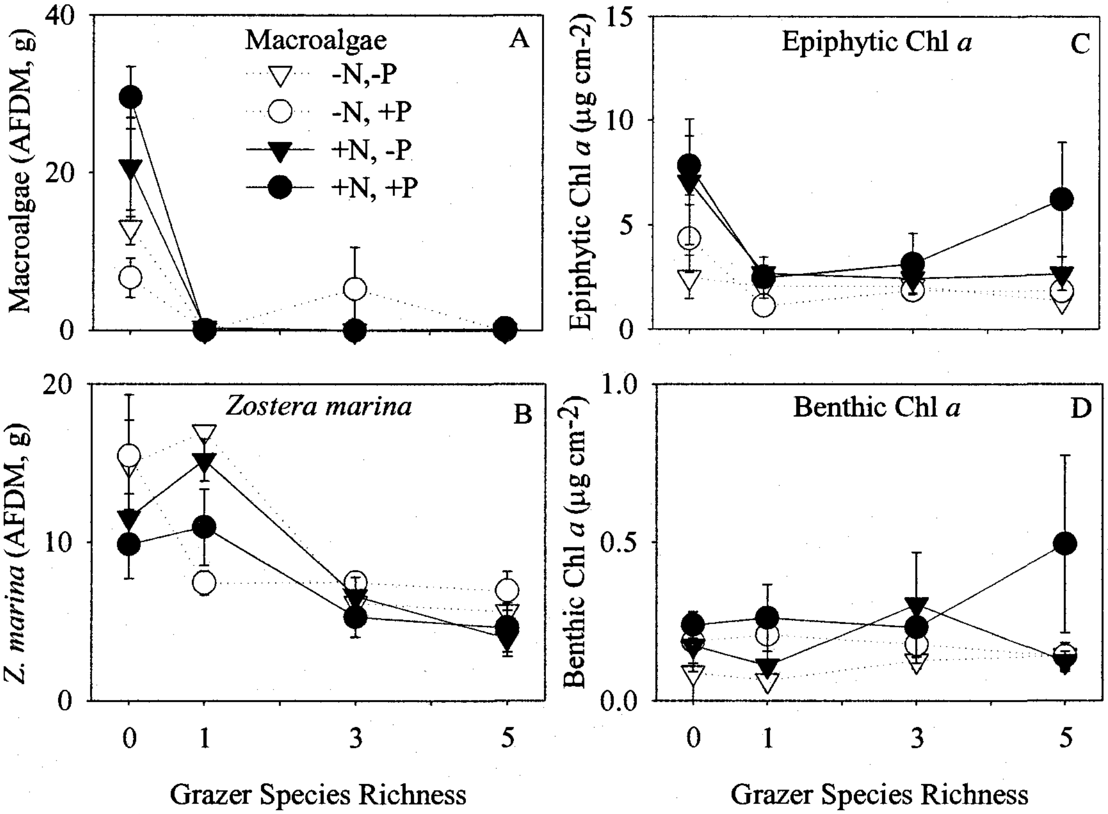
As SOM had a lower C:N than *Z. marina* or macroalgae, it is likely that SOM derived from multiple sources of varying quality.

Figure 5. (A-C) Nutrients (N) increased *G. mucronatus* %TN and %TOC, but did not affect C:N. (D-F) Nutrients decreased and predators (P) increased the %TOC of *A. valida* (E). However, both %TN and C:N were insensitive to nutrient and food web manipulations. These data indicate that grazer stoichiometric ratios were less flexible than primary producers.

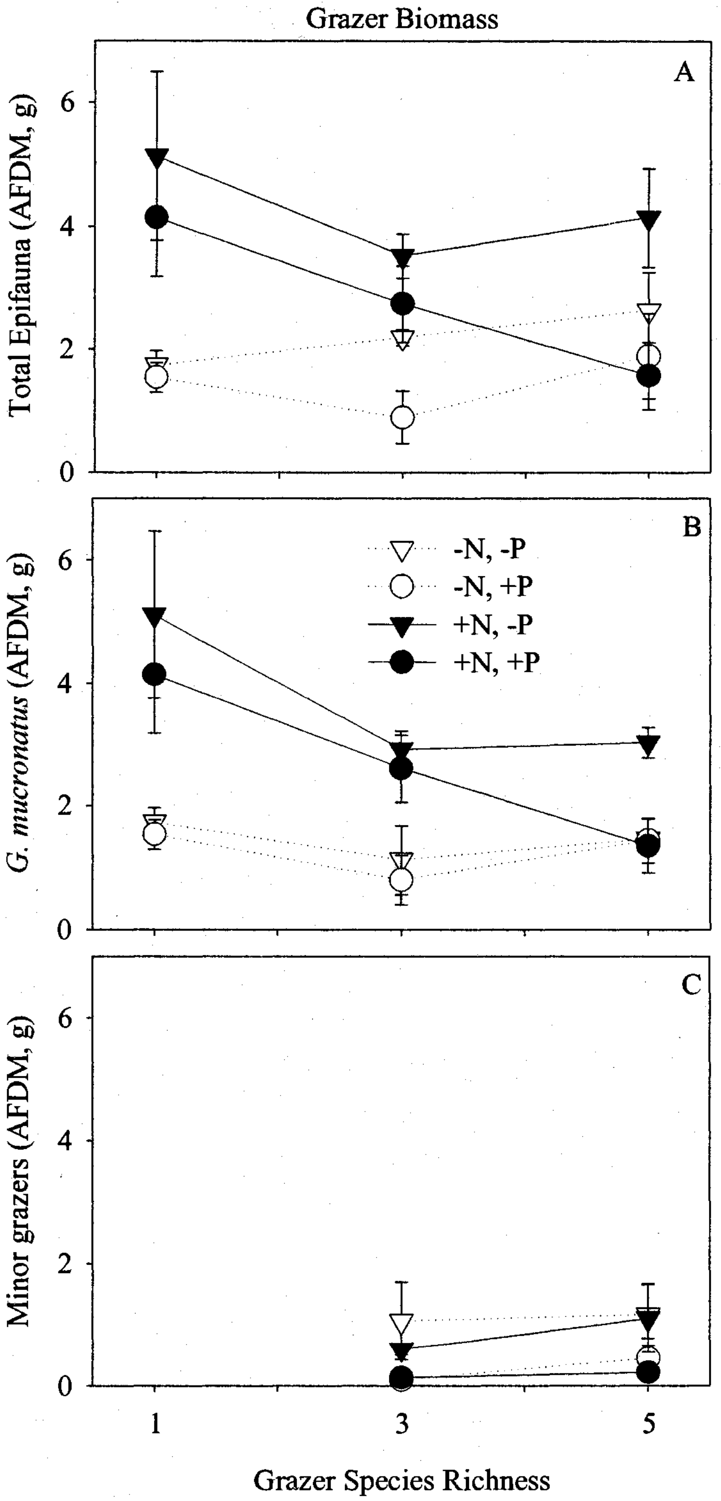
Figure 6. (A) Nutrients (N) increased and grazers (G) decreased gross ecosystem production. (B) Ecosystem respiration was increased by nutrients but decreased by grazers and predators (P). (C) The ratio of production to respiration was decreased by grazers. Values below or above one (marked by the horizontal line) are indicative of net heterotrophy or autotrophy, respectively.

Figure 7. Nutrients increased the daily flux rates of DIN (A) and PO_4^{-3} (B). DIN and PO_4^{-3} (C) were positively correlated ($r^2 = 0.64$; $p < 0.001$). The equation of the line was : $y = 15.40x + 12.16$, with a slope similar to Redfield organic matter (N:P = 16).

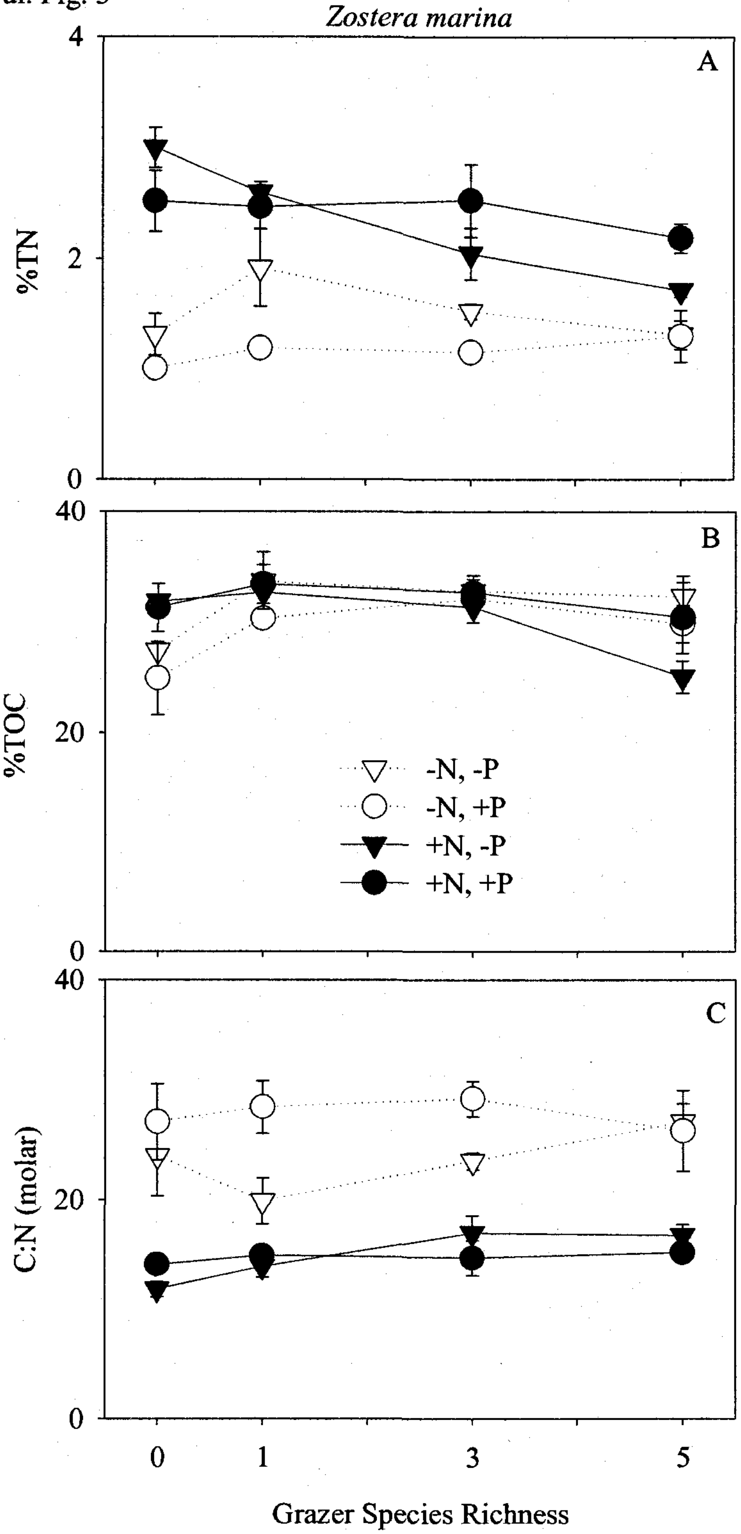
Spivak et al. Fig. 1



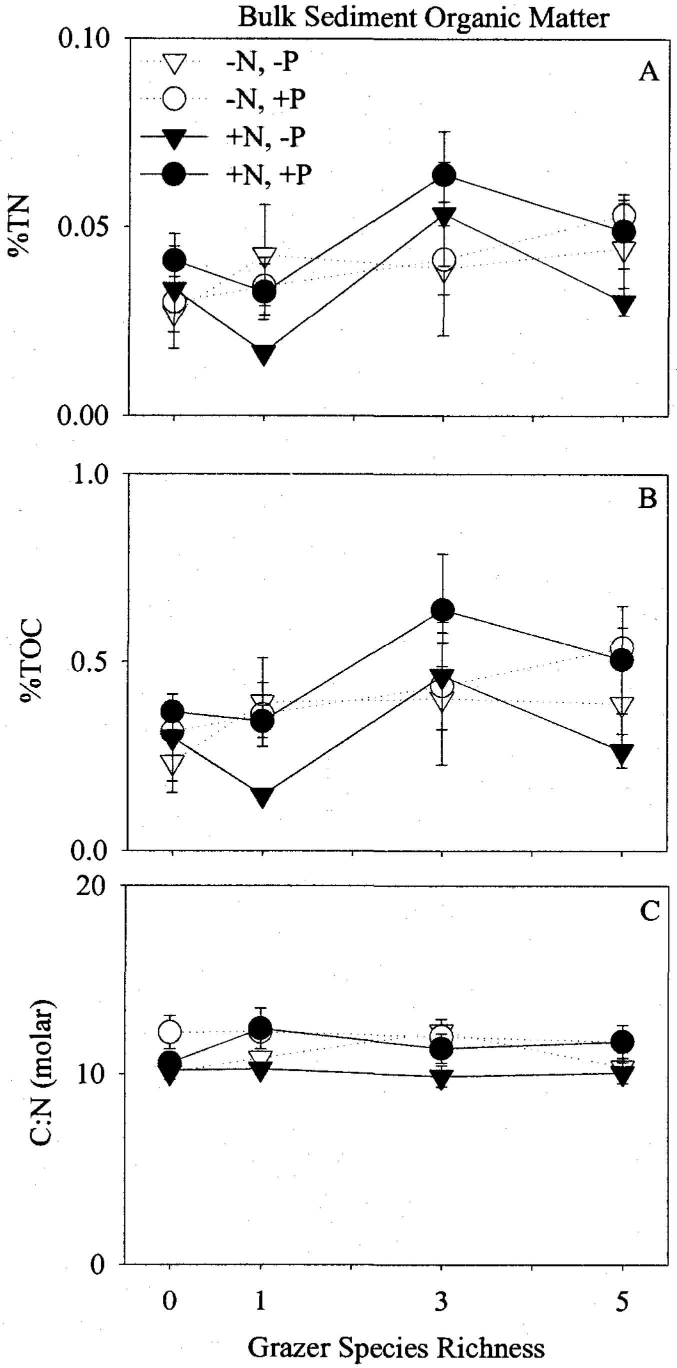
Spivak et al. Fig. 2



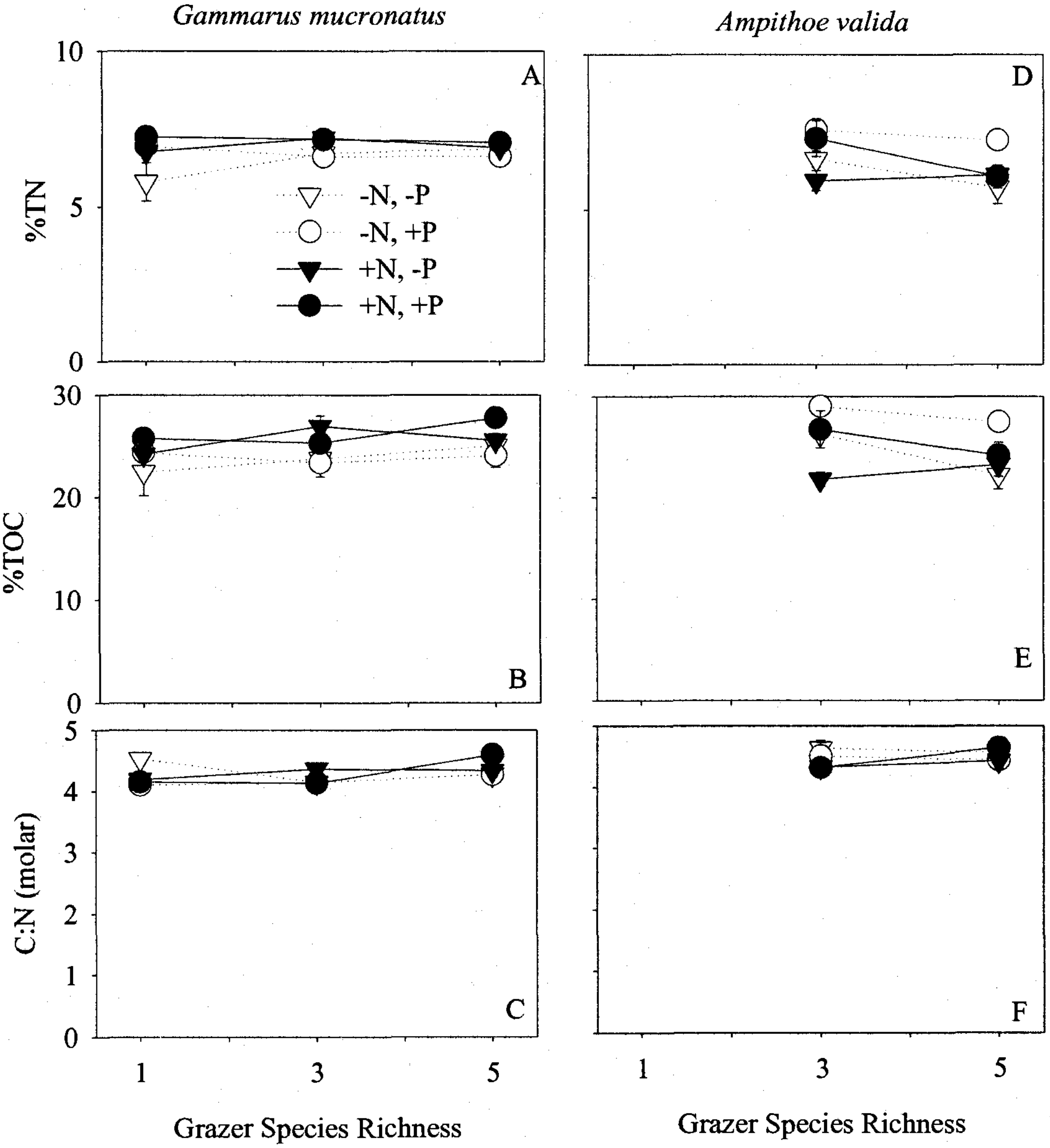
Spivak et al. Fig. 3



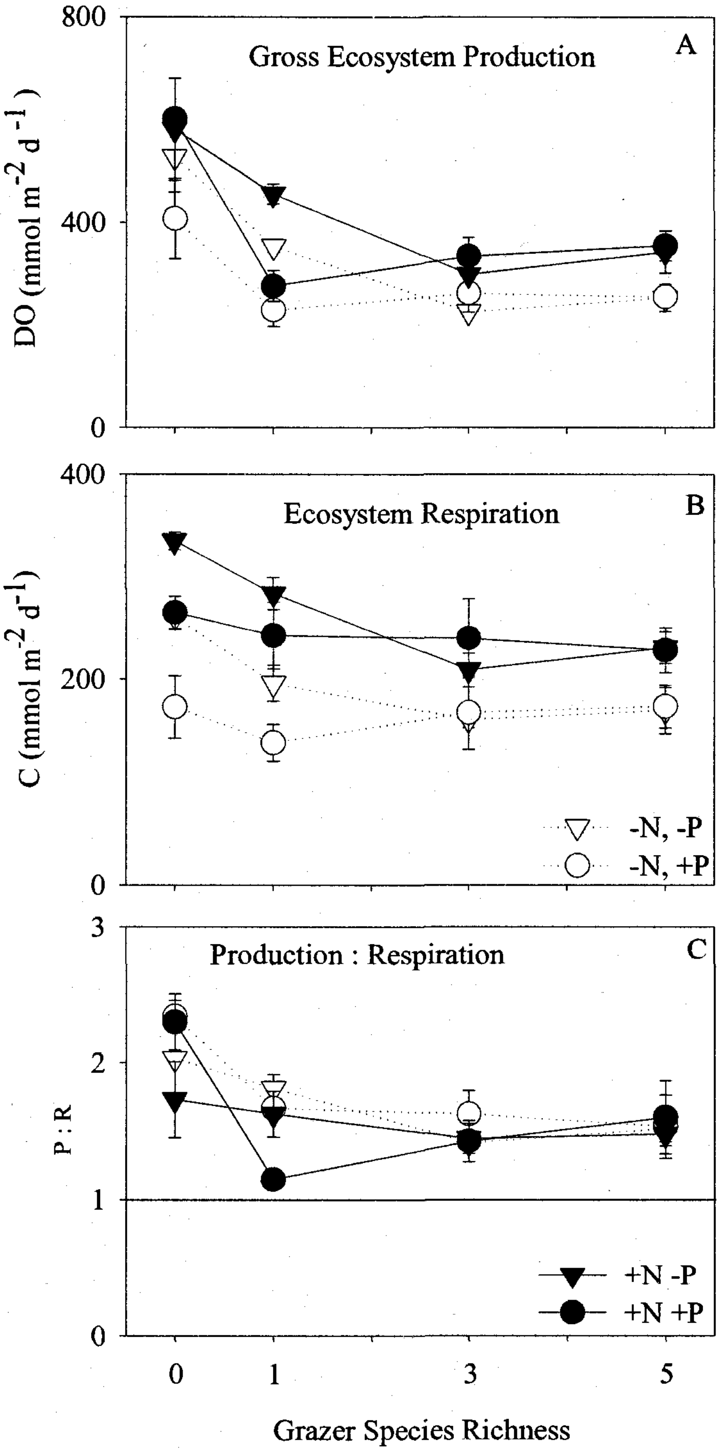
Spivak et al. Fig 4



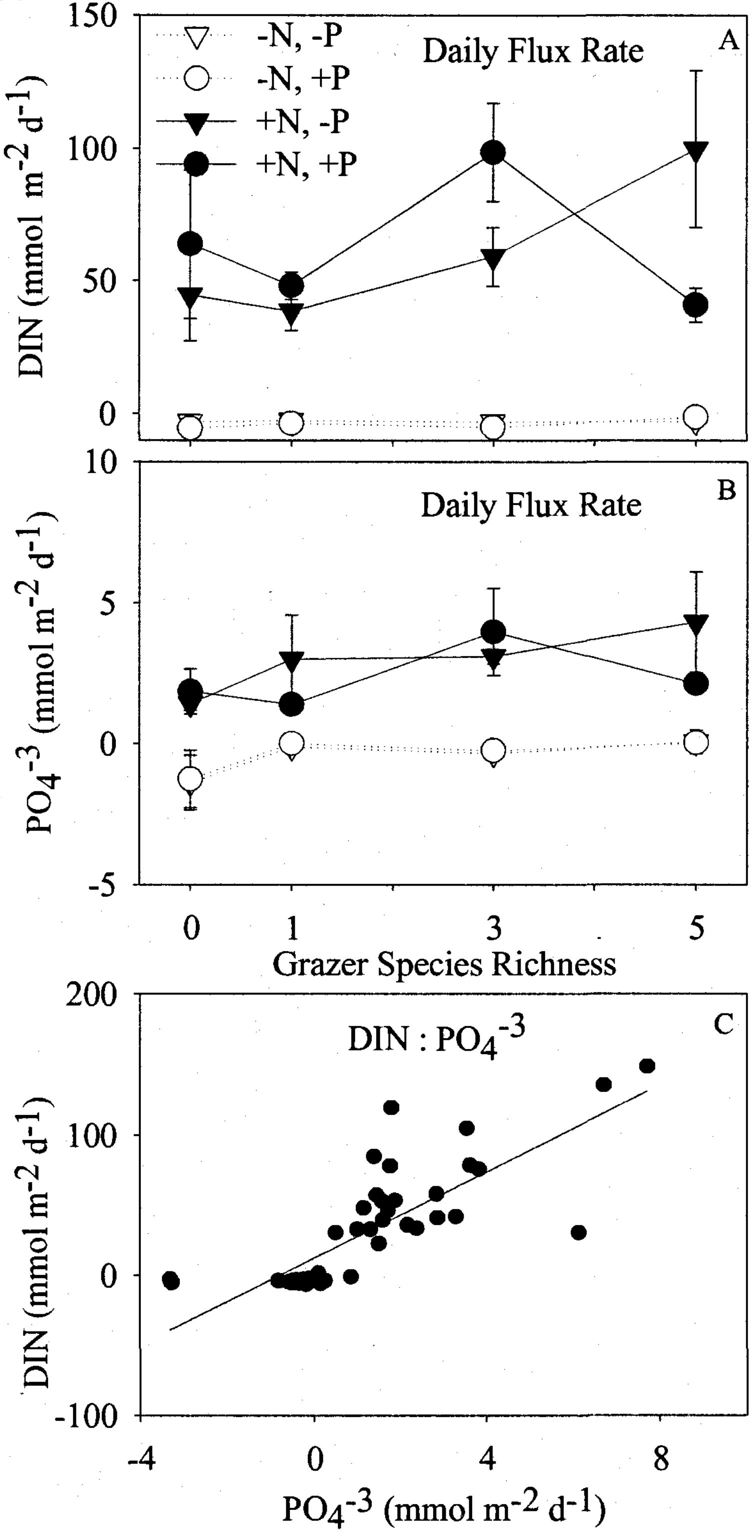
Spivak et al. Fig. 5



Spivak et al. Fig. 6



Spivak et al. Fig. 7



Chapter 5:

Community composition and nutrient enrichment influence sediment organic matter composition in an experimental seagrass ecosystem.

Amanda C. Spivak, Elizabeth A. Canuel, J. Emmett Duffy, J. Paul Richardson

Abstract.

Above-ground animal and plant communities may influence sediment microbial processes through the production of detrital organic matter (OM). Consequently, changes in OM sources and quality, as precipitated by above-ground communities, may have implications for sediment biogeochemistry. Here, we experimentally tested how sediment organic matter (SOM) composition changes in response to shifts in grazer species richness, trophic structure, and resource availability in a seagrass habitat. We manipulated community composition and nutrient levels since fishing and coastal nutrient enrichment, respectively, are two common perturbations to seagrass ecosystems. Our mesocosm experiment utilized a factorial design manipulating water column nutrient levels, food chain length (i.e. predator presence vs. absence), and grazer species richness (0, 1, 3, or 5 species). At the end of the five-week experiment, we analyzed the sources and quality of surface SOM using fatty acid (FA) biomarkers. We found that nutrient enrichment increased macroalgal and epiphytic biomass but resulted in lower abundances of algal and microbial FA in the sediments. Predator effects varied with grazer identity and did not cascade to primary producer abundance. In the sediments, predator presence increased the abundance of FA deriving from heterotrophic bacteria. In general, grazer effects on primary producer abundance and SOM composition were stronger than nutrient enrichment and food chain length.

Acknowledgements.

We would like to thank R.E. Blake, G. Blohm, M.A. Cochran, J.G. Douglass, B.W. Lerberg, and M.A. Wunderly for assistance in setting up, maintaining, and sampling the mesocosm tanks. M.A. Whalen helped sort plant, algae, and grazer samples. I.C. Anderson, D. Bronk, and J.J. Stachowicz provided valuable input on experimental goals and design. This work was supported by a NCER, STAR program, EPA grant (FP – 91656901) to A.C. Spivak, a OCE-0352343 to J.E. Duffy, and NSF DEB-0542645 to E.A. Canuel. Although the research described was partially funded by the US EPA's STAR program, it has not been subjected to EPA review and therefore does not necessarily reflect the views of the Agency. No official endorsement should be inferred. Additional support was provided by Virginia Institute of Marine Science. This is contribution XXXX of the Virginia Institute of Marine Science, College of William and Mary.

Introduction.

Declining biodiversity coupled with increasing anthropogenic stresses have prompted questions about how these disturbances affect ecosystem functioning (Hooper et al. 2005; Balvanera et al. 2006; Cardinale et al. 2006). This has generated studies exploring the effects of above-ground trophic structure (Shurin et al. 2002; Petchey et al. 2004; Byrnes et al. 2006), diversity within and between trophic levels (Tilman et al. 1997; Naeem and Li 1998; Duffy 2003), resource availability (Ware and Thomson 2005; Hulot and Loreau 2006; Cloern 2007), and their interactions (Menge 2000; Chase 2003; Borer et al. 2006) on a variety of ecosystem functions across habitats. These changes in above-ground communities and resource availability may also extend to microbial communities in terrestrial soils (Mikola and Setala 1998; Wardle et al. 2004) and marine sediments (Canuel et al. 2007; Spivak et al. 2007). The link between animals and plants above-ground and microbes in soils and sediments is often detritus. As soil and sediment bacteria govern rates of decomposition and nutrient regeneration (Boschker and Cappenberg 1998; Holmer et al. 2004; Dahllof and Karle 2005), it is important to understand how these communities are affected by changes in the quality and composition of detrital organic matter (OM) as precipitated by above-ground communities. To this end, we conducted a mesocosm experiment testing the singular and interactive effects of trophic structure, herbivore species richness, and nutrient concentrations on sediment organic matter (SOM) composition in a seagrass habitat.

We used a coastal seagrass (*Zostera marina*) ecosystem as a model habitat for several reasons. First, animal and primary producer species within seagrass habitats are well studied (Duffy 2006; Heck and Valentine 2006). Resident invertebrate grazers consume a variety of primary producers, including macroalgae, epiphytes, and occasionally seagrass blades (Duffy and Harvilicz 2001; Heck and Valentine 2006). Through their feeding habits and preferences, grazers can influence the delivery and composition of sediment organic matter (SOM) (Duffy 2003; Canuel et al. 2007). As SOM quality is an important determinant of sediment bacterial activity grazer mediated shifts in SOM composition may influence remineralization rates and carbon storage (Hansen and Blackburn 1992;(Cebrian and Duarte 2001).

Second, seagrass communities are affected by fishing efforts that reduce food-chain length (Duffy et al. 2005) and by coastal eutrophication that increases water column nutrient concentrations and reduce light availability (Cloern 2001; Orth et al. 2006). The loss of commercially important predators (e.g., fish and blue crabs) that live in seagrass systems may influence grazer community composition and strengthen grazer controls on primary producers (Heck and Valentine 2007). Coastal eutrophication is cited as a leading cause of two factors that contribute to seagrass loss, algal overgrowth and low water quality (Cloern 2001; Orth et al. 2006). Elevated water column nutrient concentrations may strengthen bottom-up controls since resource availability is a predictor of primary producer biomass and the abundances of organisms at higher trophic levels (Duarte et al. 2000; Ritchie 2000; Ware and Thomson 2005). However, in seagrass beds top-down controls by grazing invertebrates generally negate the stimulatory effects of nutrient resources on algae (Hughes et al. 2004; Armitage et al. 2005).

Finally, seagrass and benthic microalgae are sensitive to bacterial transformations of nitrogen, sulfur, and other nutrients in the sediments (Holmer et al. 2005; McGlathery et al. 2007; Perez et al. 2007). Bacterial decomposition of SOM regenerates inorganic nitrogen that may rapidly be taken up by benthic microalgae in the surface sediments (Hansen et al. 2000; Eyre and Ferguson 2002; McGlathery et al. 2007). Deeper in the sediments, or if oxygen availability is depleted, sulfate reduction may become an important pathway for OM decomposition. However, an accumulation of sulfides may negatively affect seagrass health (Calleja et al. 2007; Perez et al. 2007). Thus, changes in SOM that affect the sediment bacterial community may, in turn, influence the primary producer community.

We assessed SOM composition and quality by analyzing fatty acid biomarkers. These compounds serve as functional proxies linking OM to potential sources since they are reliably produced by specific groups of organisms (Canuel and Martens 1996; Napolitano 1998; Dalsgaard et al. 2003). Diagnostic biomarkers often have site-specific methyl groups, double bonds, or branching patterns that are useful for tracing sources of OM (Napolitano 1998; Dalsgaard et al. 2003). For example, bacteria synthesize iso-, anteiso-, and methyl-branched fatty acids while microalgae produce highly unsaturated long chain fatty acids (Volkman et al. 1998). Here, we analyzed total fatty acids (TFA) and a sub-class of the TFAs, phospholipid-linked fatty acids (PLFA), to compare OM contributions from detrital and viable or recently viable sources, respectively.

Previously, we conducted mesocosm experiments to asses the influence of community composition (Duffy et al. 2003; Canuel et al. 2007) and light availability (Spivak et al. 2007) on SOM composition. These experiments revealed that both top-down and bottom-up controls affected the relative abundance of SOM deriving from primary producers and bacteria. One of the motivations of this experiment was to determine whether the type of bottom-up control (i.e. light vs. nutrients) is important to

SOM composition. To this end, we manipulated water column nutrient levels, food chain length (predator presence vs. absence), and grazer species richness (0, 1, 3, or 5 species) and measured their effects on primary producer abundance and sediment fatty acid (FA) biomarker composition. In addition, we examined whether primary producer abundance and sediment FA responses were more or less variable at the low (0-species) or high (5-species) levels of grazer richness. Specifically, we tested three main hypotheses. First, nutrient enrichment would increase algal biomass and algal contributions to SOM. This would, in turn, increase SOM lability and sediment bacterial activity. Second, the presence of a grazer community would control algal production stimulated by nutrient enrichment. Thus, grazer feeding preferences would indirectly increase seagrass abundance, by reducing algae and increasing light, thereby influencing SOM composition. Third, the presence of predators would reduce grazer biomass and activity, thereby increasing the accumulation of algae, SOM quality, and sediment heterotrophic activity. Consequently, predators may exacerbate the effects of nutrient enrichment by negatively affecting the grazer community. Finally we compared the primary producer and SOM composition results from this mesocosm experiment to those from a previous field experiment with a similar design (Chapter 3).

Methods

Experimental Design.

We conducted a mesocosm experiment to test the main and interactive effects of nutrient availability, grazer species richness, and food chain length on sediment fatty acid biomarker composition. Results for primary producer and grazer biomass, ecosystem metabolism, and bulk SOM content are reported in Chapter 4. Water column nutrient concentrations were manipulated by adding Osmocote™ slow release fertilizer (N:P:K = 3:1:2) to half of the tanks. Grazer species richness was varied across four levels (0, 1, 3, or 5 species). The highest richness level contained five amphipod species present in the York River estuary, VA, at the time of the experiment, the intermediate level contained random combinations of three species, and the lowest richness level only had the most abundant and annually persistent species, the amphipod *Gammarus mucronatus*. The remaining four grazer species were also amphipods: *Elasmopus levis*, *Melita nitida*, *Ampithoe valida*, and *Sympleustes* spp. Food chain length was manipulated by exposing parallel sets of grazer treatments to a generalist predator, the blue crab, *Callinectes sapidus*. The 16 treatments were each replicated 3 times for a total of 48 mesocosm tanks.

The outdoor mesocosm experiment was conducted over five weeks during summer 2006 in 120 liter translucent fiberglass tanks that were continuously supplied with water from the York River estuary, VA. Water passed through a sand filter and then through 150 μm mesh before filling 'dump buckets' which regularly spilled into the tanks, providing turbulence and aeration. The filtering process eliminated larger, non-target animals while permitting passage of invertebrate larvae and algal spores, which often colonized the tanks. The tanks were filled with a mixture of sand : mud (9:2 w:w), averaging 0.80% (± 0.18 S.E.) organic matter (OM) content, to a depth of 10 cm. In contrast with previous experiments (Canuel et al. 2007; Spivak et al. 2007), we used a sediment substrate with approximately 1% OM to facilitate *Zostera marina* transplant success and growth (Koch 2001). One hundred pre-weighed eelgrass (*Z. marina*) shoots, cleaned of grazers and epiphytes, were planted in each tank. Sixteen days later, grazing invertebrates were added to each grazer mesocosm. The five-species treatment received 18 individuals of each species, the three-species treatment had 30 individuals of each species, and the one-species treatment had 90 *G. mucronatus* individuals. Eleven days later, two juvenile blue crabs were added to each predator treatment. Each nutrient treatment received 200 g of Osmocote™ slow release fertilizer in the first two weeks of the experiment and 100 g every week thereafter. We reduced the fertilizer dosage since the target concentration was five times ambient and 200 g resulted in higher than target concentrations. The 200 g and 100 g additions of Osmocote™ increased NH_4^+ concentration to 30.6 (29.23 μM) and 5.6 (14.37 μM) times ambient, respectively (Spivak et al. in prep). Nutrients were delivered through two perforated PVC tubes that were suspended from the top of the tanks. Twice a week, one nutrient PVC tube from each nutrient treatment was refreshed with new fertilizer. Water column nutrient concentrations were monitored each week by measuring NH_4^+ concentrations from five randomly chosen tanks of each nutrient treatment using the Koroleff colorimetric method. The five-week experimental incubation time was chosen to minimize the risk of invasion by non-target animals. This time period permits major changes in animal (one to two grazer generations) and plant community development and in surface sediment characteristics (Duffy et al. 2003; Canuel et al. 2007; Spivak et al. 2007). Despite limitations, this experimental infrastructure simulates several aspects of the biotic and abiotic field conditions well (Duffy et al. 2001). Results for the aboveground plant and animal community and for ecosystem metabolism and stoichiometric ratios are reported elsewhere (Duffy et al. in prep; Chapter 4).

Sediment fatty acid analyses.

At the end of the five week experiment, sediments were collected and analyzed for fatty acid biomarker composition. Three sediment cores (2.6 cm diameter) were collected from every mesocosm tank; the upper 1 cm from each was removed and combined to form a composite surface sediment sample which was stored in a pre-combusted (450 °C) jar. Samples were immediately put on ice following collection and were later frozen at -80 °C until analysis.

Fatty acids (FA) were analyzed using a revised Bligh & Dyer (1959) method (Macnaughton et al. 1997). Briefly, sediment samples were extracted with methanol:chloroform :K_2HPO_4 50 mM buffer (2:1:0.8, v:v:v) using an accelerated solvent extraction system (Dionex ASE 200). Following extraction, the samples were partitioned and the organic phase removed and allowed to sit over anhydrous Na_2SO_4 overnight to remove traces of water. The samples were concentrated to 1 mL (Zymark Turbo Vap 500). The total lipid extracts were separated into non-polar (F1/2) and polar (F3) fractions using silica gel columns; each fraction was then eluted with solvents of increasing polarity (Guckert et al. 1985). F1/2 (neutral and glyco-lipids) and F3 (phospholipids) were each saponified, using procedures described in Canuel et al. (2007). Following saponification, the residue was extracted under basic (saponified-neutral) and acidic pH (saponified-acid). The saponified acid fraction was methylated using BF_3-CH_3OH and purified using silica gel chromatography. Before analysis by gas chromatography (GC), samples were evaporated to dryness under N_2, and a small volume of hexane (100 µL for the polar fraction and 400 µL for the non-polar) was added. The FAs, as methyl esters, were analyzed by gas chromatography following previously-published methods (Canuel and Martens 1993; Zimmerman and Canuel 2001). Peaks were quantified relative to an internal standard, methyl heneicosanoate, added just prior to GC analysis. Peak identities were verified using reference standards and by combined gas chromatography-mass spectrometry using a Hewlett-Packard 6890 GC interfaced with a mass selective detector operated in electron impact mode. FAs are designated as A:BωC, where A is the total number of carbon atoms, B is the number of the double bonds, and C is the position of the first double bond from the aliphatic "ω" end of the molecule. The prefixes "i" and "a" refer to *iso* and *anteiso* methyl branched FAs (see Canuel et al. 1995 and references therein). Results for two classes of fatty acids are presented: phospholipid-linked fatty acids (PLFA) which represent viable or recently viable biomass and total fatty acids (TFA) which represent neutral, glyco-, and phospholipids and include the sum of the viable and detrital contributions.

Statistical analyses.

Results of the experiment were analyzed in a fully factorial three-way analysis of variance (ANOVA, SAS version 9.1 for Windows), with grazer treatment (df = 3), food chain length (i.e. predator presence or absence, df = 1) and nutrient availability (df = 1) as fixed factors. Data were logarithmically transformed as necessary to maintain homogeneity of variance as determined by the Cochran's C test. From the ANOVAs, we calculated the magnitude of main and interactive effects (ω^2, percent of variance explained). To determine whether abundance of sediment fatty acid groups varied among replicates, we conducted the Levene's test of homogeneity of variance (Schultz 1985). The three species treatment was excluded from the Levene's analysis as it contained random combinations of grazer species (whereas the one and five species treatments had constant composition among replicates) and, consequently, was expected to be the most variable treatment. All analyses included all three replicates of every treatment except for two: (1) one replicate of the no-nutrient, no-crab, one-grazer species treatment was excluded due to contamination by more than 500 mg of grazer ash-free dry matter; and (2) a replicate of the no-nutrient, crab, five-grazer species treatment was excluded from the total fatty acid analyses because of low internal standard recovery. Thus, we reported the type III sum of squares (SS) results from the ANOVA model. Analyses were performed on fatty acid biomarker concentrations (ng g^{-1}sediment). Results for primary producer and grazer abundances were reported in Chapter 4.

To aid data interpretation, we performed multiple regression and principal components analyses (PCA). We examined relationships between the fatty acid groups and the major primary producers (*Z. marina*, macroalgae, and epiphytic Chl *a*) and invertebrate grazers using multiple linear regressions. Since *G. mucronatus* was the most abundant grazer at all levels of richness, we divided the grazer response into two categories, *G. mucronatus* only and "minor" grazers (i.e., total epifauna less *G. mucronatus*; see Chapter 4). The partial r^2 was calculated by dividing the type III SS for each response variable by the total SS. We conducted principal components analysis (PCA; using Minitab 15) to better elucidate relationships between manipulated and response variables. We only performed PCA on SOM variables, as these responded to primary producer abundance determined by food web composition and nutrient concentrations. PCA loadings describe the relationships between the response variables and the dominant principal components. PCA loadings were also regressed against the major primary producer groups (*Z. marina*, macroalgal biomass, and epiphytic Chl *a*) to help interpret the results.

Results

Above-ground biomass.

Results for above-ground biomass of primary producers were reported in Chapter 4. Here, we present the results for grazer community composition and relative abundance in the one and five species treatments (Fig. 1). We compared the one and five grazer treatments since the one species treatment only contained *G. mucronatus* and the five species treatment included the full complement of grazers. Since *G. mucronatus* is the most perennially abundant grazer, a comparison between the monoculture and the five species treatment reflects a realistic hypothesis of grazer community composition after and before, respectively, a grazer extinction event. The three species treatment was excluded because it consisted of random grazer combinations, some of which did not include *G. mucronatus*.

Nutrients increased grazer biomass in the one and five species treatments (Fig. 1; Table 1). This effect was stronger for *G. mucronatus* in the one species treatment ($\omega^2 = 0.19$) than for total epifaunal biomass in the five grazer treatment ($\omega^2 = 0.12$). Predators reduced total epifaunal biomass but had no effect on *G. mucronatus* biomass in the one species treatment. There was no difference in total grazer biomass in the one versus five grazer species treatments, however, *G. mucronatus* achieved higher biomass in the monoculture than in the polyculture .It is possible that the changes we observed in grazer biomass reflect early successional dynamics in grazer community development and that, had the experiment run longer, different patterns might have emerged (Cardinale et al. 2007). However, the experimental duration did permit the production of several grazer generations (Duffy et al. 2003) and likely allowed for competitive interactions between grazer species.

Total fatty acids.

At the end of the experiment the abundance of total fatty acids (TFA) was lowest in the one grazer species treatment but was unaffected by nutrient enrichment or predator presence (Fig. 2A; Table 2). Variation in TFA abundance (among replicates) in the one and five species treatments was similar (Table 3). TFA abundance correlated negatively to biomasses *Z. marina* and *G. mucronatus* and positively to minor grazers (Tables 4, 5). Patterns in TFA and phosopholipid-linked FA (PLFA) were qualitatively very similar, however, PLFA abundance was not significantly affected by any of the manipulated variables (Fig. 2B; Table 2). Since TFA and PLFA derive from detrital and recently viable OM sources, respectively, we normalized the abundance of PLFA to TFA to determine the relative contributions from each OM pool (Fig. 2C). Nutrients increased PLFA:TFA which is consistent with higher abundances epiphytes in enriched treatments (Chapter 4). The ratio was not related to the abundances of any of the primary producers but was negatively correlated to minor grazer abundance (Tables 4, 5). Since the PLFA contributions to the TFA pool were small and the trends in PLFA and TFA sub-classes were similar, we only present results for the TFA hereafter.

We partitioned the TFA into five sub-classes based on FA chain length and saturation and branching patterns (Table 6). Saturated, short-chain FAs ($C_{12:0} + C_{14:0}$), which constituted 3-6% of the TFAs, are indicative of algal and microbial sources of OM. Abundance of this group was lower in treatments with nutrients but was unaffected by predators and grazers (Fig. 3; Table 2). $C_{12:0} + C_{14:0}$ was negatively correlated to *G. mucronatus* biomass (Table 5). Abundances of saturated long chain FA ($\Sigma(C_{24:0} - C_{30:0})$; 5-11% of TFA), $C_{16:0}$ (20-30% of TFA), and $C_{18:0}$ (3-9% of TFA) were insensitive to all of the experimental manipulations (data not shown).

Polyunsaturated FAs (PUFA), which are indicative of labile, algal-derived OM accounted for approximately 15% of TFA. We analyzed two PUFA groups, $C_{20:4} + C_{20:5}$ (i.e. C_{20} PUFA) and $C_{22:5} + C_{22:6}$ (i.e. C_{22} PUFA) which represent OM contributions from diatoms and dinoflagellates, respectively (Fig. 3; Table 2). Grazers were the strongest determinant of PUFA abundance as C_{20} PUFA was lowest and C_{22} PUFA was highest in the *G. mucronatus* monocultures. Minor grazer biomass correlated positively with C_{20} PUFA and negatively with C_{22} PUFA (Table 5), suggesting that grazer diet preferences influenced the composition of sedimentary PUFA.. Grazers also affected the variance of the PUFA groups (Table 3). C_{20} PUFA was more variable in the five- than in the one-species grazer treatments whereas C_{22} PUFA was more variable in the one- than in the five-species treatments. In summary, the results for saturated FAs and PUFA indicate that grazer community composition can influence the importance of different primary producer taxas to SOM through their feeding preferences.

Branched fatty acids (iso- and anteiso $C_{13:0} + C_{15:0} + C_{17:0} + C_{19:0}$; BrFA) representative of sediment heterotrophic bacteria, accounted for 5-11% of TFA (Fig. 3; Table 2). Grazer richness and predator presence increased the abundance of BrFA but there was no effect of nutrients. Abundance of this TFA sub-class correlated negatively to biomasses of *G. mucronatus* and *Z. marina* (Tables 4, 5). The data indicate that food web structure and composition, and their effect on the primary producer community, influenced the sediment heterotrophic community.

We also analyzed the ratio $C_{20:5\omega3}$: $C_{22:6\omega3}$ to estimate diatom-derived OM contributions to the sediments (Budge and Parrish 1998; Shin et al. 2000). The ratio was lower in the *G. mucronatus* (1 species treatments) suggesting that this grazer reduced FA contributions from diatoms relative to dinoflagellates (Fig. 3; Table 2). In addition, there was less variability of the ratio (across replicates) in the one versus five species treatments, suggesting that *G. mucronatus* was a more effective consumer of diatoms in the monoculture than in the polyculture (Table 3). This hypothesis is further supported by positive correlations between the ratio $C_{20:5\omega3}$: $C_{22:6\omega3}$ and minor grazer biomass (Table 5). Predators decreased the ratio $C_{20:5\omega3}$: $C_{22:6\omega3}$, but only in the three and five grazer species treatments which created a predator by grazer interaction effect. $C_{20:5\omega3}$: $C_{22:6\omega3}$ was negatively correlated to *Z. marina* biomass but not the biomass of any of the algal groups (Table 4). Thus, grazing by *G. mucronatus* and, to a lesser extent, the presence of crab predators tended to shift the composition of SOM from diatom to dinoflagellate contributions.

PCA provided a summary of TFA composition in response to grazer richness, predator presence, and nutrient availability (Fig. 4). PC1 and PC 2 described 42.6% and 17.5% of the variance, respectively and were both negatively correlated to *Z. marina* biomass (Table 7). The negative correlation between PC1 and *Z. marina* was supported by the loadings of TFA, short chain FA, C_{20} PUFA, BrFA, and $C_{20:5\omega3}$: $C_{22:6\omega3}$ (all negatively related to *Z. marina*; Table 8). PC1 tended to separate SOM variables according to grazer effects especially in nutrient enriched treatments. For instance, TFA, C_{20} PUFA, and $C_{20:5\omega3}$: $C_{22:6\omega3}$ had positive PC1 scores and were lowest in the one grazer treatments while C_{22} PUFA and PLFA:TFA had negative PC1 scores and were highest in the one grazer treatments. PC2 separated the one grazer treatment (positive scores) from all other grazer treatments (negative scores). PC2 also provided some information about predator effects as SOM C:N, C_{22} PUFA, and BrFA, had positive scores and were increased by predators.

We analyzed PC scores in the presence and absence of nutrients to determine whether enrichment affected relationships between grazer and predator treatments (Fig. 4). One grazer species treatments were distinct from the rest of the grazer treatments despite nutrient concentrations. In the absence of nutrients, the zero, three, and five grazer species treatments tended to cluster together. In the presence of nutrients, however, there were three distinct groupings according to species richness: (1) the one species treatment, (2) the zero species treatment, and (3) the multi-species treatments. The clustering of the three and five grazer treatments suggests that the species rich communities were more similar to each other than they were to the zero or one species treatments. In addition, predator effects tended to be stronger under nutrient enrichment as treatments with predators tended to have more positive PC2 scores than those with grazers only. In summary, the PCA results indicate that grazer identity (i.e. *G. mucronatus*) was a strong determinant of SOM composition. Secondarily, nutrient enrichment increased the importance of predator presence and grazer richness to sediment geochemistry. Finally, despite differences in the composition of three- and five-species treatments, they consistently grouped together.

In summary, nutrient enrichment increased the abundance of macroalgae and epiphytes (Chapter 4) and this translated into higher *G. murcronatus* biomass (Fig. 1) and a greater proportion of PLFA relative to TFA (Fig. 2). The grazer community reduced above-ground primary producer biomass (Chapter 4) but SOM composition was most influenced by grazer identity. This is suggested by low abundances of TFA, $C_{20:4} + C_{20:5}$, and $C_{20:5\omega3} : C_{22:6\omega3}$ in the *G. mucronatus* monocultures (i.e. one-species treatments; Figs. 2, 3). Predators reduced minor grazer biomass (Chapter 4) but did not initiate a trophic cascade, as evidenced by an absence of predator effects on primary producer biomass and representative FAs in the sediments. Surprisingly predator presence and grazer richness both increased BrFAs, suggesting that the above-ground trophic structure is important to the sediment heterotrophic community (Fig. 3).

Discussion.

Grazer community compostion and richness had much stronger effects, on average, than nutrient enrichment or predators, on SOM composition (Table 2). Specifically, the amphipod, *G. mucronatus,* sharply reduced the abundance of SOM deriving from diatoms in the one-species treatment (Fig. 3). However, similar SOM composition in the three and five grazer species treatments suggested that the strong effects of *G. mucronatus* were dampened in more diverse communities. It was somewhat surprising that grazer effects on sediment FA groups were stronger than nutrient enrichment since light availability, another bottom-up force, was a main determinant of SOM composition in a previous experiment (Spivak et al. 2007). It is probable that nutrient enrichment in this experiment did not lead to reduced light availability because grazers were able to control primary producer abundance (Chapter 4). Thus, grazing invertebrates appear to lessen the effects of nutrient enrichment in this seagrass habitat as shown in others (Hughes et al. 2004; Armitage et al. 2005; Heck and Valentine 2007).

Grazer species identity and richness affected SOM composition.

In this experiment, one of the clearest trends was that SOM composition differed in the one versus the three and five grazer species treatments. This strongly suggested that *G. mucronatus* exerted a much greater influence over SOM composition in the absence of competition with other grazer species. These differences may have been due to *G. mucronatus* accruing more biomass in monoculture than in a multi-species community (Fig. 1; Table 1). However, the strong effect of nutrient enrichment on *G. mucronatus* biomass and the general lack of nutrient by grazer interaction effects on SOM composition suggest that the influence of this grazer was not proportional to its abundance. Thus, despite relatively high *G. mucronatus* biomass in the five species treatments, direct or indirect interactions between grazer species attenuated the influence of *G. mucronatus* on SOM composition. This suggests that grazer diversity may weaken trophic effects that extend to SOM composition (Finke and Denno 2002; 2004). Alternatively, minor grazers may have had a disproportionate influence on SOM composition despite their low abundance. This hypothesis is in accord with other experiments suggesting that grazer identity rather than biomass is important to ecosystem properties (Duffy et al. 2001; Canuel et al. 2007; Jaschinski and Sommer 2008). However, from this dataset we can not discern which hypothesis provides the most likely explanation for differences in SOM composition between the grazer monocultures and polycultures.

Differences in SOM composition in the one- versus three- and five-species treatments hint that grazer community makeup and interactions can impact sediment biogeochemistry (Duffy and Harvilicz 2001; Canuel et al. 2007; Spivak et al. 2007). For instance, diatom-derived OM (i.e. $C_{20:4}$+$C_{20:5}$, $C_{20:5\omega3}$:$C_{22:6\omega3}$; Fig. 3) was less abundant in the grazer monocultures compared to the polycultures. This is consistent with a previous study where *G. mucronatus* decreased the accumulation of benthic microalgae (chlorophyll *a*) and the relative abundance of polyunsaturated FAs (Canuel et al. 2007). Since algal OM is particularly labile, SOM quality might have been lower in the monoculture than in the more species rich treatments (Canuel and Martens 1996). The higher abundances of diatom-derived FAs ($C_{20:4} + C_{20:5}$ and $C_{20:5\omega3} : C_{22:6\omega3}$) in the three- and five-species treatments might have been the indirect result of minor grazers reducing *Z. marina*, thereby increasing light availability and, hence, sediment microalgal production (Chapter 4). This hypothesis is supported by negative correlations of *Z. marina* with TFA and FAs indicative of diatom OM ($C_{20:4} + C_{20:5}$, and $C_{20:5\omega3} : C_{22:6\omega3}$; Table 4). Increased abundance of labile, algal-derived SOM may also stimulate sediment microbial activity as BrFA (sediment heterotrophic bacteria) abundance was higher in the mixed grazer species treatments than in monoculture (Fig. 3; Table 2). Supporting this hypothesis was the negative correlation between *Z. marina* biomass and abundance of iso- and anteiso-BrFA, which are abundant in gram positive bacteria (Kaneda 1991) (Table 4). Thus, an indirect effect of reduced *Z. marina* biomass might have been a heightened sediment bacterial response, suggesting that shifts in SOM composition precipitated by grazer effects on primary producers influenced the sediment bacterial community. Cascading effects of above-ground animals on organic matter composition and the bacterial community have been observed in soil systems as well (Lavelle et al. 1997; Bardgett et al. 1998; Wardle et al. 2004). This suggests that above-ground community composition and structure may affect biogeochemical cycles in a variety of ecosystems.

We tested whether our data supported the portfolio hypothesis, which predicts that variability will decrease as species richness increases (Tilman 1999; Lhomme and Winkel 2002), by comparing the variance of SOM properties among replicate mesocosms at low (1) and high (5) grazer species richness. There was little evidence that the five-grazer species community conferred stability since the variance of many fatty acid groups was similar in monocultures and mixed species treatments (Table 3). However, when variance in FA abundance differed between the one- and five-species treatments, the pattern was opposite of the prediction. For example, there was less variance in the abundance of diatom-derived FAs ($C_{20:4} + C_{20:5}$, $C_{20:5\omega3} : C_{22:6\omega3}$) in the one- versus five-species treatments (Fig. 3; Table 3). This was likely the result of *G. mucronatus* efficiently consuming diatoms in the one species treatment. In contrast, grazer interactions in the multi-species community, may have reduced *G. mucronatus'* ability to consume diatoms and, consequently, resulted in higher and more variable concentrations of representative FAs (i.e. $C_{20:4} + C_{20:5}$, $C_{20:5\omega3} : C_{22:6\omega3}$). While diatom FAs were less variable in the one-species treatment, dinoflagellate FAs ($C_{22:5} + C_{22:6}$) were variable in the five-species community ((Budge and Parrish 1998)Table 2). It is possible that algal sources of C_{22} PUFA were more efficiently grazed in the mixed species community than in the monoculture. Overall, these data suggested that grazer species richness did not consistently influence the variance in algal contributions to SOM.

Combined, our results indicated that grazer community composition (identity and richness) were important determinants of SOM composition. Despite the high biomass of *G. mucronatus*, relative to the minor grazers in the five species treatment, SOM patterns were not controlled solely by this species. Instead, minor grazers moderated the effects of the more abundant *G. mucronatus* and may have disproportionately affected SOM composition. Consequently, it is important to consider the entire grazer community rather than focus on the most abundant species (Jernakoff and Nielsen 1997; Matthiessen et al. 2007; Jaschinski and Sommer 2008).

Bottom-up and top-down controls on SOM composition.

Effects of nutrients and predators on primary producers and grazers in this experiment (Chapter 4) also affected SOM composition. For instance, nutrients increased the relative abundance of labile FAs (PLFA:TFA) in the sediment (Fig. 2; Table 2). Thus, algal growth, stimulated by nutrient enrichment, increased the lability and quality of SOM. Curiously, abundance of sediment microbial and algal FAs ($C_{12:0} + C_{14:0}$) was lower in nutrient enriched treatments (Fig. 3; Table 2). Predators increased sediment bacterial FA abundance (BrFA; Fig. 3; Table 2), possibly by increasing SOM lability, physically altering sediment conditions, or both. Previous studies demonstrated that grazers can stimulate sediment microbes by fragmenting POM and increasing surface area, by changing the chemical composition of OM, by irrigation and sediment resuspension which reduce build-up of metabolites, etc. (see papers by Aller; Lee 1991;

(Zimmer et al. 2002; Mermillod-Blondin et al. 2003; Zimmer et al. 2004) While we are unable to resolve the mechanism, the positive effect of predators on bacterial FAs is consistent with previous experiments (Canuel et al. 2007; Spivak et al. 2007) and suggests that food chain length was an important determinant of the sediment heterotrophic bacterial community and microbial processes. Shifts in sediment bacterial activity may have important implications for *Z. marina* and algal productivity. For instance, an increase in sediment bacteria that leads to anoxic conditions and a build up of sulfides may negatively affect seagrass health (Holmer et al. 2006; Calleja et al. 2007; Perez et al. 2007). Alternatively, an increase in sediment bacteria and bacterial activity in aerated surface sediments may lead to higher rates of mineralization and nitrogen availability to benthic microalgae (Eyre and Ferguson 2002; McGlathery et al. 2007).

Although there were few main predator effects on SOM variables, it is possible that the influence of predators was moderated by nutrient enrichment. Evidence for this comes from PCA (Fig. 4). There was little distinction between treatments according predator presence in the absence of nutrients, whereas treatments separated along PC2 according to crab presence in nutrient enriched treatments (Fig. 4). In addition, SOM variables increased by predators (BrFA, SOM C:N) had positive PC 2 loadings (Table 8). This suggests that interactions between bottom-up and top-down controls may produce different SOM patterns than either variable singularly.

Although primary producer abundance and SOM composition were sensitive to bottom-up (i.e. nutrient enrichment) and top-down (i.e. food web composition) controls, grazer effects were generally stronger and more pervasive (see ω^2 values in Table 2). The importance of grazer effects was also supported by the PCA as the one-species treatment was consistently separated from the other treatments despite nutrient enrichment or predator presence. Thus, the grazing community was likely a stronger determinant of ecosystem properties than resource availability and trophic structure. The importance of grazing, relative to nutrient enrichment and predation, is consistent with previous studies and suggests that grazers may play a pivotal ecological role in seagrass habitats (Heck et al. 2000; Hughes et al. 2004; Armitage et al. 2005) and in other systems (Hillebrand et al. 2000; 2002; Borer et al. 2006; Burkepile and Hay 2006).

Experimental comparisons.

Although mesocosm experiments allow for controlled manipulations, their value partly depends on how accurately the system mimics the natural environment. To this end, we tested the interactive effects of nutrient enrichment and seagrass community composition on ecosystem functioning in a mesocosm (Chapter 4; this study) and a field experiment (Douglass et al. 2007; Chapter 3).

In both the mesocosm and field experiments, nutrients increased above-ground algae and reduced *Z. marina* biomass (Douglass et al. 2007; Chapters 3, 4) as often found in other experiments (McGlathery 1995; Hauxwell et al. 2003; Hughes et al. 2004). In addition, changes in the primary producer community were reflected in SOM composition. For instance, nutrients decreased the abundance of FAs deriving from algae and microbes (short-chain FA) in both this mesocosm study and in the field experiment (Chapter 3). The declines in *Z. marina* abundance and benthic algal and microbial production were likely the indirect results of nutrients reducing light availability by stimulating above-ground epiphytic algal growth (Havens et al. 2001; Bintz et al. 2003; Hauxwell et al. 2006).

In both the mesocosm and field experiments, the above-ground animal community strongly influenced primary producers and SOM composition. For instance, grazers decreased epiphytic Chl *a* but had no effect on benthic microalgae. The latter result may seem surprising since grazers reduced benthic Chl *a* in two previous mesocosm experiments (Canuel et al. 2007; Spivak et al. 2007). Instead grazer effects on above-ground algae translated into changes in SOM composition and quality. For example, diatom-derived contributions to SOM, as indicated by $C_{16:1\omega7}$: $C_{16:0}$, and $C_{20:5\omega3}$: $C_{22:6\omega3}$, were reduced in the mixed grazer community of the field experiment (Chapter 3) and in the one species treatment of this study. It was curious that the mixed grazer community did not decrease diatom-derived OM in both the mesocosm and field experiments. However, the mixed grazer treatments in each experiment contained different grazer species. The field experiment included one amphipod (*G. mucronatus*) and two isopods (*Erichsonella attenuata*, *Idotea balthica*) while this study contained five different amphipod species.

These differences in the deposition of plant derived OM may be a function of grazer feeding preferences and interactions. The importance of grazer identity on SOM composition was demonstrated in a previous mesocosm experiment. Duffy and Harvilicz (2001) showed that grazer feeding preferences significantly influenced the accumulation of different types of macroalgae. For example, red algae, such as *Polysiphonia*, increased significantly in treatments with the amphipod *G. mucronatus*. Canuel et al. (2007) found that long chain fatty acids, indicative of vascular plant OM, were more abundant in *G. mucronatus* monocultures while short chain fatty acids, deriving from algae and microbes, were more abundant in monocultures of the isopod *Erichsonella attenuata*. In monoculture, *G. mucronatus* and *E. attenuata* had strong effects on FA sub-groups. SOM composition in grazer species polycultures, however, largely reflected the entire community rather than a single species (Canuel et al. 2007). The averaging effect of a mixed grazer species on SOM composition was largely consistent with the results of this experiment. For example, the abundance of C_{20} PUFA and the ratio $C_{20:5\omega3} : C_{22:6\omega3}$ were lowest in the one grazer species treatment but were more abundant in the mixed species treatments. Thus, despite the high *G. mucronatus* biomass, minor grazers strongly influenced SOM composition. Consequently, it may be important to consider the effects of the entire grazer community rather than the influence of the most abundant species.

SOM composition was also influenced by food chain length in both the field and mesocosm experiments. Abundances of BrFA and MeBrFA (sulfate reducing bacteria) were increased by predators in both experiments. Since this result was congruous with previous mesocosm experiments (Canuel et al. 2007; Spivak et al. 2007), it is likely that predators enhance sediment heterotrophic activity by increasing SOM quality or by physically altering the sediment environment (Mermillod-Blondin et al. 2003; Wardle et al. 2004; Zimmer et al. 2004). For example, crab burrowing may increase oxygen penetration into the sediments, creating more favorable conditions for microbial decomposition (Morrisey et al. 1999; Fanjul et al. 2007). Crabs may also fragment plant detritus increasing the surface area available for grazing. Thus, heavy harvesting of this invertebrate may have implications for rates of OM decomposition and carbon storage in the sediments.

Overall, SOM patterns in the field experiment (Chapter 3) and in this study were largely consistent. While field experiments would be preferable to mesocosm experiments, the mesocosm setup allowed us to control grazer community composition and measure ecosystem metabolism (Chapter 4) which would have been unfeasible in the field. Risk of contamination by non-target grazers species in the field experiment prevented us from manipulating grazer species more precisely than the presence or absence of a mixed species community. Thus the use of complementary mesocosm and field experiments yielded information about grazer species and community effects on SOM composition and demonstrated that nutrient enrichment and trophic structure can rapidly influence SOM quality, despite the presence of previously deposited OM and variance in environmental conditions typical of field situations.

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Table 1. Tests of significance and estimated magnitude of effect (w2) of nutrient enrichment, food chain length, and species richness on grazer community composition. We only analyzed differences in grazer abundance in the one versus the five-species treatments. Data were log transformed to obtain homogeneity of variance. Significant p (<0.05) values are in bold.

Response	Nutrient enrichment			Food chain length			Grazer Richness (1 vs. 5)			Interactions	Model error	
	p	MS	ω^2	*p*	MS	ω^2	*p*	MS	ω^2		MS	ω^2
log *G. mucronatus* biomass +1	**0.004**	0.39	0.19	0.097	0.10	0.04	**0.021**	0.21	0.10		0.03	0.63
log total epifauna biomass + 1	**0.017**	0.29	0.12	**0.046**	0.19	0.07	0.345	0.04	0.00		0.04	0.73

Table 2. Tests of significance and estimated magnitude of effects (ω^2) of nutrient enrichment, food chain length, and grazer community on SOM composition. In order to determine whether grazer-free controls and grazer richness levels differed in their effects on the response variable we conducted Student-Newman-Keuls (SNK) analyses; different means are designated by letters. When an interaction was significant, the dataset was divided according to the interaction (i.e. with vs. without nutrients or with vs. without predators) and the ANOVA was run again. Significant interactions are followed by the *p* value for significance and the mean squared in parentheses. N refers to nutrient enrichment; G to grazer community; P to predators. Fatty acid analyses were conducted on abundance normalized to sediment (ng g^{-1}). See text for description of fatty acid organic matter sources.

Response		Nutrient enrichment			Food chain length			Grazer community			Interactions	Model error		SNK
		p	MS	ω^2	*p*	MS	ω^2	*p*	MS	ω^2		MS	ω^2	
Total FA		0.242	2.80E+08	0.01	0.251	2.70E+08	0.00	**0.002**	1.19E+09	0.17		1.97E+08	0.88	$0^a1^b3^a5^a$
PLFA		0.838	208244.11	0.00	0.317	5053530.36	0.00	0.109	10709661.01	0.04		4883030.50	0.97	$0^{ab}1^b3^{ab}5^a$
PLFA : TFA		**0.022**	0.00	0.05	0.967	0.00	0.00	**0.002**	0.01	0.15		0.00	0.76	$0^a1^b3^a5^a$
$C_{12:0} + C_{14:0}$		**0.033**	3.38E+06	0.05	0.531	2.74E+05	0.00	0.095	1.58E+06	0.05		6.80E+05	0.96	$0^a1^a3^a5^a$
$\Sigma(C_{24:0} - C_{30:0})$		0.829	7.69E+04	0.00	0.161	2.03E+06	0.01	0.768	3.75E+05	0.00		9.86E+05	1.03	$0^a1^a3^a5^a$
$C_{20:5} + C_{20:4}$		0.992	7.83E+01	0.00	0.979	5.31E+02	0.00	**<0.001**	2.82E+07	0.58		7.79E+05	0.44	$0^a1^b3^c5^d$
$C_{22:6} + C_{22:5}$		0.187	7.74E+04	0.00	0.410	2.96E+04	0.00	**<0.001**	1.90E+06	0.63		4.25E+04	0.38	$0^a1^b3^a5^a$
BrFA		0.095	8.16E+06	0.02	0.066	1.00E+07	0.03	**0.010**	1.24E+07	0.12		2.75E+06	0.90	$0^a1^a3^{ab}5^b$
odd BrFA*		0.142	2.90E+06	0.01	**0.031**	6.75E+06	0.05	**0.006**	6.56E+06	0.13		1.31E+06	0.87	$0^a1^a3^{ab}5^b$
log even BrFA†		0.108	1.20E+00	0.02	0.095	1.31E+00	0.02	0.052	1.27E+00	0.07		4.40E-01	0.96	$0^a1^a3^a5^a$
Me BrFA§		0.115	3.51E+04	0.02	**0.038**	6.29E+04	0.05	0.145	2.58E+04	0.03		1.33E+04	0.98	$0^a1^a3^a5^a$
$C_{16:1\omega7} : C_{16:0}$		**0.004**	0.71	0.05	0.550	0.03	0.00	**<0.001**	1.72	0.42	NxG 0.023 (0.27)	0.07	0.49	$0^a1^b3^a5^a$
	nutrients				0.637	0.02	0.00	**0.002**	0.78	0.48		0.09	0.59	$0^a1^b3^a5^a$
	no nutrients				0.182	0.13	0.03	**<0.001**	1.18	0.72		0.05	0.27	$0^a1^b3^a5^a$
$C_{20:5\omega3} : C_{22:6\omega3}$		0.250	12.42	0.00	0.318	9.33	0.00	**<0.001**	835.14	0.72	NxG 0.013 (38.15)	9.04	0.21	$0^a1^b3^c5^d$
	nutrients				0.091	22.02	0.01	**<0.001**	466.30	0.86		6.81	0.12	$0^a1^b3^a5^a$
	no nutrients				0.948	0.05	0.00	**<0.001**	420.49	0.73	PxG 0.012 (61.34)	11.58	0.19	$0^a1^b3^c5^c$
	crabs				0.972	0.01	0.00	**<0.001**	349.88	0.82		7.68	0.19	$0^a1^b3^a5^c$
	no crabs				0.151	23.85	0.01	**<0.001**	562.90	0.79	NxG 0.021 (45.35)	10.40	0.15	$0^a1^b3^c5^d$

* iso-, anteiso- $\Sigma(C_{13:0} + C_{15:0} + C_{17:0} + C_{19:0})$

† iso- $(C_{14:0} + C_{16:0})$

§ 10Me17:0 + 10Me19:0

Table 3. Results from Levene's test of homogeneity of variance for fatty acid biomarker composition. Grazer richness treatments (i.e. 1 or 5 species) are listed in the Variance column according to whether the treatments were more or less variable relative to each other. The mean and standard deviation (SD) are listed for each treatment as well as the p for the Levene's test. See text for description of fatty acid organic matter sources. Fatty acid analyses were conducted on abundance normalized to dry sediment (ng g^{-1}).

Response	Variance			1 grazer		5 grazers		Levene's HOV
	Less		More	mean	S.D.	mean	S.D.	p
Total FA		=		24057.71	11214.17	49379.96	16191.87	0.467
PLFA : TFA		=		0.17	0.03	0.13	0.02	0.565
PLFA		=		4044.31	1807.35	6546.20	2372.89	0.128
$C_{12:0} + C_{14:0}$		=		1436.41	812.43	2300.15	964.05	0.745
$\Sigma(C_{24:0} - C_{30:0})$		=		2447.22	1088.83	2830.69	996.86	0.242
$C_{20:5} + C_{20:4}$	1	<	5	350.81	199.13	4231.04	1125.35	**0.006**
$C_{22:6} + C_{22:5}$	5	<	1	1058.60	344.06	272.17	106.98	**0.001**
BrFA		=		3096.35	1513.49	5150.83	2102.11	0.392
odd BrFA*		=		2307.47	1141.82	3654.77	1347.07	0.610
log even BrFA†		=		6.17	0.59	6.91	0.62	0.754
Me BrFA§		=		235.69	110.58	297.43	126.90	0.903
$C_{16:1\omega7} : C_{16:0}$	1	<	5	0.00	0.00	0.88	0.08	**0.001**
$C_{20:5\omega3} : C_{22:6\omega3}$	1	<	5	0.00	0.00	20.81	4.17	**<0.001**

* iso-, anteiso- $\Sigma(C_{13:0} + C_{15:0} + C_{17:0} + C_{19:0})$

† iso- $(C_{14:0} + C_{16:0})$

§ 10Me17:0 + 10Me19:0

Table 4. Results of regression analyses of fatty acid biomarker groups against the biomass of the major primary producers. The coefficient indicates the directionality of the relationship. Partial r^2 calculated by dividing the type III SS by the corrected total SS of the model. See text for description of fatty acid organic matter sources. Analyses were conducted on fatty acid abundance normalized to dry sediment ($ng\ g^{-1}$).

Response	*Zostera marina* (AFDM, g)			Macroalgae (AFDM, g)			Epiphytic Chl *a* ($\mu g\ cm^{-2}$)			Total Model
	Coefficient	Partial r^2	*p*	Coefficient	Partial r^2	*p*	Coefficient	Partial r^2	*p*	r^2
Total FA	-1514.08	0.19	**0.002**	-178.73	0.01	0.515	1052.53	0.03	0.237	0.23
PLFA	-146.65	0.08	**0.047**	-35.84	0.01	0.400	206.90	0.05	0.136	0.14
PLFA : TFA	0.00	0.07	0.088	0.00	0.01	0.485	0.00	0.01	0.488	0.09
$C_{12:0} + C_{14:0}$	-53.56	0.08	0.054	-18.09	0.03	0.262	37.40	0.01	0.470	0.12
$\Sigma(C_{24:0} - C_{30:0})$	-46.47	0.05	0.139	-9.28	0.01	0.612	97.13	0.06	0.104	0.11
$C_{20:5} + C_{20:4}$	-186.71	0.29	**<0.001**	-3.84	0.00	0.884	23.71	0.00	0.780	0.29
$C_{22:6} + C_{22:5}$	28.51	0.10	**0.035**	-11.74	0.05	0.137	16.89	0.01	0.501	0.16
Branched FA	-111.96	0.16	**0.004**	-39.30	0.06	0.008	80.54	0.02	0.259	0.24
odd BrFA*	-111.96	0.16	**0.004**	-39.30	0.06	0.079	80.54	0.02	0.259	0.24
log even BrFA†	-0.06	0.16	**0.003**	-0.02	0.06	0.071	0.09	0.09	**0.022**	0.31
Me BrFA§	-5.23	0.04	0.171	-2.47	0.03	0.272	1.00	0.00	0.889	0.07
$C_{16:1\omega7} : C_{16:0}$	-0.02	0.02	0.319	0.00	0.01	0.624	-0.03	0.02	0.315	0.05
$C_{20:5\omega3} : C_{22:6\omega3}$	-1.02	0.30	**<0.001**	0.05	0.00	0.700	-0.04	0.00	0.932	0.31

* iso-, anteiso- $\Sigma(C_{13:0} + C_{15:0} + C_{17:0} + C_{19:0})$

† iso- $(C_{14:0} + C_{16:0})$

§ 10Me17:0 + 10Me19:0

Table 5. Results of regression analyses of fatty acid biomarker groups against the biomasses of *G. mucronatus* and minor grazers. The coefficient indicates the directionality of the relationship. Partial r^2 calculated by dividing the type III SS by the corrected total SS of the model. See text for description of fatty acid organic matter sources. Analyses were conducted on fatty acid abundance normalized to dry sediment (ng g^{-1}).

Response	*G. mucronatus* (mg)			log Minor grazers (mg)			Total Mode
	Coefficier	Partial r^2	*p*	Coefficient	Partial r^2	*p*	r^2
Total FA	-3.96	0.13	**0.036**	7288.24	0.14	**0.026**	0.27
PLFA	-0.28	0.03	0.350	653.14	0.06	0.192	0.09
PLFA : TFA	0.00	0.13	**0.020**	-0.02	0.23	**0.003**	0.36
$C_{12:0} + C_{14:0}$	-0.20	0.13	**0.042**	253.16	0.07	0.136	0.20
$\Sigma(C_{24:0} - C_{30:0})$	-0.14	0.05	0.270	63.59	0.00	0.772	0.05
$C_{20:5} + C_{20:4}$	-0.32	0.08	0.055	1153.65	0.34	**<0.001**	0.42
$C_{22:6} + C_{22:5}$	0.05	0.04	0.159	-289.80	0.42	**<0.001**	0.46
Branched FA	-0.48	0.13	**0.045**	434.97	0.04	0.277	0.17
odd BrFA*	-0.35	0.14	**0.038**	290.50	0.03	0.299	0.18
log even BrFA†	0.00	0.16	**0.029**	0.14	0.04	0.254	0.20
Me BrFA§	-0.02	0.09	0.123	-3.00	0.00	0.910	0.09
$C_{16:1w7} : C_{16:0}$	0.00	0.16	**0.005**	0.27	0.31	**<0.001**	0.47
$C_{20:5w3} : C_{22:6w3}$	0.00	0.06	**0.018**	7.95	0.61	**<0.001**	0.66

* iso-, anteiso- $\Sigma(C_{13:0} + C_{15:0} + C_{17:0} + C_{19:0})$

† iso- $(C_{14:0} + C_{16:0})$

§ 10Me17:0 + 10Me19:0

Table 6. Names and sources of fatty acid (FA) groups analyzed in this experiment.

Fatty Acid (FA) Group		Likely source	Reference
Short chain FA	$C_{12:0} + C_{14:0}$	Algae and microbes	Viso and Marty 1993
C_{20} Polyunsaturated FA	$C_{20:4} + C_{20:5}$	Diatoms	Viso and Marty 1993; Budge and Parrish 1998
C_{22} Polyunsaturated FA	$C_{22:5} + C_{22:6}$	Dinoflagellates	Viso and Marty 1993; Budge and Parrish 1998
Branched FA	iso, anteiso odd $\Sigma(C_{13:0} - C_{19:0})$	Heterotrophic bacteria	Volkman et al. 1980

Table 7. Results from regression analyses of principle components (PC) against the major primary producer groups. The coefficient indicates the directionality of the relationship. Partial r^2 was calculated by dividing the type III SS by the corrected SS of the model.

PC	*Zostera marina* (AFDM, g)			Macroalgae (AFDM, g)			Epiphytic Chl *a* ($\mu g\ cm^{-2}$)			Total Model
	Coefficient	Partial r^2	*p*	Coefficient	Partial r^2	*p*	Coefficient	Partial r^2	*p*	r^2
PC1	-0.30	0.27	**<0.001**	-0.05	0.02	0.260	0.15	0.02	0.254	0.31
PC2	-0.12	0.11	**0.029**	0.05	0.05	0.136	-0.07	0.01	0.504	0.16

Table 8. Loadings of principal components 1 (PC1) and 2 (PC2) for concentrations of total fatty acid (TFA) groups. Fatty acids are expressed as abundance normalized to dry sediment (ng g^{-1}). See text for description of organic matter sources of fatty acids.

Variable	PC1	PC2
SOM C:N (mol:mol)	0.02	0.11
TFA	0.39	0.11
PLFA : TFA	-0.17	0.25
Monounsaturated FA	0.37	-0.15
$C_{12:0} + C_{14:0}$	0.35	0.22
$\Sigma(C_{24:0} - C_{30:0})$	0.25	0.37
$C_{20:5} + C_{20:4}$	0.34	-0.19
$C_{22:6} + C_{22:5}$	-0.11	0.49
odd BrFA*	0.35	0.23
log even BrFA†	0.33	0.18
Me BrFA§	0.21	0.19
$C_{16:1\omega7} : C_{16:0}$	0.20	-0.40
$C_{20:5\omega3} : C_{22:6\omega3}$	0.23	-0.39

* iso-, anteiso- $\Sigma(C_{13:0} + C_{15:0} + C_{17:0} + C_{19:0})$

† iso- $(C_{14:0} + C_{16:0})$

§ 10Me17:0 + 10Me19:0

Figure Captions.

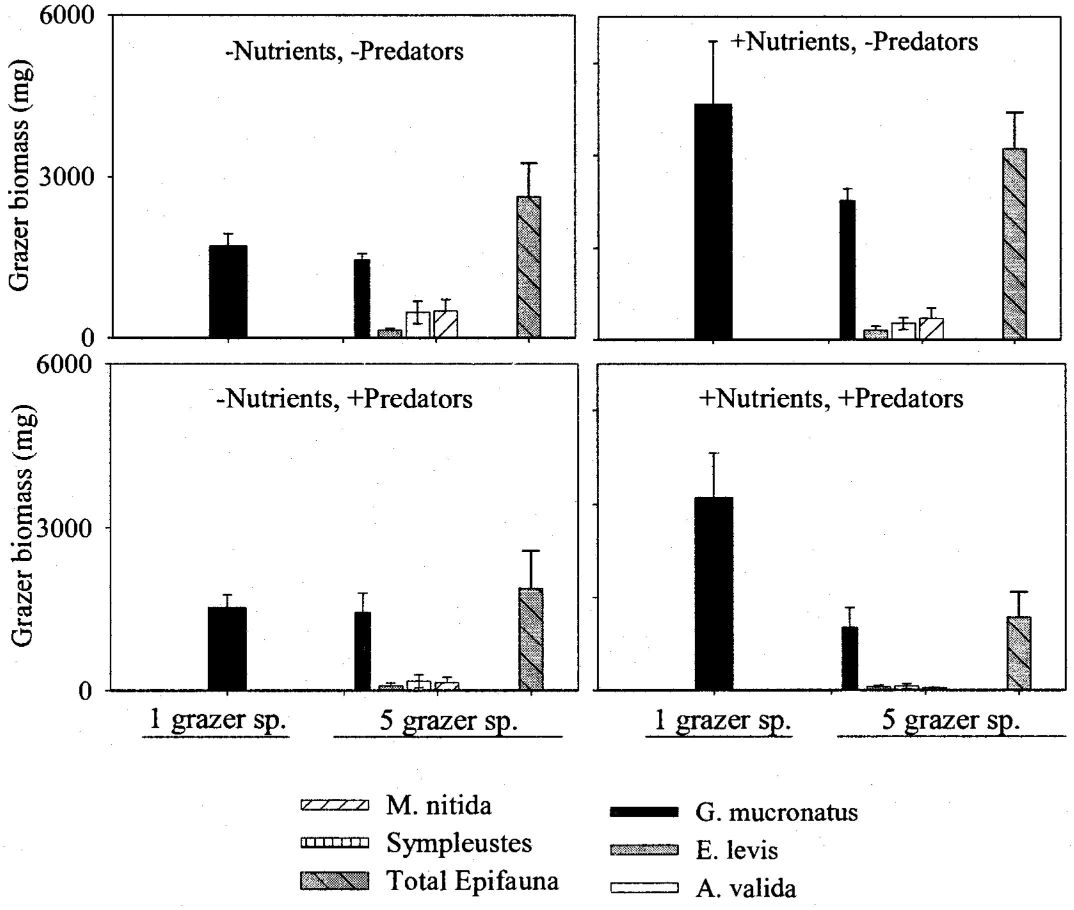
Figure 1. Biomass distribution of individual grazer species. Results are only presented for the one and five species treatments since those contained grazer communities of constant composition while the three grazer treatment contained random combinations of species.

Figure 2. Effects of nutrient enrichment, food chain length, and the grazer community on the abundances of total fatty acids (TFA) and phospholipid linked fatty acids (PLFA) as well as the ratio PLFA:TFA. Results are presented for fatty acid abundance normalized to dry sediment (ng g^{-1}). See text for organic matter source assignment of each fatty acid biomarker subgroup.

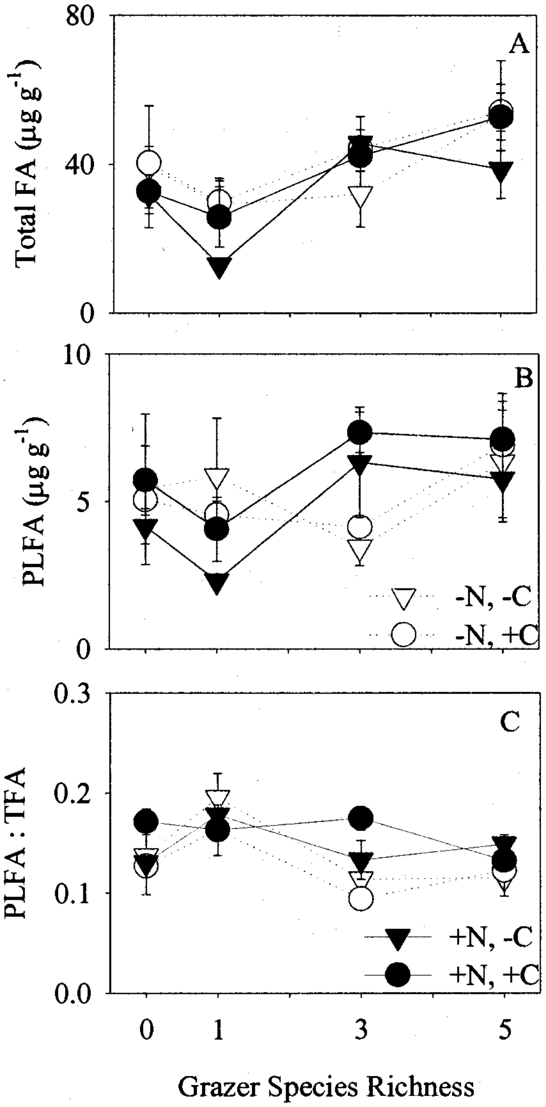
Figure 3. Effects of nutrient enrichment, food chain length, and the grazer community TFA sub-classes. (A) Short-chain FA ($C_{12:0} + C_{14:0}$) abundance was reduced by nutrients and grazers. (B) C_{20} PUFA ($C_{20:4}$+$C_{20:5}$), representative of diatom OM, was least abundant in the one species treatment. (C) C_{22} PUFA ($C_{22:5}$+$C_{22:6}$), common in dinoflagellates, was more abundant in the grazer monoculture than the polycultures. (D) Branched FA (i, a $\Sigma(C_{13:0} - C_{19:0})$), from heterotrophic bacteria, were increased by predators and grazers. (E). $C_{20:5\omega3}$: $C_{22:6\omega3}$, indicative of diatom OM, was least abundant in the one-species treatments. Results are presented for fatty acid abundance normalized to dry sediment (ng g^{-1}).

Figure 4. Principal component scores for total fatty acid groups in treatments with and without nutrients. PC2 separated the grazer monoculture treatments from the grazer-free controls and three and five species treatments. PC1 tended to separate the treatments with three or five grazer species from the monocultures and controls; this effect was strongest in nutrient treatments.

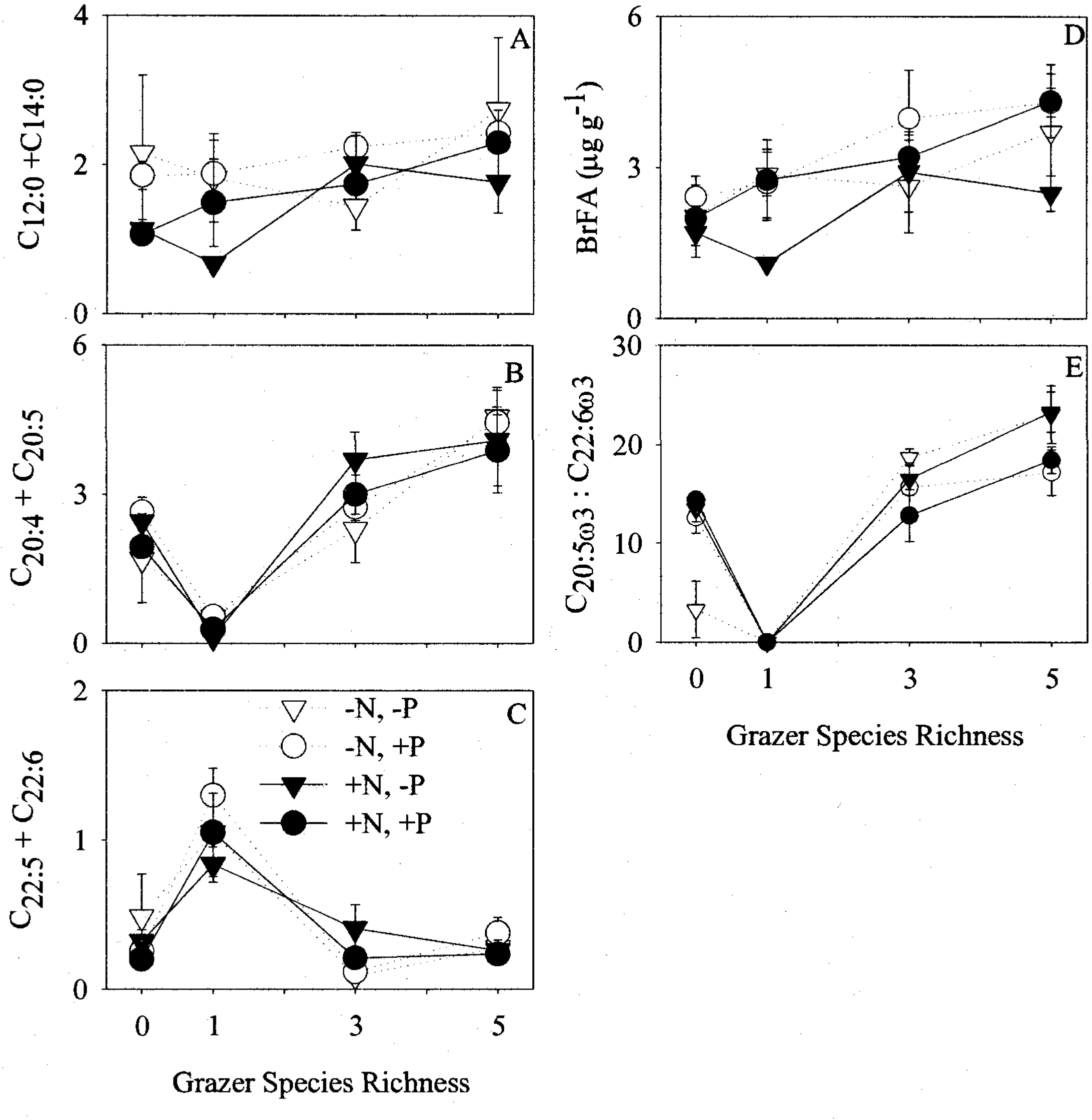
Spivak et al. Fig. 1



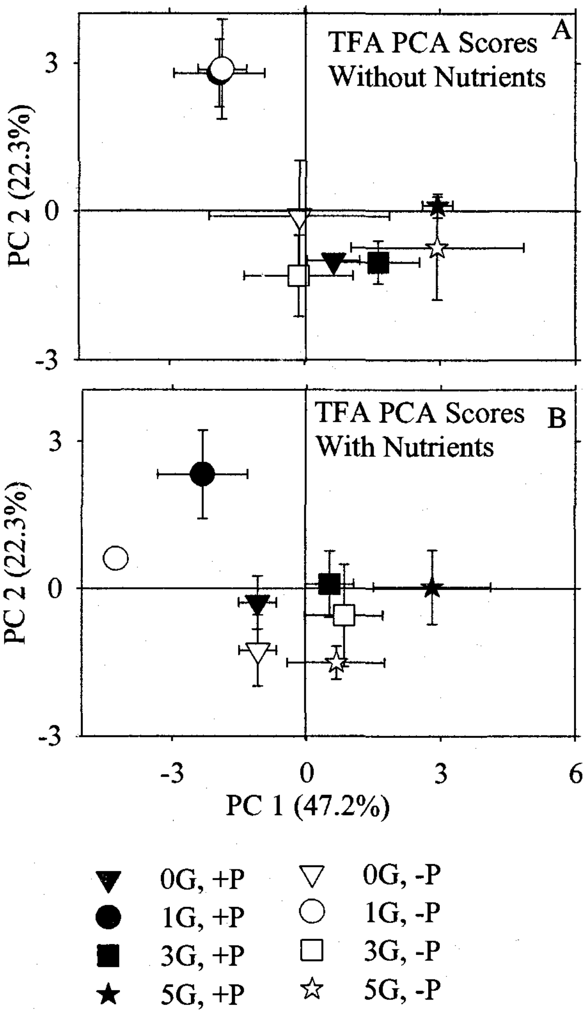
Spivak et al. Fig. 2



Spivak et al. Fig. 3



Spivak et al. Fig. 4



Chapter Six: A Summary

Amanda C. Spivak

Introduction.

The rapid loss of global biodiversity combined with changing environmental conditions has spurred research investigating interactions between biodiversity (Chapin et al. 1998; Balvanera et al. 2006; Bunker and Naeem 2006), community structure (Chase 2003; Burkepile and Hay 2006; Byrnes et al. 2006), and ecosystem functioning (Tilman et al. 2001; Downing 2005; Hooper et al. 2005). Changes in above-ground plant and animal communities that influence ecosystem functioning may also affect processes in soils and sediments (Wolters 2000; Liiri et al. 2002; Heemsbergen et al. 2004; Wardle et al. 2004). Detrital organic matter (OM) produced by above-ground communities often serves as substrate to below-ground organisms and, therefore, functionally links the two communities. The quality of sediment organic matter (SOM) is a partial determinant of sediment bacterial activity (Boschker and Cappenberg 1998; Holmer et al. 2004; Bouillon and Boschker 2006). Thus, changes in SOM quality that influence the sediment microbial community may have implications for nutrient cycling and regeneration. Thus, a goal of my dissertation was to address the role of SOM as a link between above- and below-ground communities. I tested the interactive effects of above-ground community composition and resource availability on (1) SOM quality; and (2) ecosystem metabolism and nutrient dynamics in a seagrass habitat. I used a seagrass (*Zostera marina*) ecosystem as a model system because (1) the animal and plant communities are well studied (Valentine and Heck 1999; Duffy 2006; Heck and Valentine 2006); and (2) seagrass habitats are commonly influenced by perturbations that affect resource availability (i.e. eutrophication) and trophic structure (i.e. fishing) (Cloern 2001; Orth et al. 2006). The results from my dissertation will increase our understanding of seagrass ecosystem functioning and will better elucidate the role of SOM as a link between above- and below-ground communities.

Experimental Design.

I examined the effects of resource availability and food web composition on seagrass ecosystem functioning in two mesocosm experiments and one field experiment. The first mesocosm experiment varied light levels, food chain length (i.e. predator presence), and grazer species richness (0, 2, or 4 species) in a factorial design (Chapter 2). This experiment ran for six weeks during Summer 2003. At the conclusion of this experiment I analyzed changes in gross ecosystem production (GEP), primary producer biomass, and bulk SOM content and composition. The second mesocosm experiment manipulated nutrient levels, food chain length, and grazer species richness (0, 1, 3, or 5 species) in a factorial design (Chapters 4-5). This experiment lasted 5 weeks in Summer 2006. I measured flux rates of dissolved oxygen (DO), dissolved inorganic nitrogen (DIN), and phosphate as well as changes in primary producer and grazer biomass and SOM composition. The field experiment had a similar design to the second mesocosm experiment; except that the presence (not richness) of the grazer community was varied (Chapter 3). The design of the field experiment was less complex that those of the mesocosm experiments due to the difficulty in maintaining grazer treatments and preventing contamination by non-target grazers. Field cages were situated in an eelgrass (*Zostera marina*) bed at Goodwin Islands in the York River, VA. This experiment ran for 4 weeks during Summer 2005. At the end of the field experiment I analyzed primary producer abundance and SOM composition. In all three experiments, SOM composition was evaluated using fatty acid (FA) biomarkers. Please see the previous chapters for a more detailed explanation of FA biomarkers and their use. The remainder of this chapter is devoted to describing similarities and differences in the results of the three experiments and to describing the conclusions from this dissertation.

Discussion.

In general, grazer identity and community composition were stronger the determinants of FA composition than resource levels and predator presence. Predator effects on SOM composition were generally weak, suggesting that above-ground trophic cascades may not consistently affect plant contributions to SOM. Finally, resource identity was important; light availability was a stronger determinant of SOM composition than nutrient levels. The presence of interactive effects between food web composition and resource levels indicates that these factors should not be considered in isolation.

Grazers.

Grazers reduced algal biomass in all three experiments but only reduced *Z. marina* biomass in mesocosm experiment 2 (Tables 1, 2; Chapters 2-4). Grazer effects on the primary producer community often translated into changes in SOM composition. In mesocosm experiment 1, grazers reduced macroalgae and benthic Chl *a* as well as the relative abundance of algal and microbial FA ($C_{12:0} + C_{14:0}$; Table 1; Fig. 1). In mesocosm experiment 2, grazers reduced epiphytes and the relative abundance of FAs deriving from diatoms ($C_{20:4} + C_{20:5}$; Table 2). Although grazers strongly influenced both primary producer abundance and SOM composition, patterns of FA abundance were not consistent in grazer treatments across experiments (Tables 1, 2). For instance, the relative abundance of long chain FA (vascular plant OM) was decreased by grazers in ambient light treatments of mesocosm 1 ($C_{24:0}$; Chp. 2), was increased by grazers in the field experiment ($C_{24:0}$-$C_{28:0}$; Chp.3), and was unaffected by grazers in mesocosm 2 ($C_{24:0}$-$C_{28:0}$; Chp. 5). The relative abundance of short chain FAs (algal and microbial OM) was decreased by grazers in mesocosm experiment 1 ($C_{12:0}$+$C_{14:0}$; Chp. 2) but was increased by grazers in the field experiment ($C_{12:0}$+$C_{14:0}$; Chp. 3; Tables 1, 2; Fig. 1). While this is curious, differences in SOM composition between experiments may be the result of grazer community composition rather than grazer species richness. For example, mesocosm experiment 1 included two amphipod species (*Ampithoe longimana, G. mucronatus*) and two isopods (*Idotea baltica* and *Erichsonella attenuata*). The grazer community in the field experiment consisted of *G. mucronatus, I. baltica,* and *E. attenuate*. Finally, in mesocosm experiment 2, I used five amphipod species: *G. mucronatus, Elasmopus levis*, *Melita nitida*, *Ampithoe valida*, and *Sympleustes* spp. While there was some overlap in species composition between experiments (mainly *G. mucronatus*), none of the experiments used the same grazer community. Thus, differences in SOM patterns between experiments may be due to grazer community composition and the diet preferences of particular grazer species.

Previous studies demonstrated that grazer identity is important to multiple ecosystem properties (Duffy et al. 2001; Matthiessen et al. 2007; Jaschinski and Sommer 2008), including SOM composition (Duffy et al. 2003; Canuel et al. 2007). Canuel et al. (2007) found that the relative abundance of long chain FA (vascular plant OM) and short chain FA (algal and microbial OM) was higher in *G. mucronatus* and *E. attenuate* monocultures, respectively. While these two grazer species had strong effects on FA subgroups in monoculture, SOM composition largely reflected the entire community, rather than a single species, in grazer polycultures (Canuel et al. 2007). This suggests that grazer diversity may weaken trophic effects that extend to SOM composition (Finke and Denno 2002; 2004). The averaging effect of a mixed grazer species on SOM composition was largely consistent with the results of mesocosm experiment 2 (Chp. 5). For example, C_{20} PUFA abundance and the ratio $C_{20:5\omega3}$: $C_{22:6\omega3}$ were lowest in the one grazer species treatment but were more abundant in the mixed species treatments. Consequently, it is important to consider the effects of the entire grazer community rather than the influence of the most abundant species.

Another trend was that multi-species grazer communities tended to have more similar SOM composition than treatments without grazers or with only one species. For instance, in mesocosm experiment 2, principal component (PC) scores of treatments with two- or four-grazer species were more similar to each other than either was to the grazer free controls in ambient light treatments (Chapter 2; Fig. 2). In mesocosm experiment 2, PC scores of treatments with three and five grazer species were consistently different from the scores of one grazer treatments (Chapter 5; Fig. 2). This trend was more evident with nutrient enrichment. However, it is important to note that *G. mucronatus* was the only grazer in the monoculture treatments and it was the most abundant grazer in the five species polyculture. Despite the high abundance of *G. mucronatus*, SOM patterns in the five species community did not resemble SOM patterns in the monocultures. This suggested that grazer identity rather than biomass is important to ecosystem properties (Duffy et al. 2001; Canuel et al. 2007; Jaschinski and Sommer 2008).

Predators.

In all three experiments, I initially predicted that the presence of crab predators would initiate a trophic cascade, whereby grazer biomass would be reduced and primary producer abundance increased. However, crab predators only had a positive effect on macroalgal biomass in mesocosm experiment 1 (Table 1; Chapter 2). This was somewhat surprising and suggested that the effect of predators may depend on the species composition of the grazer community. For instance, crabs sharply reduced total epifaunal biomass in mesocosm experiment 1 but not in mesocosm experiment 2 (Fig. 3). Thus differences in grazer community composition and grazer species susceptibility to predation by crabs likely affected the propagation of predator affects to lower trophic levels.

Positive predator effects on plants and algae may translate into increased labile algal contributions to SOM which could, in turn, stimulate sediment bacterial activity. For instance, Canuel et al. (2007) found higher abundances of polyunsaturated FA (PUFA), indicative of labile algal OM, and branched FA, deriving from heterotrophic bacteria, in treatments with predators. This suggested that predators indirectly influenced sediment biogeochemistry. However, there was no evidence of a positive predator effect on PUFA in any of the experiments described in this dissertation. Instead, predators decreased the relative abundance of PUFA in low light treatments of mesocosm 1 (Chp. 2) and in the field experiment ($C_{22:5} + C_{22:6}$; Chapter 3).. However, in both mesocosm experiments and in the field experiment, predators increased the relative abundance of branched FA (Fig. 4). Instead of increasing labile algal contributions to SOM, predators may have influenced sediment bacteria through other processes such as fragmenting POM and increasing surface area, changing the chemical composition of OM, irrigation and sediment resuspension which reduce build-up of metabolites, etc. (Zimmer et al. 2002; Mermillod-Blondin et al. 2003; Zimmer et al. 2004). Shifts in sediment bacterial activity may have important implications for *Z. marina* and algal productivity. For instance, an increase in sediment bacteria that leads to anoxic conditions and a build up of sulfides may negatively affect seagrass health (Holmer et al. 2006; Calleja et al. 2007; Perez et al. 2007). Alternatively, an increase in sediment bacteria and bacterial activity in aerated surface sediments may lead to higher rates of mineralization and nitrogen availability to benthic microalgae (Eyre and Ferguson 2002; McGlathery et al. 2007). Consequently the positive effect of predators on the bacterial community may have implications for sediment biogeochemistry and the primary producer community.

Resources.

High resource levels increased above-ground macroalgal and epiphytic abundance in all three experiments while only light increased sediment microalgal abundance in mesocosm experiment 1 (Chps. 2-4; Tables 1, 2; (Douglass et al. 2007)). *Z. marina* biomass was increased by high light levels (mesocosm expt. 1; Chapter 2) but was decreased by high nutrient levels (field experiment; Chapter 3; Tables 1, 2). High nutrient levels increased epiphytes early in the field experiment (Douglass et al. 2007) and likely reduced *Z. marina* biomass by reducing light availability.

Changes in the primary producer community were reflected in SOM composition. For instance, algal and microbial fatty acids (FA) ($C_{12:0}$+$C_{14:0}$) were increased by high light availability (mesocosm expt. 1) but were decreased by nutrient enrichment (mesocosm expt. 2 and field expt.; Tables 1, 2; Fig. 1; Chps. 2-3, 5). High nutrient levels may have indirectly reduced algal and microbial FAs in the sediments by increasing shading by above-ground macroalgae. In general, however, the effects of light availability on SOM content and composition were stronger than nutrient enrichment. For example, a greater number of FA sub-groups (i.e. short and long chain FA, branched FA, polyunsaturated FA) were affected by light availability than by nutrient levels (short chain FA and branched FA in the field experiment). In addition, light availability strongly influenced where sediment FA sub-classes clustered in principal components analysis (PCA) while nutrient levels had little influence on FA groupings (Fig. 2; Chapters 2, 5). In ambient light, grazer-free treatments were clearly distinct from communities with two- or four-grazer species (Chp. 2). In low light, though, treatments were not separated by grazer richness but by predator presence or absence (Chp. 2). Combined, these results suggested that, in ambient light, treatments with grazers had more similar SOM compositions than grazer-free controls while, in low light, treatments with predators were more similar to one another than treatments without predators. Nutrient enrichment, however, had little effect on the PCA scores (Chp. 5). The results of these analyses suggested that light availability was a more important determinant of SOM composition than nutrient concentrations.

Although light was a stronger determinant of SOM composition, nutrient enrichment influenced both primary and secondary production as well as plant elemental content and dissolved nutrient fluxes (Chp 4). For instance, while light and nutrients both increased total algae in the mesocosm experiments, only nutrient enrichment extended up a trophic level to increase biomass of the grazer *G. mucronatus* (Fig. 3). The positive effect of nutrients on *G. mucronatus* biomass might have been the result of higher abundance or higher quality of primary producers (i.e., lower C:N; Chp. 4). Consequently, both light and nutrients may be equally important determinants of ecosystem functioning but they may affect different ecosystem properties and processes.

Conclusions.

Overall, food web composition and resource availability were important determinants of seagrass ecosystem metabolism and SOM composition (Fig. 5). Importantly, resource identity had a strong influence on ecosystem nutrient fluxes, animal and plant biomass, and SOM composition. In general, light was a more important determinant of SOM composition than nutrient concentrations. However, nutrient enrichment strongly influenced nutrient storage in biomass and ecosystem metabolism (Chp. 4). Predator effects on SOM composition were generally weak and tended to vary with grazer community composition, suggesting that grazers differed in their susceptibility to predation by blue crabs. Finally, my results indicated that grazer species identity and community composition strongly influenced SOM composition. While individual grazer species may differ in their effects on FA sub-classes, multi-grazer species communities tended to have similar patterns of SOM composition, as indicated by PCA (Fig. 2). In addition to the main effects of resources and food web composition, there were a variety of interactions indicating that seagrass ecosystem functioning is influenced by multiple factors that should not be considered in isolation.

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Table 1. Comparison of results between mesocosm experiments 1 and 2. Resources were light and nutrients in experiments 1 and 2, respectively. Arrows indicate whether resource, grazers, or crabs increased or decreased the response variables. Fatty acid (FA) data are presented as percent of total FA abundance.

	Resource	**Grazers**	**Crabs**
Macroalgae	⇧ ⬆	⇩ ⬇	⇧
Z. marina	⇧	⬇	
Benthic Chl *a*	⇧	⇩	
GEP	NA ⬆	⇩ ⬇	⇧
TFA : TOC	⇧		
%Short chain FA	⇧ ⬇	⇩	⇧
%Long chain FA	⇧		
%Branched FA	⇩	⬆	⇧ ⬆

☐ **Mesocosm Expt. 1** ■ **Mesocosm Expt. 2**

Table 2. Comparison of results between the field experiment and mesocosm experiment 2. Arrows indicate whether nutrients, grazers, crabs increased or decreased plant biomass or fatty acid (FA) response variables. FA data are reported as percent of total FA abundance.

	Nutrients	**Grazers**	**Crabs**
Epiphytes	⇧	⬇ ⇩	
Z. marina	⬇	⇩	⬇
%Short chain FA	⬇ ⇩	⬆	⬇
%Long chain FA		⬆	
%Branched FA	⬆	⇧	⬆ ⇧
%C_{20} PUFA		⬇ ⇩	
%C_{22} PUFA		⇧	⬇
Diatom : Dino.		⬇ ⇩	⬆

■ **Field Expt.** ▨ **Mesocosm Expt. 2**

Figure Captions.

Figure 1. Comparison of short chain fatty acids (FA; $C_{12:0} + C_{14:0}$) abundance across experiments. Both nutrients and light reduced short chain FA, which are indicative of algal and microbial sources of OM. Significant ($p < 0.05$) effects of resources, crab predators, and grazers are indicated in the upper corner of each graph by R, C, or G, respectively. Treatments with predators are circles, without predators are triangles, with resources are closed, without resources are open.

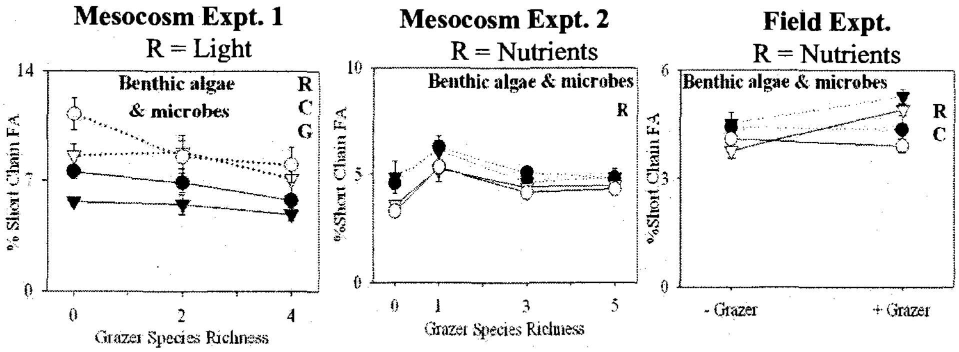
Figure 2. Comparison of PCA scores from two mesocosm experiments, one varying light availability and the other varying nutrient enrichment. In mesocosm experiment 1, circles represent treatments with crab predators and triangles represent treatments without crab predators. Open symbols represent treatments with zero grazers, shaded symbols are 2 grazers, and closed symbols are 4 grazers. In mesocosm experiment 2, triangles are zero grazers, circles one grazer, squares three grazers, and stars five grazers. Open symbols are treatments without crab predators while closed symbols denote treatments with predators.

Figure 3. Comparison of grazer biomass in two mesocosm experiments. Nutrient enrichment increased *G. mucronatus* biomass, suggesting that bottom-up forces may ascend the food web. Light availability, however, did not affect grazer biomass. Significant ($p < 0.05$) effects of resources, crab predators, and grazers are indicated in the upper corner of each graph by R, C, or G, respectively.

Figure 4. Comparison of branched FA abundance across experiments. Predators had a positive effect on branched fatty acids in all three experiments. Significant ($p < 0.05$) effects of resources, crab predators, and grazers are indicated in the upper corner of each graph by R, C, or G, respectively. Treatments with predators are circles, without predators are triangles, with resources are closed, without resources are open.

Figure 5. Comparison of the effects of resource levels, grazer richness, and predator presence on gross ecosystem production and sediment organic matter (SOM) content and composition in mesocosm experiments 1 and 2. Solid lines represent direct effects while broken lines are indirect effects. Dark lines represent main effects while light lines are interactive effects. Short chain fatty acids (FA), representing algal and microbial OM, are $C_{12:0} + C_{14:0}$. Bacterial FAs are iso, anteiso $\Sigma(C_{13:0} + C_{15:0} + C_{17:0} + C_{19:0})$. Polyunsaturated FAs, representing labile algal OM, are $\Sigma(C_{18:4} + C_{20:4} + C_{20:5} + C_{22:5} + C_{22:6})$ except in mesocosm experiment 2 which does not include $C_{18:4}$.

Spivak. Figure 1

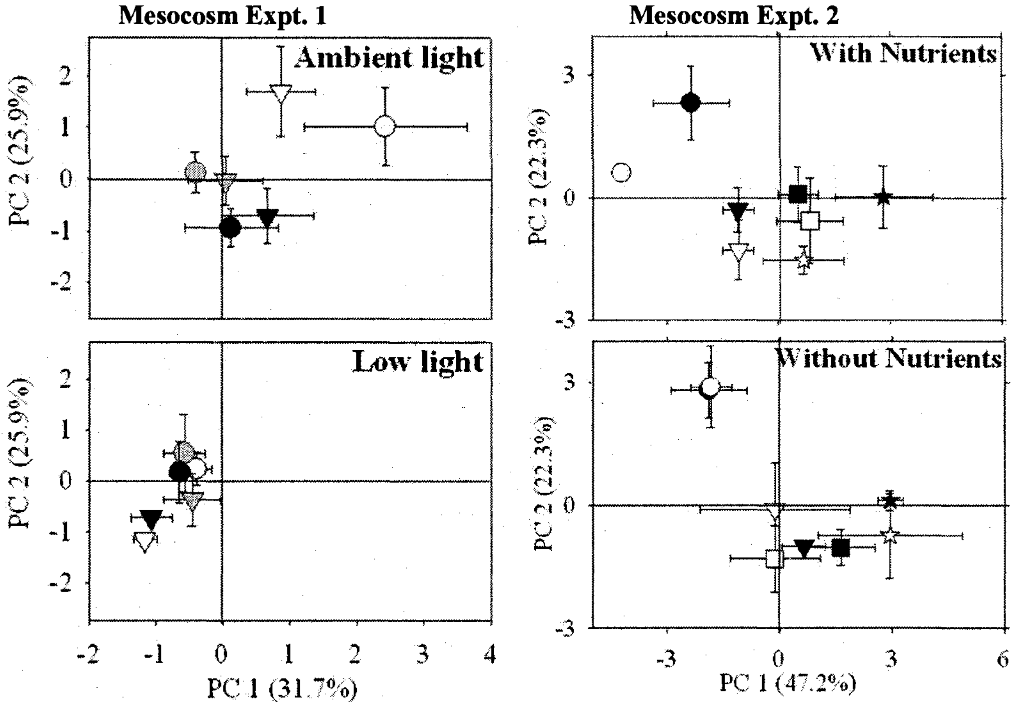


Mesocosm Expt. 1
R = Light

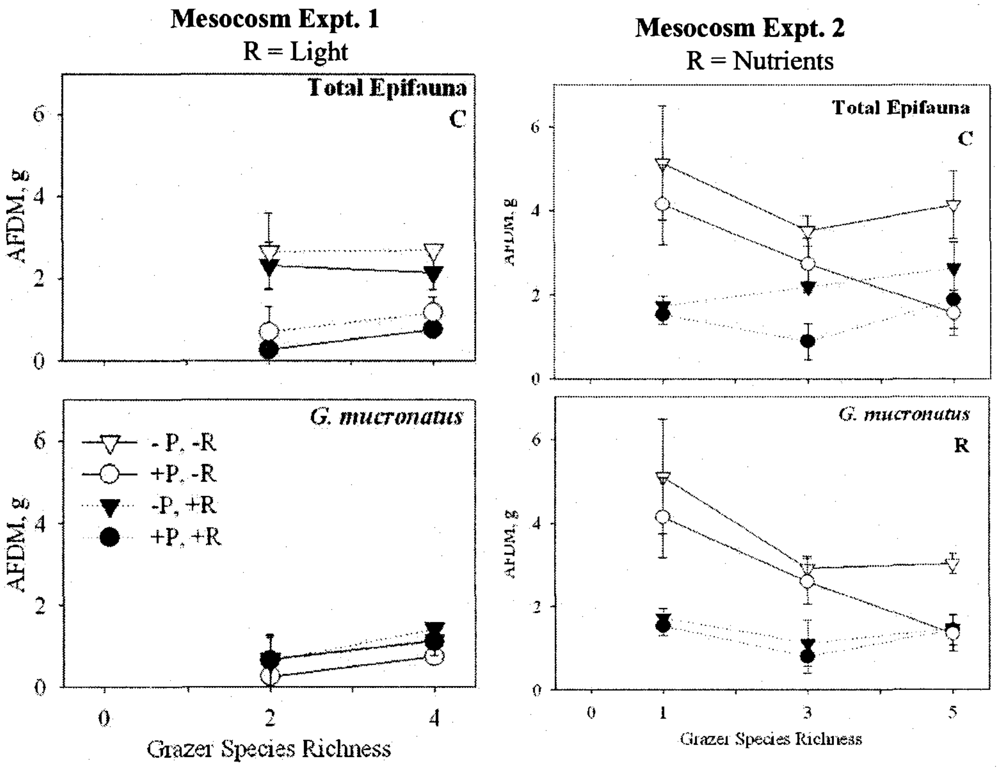
Mesocosm Expt. 2
R = Nutrients

Field Expt.
R = Nutrients

Spivak. Figure 2



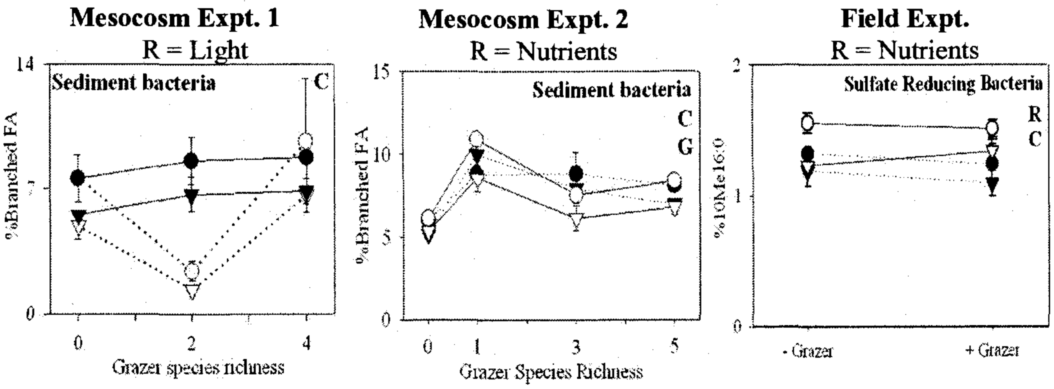
Spivak. Figure 3



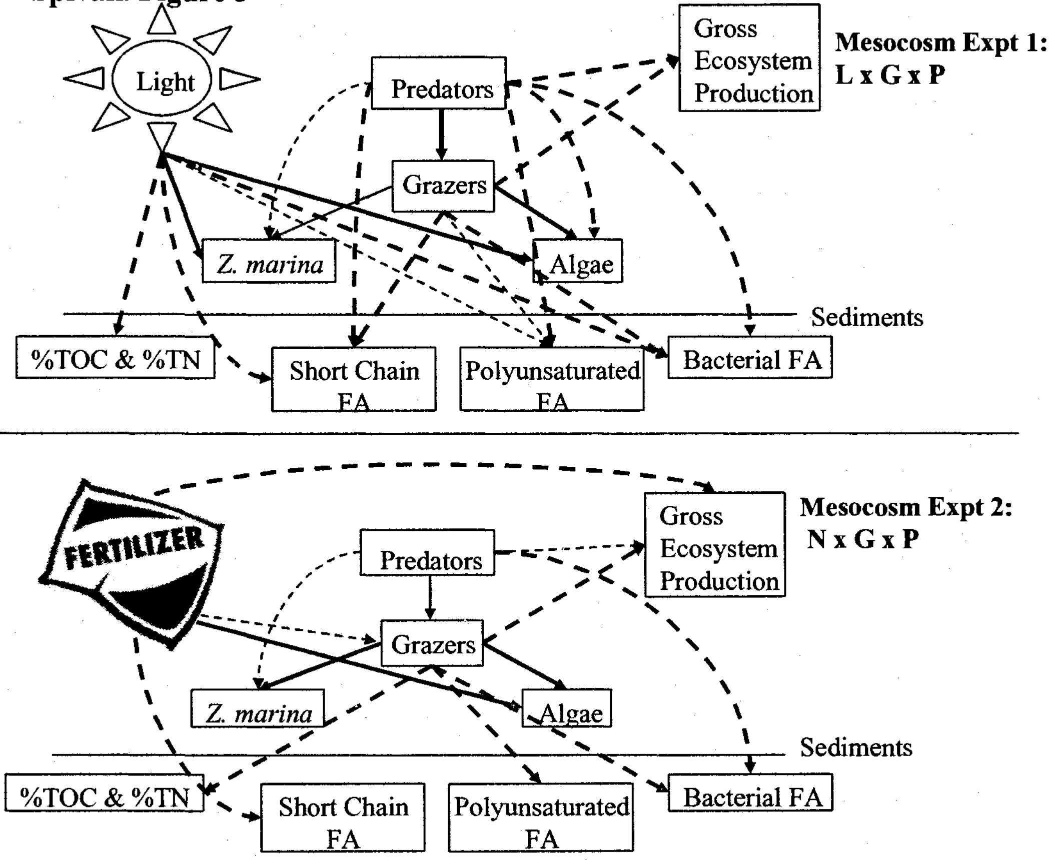
Mesocosm Expt. 1
R = Light

Mesocosm Expt. 2
R = Nutrients

Spivak. Figure 4



Spivak. Figure 5



Mesocosm Expt 1: L x G x P

Mesocosm Expt 2: N x G x P

Appendix 1. Raw DO data from Chapter 2.

L/D	Tank	Cylinder	# spp	grazer	crabs?	L/D	Water Vol (cm^3)	water vol (m^3)	DO at T=0	DO (mg/L) (T=1)	DO (mg/L) (T=2)	DO (mg/L) (T=3)	DO (mg/L) (T=4)	[DO] (mM) T=0	[DO] (mM) T=1	[DO] (mM) T=2	[DO] (mM) T=3	[DO] (mM) T=4	Elapsed Time (h) T = 0	Elapsed Time (h) T =1	Elapsed Time (h) T= 2	Elapsed Time (h) T = 3	Elapsed Time (h) T = 4
L	2	2	0	CON	CRAB	L	141371.67	0.14	13.53	17.61	19.37	18.90		0.44	0.57	0.62	0.61		0.00	0.60	1.48	2.35	
L	4	3	0	CON	CRAB	L	141371.67	0.14	13.46	15.41	17.90	22.10		0.43	0.50	0.58	0.71		0.00	0.60	1.62	2.36	
L	6	6	0	CON	CRAB	L	141371.67	0.14	13.99	15.45	20.29	21.71		0.45	0.50	0.65	0.70		0.00	0.85	1.92	2.46	
L	8	3	0	CON	CRAB	L	141371.67	0.14	10.43	11.86	15.72	18.30		0.34	0.38	0.51	0.59		0.00	0.68	1.80	2.41	
L	10	4	0	CON	CRAB	L	141371.67	0.14	12.46	15.23	17.21	18.93		0.40	0.49	0.56	0.61		0.00	0.65	1.78	2.41	
L	2	4	0	CON	Nocrab	L	141371.67	0.14	11.40	12.65	13.45	18.04		0.37	0.41	0.43	0.58		0.00	0.60	1.53	2.35	
L	4	4	0	CON	Nocrab	L	141371.67	0.14	13.36	16.57	17.30	21.58		0.43	0.53	0.56	0.70		0.00	0.60	1.70	2.38	
L	6	2	0	CON	Nocrab	L	141371.67	0.14	12.91	16.30	19.30	20.77		0.42	0.53	0.62	0.67		0.00	0.80	1.90	2.45	
L	8	6	0	CON	Nocrab	L	141371.67	0.14	12.97	16.22	20.10	22.59		0.42	0.52	0.65	0.73		0.00	0.72	1.87	2.42	
L	10	3	0	CON	Nocrab	L	141371.67	0.14	14.29	13.74	17.75	19.71		0.46	0.44	0.57	0.64		0.00	0.62	1.75	2.38	
L	6	5	2	AE	CRAB	L	141371.67	0.14	10.92	13.03	16.40	17.71		0.35	0.42	0.53	0.57		0.00	0.80	1.88	2.45	
L	10	2	2	AI	CRAB	L	141371.67	0.14	14.03	16.70	18.25	21.78		0.45	0.54	0.59	0.70		0.00	0.63	1.77	2.39	
L	4	6	2	CB	CRAB	L	141371.67	0.14	14.78	17.69	19.10	21.92		0.48	0.57	0.62	0.71		0.00	0.60	1.72	2.38	
L	8	4	2	CE	CRAB	L	141371.67	0.14	13.03	16.62	20.60	22.60		0.42	0.54	0.66	0.73		0.00	0.72	1.87	2.42	
L	2	3	2	GI	CRAB	L	141371.67	0.14	9.76	13.18	16.25	20.10		0.31	0.43	0.52	0.65		0.00	0.60	1.47	2.35	
L	6	4	2	AE	Nocrab	L	141371.67	0.14	11.29	13.81	15.62	17.45		0.36	0.45	0.50	0.56		0.00	0.85	1.93	2.45	
L	10	6	2	AI	Nocrab	L	141371.67	0.14	9.01	9.60	11.47	13.52		0.29	0.31	0.37	0.44		0.00	0.67	1.78	2.41	
L	4	1	2	CB	Nocrab	L	141371.67	0.14	13.40	14.13	16.50	20.11		0.43	0.46	0.53	0.65		0.00	0.57	1.57	2.30	
L	8	5	2	CE	Nocrab	L	141371.67	0.14	9.48	12.05	15.02	17.05		0.31	0.39	0.48	0.55		0.00	0.68	1.83	2.41	
L	2	5	2	GI	Nocrab	L	141371.67	0.14	8.23	9.72	11.75	11.27		0.27	0.31	0.38	0.36		0.00	0.73	1.62	2.35	
L	2	6	6	ALL	CRAB	L	141371.67	0.14	15.47	14.47	18.88	22.90		0.50	0.47	0.61	0.74		0.00	0.62	1.58	2.36	
L	4	2	6	ALL	CRAB	L	141371.67	0.14	10.97	12.72	16.25	20.07		0.35	0.41	0.52	0.65		0.00	0.60	1.67	2.36	
L	6	3	6	ALL	CRAB	L	141371.67	0.14	9.30	11.69	15.15	17.40		0.30	0.38	0.49	0.56		0.00	0.75	1.87	2.43	
L	8	1	6	ALL	CRAB	L	141371.67	0.14	10.26	10.38	14.24	17.12		0.33	0.33	0.46	0.55		0.00	0.68	1.80	2.41	
L	10	1	6	ALL	CRAB	L	141371.67	0.14	10.86	11.44	14.20	18.99		0.35	0.37	0.46	0.61		0.00	0.60	1.73	2.36	
L	2	1	6	ALL	Nocrab	L	141371.67	0.14	7.50	7.94	9.10	10.27		0.24	0.26	0.29	0.33		0.00	0.63	1.50	2.35	
L	4	5	6	ALL	Nocrab	L	141371.67	0.14	7.95	8.52	9.58	11.05		0.26	0.27	0.31	0.36		0.00	0.65	1.67	2.41	
L	6	1	6	ALL	Nocrab	L	141371.67	0.14	8.08	8.70	9.98	11.38		0.26	0.28	0.32	0.37		0.00	0.75	1.85	2.43	
L	8	2	6	ALL	Nocrab	L	141371.67	0.14	8.10	8.73	9.96	11.05		0.26	0.28	0.32	0.36		0.00	0.70	1.85	2.41	
L	10	5	6	ALL	Nocrab	L	141371.67	0.14	8.76	9.19	10.77	11.77		0.28	0.30	0.35	0.38		0.00	0.63	1.77	2.39	
D	2	2	0	CON	CRAB	D	141371.67	0.14	7.15	6.58	5.72	5.33	4.40	0.23	0.21	0.18	0.17	0.14	0.00	0.78	1.62	2.42	3.15
D	4	3	0	CON	CRAB	D	141371.67	0.14	7.77	7.00	6.02	5.16	4.40	0.25	0.23	0.19	0.17	0.14	0.00	0.77	1.57	2.38	2.95
D	6	6	0	CON	CRAB	D	141371.67	0.14	12.72	11.77	9.96	9.15	8.38	0.41	0.38	0.32	0.30	0.27	0.00	0.70	1.47	2.27	2.93
D	8	3	0	CON	CRAB	D	141371.67	0.14	12.45	11.13	9.46	8.49	8.69	0.40	0.36	0.31	0.27	0.28	0.00	0.78	1.60	2.40	3.07
D	10	4	0	CON	CRAB	D	141371.67	0.14	8.50	7.65	6.30	5.66	5.06	0.27	0.25	0.20	0.18	0.16	0.00	0.70	1.50	2.32	2.98
D	2	4	0	CON	Nocrab	D	141371.67	0.14	5.78	5.06	4.30	3.46	2.95	0.19	0.16	0.14	0.11	0.10	0.00	0.78	1.60	2.40	2.93
D	4	4	0	CON	Nocrab	D	141371.67	0.14	5.06	4.79	3.87	3.00	2.45	0.16	0.15	0.12	0.10	0.08	0.00	0.77	1.57	2.38	2.85
D	6	2	0	CON	Nocrab	D	141371.67	0.14	12.72	12.20	11.10	10.63	9.68	0.41	0.39	0.36	0.34	0.31	0.00	0.77	1.53	2.33	3.00
D	8	6	0	CON	Nocrab	D	141371.67	0.14	7.12	6.05	5.22	3.89	3.41	0.23	0.20	0.17	0.13	0.11	0.00	0.80	1.62	2.42	3.08
D	10	3	0	CON	Nocrab	D	141371.67	0.14	10.07	8.15	7.65	6.23	4.75	0.32	0.26	0.25	0.20	0.15	0.00	0.73	1.53	2.35	3.02
D	6	5	2	AE	CRAB	D	141371.67	0.14	6.05	6.32	5.66	4.90	4.35	0.20	0.20	0.18	0.16	0.14	0.00	0.68	1.45	2.25	2.92
D	10	2	2	AI	CRAB	D	141371.67	0.14	6.29	5.49	4.54	3.64	3.20	0.20	0.18	0.15	0.12	0.10	0.00	0.77	1.57	2.38	2.88
D	4	6	2	CB	CRAB	D	141371.67	0.14	11.54	10.77	9.71	9.20	8.71	0.37	0.35	0.31	0.30	0.28	0.00	0.72	1.52	2.33	3.00
D	8	4	2	CE	CRAB	D	141371.67	0.14	11.68	10.62	10.22	9.14	8.55	0.38	0.34	0.33	0.29	0.28	0.00	0.78	1.60	2.40	3.07
D	2	3	2	GI	CRAB	D	141371.67	0.14	8.15	7.36	6.17	4.77	3.30	0.26	0.24	0.20	0.15	0.11	0.00	0.78	1.63	2.43	3.17
D	6	4	2	AE	Nocrab	D	141371.67	0.14	10.60	9.60	7.88	7.19	6.49	0.34	0.31	0.25	0.23	0.21	0.00	0.70	1.47	2.27	2.93
D	10	6	2	AI	Nocrab	D	141371.67	0.14	6.70	6.00	5.12	4.58	4.00	0.22	0.19	0.17	0.15	0.13	0.00	0.72	1.52	2.33	3.00
D	4	1	2	CB	Nocrab	D	141371.67	0.14	10.46	9.32	7.79	6.94	6.98	0.34	0.30	0.25	0.22	0.23	0.00	0.78	1.60	2.40	3.07
D	8	5	2	CE	Nocrab	D	141371.67	0.14	6.55	5.37	3.60	2.70	2.04	0.21	0.17	0.12	0.09	0.07	0.00	0.77	1.58	2.40	3.07
D	2	5	2	GI	Nocrab	D	141371.67	0.14	7.21	6.91	6.37	5.89	5.41	0.23	0.22	0.21	0.19	0.17	0.00	0.78	1.63	2.43	3.15
D	2	6	6	ALL	CRAB	D	141371.67	0.14	6.73	6.33	5.68	4.96	4.35	0.22	0.20	0.18	0.16	0.14	0.00	0.78	1.52	2.32	3.03
D	4	2	6	ALL	CRAB	D	141371.67	0.14	6.32	5.43	4.51	3.66	3.05	0.20	0.18	0.15	0.12	0.10	0.00	0.77	1.57	2.38	2.90
D	6	3	6	ALL	CRAB	D	141371.67	0.14	6.20	5.39	4.66	3.88	3.30	0.20	0.17	0.15	0.13	0.11	0.00	0.77	1.53	2.33	3.00

D	8	1	6	ALL	CRAB	D	141371.67	0.14	13.58	12.76	11.64	11.05	10.61	0.44	0.41	0.38	0.36	0.34	0.00	0.78	1.60	2.40	3.07
D	10	1	6	ALL	CRAB	D	141371.67	0.14	12.10	10.35	9.51	8.90	7.92	0.39	0.33	0.31	0.29	0.26	0.00	0.72	1.52	2.33	3.00
D	2	1	6	ALL	Nocrab	D	141371.67	0.14	6.57	6.20	5.69	5.12	4.56	0.21	0.20	0.18	0.17	0.15	0.00	0.78	1.63	2.43	3.15
D	4	5	6	ALL	Nocrab	D	141371.67	0.14	6.40	5.83	5.23	4.58	4.12	0.21	0.19	0.17	0.15	0.13	0.00	0.77	1.57	2.38	3.08
D	6	1	6	ALL	Nocrab	D	141371.67	0.14	6.60	6.01	5.50	5.00	4.56	0.21	0.19	0.18	0.16	0.15	0.00	0.77	1.53	2.33	3.00
D	8	2	6	ALL	Nocrab	D	141371.67	0.14	6.76	6.10	5.52	4.94	4.46	0.22	0.20	0.18	0.16	0.14	0.00	0.78	1.60	2.40	3.07
D	10	5	6	ALL	Nocrab	D	141371.67	0.14	8.67	8.08	7.43	7.03	6.50	0.28	0.26	0.24	0.23	0.21	0.00	0.72	1.52	2.33	3.00

Appendix 2. Total fatty acid (ng g^{-1}) data from Chapter 2.

Light	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
crabs	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
grazers	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	2	2	2	2	2	6	6	8
Componen	2-2	4-3	6-6	8-3	10-4	2-4	4-4	6-2	8-6	10-3	2–3	4–6	6–5	8–4	10–2	2–5	4–1	6–4	8–5	10–6	2-1	4-5	6-1
12:0	114.0797	59.75496	45.82272	90.12443	92.45476	45.98916	10.4399	22.1732	99.42665	82.97306	62.15443	23.13836	97.82843	82.3671	63.66233	21.70172	50.00792	10.32368	58.98767	84.41047	80.33031	151.2977	32.02109
i13	62.40354	23.86206	25.32326	0	39.21832	21.51105	0	0	4.012626	51.49439	10.51539	2.475174	8.425274	7.662027	11.75926	1.511401	6.580596	0	4.739551	7.748622	1.801001	63.17126	0
a13	37.0297	14.30587	8.362102	0	17.05803	12.69815	0	0	3.380008	21.44276	4.616063	0	3.920763	4.11103	4.505535	0	3.065349	6.079501	0	0	0	31.12424	0
13:0	12.60645	9.583698	12.26708	10.18229	11.48884	7.491383	8.993098	8.61467	11.90468	11.72579	52.11796	19.18107	44.68572	36.98092	33.70962	14.36056	21.54728	36.84634	32.03407	36.07826	54.27411	74.16773	33.87682
14:1	22.23586	3.600786	15.70373	164.0266	20.49645	1.084682	16.83588	108.3982	28.30712	57.49591	38.49278	4.794433	26.54493	16.14164	20.20518	10.57487	18.74926	21.33867	10.10565	20.91874	17.81669	40.93722	10.80597
14:0	2819.669	2168.593	1996.56	3045.808	1830.103	1187.303	824.3905	1351.024	2718.934	2809.66	958.0995	423.3982	1641.971	1133.722	1056.807	700.3335	949.585	1718.832	1724.668	1568.418	1412.946	2419.321	778.4424
i15	1375.012	904.106	832.7698	589.481	880.8504	8.809822	304.265	480.3906	1121.891	166.8642	279.5895	71.14255	116.782	102.334	171.8099	58.9165	143.5553	125.8891	121.0557	117.5193	599.046	1190.989	207.6099
a15	679.1332	358.0367	368.1273	276.4698	473.4164	40.53429	165.6578	228.3868	567.4556	1367.579	176.3668	42.59274	61.25209	68.85842	90.84369	36.02801	88.17593	26.79933	61.43641	83.4742	409.6801	726.4981	130.7316
15:1	116.87	38.88702	29.65093	0	104.2147	0	0	2.319484	105.6652	32.13626	125.466	37.07599	121.644	108.2722	90.91016	21.23033	88.44958	68.27794	90.5712	87.04735	194.2665	169.0337	37.75828
15:0	943.8748	628.5864	628.7791	939.3221	646.2334	325.2143	467.6987	531.0256	769.8122	904.8671	517.5844	210.2493	689.4526	494.4047	496.3989	219.6957	321.8372	343.1355	540.0329	575.0873	572.3151	975.7748	381.5601
16:4	4.558554	54.09237	0	14.9058	3.083883	30.85831	8.901788	24.72689	0	5.951236	33.08462	8.859332	0	22.24755	36.53303	0	25.3269	2.458756	23.38826	31.5211	0	54.75743	0
16:3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8.190472	0
16:2	0	305.3641	31.01813	139.6246	0	0	80.9972	25.82697	0	0	178.5284	50.49823	0	181.5206	169.2646	0	169.0314	0	0	134.3245	0	171.8275	24.65062
i16	43.44156	13.30586	22.23137	6.168572	22.91452	25.7528	2.276306	192.9617	51.1137	35.72557	130.4586	84.15299	0	171.2625	221.9921	17.43381	205.6406	25.5676	205.97	247.6698	57.98652	1144.613	294.8659
16:1w7	278.7599	104.9463	346.8677	556.5917	183.7144	30.16658	95.36056	851.1706	397.5192	1167.355	3312.449	1626.688	0	3874.615	3090.682	450.0981	3298.421	137.272	5417.831	5656.317	1059.526	7727.303	3190.24
16:1w9	176.0949	3633.25	182.2764	0	818.8382	299.592	0	135.4346	1282.478	721.2976	205.6131	72.99601	289.8864	201.3355	271.5779	2787.321	410.6406	81.36042	211.8964	284.9557	63.87318	41.88042	98.9035
16:0	1139.903	7846.65	3129.379	14900.25	7854.253	1687.619	5205.806	7585.194	10758.53	10756.08	3647.196	2128.653	7045.316	3628.346	3578.637	3369.639	3485.079	5272.819	1212.281	6056.368	1104.2	8732.342	3415.907
10me17	59.46817	126.0684	43.64146	44.64683	26.67767	11.5483	52.78028	80.15597	8.549097	28.6409	20.3086	3.475472	3.116678	7.456503	27.73241	9.271314	5.543835	753.7951	11.52955	15.14186	13.11702	138.3875	30.49304
i17	199.3715	178.9505	22.08331	6.137692	41.91045	21.19419	89.98025	123.3843	58.07902	76.06445	40.80051	38.66935	20.18467	24.06744	42.36182	25.90517	24.65827	12.83561	10.44106	86.96377	46.89995	163.0995	37.33386
a17	108.4377	107.7234	51.58434	70.05434	77.56115	60.74141	55.29985	20.51868	133.8975	134.4485	43.29574	21.1004	11.96527	69.51863	30.5268	7.938608	34.74303	6.832811	81.07768	3.962222	120.3581	413.8663	123.0219
17:1	394.348	111.8382	102.5959	36.75297	176.8171	49.30915	11.23511	24.2442	221.2191	252.8634	166.1589	7.726485	313.2609	104.8221	139.7236	81.51396	20.66129	235.756	106.8504	13.15319	308.5471	236.1828	61.07501
17:0	293.2744	350.867	108.8827	378.6179	263.4191	160.6859	270.7472	311.41	476.8457	587.0902	156.8997	44.28289	20.14442	139.5089	217.2036	46.99787	56.43841	12.16302	214.6864	127.5574	50.92595	490.7345	161.2892
18:4	199.8547	0	44.54688	0	107.1832	0	0	2.716802	190.1093	210.3252	86.1062	82.62687	169.3928	111.3103	73.94578	55.19978	184.0851	0	149.8818	240.6431	0	201.6795	50.47645
18:3	0	1299.216	13.85696	11.67817	337.6191	164.6555	2373.935	2030.83	359.4853	213.6571	242.777	199.6852	275.828	232.8828	221.4254	205.3599	512.363	333.4083	388.5998	569.2064	268.2605	516.0921	109.1367
18:2	1507.014	318.8936	2146.884	338.2522	917.8531	2039.614	213.2197	332.1297	1613.46	630.3714	482.8643	412.5193	542.3448	387.294	361.0214	491.8396	735.1614	58.17992	629.1251	986.879	81.18996	964.0847	60.36281
18:1w9c	1387.847	289.4523	396.3816	191.9654	789.1896	244.9406	160.2793	235.5649	1195.252	444.8869	662.5089	221.7466	419.6704	390.6357	506.9992	171.346	175.5906	1264.444	888.1402	470.2611	647.1902	932.161	347.0787
18:1w9t	976.8728	989.1965	657.0201	106.6726	1442.911	460.3876	107.6535	283.1443	2411.81	2217.57	1042.117	101.0874	755.5204	758.2377	229.2098	153.927	220.727	1016.299	1290.647	253.8159	1243.806	425.1973	360.857
18:0	1888.678	1677.373	1123.994	961.2371	787.5637	807.403	770.0804	897.9676	1685.648	566.4345	392.7469	63.00371	541.8189	627.407	168.5213	164.7822	63.32283	667.12	739.5735	159.1205	915.659	1371.037	436.8032
i19	127.1381	64.41961	35.11235	85.73312	20.88865	75.95868	67.90859	60.84754	44.00317	68.98492	21.67831	0	6.590062	1.676775	0	3.87427	0.675837	3.907096	0	4.916443	11.67777	79.54635	0
a19	39.1012	0	0	0	0	0	0	2.342128	40.21777	49.05656	0	0	1.978641	2.70571	5.28381	0	22.89693	7.129503	8.564107	3.361528	0	0	6.873656
19:1	147.4922	82.68586	46.88358	95.9293	45.92315	26.48879	15.26468	53.46091	120.2515	150.1717	46.05832	14.66985	23.1853	19.35432	56.83859	14.9481	33.53983	42.73925	103.4581	38.49195	0	37.58948	64.86133
19:0	1496.861	1204.492	1209.304	1233.184	1186.213	1191.746	1236.521	1017.937	1558.214	1386.351	736.9082	895.9297	795.5914	788.1588	963.2969	967.1932	747.1742	685.6356	851.2299	1058.296	1094.877	1342.849	1425.259
20:5w6	1383.181	308.3948	209.7768	5.907912	656.7846	177.5745	3.808637	47.80038	980.3509	1009.09	338.7644	201.4205	656.0897	426.9177	563.1853	191.9452	632.317	84.36336	546.1933	572.6971	0	391.6758	3.112707
20:4w6	253.9057	749.1835	425.626	7.799138	1881.705	383.1155	3.608898	76.51312	2416.309	2467.802	64.71934	459.5705	1345.821	1084.33	1235.512	674.3937	17.10929	1364.811	1477.205	1748.466	810.6222	2718.057	331.4631
20:5w3	196.6308	71.14423	109.2746	0	116.1523	8.588884	0	10.77227	238.8092	226.3054	136.197	48.76098	117.9225	93.04236	151.7359	80.11049	39.77061	94.68365	172.631	229.4025	1508.749	185.6584	735.1089
20:3	223.0813	193.9013	199.669	0	107.1708	324.9087	241.6675	242.0703	139.0164	191.484	66.63609	32.37469	74.36784	51.74921	76.11992	39.69197	49.82433	101.5278	74.49392	101.7898	59.44787	117.1294	44.44074
20:2	364.2568	341.4839	356.4611	641.9583	77.88458	539.9383	355.7109	396.6631	80.06336	85.8901	29.67239	15.83286	33.4148	3.325659	25.11166	20.48043	13.99454	49.28496	23.96108	11.19856	6.808821	18.94787	0
20:1w7	53.62286	96.35635	98.74572	34.3048	33.76122	82.82611	12.99328	3.359776	14.92288	66.30979	22.33369	18.30824	24.56674	16.38294	29.19294	37.89193	36.12277	55.97073	81.75683	45.67445	75.06458	113.4148	13.14851
20:0	1696.733	1331.908	1313.64	1256.016	1198.98	1265.818	1213.238	939.35	1719.827	1666.703	868.0251	925.8501	887.6537	669.4764	1079.482	1239.801	813.3651	883.9331	1011.179	1302.233	1410.262	1976.69	1410.126
21:0	369.8346	321.2825	353.8904	423.1076	392.3153	366.1975	473.9933	471.2486	376.5791	382.977	521.3775	396.3527	414.7933	565.3508	500.235	409.2548	433.1152	178.9839	769.6179	523.0548	339.6965	687.3176	624.6545
22:6w6	188.2319	68.72821	38.48082	0	98.63044	55.35907	0	0	167.5253	172.4938	27.03213	20.5177	63.80556	50.23067	105.3704	12.29765	60.95655	82.9433	95.59276	90.95855	0	205.3564	0
22:6w3	349.9802	137.9341	73.0095	0	409.0171	98.32411	18.37949	0	514.7531	643.4588	146.1245	113.1603	241.369	236.7937	343.521	89.42597	215.9219	280.6085	442.9067	406.9807	408.6475	705.8287	0
*22:5w6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22:5w3	98.90826	75.38913	29.37336	0	124.9549	34.14964	0	0	200.1143	216.3041	45.21973	22.86837	59.78288	40.88161	65.65691	24.34749	39.75945	90.91734	98.07837	97.51967	0	202.7029	0
22:2	24.63501	55.24187	0	0	0	22.60769	345.1	301.8755	38.44834	77.21002	6.888659	2.153457	11.98567	0	0	0	0	11.76055	59.3898	22.51066	0	0	0
22:1w9	33.45335	22.19528	0	0	11.57907	22.19339	10.18008	94.17645	491.1421	498.2888	23.59702	18.97041	11.45738	3.019969	7.711331	15.63968	27.7742	24.56752	48.21365	22.88494	21.90178	383.0884	0
22:0	951.1193	388.9305	420.1666	262.4279	273.9459	268.0776	140.1474	145.3623	483.094	558.4754	208.5493	65.5544	153.924	136.0427	190.7254	104.795	134.5438	233.1161	185.252	249.357	359.1454	767.9847	129.4894
23:0	271.3018	181.3865	192.2701	197.5007	186.8521	194.4351	173.7412	139.0929	218.3821	239.1639	160.1446	164.3967	157.0524	161.6785	188.1798	163.0813	150.5854	172.4706	165.6343	184.4604	196.7324	264.8104	209.9762
24:1	63.76675	44.90725	14.80615	0	35.68356	3.149778	25.98063	3.889421	49.59811	87.5367	10.95216	7.250332	14.53671	3.687712	14.2316	8.867243	12.80878	35.14258	30.87927	45.8557	28.08308	120.545	38.18815
24:0	1827.403	815.0405	1223.005	808.4705	549.747	569.2666	367.5511	218.8559	1173.98	898.174	293.4186	108.7643	408.3511	248.7116	295.4129	207.38	202.7698	477.8656	344.9494	508.1518	591.2155	1585.283	279.9422
25:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26:0	400.5607	182.8108	166.1577	156.2793	140.938	552.2455	91.63649	44.6855	176.908	256.19	102.7185	39.32691	76.11381	83.83319	107.9052	73.91081	78.77504	105.3129	98.36436	90.53448	198.4702	378.6438	97.8508
27:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28:0	165.3921	80.69282	76.4644	63.6898	58.06641	322.2112	48.03046	32.45959	73.17469	119.9118	50.24141	28.8857	36.21409	36.69932	71.20779	41.13635	36.62396	52.02014	59.94807	82.37497	105.7018	165.9774	54.34683
29:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	21753.01	25393.94	16109.84	25033.47	22405.88	11269.97	13038.68	17600.73	33707.46	31380.3	14736.51	7418.197	16802.44	15536.61	14794.6	10685.06	12856.48	15440.35	18169.07	22291.86	13509.35	37772.98	12231.92

1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
6	6	6	6	6	6	6	0	0	0	0	0	2	2	2	2	2	6	6	6	6	6	0	0
8-2	10-5	2-6	4-2	6-3	8-1	10-1	1-3	3-2	5-2	7-6	9-2	1-6	3-4	5-6	7-5	9-3	1-2	3-1	5-4	7-1	9-1	1-5	3-3
69.30891	21.70784	58.98011	120.7329	38.8934	34.89454	50.25958	38.46117	27.5474	60.28642	59.60327	37.33382	65.28501	20.49895	0	75.35053	13.96325	24.21191	38.23713	52.83178	2.342465	36.23579	42.96439	60.09236
43.07087	0	0	60.22078	0	0	25.1443	0	0	0	0	0	1.837555	0	0	0	0	0	0	0	0	0	0	0
0	0	0	26.04714	0	0	7.663832	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47.22721	15.35643	36.11514	69.72425	29.10835	32.84195	43.22096	22.08417	32.44759	32.849	28.68953	28.40247	38.52197	16.87185	46.49609	37.0357	13.37432	64.61801	26.33959	25.91687	22.99348	19.09961	25.18202	26.98211
131.2002	37.89341	131.6265	32.25835	10.02003	33.06961	13.18115	145.4435	284.1352	65.60567	144.1048	131.9749	9.820413	0	6.062425	30.93544	68.55247	42.64015	72.8397	84.27016	27.38136	112.7974	87.12584	184.6067
863.1259	772.6313	1543.225	2345.484	776.3611	1024.576	1567.202	1299.271	700.9275	1541.158	1309.556	1213.82	947.7766	528.141	508.5628	1623.056	229.8678	606.5937	574.463	827.0167	217.5727	811.9179	1114.599	1688.866
852.3595	222.3773	873.1092	1264.7	227.3769	262.7189	671.4481	559.1013	259.2144	697.278	834.0477	585.6497	591.7787	257.2997	248.7316	683.9582	33.64258	263.6002	222.112	497.3015	92.66589	355.3795	371.9252	1106.357
537.9408	142.6481	554.2263	771.7834	131.2358	156.1631	416.24	281.4583	149.6536	377.899	350.901	334.7643	593.73	151.4119	170.7187	447.5724	66.03385	210.3008	150.5576	453.3932	68.14305	286.1848	222.3019	14.61856
455.6085	46.187	112.0007	295.4535	48.3327	69.81013	134.6474	48.08401	12.64732	40.51453	40.41764	43.37191	81.51775	23.19775	68.82295	78.92937	32.66332	35.32063	17.66533	50.30698	19.5419	36.72788	35.13657	7.878982
408.358	291.492	619.3108	1164.548	410.2201	533.9375	760.4534	328.1976	165.0168	410.9071	362.4972	350.5677	418.2113	209.3634	244.1361	509.8221	70.49835	267.5491	215.2682	302.3781	148.6653	269.6633	281.7811	41.68228
60.08492	0	5.83521	4.814031	11.68011	0	36.61335	0	0	29.32369	0	0	3.363267	0	0	24.13051	0	0	0	22.84372	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	304.5384	0	2.903325	65.03314	84.29329	151.3571	197.214	64.30839	186.3729	0	253.2198	67.4279	175.8536	0	159.5866	0	0	0	0	0	0	261.1995	0
250.2796	13.88263	11.4581	319.0967	402.1553	451.6041	716.2419	1392.934	436.4954	1881.975	1189.245	1302.475	765.788	802.4266	732.5534	1359.418	71.71959	621.9188	434.8003	812.8279	233.687	622.5559	1316.133	7.950008
1536.002	2974.646	783.0573	1516.228	3453.992	4168.173	6864.397	4945.175	1790.744	5771.402	4760.114	4295.378	3113.368	2678.142	2961.45	6402.999	590.4025	2413.224	2112.014	2791.081	1336.35	2600.685	4095.245	4726.211
573.7459	132.2278	20.19913	27.99026	112.7671	148.886	520.8699	16.54405	0	479.2905	336.738	302.4927	47.12602	15.30715	157.4451	41.11597	0	6.427124	10.15084	34.92757	5.037072	16.95734	17.43838	0
6220.358	3225.734	1051.718	1175.018	3236.387	3960.61	6821.343	5199.916	2756.655	5758.13	5217.348	4885.708	4121.915	3109.466	3199.037	6554.401	938.2838	2535.824	2399.236	3413.887	1740.601	4053.505	4985.397	7059.269
41.38368	34.1044	11.81217	151.0745	17.49078	24.7351	108.9752	74.54746	61.82577	122.4928	143.1271	88.97547	80.37146	44.2156	7.690635	140.4177	15.14663	56.57817	113.4086	65.34945	23.56878	47.849	95.93435	169.4877
157.5973	59.01598	70.27566	65.31753	49.80147	45.43009	113.4883	138.4125	68.66088	212.6286	158.3318	159.6634	140.3761	67.12567	65.25304	202.6663	16.79203	64.65842	63.76823	106.999	38.90123	120.5562	147.943	217.3647
200.0842	128.629	251.7013	506.4999	150.155	223.3359	349.9262	245.783	89.45696	282.6336	148.8407	159.9322	300.6954	150.3543	177.9571	342.1384	19.63733	210.2361	155.5918	184.7799	128.0586	173.801	245.9663	108.1677
259.2785	66.03774	202.7814	412.0277	78.89044	102.3435	200.4823	61.96266	43.20147	104.9542	81.84286	104.1296	139.0926	40.16844	67.36361	121.6132	30.24973	56.93649	53.3927	99.30276	32.43956	74.65333	72.42154	90.57995
292.9282	167.1822	264.0989	477.8158	146.0874	252.1462	292.9207	195.5127	187.4612	275.5904	309.1856	289.7265	286.3692	240.3288	184.2255	366.1604	70.42934	248.2188	137.1579	311.914	155.7215	196.9851	331.619	208.9954
0	45.27554	0	213.2131	68.02871	106.5556	111.0797	0	0	129.1785	84.78375	126.9574	0	2.865195	86.03951	130.5396	0	0	0	99.06061	115.7681	95.12511	0	0
469.4891	109.1414	32.95808	597.1899	148.8652	186.8982	281.204	139.2092	35.57821	401.2234	262.7182	254.5077	323.7667	18.06829	201.2849	363.9353	13.94502	158.8974	49.87756	180.239	6.144618	201.267	125.8624	7.951437
54.43916	251.5326	53.48952	1208.875	66.19039	439.7744	67.63857	361.0382	101.7417	1192.516	581.8962	558.8572	335.2133	182.8201	371.1986	987.7329	46.02829	178.6626	225.0233	406.9537	122.875	694.1798	312.9108	602.4362
502.4725	327.1931	749.1839	1133.816	337.4334	476.3978	645.5049	1375.011	507.3071	1362.754	1257.266	1243.912	1038.493	670.3837	580.9777	1578.13	203.1045	575.4915	580.878	956.6977	319.1158	1976.781	185.247	916.7514
1351.707	561.7625	1334.081	2445.858	475.008	585.1572	1138.907	955.1746	693.9115	118.9209	1266.299	1281.407	432.0057	621.1932	647.2122	1453.495	176.8259	567.6864	406.3491	799.9066	265.8221	900.6315	244.7994	1056.343
1554.689	437.2931	761.9384	1105.529	401.7295	866.9026	628.131	204.4238	1175.063	108.9834	862.7574	984.7844	140.18	586.8535	420.3537	948.6016	272.1717	654.1184	449.9635	600.5757	414.2443	869.0866	393.5045	1072.387
18.0491	8.723269	0	7.028294	4.636346	0	38.6117	0	845.6292	0	95.86647	1.165869	0	0	0	70.47653	110.9236	0	391.9402	0	63.97712	0	15.85258	7.404516
0	0	1445.861	66.49668	0	0	5.826604	0	0	12.75538	8.100272	0	7.584149	12.65007	0	0	0	0	0	4.276048	0	0	0	0
44.72786	20.32594	34.16238	80.50265	12.51273	19.08326	57.11108	31.17576	7.695242	70.53582	41.5729	0	18.52291	5.477182	0	51.98561	0	0	0	5.94167	0	0	28.8334	77.79388
99.00191	1284.724	451.6078	1488.205	812.8495	1237.824	1332.307	2939.585	2784.505	2701.448	2281.006	2492.553	3160.496	2859.961	2591.357	3119.172	2933.051	2440.12	2589.477	2203.496	2844.252	2782.724	2919.58	2356.589
1506.167	252.8106	631.1671	27.27689	3.815951	0	643.1123	768.7085	7.29611	1125.541	784.8245	24.55908	0	23.60302	0	1047.645	0	0	8.143348	24.14906	145.1045	0	0	0
680.5714	31.27217	144.4295	1395.276	483.9461	514.7374	1554.089	2275.805	225.6891	2898.506	1561.6	897.5902	463.6696	536.1161	562.1106	1999.823	15.51887	408.8348	295.8506	600.1262	343.6435	597.3518	771.4666	522.7054
550.4393	12.71369	86.90887	2280.617	903.6571	985.3316	129.8393	64.68674	334.8939	128.8645	99.65842	1849.075	1308.797	848.4217	1204.673	183.7705	46.96072	801.7429	715.6512	1095.841	27.03704	1845.579	1545.802	890.5013
15.4757	0	115.6406	125.4484	28.13553	28.00133	75.15661	2.491062	0	0	106.0465	33.10274	28.56795	19.32652	45.5507	64.76239	0	70.17836	22.69784	0	0	39.78575	54.32424	60.65229
25.59999	27.11851	601.3526	72.79156	11.70283	15.70195	0	75.98402	0	98.41631	135.2234	51.06197	49.246	19.37225	44.42792	17.42653	0	136.5478	20.11081	38.7648	35.06606	65.05593	78.69824	196.7958
47.19349	47.56057	332.1408	127.6382	61.80173	66.19795	35.48058	86.52298	24.37728	104.8981	80.90403	78.19595	42.51758	22.27087	26.85776	101.0679	10.99748	43.13608	31.78012	27.6312	16.69147	52.30526	72.90169	2.214528
449.8292	1356.815	14.55391	1690.553	50.96727	1246.969	1401.895	1702.225	65.39836	1609.452	1314.659	1466.48	2035.763	1578.442	1485.019	1671.065	1608.214	1443.864	1496.444	1417.821	1593.633	1698.105	1658.907	1445.723
1102.372	612.6404	309.5077	501.9821	599.1971	655.3963	622.0144	559.9251	1782.617	748.4731	778.521	757.9081	644.9938	965.21	1867.488	736.568	754.3444	678.9381	878.434	748.4467	819.9048	741.5755	802.7058	431.3547
0	28.61587	4.377393	303.822	0	0	117.481	0	0	175.0799	113.1117	104.7768	4.983712	0	71.48718	123.237	0	1.217853	0	75.03817	11.20423	35.81198	0	0
173.5943	234.8768	15.27366	749.3383	124.3916	346.5424	400.6219	583.3905	0	823.9416	519.567	556.9015	426.0954	152.5903	309.2961	558.8061	16.17712	204.3015	186.7184	291.5099	65.63218	275.1438	442.0052	170.7602
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
355.5861	44.9799	62.17398	197.9515	35.59222	45.58806	109.6188	110.5718	0	198.6523	157.3698	231.5724	98.17978	23.33346	78.52316	165.8517	8.442917	80.36069	51.13388	82.44222	22.20084	134.8722	127.4927	51.76252
270.3773	0	559.7479	0	0	0	0	0	0	38.67067	10.6815	0	33.40662	0	0	96.908	0	0	0	0	0	0	57.79119	21.05173
170.6776	18.86591	94.50214	75.21077	10.76059	16.51126	10.29467	22.45812	1.921803	38.89627	3.36316	24.10643	37.8938	4.456683	14.95126	175.9172	33.83178	14.37847	9.338441	394.7675	12.39111	20.98744	628.3304	10.26538
77.19455	167.5852	86.36687	516.1896	82.6653	119.9145	297.8929	127.2505	85.12363	255.5208	174.88	213.7889	374.9057	118.7379	160.4407	254.2993	58.70503	134.253	96.68184	339.6188	88.67566	278.163	140.1825	330.8958
362.9116	201.8299	718.5732	240.4959	155.7386	221.6703	220.2091	118.8469	147.7967	128.3096	136.4717	121.6291	149.5193	119.9123	113.54	138.1304	148.6484	107.5537	135.2409	120.2215	122.7439	131.8529	124.1174	112.7883
38.69341	44.06518	13.66093	77.41838	31.81035	62.65267	68.58271	25.49979	14.65687	48.38755	20.56358	42.16742	23.26644	12.72161	39.38195	44.68239	78.07058	16.01127	15.51367	38.99502	2.598558	25.09436	22.35073	31.15835
620.0596	348.8004	210.8071	753.4168	224.0713	288.3077	783.0338	233.7058	145.1006	416.6029	236.1713	306.303	574.7051	167.8187	260.6428	367.2924	194.6924	225.9477	175.353	428.117	125.6842	344.2633	158.0441	549.3697
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
83.30625	111.2552	84.94482	239.9209	62.44179	58.48073	209.5438	65.02198	21.90434	98.83664	50.85408	54.2734	84.18547	31.23361	0	71.37611	0	16.38498	0	36.49489	0	27.72524	32.49925	240.9095
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28.03986	84.69081	0	126.0608	35.10674	2.058931	94.51301	0	0	39.29863	0	10.50404	0	0	0	0	0	0	0	0	0	5.789725	27.08625	16.25619
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21638.69	11862.57	14036.71	24726.62	12980.09	16820.35	27369.35	22718.23	11358.49	28205.77	23882.65	23477.18	17656.58	12608.31	13973.92	30069.09	3567.353	12024.81	10572.19	16842.17	6467.929	18319.35	19216.08	22723.47

0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	2	2	2	2	2	6	6	6	6	6
5-3	7-3	9-6	1-4	3-6	5-1	7-2	9-5	1-1	3-5	5-5	7-4	9-4
109.7865	37.75775	51.44886	17.9756	99.20396	96.80416	26.56317	10.43032	5.860611	70.58377	67.11063	80.31457	60.16691
0	0	0	0	0	0	0	0	0	0	1.398464	0	3.690162
0	0	0	0	0	0	0	0	0	0	1.579018	0	0
47.28471	20.06216	25.17785	17.00644	41.7723	35.05783	23.91731	10.22965	10.14726	36.47944	44.59161	31.63969	34.30444
105.4857	80.15156	124.9582	28.0745	143.0931	176.4174	159.3665	140.5566	34.34402	57.73871	34.61494	184.2231	57.59761
2280.96	863.6661	1439.396	480.5088	2069.384	1450.946	1807.298	297.0778	229.1392	1606.436	1250.489	1402.503	1129.122
1271.098	444.3572	794.1735	376.6732	1378.19	894.5345	1007.616	111.3597	168.4312	1037.816	915.493	916.424	817.468
865.0861	248.6181	486.9439	243.634	629.8032	662.416	567.6144	75.49785	94.96812	660.4837	700.0289	584.3298	617.9842
128.1343	11.68565	38.76954	0	108.1265	102.622	71.28996	16.33411	3.046482	77.67073	120.0189	61.99442	110.2728
741.0736	295.6853	376.1948	254.0703	569.1472	531.0667	460.413	86.23836	122.1977	537.7446	635.0795	395.8556	542.0845
59.65108	12.7927	26.96948	0	73.87143	39.43072	31.25602	0	0	53.68982	0	34.0353	34.03612
0	0	0	0	0	0	0	0	0	0	0	0	0
0	4.065941	3.981834	0	0	186.3567	7.718666	0	4.723415	124.7473	247.8001	0	122.9989
1974.082	175.2606	760.5201	91.55824	1897.747	1205.861	2036.935	33.01175	43.39399	654.0935	191.7625	926.9735	1043.531
9077.705	12.56404	3277.054	80.66604	8257.102	4935.195	6721.669	4.953648	7.998433	4971.891	5172.49	5655.257	4310.617
491.7198	965.3331	201.3498	0	45.91153	47.76607	358.5288	30.16874	0	13.27078	284.6172	333.2601	303.6666
8341.1	4185.751	5490.86	2428.277	8242.699	5970.709	7498.919	1315.305	1416.987	6275.488	6890.246	5724.076	4727.013
292.4286	43.0667	36.63147	0	173.0886	141.9335	157.894	16.79162	17.44644	134.9006	110.2131	255.1201	127.6314
273.7034	102.5043	97.51001	103.5277	27.56194	217.7386	222.2243	33.15832	56.96454	253.1411	216.3771	190.4611	193.4795
543.2055	64.59266	103.6457	59.0492	15.53576	417.7341	284.9882	32.13128	27.76889	387.2937	434.3299	253.6624	408.3313
235.7334	3.289221	0	15.81061	17.87073	189.2117	135.9358	11.59589	0	153.5978	194.7635	125.8707	200.0792
429.2204	99.67732	86.74241	216.6092	213.777	298.6722	277.9013	61.58436	176.112	351.088	413.4398	216.2518	387.6466
296.6307	819.849	655.9069	0	0	146.4914	0	311.8362	5.981843	0	0	108.5621	123.0967
314.3564	13.39264	408.0325	762.7793	409.211	260.4567	1007.21	11.21953	432.1676	830.2166	776.2894	235.6033	244.9148
689.5617	0	646.8314	0	68.3443	642.841	548.7761	32.46977	0	19.57896	21.88908	701.758	412.065
1687.051	291.2599	752.5997	187.8054	225.2687	1389.914	1040.852	112.8041	57.05306	1896.312	2819.603	1398.139	1281.712
1390.001	77.2403	85.24179	64.387	339.7883	1622.861	1239.081	129.971	66.92671	1214.12	1616.067	643.1585	306.9184
730.041	897.9077	193.0945	357.2163	1139.305	843.1629	997.4573	670.5906	513.148	1037.844	1037.146	168.2519	173.2075
89.09805	7.820887	3.666164	0	6.975254	96.21047	13.96963	4.948708	6.665151	10.78064	0	0	52.22122
8.580433	0	0	0	0	5.052008	6.035329	0	6.33331	0	4.715778	0	0
70.16559	33.28909	68.69095	16.71308	79.69107	16.70496	128.8897	0	11.53692	51.99206	31.34847	50.22037	43.94378
2732.597	2908.268	2619.128	2527.252	2931.098	2742.864	1989.28	2951.556	2293.838	3091.075	2750.613	2874.166	2565.902
1236.195	56.12345	333.2531	0	0	45.12279	1102.582	0	0	0	0	0	0
1772.145	66.5182	518.2049	0	1098.683	937.1372	1556.736	0	0	11.00469	919.8913	660.9823	793.46
102.4719	0	22.51019	16.81023	1920.762	1352.275	104.8306	2.058237	0	1670.704	1863.162	153.4255	1357.651
5.376228	101.7661	62.6356	0	78.68483	70.89693	138.9942	48.90826	79.87799	162.0461	163.8271	6.276774	54.90128
33.11222	163.6013	110.4065	240.2468	100.2163	72.97624	129.3216	59.20149	159.7146	134.021	98.43199	66.49561	63.06645
109.9623	8.463121	15.20603	8.367115	79.38286	49.92107	43.8102	11.94823	19.55113	32.95144	63.30243	59.22643	43.19226
1837.154	1615.049	1561.975	1403.628	1803.319	1734.987	1274.792	1586.851	1275.187	2022.038	1747	1757.04	1643.353
755.6388	413.5224	437.3796	420.5249	762.3827	719.3071	691.3729	458.127	297.3458	443.3765	444.781	755.6072	746.5095
211.0537	0	56.72048	0	8.05987	127.1621	130.6312	0	0	0	118.4134	110.4057	5.914623
398.9321	11.84338	149.2491	6.916863	447.1091	414.0518	369.7182	0	14.98356	475.9681	499.3333	257.2913	387.8618
0	0	0	0	0	0	0	0	0	0	118.7113	0	0
117.416	6.445904	35.04846	0	88.67682	89.64432	59.24277	0	0	34.82475	49.68297	63.73445	9.406784
0.721822	15.29236	60.17229	33.37229	0	25.55259	22.89904	19.70963	22.62107	42.34412	337.2471	0	553.5139
628.2415	312.4133	137.2595	0	171.9415	35.43564	234.4564	2.92872	11.04086	29.67202	31.17058	20.93913	19.99888
331.1118	113.8255	216.9758	90.6437	390.3715	325.2524	245.0001	34.39434	70.39777	366.2198	342.7197	266.4699	266.3045
143.2106	125.4962	132.3543	135.6431	145.9533	141.1836	146.3961	130.8143	128.1133	190.5343	169.7497	141.3346	160.7602
29.80586	15.86926	17.57466	21.05076	29.50757	25.4755	47.68354	4.029808	35.01309	69.82593	14.7034	47.78407	46.28149
589.3706	205.0469	485.7305	155.6187	498.1694	426.2346	445.0075	49.15351	81.93761	623.4681	389.8477	433.6561	394.1213
0	0	0	0	0	0	0	0	0	0	0	0	0
214.893	21.52423	108.3122	0	273.2853	103.4507	219.2723	4.608135	4.092857	128.3007	59.10622	155.1643	49.26029
0	0	0	0	0	0	0	0	0	0	0	0	0
10.15944	23.36187	32.72737	0	0	20.07629	46.86186	4.408021	6.817388	22.53631	26.78923	8.595819	13.40589
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0
38329.91	10935.54	18604.38	6367.489	31655.52	26724.03	31757.27	3621.011	4025.41	26313.9	29329.91	22988.37	21928.14

Appendix 3. Phospholipid-linked fatty acid (ng g^{-1}) data from Chapter 2.

Light	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
crabs	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
grazers	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	2	2	2	2	2	6	6	6	6
Componen	2-2 f 3-4	4-3 f 3-4	6-6 f3-4	8-3 f3-4	10-4 f3-4	2-4 f 3-4	4-4 f 3-4	6-2 f 3-4	8-6 f3-4	10-3 f3-4	2--3	4--6	6--5	8--4	10--2	2--5	4--1	6--4	8--5	10--6	2-1 f3-4	4-5 f3-4	6-1 f3-4	8-2 f3-4
12:0	17.56067	4.280259	5.447782	0	1.286536	13.58944	0	5.507939	38.22717	3.524331	2.441293	1.221241	1.454494	0	2.048563	0	0	6.774623	0	0	2.063934	4.876853	2.430715	36.1545
i13	2.682456	0	0	0	0	0	0	0	4.012626	1.325869	1.428103	0	0	0	0.743511	0	0	0	0	0	1.601001	0	0	25.8521
a13	2.665312	4.699035	0	0	0	3.663699	0	0	3.380008	0	0	0	0	0	0	0	0	1.563242	0	0	0	3.582978	0	0
13:0	2.862235	2.624108	5.222498	0	2.358957	1.920346	6.121138	2.11532	3.560098	1.918153	2.119254	5.759731	0.987294	1.293403	2.553292	0	0	2.433338	0	2.103694	3.10514	4.831777	2.819038	26.09556
14:1	0.834129	3.600786	5.746237	3.415745	4.490255	1.084682	3.203516	3.254485	9.050477	5.943091	23.24265	0	6.568691	0.725332	9.628617	0	6.4131	1.071966	0	6.636657	0	7.228066	3.769681	0
14:0	157.0384	60.75591	113.0647	36.25822	63.12731	27.98709	11.28895	78.84014	222.9394	155.4345	109.2473	29.61491	64.3366	71.1637	123.4841	51.35158	42.45716	150.5807	178.5264	124.9194	159.988	169.6048	40.87778	839.1118
i15	93.35435	26.87045	66.45294	10.97163	66.71935	8.809822	3.580058	28.22169	124.5094	78.84325	127.4368	25.71535	3.079309	0	5.844715	27.42762	40.76097	13.68833	37.41753	0	104.9056	160.8779	37.44415	627.3429
a15	44.72891	11.04738	21.4886	5.394612	29.61575	5.209033	2.493859	11.98367	51.09613	31.79944	86.29371	14.28063	0	3.610378	0	14.45645	24.99414	0	16.50816	2.731726	7.590239	85.53276	18.51719	508.5427
15:1	1.860133	2.132062	0	0	1.3556	0	0	2.319464	2.541336	2.233015	11.86252	1.581771	2.346458	0	7.282329	0	2.143366	0	6.682346	4.506135	77.03395	4.593833	0	37.98089
15:0	34.14338	17.48363	22.49886	13.20558	24.81584	9.420399	6.559952	19.50274	52.98149	36.784	75.619	18.92323	51.01786	40.92635	154.5375	28.71128	24.84474	124.0958	72.55671	97.43508	6.752095	59.80299	21.7075	334.0764
16:4	4.558554	0	0	0	3.083683	0	0	6.762951	0	5.951236	0	0	0	0.888007	0	0	5.705737	2.458756	0	0	0	0	0	35.66831
16:3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8.190472	0	0
16:2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
i16	43.44156	13.30585	22.23137	6.188572	22.91452	7.175242	2.276306 s		51.1137	35.72557	5.886522	0	0	2.966654	0	17.43381	21.56303	8.993993	17.06882	0	57.98652	48.03428	13.16788	220.1042
16:1w7	278.7599	104.9463	17.60603	56.98256	183.7144	3.7161	9.382889	7.775511	397.5192	269.7156	56.24664	120.5684	0	2.065033	7.848244	201.4198	11.24071	0	440.2481	0	350.5629	276.0734	95.52775	1493.102
16:!w9	18.76863	5.900911	182.2764	0	11.46364	21.47523	0	99.92408	0	19.8293	22.87662	0	20.5745	31.82268	68.18981	10.46771	230.8557	81.36642	38.13007	45.03721	63.87318	41.88042	6.666372	196.1717
16:0	647.0378	275.4824	490.0904	141.8829	492.8604	114.4092	65.05752	331.731	1053.613	903.4256	34.92227	307.1768	163.7208	211.4459	368.7775	627.8091	493.1814	322.5573	1200.254	378.3871	811.0993	806.5942	226.0999	3124.491
10me17	12.72365	0	10.02776	0	5.727628	0	1.298041	3.601954	8.549097	9.827294	0	0	0	1.01316	0	4.794349	0	746.5514	6.239882	0	13.11702	16.89653	5.491549	41.38368
i17	13.64409	4.517149	7.558912	6.137692	8.976549	5.593331	5.714394	5.33614	20.61373	14.40804	13.61208	6.929505	20.18467	7.383307	3.873232	0	12.12094	0	10.44106	13.65269	18.26246	16.75928	6.267438	94.69516
a17	6.635057	0	15.94838	6.310377	4.137724	0	0	1.722428	26.18786	5.299662	0	5.282763	5.711874	8.292789	11.28036	0	13.29964	6.832811	8.728873	3.952222	13.51097	12.12048	3.919725	168.3992
17:1	12.86077	2.876793	11.55041	3.604822	6.149614	2.047327	0	4.301008	14.54421	9.040009	0	7.726485	1.521422	4.675962	11.92173	10.64495	20.66129	15.70717	23.37418	1.494265	25.78223	17.13873	5.94034	108.3172
17:0	25.42602	12.61757	17.91218	10.90178	16.81446	7.369269	5.579808	20.86148	68.64467	106.8166	23.91571	17.36581	13.58706	17.90899	39.25198	10.92547	14.62585	4.563233	59.39858	21.02324	41.20531	83.64459	14.90926	143.0845
18:4	28.05438	0	4.621607	0	0	0	0	2.718862	0	18.67724	8.76569	0	0	0	0	0	6.150103	0	0	0	0	28.01524	0	0
18:3	0	10.97205	13.85696	11.67817	14.03648	7.120604	8.137155	7.033526	0	0	47.89911	11.95866	0	3.338454	7.646959	0	13.92117	0	43.54225	4.380239	21.34014	99.46655	0	439.4376
18:2	210.3381	318.8936	756.6208	27.82528	247.2396	160.0737	31.72435	35.46223	502.9567	189.1042	79.81388	17.1196	16.46686	24.22667	36.11846	0	37.6596	56.17992	75.1952	27.95027	81.18998	0	80.36281	0
18:1w9c	115.1401	109.0727	214.8496	71.80861	100.2489	69.33891	59.58962	104.4369	169.6499	125.6268	220.2472	64.37456	21.49802	29.38945	58.90367	29.95025	152.893	496.4663	357.2189	62.54725	108.613	174.2278	27.5693	438.1597
18:1w9t	225.2861	64.84344	117.7851	38.86137	118.1122	26.74909	0	105.2593	304.1726	280.8723	361.0722	86.04532	87.68149	114.3562	229.2096	146.0698	206.4478	0	507.6305	230.6748	251.1483	327.4629	0	982.2879
18:0	107.1328	57.96339	114.8358	45.11082	65.14591	33.01801	17.72929	119.0953	360.6542	504.1711	22.73479	45.80787	76.342	79.29877	109.1971	148.8127	22.10769	1.149084	190.4777	114.4723	99.37306	180.2091	3.14961	365.8545
i19	5.635418	0	6.839127	0	0	5.227604	0	3.58718	11.71121	14.64702	15.52476	0	0	1.876775	0	3.87427	0	3.907096	0	0	11.67777	17.49717	0	18.0491
a19	2.276678	0	0	0	0	0	0	2.342128	11.03361	5.509288	0	0	1.978841	2.70571	1.468809	0	22.89693	7.129503	3.795827	3.361526	0	0	6.873656	0
19:1	11.92779	0	0	0	0	0	0	0	0	11.42045	26.96608	0	0	0	0	0	6.777903	0	58.64205	0	0	0	50.37433	44.72786
19:0	9.285042	6.897658	7.306808	7.301171	5.140868	6.441179	3.698018	5.110836	11.80182	8.150012	3.923842	3.529617	3.929147	4.517572	7.670433	7.195117	4.152549	7.863195	11.21409	5.879825	7.555844	6.726472	5.83531	53.125
20:5w6	0	10.66285	0	5.907912	0	0	3.608637	0	0	0	0	0	0	0	0	0	95.66063	64.36336	0	0	0	0	3.112707	0
20:4w6	46.74492	23.43857	23.55358	7.799138	0	8.647078	3.608698	7.242483	38.41269	23.59635	45.83324	14.62696	23.72702	29.53061	50.49631	31.16309	0	160.4321	43.37241	48.88078	37.23754	37.68183	17.33128	175.1113
20:5w3	53.76842	0	43.05061	0	16.4263	8.588864	0	10.77227	62.82365	48.38616	82.74988	24.27142	40.16301	48.50623	99.70452	60.11049	0	5.195088	106.3195	146.9489	56.86562	73.75226	0	550.4393
20:3	4.889927	3.75099	0	0	0	0	0	0	5.759763	1.683954	4.023134	1.899013	1.694603	2.157351	4.205924	2.57936	0	13.40368	0	7.922151	0	7.913624	1.373216	15.4757
20:2	9.731159	0	5.004956	6.501861	0	0	10.27801	0	11.80123	4.438907	4.25193	4.187156	1.387972	3.325659	3.725518	2.992515	0	18.52457	0	11.19858	6.808821	3.571262	0	25.59999
20:1w7	2.531845	5.181099	3.620349	2.464456	3.360526	2.880998	2.87165	3.359776	14.92268	1.52255	2.363769	2.118622	1.218205	2.082534	2.955087	1.264597	1.650568	5.517571	27.14312	4.19788	1.633209	7.929469	1.781768	37.99082
20:0	16.79515	11.05532	16.04145	9.758067	11.35343	5.286603	18.41308	6.409334	17.60752	16.02522	17.68482	6.858928	8.94392	12.02759	17.78945	21.30965	12.00254	21.75946	31.8437	20.87427	17.30851	20.95195	14.2809	62.76497
21:0	56.29233	54.32259	53.46761	112.4418	86.49476	68.15794	170.1112	96.2041	66.81195	79.08448	144.2347	148.2253	114.2514	124.7087	215.862	165.6533	174.5837	11.06233	431.6523	166.6293	113.9118	124.5849	105.7481	708.5066
22:6w6	3.807732	0	0	0	0	0	0	0	0	0	0	0	2.604044	4.652728	11.72299	0	0	1.39888	12.24345	9.360171	0	6.305388	0	0
22:6w3	10.43554	3.220827	10.72837	0	2.039124	0	0	0	12.60713	7.983467	16.87919	7.295393	10.23866	16.33014	33.08547	19.22819	12.3766	4.124085	46.46867	47.18605	5.454762	22.38249	0	120.0452
*22:5w6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22:5w3	4.873449	3.173196	7.568694	0	3.497498	0	0	0	0	3.392915	4.26266	0	3.41615	2.310861	7.198544	3.057274	0	0	12.73077	14.88499	0	5.896804	0	126.322
22:2	0	0	0	0	0	22.50769	0	0	0	0	0	2.153457	3.085248	0	0	0	0	0	6.228011	6.952395	0	0	0	20.78829
22:1w9	4.412328	4.14282	0	0	1.040536	0	3.296674	74.485	454.5252	422.0297	6.198021	5.388188	0	3.019969	2.273827	2.436122	8.929243	0	11.76385	0	0	319.7965	0	24.84426
22:0	14.08494	5.677383	15.41065	8.0476	9.992972	5.844424	2.067166	17.99412	56.42186	35.40838	14.88315	4.393242	8.710573	11.12204	13.05236	6.762827	8.798687	17.95	21.06982	15.68825	14.59082	28.25335	5.832129	37.18664
23:0	78.1702	63.43968	75.01166	77.49709	76.24507	74.4166	75.88946	75.6532	77.2729	75.7644	80.07229	82.19833	78.52621	60.83924	81.28089	81.54063	75.29268	86.23529	80.52298	64.69609	78.74832	78.80197	75.4046	84.82586
24:1	2.601061	15.86888	14.80616	0	5.296279	3.149778	0	3.889421	2.305823	6.429851	0	2.441423	0	3.687712	0	0	0	6.72723	0	2.539994	0	29.26495	0	23.03426
24:0	37.53227	0	71.85732	9.906336	31.98836	9.391798	4.347877	25.81478	86.75456	30.03691	18.29687	8.308018	23.97792	19.61684	15.76393	11.98299	11.64974	38.36698	24.81132	27.6002	31.68209	54.06717	13.0422	76.59714
25:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26:0	7.537584	0	0	0	5.725205	0	0	2.731345	6.486218	5.981881	0	0	0	1.772713	0	0	0	0	0	2.375896	8.610964	8.807801	0	26.91708
27:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28:0	2.053608	0	0	0	0	0	0	0	2.083494	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21.91469
29:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
corr total	2332.182	1190.008	2430.133	537.1461	1573.763	595.0091	283.8948	1169.014	4248.367	3438.964	1582.056	862.5356	681.3017	809.7091	1504.193	1496.547	1572.787	2435.715	3664.269	1491.212	2496.866	3260.567	716.3592	11837.36

1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	
6	6	6	6	6	0	0	0	0	0	0	2	2	2	2	2	6	6	6	6	6	0	0	0	
10-5 f3-4	2-6 f3-4	4-2 f3-4	6-3 f3-	8-1 f3-4	10-1 f3-4	1-3 plfa	3-2 plfa	5-2 plfa	7-6 plfa	9-2 plfa	1-6 plfa	3-4 plfa	5-6 plfa	7-5 plfa	9-3 plfa	1-2 plfa	3-1 plfa	5-4plfa	7-1 plfa	9-1 plfa	1-5 plfa	3-3 plfa	5-3 plfa	7-3 plfa
1.927886	1.101571	0	5.590788	0.801801	1.801975	1.856091	3.950075	0	3.582362	4.292162	3.862179	0	0	1.791825	0	0	2.141562	2.558011	2.342465	0	4.162515	0	10.14496	0
0	0	0	0	0	0	0	0	0	0	0	1.837555	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1.513057	0.888236	2.398722	0.778192	0	2.853488	17.37024	3.870031	3.073224	7.128079	2.743096	1.691722	4.314804	2.472301	4.754959	1.273426	2.688959	4.873059	4.200279	0.896974	4.000656	5.770994	4.956034	2.343451
10.82933	110.8572	0	10.02003	5.305883	0	16.0746	231.4432	6.849686	98.98785	85.55899	9.820413	0	8.062425	9.751259	0	11.46902	18.7998	51.14781	5.26691	18.03883	34.99561	70.70323	67.56142	43.02081
57.41165	1.771844	76.28395	59.28361	64.02719	92.06062	97.66777	217.981	40.55964	171.2219	105.2079	95.32657	58.76296	47.36142	132.8077	7.464078	35.7184	49.30322	97.85981	36.02706	43.93993	108.1683	59.50455	277.3883	51.47187
40.35739	102.1663	105.6177	36.73948	34.17885	104.4799	56.93164	53.52602	36.64217	97.0919	43.9618	88.8526	41.36164	41.87008	98.88049	8.794577	41.06792	40.34916	73.11433	22.69151	35.64033	49.35646	0	213.0536	19.72887
21.20636	58.65626	61.74978	16.89356	17.97178	51.90331	25.45607	35.55195	19.74423	56.81288	26.21679	88.94844	25.39299	28.70577	54.77978	6.095723	23.2105	24.60281	61.22701	16.22663	27.65505	27.06202	14.61856	133.4998	12.24347
6.100907	3.174663	8.013546	0	2.032487	3.24439	2.555369	0	2.035437	6.864976	0	7.514102	3.244053	2.26043	2.135862	0	0	0	4.62587	5.09514	0	4.093743	7.878982	9.284474	3.499028
26.40646	39.02094	50.57875	23.75647	24.92948	37.24223	17.79929	30.21381	14.61008	33.3184	17.91903	36.00368	19.15416	16.2474	39.83175	5.752038	15.3001	16.00338	26.57373	11.30108	15.96982	26.52167	7.41625	61.193	10.6264
0	5.83521	4.814031	11.68011	0	5.724389	0	0	0	0	0	3.303267	0	0	0	0	0	0	0	0	0	0	0	-7.881524	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	2.903325	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4.065941
13.88263	11.4581	40.54282	0	0	28.56988	25.82322	22.28084	22.10769	49.39379	19.81519	36.08404	21.67714	21.22963	0	4.665064	15.7213	14.24898	29.82118	8.343022	16.58448	27.06663	7.950008	92.16824	6.68604
113.386	295.9181	248.3578	109.51	13.91074	9.885297	221.4329	132.5107	6.412548	295.1098	152.2298	216.9912	160.7632	170.6474	354.5048	19.07723	104.6616	94.15298	186.5473	69.36823	119.7867	229.6518	10.63662	605.1821	12.56404
9.433278	20.19913	27.99026	6.002999	0	227.6827	16.54405	0	149.3807	29.19407	16.93607	47.12607	15.30715	16.96763	41.11597	0	8.427124	10.15084	34.92757	5.037072	16.95734	17.43838	0	60.14956	8.772164
235.3894	707.694	726.4173	296.2173	130.1116	428.829	433.8516	941.4798	259.1402	654.0157	353.2444	440.173	452.742	239.3998	29.76446	91.36964	243.0195	266.1709	335.8976	220.2654	296.2726	703.1452	257.3267	1050.035	267.9428
0	11.81217	15.24012	4.399715	0	6.769918	5.057003	10.68424	8.244865	19.89246	5.632557	12.75806	4.886338	7.690635	37.15078	2.28567	7.949624	7.295817	8.98279	2.954301	6.203976	9.348431	0	27.25617	0
2.645309	11.59358	16.79447	4.366253	0	8.845239	12.95774	17.47971	10.74971	23.24178	11.34644	18.6073	10.82592	8.786447	18.64572	3.931262	6.815123	10.00641	10.24717	9.493263	6.633595	14.02692	6.822335	43.62951	5.234195
0	6.992356	12.29252	4.364431	15.55487	6.442164	16.80593	0	11.85253	12.8771	16.66727	32.95073	21.75011	15.59549	17.30745	0	13.77207	18.74741	0	14.44631	0	30.25653	7.523137	24.92484	7.019504
0	14.9921	26.37318	4.390336	6.580112	11.22914	7.013233	5.22347	5.432026	8.498436	7.103097	16.01451	7.61167	7.251319	0	2.860474	3.553835	5.683651	12.2825	4.768466	6.929763	3.947203	1.619758	27.88789	3.289221
27.5657	27.27148	30.51212	14.80901	34.89409	16.37039	17.88771	43.9288	34.86814	30.38557	21.6443	66.11754	103.5987	13.34032	44.39679	13.43001	12.07613	25.6751	85.68516	63.15344	27.82803	127.1868	26.58331	147.294	13.39268
0	0	12.83805	0	7.984135	0	0	0	0	0	0	0	2.885195	0	0	0	0	0	0	0	0	0	0	59.24499	0
0	32.95808	9.103053	4.556248	12.72812	0	15.92973	10.56171	14.96887	28.89046	11.86229	23.93987	18.08829	15.72337	30.1592	0	0	0	19.04866	6.144618	7.283079	28.9571	7.951437	0	13.39264
13.45506	53.48952	85.91534	56.19039	113.7442	67.63857	32.05562	22.89547	17.985	52.54927	17.56294	104.6245	26.36265	18.83318	54.34255	4.37906	11.63332	16.22388	0	20.6763	57.2633	61.97435	0	51.31718	0
53.75365	86.80777	90.17184	52.2623	87.83798	56.55104	94.01562	140.4231	55.04072	174.8526	85.38404	223.3143	104.9345	56.10557	127.1327	19.9296	55.38466	57.71723	163.0235	56.65437	150.5831	185.247	51.55535	508.6976	42.06023
92.93147	188.4288	237.1614	72.93304	0	110.9334	135.501	313.4202	87.11002	233.1119	140.7043	173.7674	189.2525	93.44676	190.6952	18.31576	70.45666	77.51869	133.7722	58.64687	88.01698	217.7817	97.58864	22.91795	77.2403
53.77915	73.44391	91.73095	85.40007	482.242	52.67451	161.0759	801.2965	46.379	143.1895	191.3217	101.4608	248.581	41.50262	64.69718	25.27662	72.50109	101.293	96.66341	203.8062	123.0508	334.8843	305.5614	34.92183	218.4142
8.723269	0	7.028294	4.636346	0	0	0	30.65197	0	0	1.165869	0	0	0	0	0	0	6.866929	0	4.971078	0	15.85258	7.404516	0	7.820887
0	5.575435	0	0	0	5.826604	0	0	12.75538	8.100272	0	7.584149	12.65007	0	0	0	0	0	4.276048	0	0	0	0	6.580433	0
0	34.16238	18.39922	0	0	32.73525	0	7.095242	7.570129	1.795015	0	0	5.477182	0	0	0	0	0	5.94167	0	0	0	0	22.12336	0
6.357043	8.251516	5.552805	3.627366	7.124173	5.714761	6.368088	9.401734	13.05068	25.33748	9.383636	10.43484	7.439875	5.573579	5.48886	10.53872	3.405851	8.19484	6.143601	6.271707	8.071478	10.21785	7.677002	10.87916	6.552701
0	0	27.27689	3.815951	0	0	0	7.29611	4.483961	0	0	0	23.60302	0	0	0	0	8.143348	24.14906	0	0	0	0	73.95566	0
5.8988	47.56412	60.21863	20.52339	9.716957	24.07689	21.71587	17.76939	22.08158	0	20.61929	24.16569	51.08362	22.91192	42.68065	0	9.644386	18.27462	67.14031	3.636765	32.4486	25.92869	0	134.4653	0
12.71369	86.90887	3.125803	0	15.4017	46.20622	0	1.733529	48.58576	40.44025	60.82305	68.84016	0	67.70124	109.8805	0	0	2.172741	4.805835	6.678944	122.7363	72.7441	0	3.431525	0
0	4.103969	0	3.898869	0	0	2.491062	0	0	106.0485	0	0	0	0	2.040891	0	2.640243	0	0	0	0	0	0	5.376228	0
2.375337	2.270606	3.60552	0	1.127938	0	0	0	2.191393	0	3.337704	3.613816	0	3.75919	5.752367	0	0	0	0	6.816527	3.305775	15.70049	0	0	3.607787
14.40956	5.893737	2.042876	8.494539	10.36238	5.627387	2.582342	7.823504	3.148197	13.87538	12.08137	13.48784	1.354802	6.75141	8.659302	2.301196	0.948349	4.069737	2.488378	2.488096	9.422927	8.050368	2.214528	5.578939	1.525041
9.994671	14.55391	12.88266	4.03482	16.94724	11.05497	11.81868	36.73532	10.78092	11.08238	12.037	15.99638	11.54659	6.1239	6.381249	7.094722	4.733337	7.622528	22.67033	7.812391	12.92453	18.86999	5.457124	21.26689	6.536433
99.14781	88.31029	98.25221	95.79866	59.60003	108.303	108.1412	106.7783	106.6277	106.1379	108.1848	107.2086	106.6779	107.0387	104.9572	107.6703	103.4564	102.8565	108.6239	107.8578	105.8534	106.5083	108.1193	108.1507	102.9224
0	4.377393	6.707319	0	0	0	0	0	3.690054	6.793121	0	4.983712	0	4.736769	5.553424	0	1.217853	0	0	0	0	0	0	11.60751	0
0	15.27366	15.25296	0	2.978661	5.752462	21.01654	0	16.8022	33.36998	22.13033	31.46492	6.67017	23.88682	32.95921	0	4.722088	6.297527	24.51808	0	22.6034	20.14011	0	31.85454	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	4.256755	3.858558	0	0	0	2.518781	0	1.772694	15.5349	6.349472	12.12258	0	6.925295	0	0	3.307143	2.191106	0	0	4.923844	6.66209	0	4.450172	0
0	0	0	0	0	0	0	0	0	10.8815	0	0	0	0	0	0	0	0	0	0	0	0	0	0.721822	0
0	0	1.187127	0	2.213064	0	4.646633	1.921803	0	3.36315	9.264434	0	4.456683	4.892478	117.9912	4.129875	0	0	377.3497	0	0	541.2801	0	561.0554	0
5.535346	14.46971	13.38823	4.288852	6.968648	10.82615	7.72888	8.828643	7.752223	8.949509	8.567835	13.75655	11.58897	5.377406	7.454494	5.457482	2.610777	5.128409	8.660713	4.813124	10.03539	24.57693	5.956155	16.19556	3.506566
74.72713	85.19345	78.15931	73.15108	107.8023	74.75897	40.33331	69.59591	36.20343	58.73984	31.28385	33.8076	41.48026	34.84263	35.53876	70.08582	31.55603	59.75197	31.72021	44.0465	39.17131	45.8778	17.97297	45.42161	42.07578
7.715991	13.66093	2.152268	0	1.581285	0	7.618406	3.968582	13.58957	0	9.683379	4.780656	6.865251	7.307598	2.631543	0	0	0	4.138624	2.598558	0	6.460381	6.218937	8.522009	6.525793
14.43748	31.41877	27.26272	13.36306	23.19135	40.91657	18.24718	19.06946	3.865272	12.86788	12.41192	16.5007	9.439363	9.572723	11.6263	4.351697	5.542535	9.00088	11.14367	4.860719	12.79032	14.44987	4.326071	3.690563	5.812805
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	7.447185	7.162533	3.17577	6.172235	6.774617	0	0	0	0	10.1593	0	0	0	0	0	0	0	0	0	0	0	8.933134	7.090893	7.588224
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19.37869	0	2.022961	0	2.058931	0	0	0	6.007379	0	10.50404	0	0	0	0	0	0	0	0	0	5.769725	27.08625	0	10.15944	7.144445
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
865.6498	2144.538	2164.982	943.9618	1139.367	1509.622	1505.711	3158.999	1008.279	2487.995	1528.857	2057.704	1692.023	1032.165	1699.804	254.4422	766.6447	921.8591	1973.891	883.7726	1291.57	3028.215	984.0642	4447.45	868.5194

9-6 plfa	1-4 plfa	3-6 plfa	5-1 plfa	7-2 plfa	9-5 plfa	1-1plfa	3-5 plfa	5-5 plfa	7-4 plfa	9-4 plfa
0	0	3.243991	5.756961	3.682631	0	0	2.611853	2.158451	6.137615	4.630076
0	0	0	0	0	0	0	0	1.398464	0	3.690162
0	0	0	0	0	0	0	0	1.579018	0	0
3.326671	0	3.073962	3.978431	6.292796	1.964555	3.017897	2.468095	2.068509	3.95303	3.453821
36.16847	0	32.44735	113.9928	85.47178	55.20583	7.616705	5.859143	10.12193	59.44476	32.83173
37.10303	4.958955	180.3173	226.3874	128.106	58.34124	26.43944	66.33768	49.84056	185.8751	136.5733
5.501561	10.40352	150.8304	163.7198	54.92845	10.4088	11.56106	71.7694	57.44213	188.2313	137.1127
5.556895	5.979607	92.64906	118.5863	33.31091	10.2256	7.193574	43.67189	39.56138	111.4773	98.68274
4.357881	0	5.136227	10.11062	11.29508	5.597767	3.046482	5.23286	6.193687	3.238624	7.606438
6.602844	5.185986	41.00397	50.4061	21.87616	8.166045	9.204666	24.14612	24.50874	49.85944	47.67442
0	0	6.286585	6.507833	0	0	0	0	0	5.683767	5.107568
0	0	0	0	0	0	0	0	0	0	0
3.981834	0	0	0	7.718666	0	4.723415	6.52107	7.848187	0	0
0	4.321488	70.81995	64.66748	23.31	4.00773	3.827631	26.81541	21.99459	80.00106	52.33188
11.65996	4.933357	481.7949	409.5884	112.5269	4.953648	7.998433	103.8991	102.5733	438.6491	307.5958
6.223241	0	45.91153	47.76607	12.21008	5.575593	0	13.27078	11.47849	47.84614	36.42574
142.9181	88.0444	809.024	870.8121	472.5528	196.2079	239.582	360.8468	313.8631	826.1931	606.7238
0	0	16.08849	20.32636	0	0	0	6.313884	7.447559	25.46796	21.88878
0	4.958897	27.56194	29.93567	9.797576	3.765971	5.11136	15.74311	10.95746	31.82131	31.40134
0	3.04179	15.53575	43.89043	0	6.04901	0	17.67492	0	0	22.29721
0	4.776226	17.87073	23.33812	7.75066	2.044811	0	7.232693	7.923429	18.14499	23.61977
18.91974	5.389798	49.9586	39.53283	43.41351	10.9475	100.8629	70.65208	82.3175	42.69222	37.22497
0	0	0	29.59519	0	0	5.981843	0	0	0	0
4.944835	18.67264	41.4143	0	28.2631	11.21953	11.85119	27.28676	25.24547	33.42639	28.59367
0	0	68.3443	59.43124	0	2.610382	0	19.57896	21.86908	228.316	44.4379
32.51674	10.77134	225.2687	229.3808	99.23436	29.5462	41.95796	120.5659	62.26334	307.4382	146.4367
48.27472	2.567601	339.7883	329.6125	174.0131	53.14201	66.92671	3.758473	96.75856	0	264.2812
126.5528	21.8166	141.3577	20.92986	311.1091	168.8609	228.0224	87.05168	70.83719	98.99458	115.6709
3.666164	0	6.975254	0	13.96963	4.948708	6.665151	10.78864	0	0	0
0	0	0	5.052008	6.035329	0	6.33331	0	4.715778	0	0
0	0	0	16.70496	5.104419	0	0	0	0	0	0
4.971693	6.246635	9.104047	9.319083	12.48718	4.288691	7.998772	7.519231	8.909267	9.086222	14.02415
0	0	0	45.12279	0	0	0	0	0	0	0
0	0	62.83806	96.25296	9.183885	0	0	11.00469	11.74492	50.8455	33.7614
0	0	136.0382	4.32937	16.73141	2.058237	0	21.33829	23.66289	65.13964	68.44288
0	0	3.580819	4.502655	0	0	0	0	4.199868	6.276774	7.896902
0	2.734395	5.483951	0	6.976356	2.678769	8.65624	6.045789	6.44545	8.797627	0
2.087578	0	8.828723	4.238734	7.687415	1.884809	6.735878	1.032056	0.68544	6.419417	4.966333
3.214852	6.017385	14.90035	19.79429	12.05998	3.687203	8.303088	9.890838	12.73014	11.24132	34.36941
108.7113	105.275	108.782	102.9507	222.474	105.7828	121.9923	109.8596	110.1432	107.7255	106.1525
0	0	8.05967	5.101521	0	0	0	0	0	4.396592	5.914623
0	0	25.36943	20.52629	0	0	0	8.799057	6.906037	21.28331	21.46346
0	0	0	0	0	0	0	0	0	0	0
0	0	1.883334	2.825736	0	0	0	3.934449	0	2.533841	9.406784
0	0	0	3.761638	0	6.341851	0	4.35151	0	0	5.379556
107.4706	0	148.8004	5.036677	209.2072	2.92872	3.809861	0	12.26908	3.484063	11.90435
8.064086	4.585439	14.8639	11.64681	13.76218	3.768287	16.29208	9.676489	15.5821	9.362015	20.69439
48.03051	57.5623	43.3655	38.36612	65.26897	53.55705	53.98892	65.03014	65.73447	40.24136	69.40097
8.12709	0	1.07379	4.190724	12.17353	4.029808	15.65456	5.762388	5.724679	9.495026	3.727615
3.580143	4.638522	21.88103	16.58102	9.858035	2.767125	3.388526	15.81958	9.302696	16.36208	18.65338
0	0	0	0	0	0	0	0	0	0	0
5.428098	0	7.808642	3.185652	8.578534	4.606135	4.092857	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
17.15655	0	0	10.95074	7.851335	4.408021	6.817388	0	11.59958	8.595819	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0
650.1896	207.7806	3319.213	3177.066	1973.983	689.2616	863.3715	1207.662	1151.107	3007.886	2426.704

Appendix 4. Total fatty acid (ng g^{-1}) data from Chapter 3.

cage	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
crab	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
grazer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
nutrient	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
Component	5 TFA	9 TFA	20 TFA	37 TFA	41 TFA	17 TFA	30 TFA	33 TFA	45 TFA	46 TFA	1 TFA	7 TFA	22 TFA	27 TFA	40 TFA	6 TFA	8 TFA	25 TFA	28 TFA	48 TFA	4 TFA	29 TFA	34 TFA	35 TFA	43 TFA
12:0	155.9491	152.933	76.49471	307.6976	217.9198	151.7103	123.7654	137.1422	163.3417	165.5474	136.4997	91.3203	207.5444	168.8508	150.9719	163.4808	137.5723	65.16268	89.36157	143.1363	389.1624	94.79611	278.785	195.8774	175.0761
i13	70.76484	65.59198	38.77458	93.67138	108.3891	71.6418	48.04313	66.64131	60.95789	67.44884	55.6292	32.65431	75.06108	68.78173	61.61191	85.44808	61.26823	29.90813	44.40866	75.59565	147.8702	37.34102	104.319	79.52836	69.38058
a13	31.1393	28.53665	25.21564	43.85799	52.07119	32.22024	19.75595	35.69886	34.39384	34.07938	14.65692	13.26581	40.83063	35.13925	25.40659	41.47518	23.87882	17.70921	31.73959	40.9965	97.70433	23.68441	72.92945	58.09555	41.26304
13:1	23.65414	38.76906	31.76265	32.3419	39.84132	24.60809	26.08954	25.56165	32.53405	31.86621	12.19835	12.92675	20.02881	22.41407	28.78263	25.51291	14.75808	0	20.46897	25.02538	27.18998	0	0	0	26.02625
13:0	97.05199	106.7083	72.55716	145.5238	173.0622	114.2382	102.7243	117.73	91.82659	122.4614	94.79526	92.30099	108.7146	123.7217	106.8598	142.6597	112.2312	61.06892	72.33086	115.1935	202.142	69.86577	149.5638	119.2533	112.1384
i14	515.9976	518.5846	308.1536	673.9956	752.1951	569.5433	422.7535	478.8622	495.8964	499.9778	395.0411	231.3096	509.934	480.9633	372.2908	557.4451	433.0114	233.7191	370.7937	553.0749	871.4685	259.7632	605.1604	472.1736	502.5159
14:1	94.36454	100.789	58.29828	143.926	163.0555	108.9874	74.79505	89.66022	105.641	149.6436	80.95929	73.80772	105.4752	126.5222	100.0708	127.8106	100.3809	55.89591	53.21076	112.6001	293.2859	73.30944	166.0104	145.4471	104.3389
14:0	2080.786	2173.561	969.0043	2451.336	2681.619	2252.274	1978.586	2421.806	1508.718	1955.571	1739.425	1398.598	1846.254	2363.135	1848.727	2197.652	1313.629	1188.264	1393.194	2010.192	3118.941	1146.946	2409.177	1780.969	1549.633
i15	1520.269	1469.985	901.6061	1791.822	2159.788	1627.231	1300.913	1483.213	1427.47	1361.002	1229.372	813.3439	1417.579	1391.047	1140.007	1977.986	1327.765	651.0137	1110.483	1674.315	2261.852	812.6131	1768.617	1339.303	1382.251
a15	2022.892	2000.317	1420.728	2346.437	2889.375	2232.346	1781.79	1898.655	1931.415	1878.043	1692.709	1406.152	2011.393	1882.634	1629.523	2457.418	1840.535	1107.411	1571.319	2200.35	2853.841	1116.405	2271.577	1864.984	1631.325
15:1	153.8312	161.1777	26.31694	211.9828	248.326	205.903	223.0783	205.6486	187.9643	219.2992	126.374	274.8692	115.9795	202.0781	31.62763	295.6911	217.9476	27.00027	128.6321	137.7322	178.8625	44.49518	157.1895	115.3587	124.8685
15:0	1038.312	1154.483	884.4854	1391.335	1783.071	1463.551	1504.391	1348.757	1165.082	1261.621	993.9578	1412.329	910.6801	1355.842	1193.276	1751.325	1429.308	713.2962	885.481	1064.128	1546.681	817.9748	1313.109	960.4535	876.206
16:4	82.94488	79.86584	59.12464	95.81309	126.3597	91.66608	12.96996	67.48017	75.76973	75.96473	115.2419	53.29809	82.64223	83.55427	71.95702	113.5138	76.63182	36.99191	59.31831	89.95765	117.7351	34.19822	93.49398	73.70628	81.65637
16:3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16:2	9.528323	15.83972	0	0	0	18.71998	0	0	15.77808	0	13.76701	0	0	606.2821	17.57902	840.2864	451.1538	302.5997	0	0	938.5007	92.94264	744.7524	0	209.2208
i16	784.6933	811.9538	533.1119	893.3969	1078.534	996.736	820.9999	776.1246	826.0024	737.4071	695.4951	1150.878	717.4827	739.9087	635.8504	1091.772	834.6029	506.3013	592.0298	904.8057	674.9032	312.92	539.3367	684.2286	506.7084
16:1w7	8436.381	6501.338	5577.158	8153.528	9819.267	8875.467	8680.467	8819.842	6812.764	7129.911	5218.195	6816.797	5088.965	7259.565	6823.284	10124.23	8800.253	4152.26	5435.677	6385.327	7148.958	2241.114	6007.89	4298.926	5342.458
16:1w9	368.5281	344.561	203.8212	435.1867	395.907	350.0507	354.4815	43.32657	317.1976	257.6831	286.5501	0	291.7047	307.9152	258.2853	383.2863	0	201.2858	226.7372	377.4239	503.3327	631.9181	295.7113	263.7513	70.26023
16:0	8148.682	9438.02	6075.989	9812.079	12296.92	10907.28	10567.46	10638.73	8670.322	8511.251	8286.051	7142.649	7351.341	9277.146	8278.136	10495.59	8047.331	5601.821	6705.639	8406.251	11988.27	3616.291	9542.242	7271.427	6440.729
10Me17br	537.1932	533.8413	356.8805	538.371	773.3399	620.1678	560.7653	508.7736	511.8767	459.2014	466.2165	492.2787	616.1146	511.3085	469.355	798.6683	612.9527	334.8066	448.7258	592.1622	750.7451	245.9726	457.9068	319.1377	526.3011
i17	429.6717	423.8891	265.525	453.5231	619.3659	550.9292	403.6811	439.4103	462.0994	360.8883	547.9716	296.9043	429.7848	518.6206	411.9659	642.0515	432.9457	374.8887	395.7038	507.4936	754.7695	210.7971	591.3979	434.5568	397.9006
a17	888.0133	1087.542	1036.927	1163.344	1630.984	1485.788	1645.683	1324.257	1151.478	1254.198	831.6165	1872.902	807.7424	1300.304	1270.484	1854.429	1666.95	756.604	834.9187	824.0609	969.6821	438.5133	1005.204	481.0326	712.1418
17:1	280.714	366.5959	289.3124	412.0417	446.9841	362.7587	401.3899	326.822	286.8499	320.0226	215.6374	402.5663	242.3218	387.1785	276.1953	528.4986	416.5168	200.5977	241.7979	357.9964	348.5474	134.2716	270.2975	211.2191	248.6594
17:0	697.0371	790.6765	493.6554	803.0907	1118.784	1103.45	814.5131	764.8262	818.2083	738.8227	1052.901	697.729	779.4588	1068.301	861.1506	1190.945	813.7428	677.229	781.7477	980.984	1324.421	446.233	1141.254	860.9845	707.1303
18:4	159.9339	195.5091	143.4573	207.4553	254.6999	247.6407	269.3683	291.9091	179.008	202.8534	119.0603	185.9026	106.8368	183.0417	154.208	236.4971	175.4794	115.7296	128.7278	118.7034	145.2233	38.48831	105.3451	74.56415	83.49394
18:3	387.4389	389.9433	358.5765	429.1431	509.3006	551.5924	512.7635	530.8949	382.7049	402.9661	356.008	343.6423	284.8236	469.0522	383.1898	499.6347	349.296	286.683	295.2375	336.8607	572.8687	215.8606	497.151	357.8729	247.2623
18:2	729.3638	789.8379	702.5173	1739.309	1078.909	1131.297	1037.592	1073.995	1473.295	907.8892	974.5956	500.4428	1007.096	972.0244	911.227	991.58	690.645	513.7076	751.6146	782.899	1107.386	382.0466	1127.92	623.4759	1141.635
18:1w9c	2620.43	2931.697	2032.458	3066.155	3310.664	3555.763	3141.455	2679.185	2938.679	2492.313	2456.152	1692.897	2135.778	2566.295	2733.191	2883.973	2072.794	1430.305	1949.405	2363.923	3203.931	1055.042	2436.418	1983.17	2279.295
18:1w9t	3368.966	4199.263	2425.683	3856.075	5244.287	4180.969	3824.62	3611.892	3506.036	3357.151	3425.833	2676.437	3721.531	3413.969	3326.398	5042.979	3171.92	2232.266	2723.024	3736.845	4609.728	1505.267	3521.988	3313.523	3393.436
18:0	2018.808	3037.853	1572.216	1907.701	2857.291	2424.371	2084.58	2020.05	2142.793	2431.181	2376.686	1443.18	1806.095	2655.863	2739.983	2428.735	1821.788	1692.659	1747.256	2551.774	2984.502	1082.802	2582.312	2011.736	1634.905
i19	88.2041	19.7641	21.34465	26.9276	33.09669	0	80.42127	189.8603	0	54.68658	23.12197	0	136.5904	40.45369	141.1988	124.9175	33.33745	0	34.33996	4.833238	73.2312	10.92725	77.41826	52.00074	7.508529
a19	68.33805	69.3482	63.19354	76.10682	96.28326	97.67023	69.18578	75.18303	109.2297	68.14467	127.9557	54.75023	82.09544	122.5818	104.5176	130.4909	75.27231	76.83656	98.48745	109.6573	121.2319	33.97142	116.3567	112.4763	88.91318
19:1	31.5331	52.54722	12.95016	55.67647	89.44124	79.30027	47.35815	72.28976	105.5036	54.74934	89.32461	15.59548	78.89772	15.67042	77.75304	123.2279	61.32239	33.26529	50.64768	35.01909	64.7788	21.90999	70.44917	57.43254	82.5275
19:0	4506.248	4613.555	4086.518	4008.413	6176.625	5681.333	5035.999	4339.031	4523.147	3655.353	3713.36	5059.219	4321.133	4015.005	4864.411	4734.516	5511.157	4834.625	3805.307	5375.002	4968.932	2264.53	4267.678	3940.652	3066.634
20:5w6	9.88942	25.85586	39.49579	56.77219	53.75809	0	13.45541	14.73973	0	68.81465	11.01904	0	60.07489	43.30442	36.00712	44.70769	25.36314	19.10475	26.80116	0	144.4529	37.029	179.1077	55.16774	64.17175
20:4w6	1361.466	1590.148	1561.573	1975.732	2342.701	2503.001	2357.886	1951.683	1915.144	1908.751	1489.938	1990.081	1243.255	2195.446	1815.334	2731.494	1916.259	1640.704	1665.486	1411.203	1803.738	458.1353	1489.632	905.3547	994.2501
20:5w3	1991.145	2321.713	1884.896	2804.194	2656.731	3556.893	3445.922	2854.077	2560.341	2370.707	3126.667	2036.902	1763.99	3353.414	2530.168	3946.156	2165.889	2584.045	2682.255	2306.747	2894.462	755.4513	2428.864	1500.43	1678.238
20:3	107.1511	118.731	111.4862	124.6829	130.7764	186.5371	190.0572	157.7226	170.0897	111.9201	888.5623	159.6522	91.65349	170.6393	439.7414	189.5853	134.5413	108.5328	117.8986	131.2194	166.9803	41.9868	109.2098	64.30395	90.32479
20:2	91.67676	110.7238	90.99657	112.3836	121.4437	231.9197	144.9217	176.3903	237.5749	106.0702	292.7958	141.0351	102.075	289.4578	165.5036	171.9123	184.4116	172.5224	197.8653	113.4733	374.7532	81.31785	304.8276	26.22022	88.27178
20:1w7	99.38824	130.4843	94.20498	108.3638	126.9234	136.9783	113.23	145.839	167.2914	105.8811	226.3155	145.4156	160.3568	209.3854	191.5364	258.7354	170.4603	224.1559	136.4988	221.6582	363.4415	72.28955	245.6706	174.4891	89.85427
20:0	2784.825	2976.272	2561.902	2931.05	4166.81	3609.4	3092.266	2888.5	3078.58	2627.849	2336.861	2707.821	2975.552	2638.348	3044.1	3277.219	3200.704	2556.001	2330.514	3311.923	3936.008	1676.056	3181.7	2999.323	2611.342
21:0	2864.215	2758.492	2526.962	2680.317	2958.105	3098.193	2643.384	2549.724	2480.586	2421.451	1307.527	1366.864	1307.144	1427.856	2549.951	1407.474	1731.517	1430.359	1361.385	2929.804	1422.747	1093.304	1502.276	1592.034	1690.733
22:6w6	8.258918	7.320803	10.30157	9.418606	82.38139	27.31744	8.328196	27.39042	29.17938	0	0	0	0	0	38.82711	0	0	0	0	0	0	0	0	0	0
22:6w3	153.0756	163.8052	117.3416	160.1028	187.0344	236.375	199.7324	179.2604	223.2987	166.1543	236.385	132.3355	145.0759	257.9865	187.9377	326.0435	174.9905	196.8907	211.4718	220.8574	403.4577	175.2492	280.2229	245.6934	181.2206
*22:5w6	106.1255	142.86	125.9033	165.7077	147.7326	620.979	216.9426	167.6846	382.6584	179.7622	777.2876	215.3997	204.7857	767.4352	348.529	671.5615	227.9499	371.0521	429.8419	379.4952	288.8982	121.4613	324.3558	336.8611	119.1729
22:5w3	126.6392	157.2202	127.0251	186.002	155.9524	412.2101	248.028	192.76	305.1159	173.6016	654.3946	208.6875	210.2097	624.3752	372.4709	566.8649	221.7075	392.2289	425.8636	373.4978	312.8526	127.4775	331.3157	256.8549	219.0259
22:2	34.56524	32.8165	27.16458	38.45113	4.808738	69.55428	35.73764	28.80591	30.50422	36.45973	107.9737	37.7859	44.79083	94.96612	39.6095	69.81876	29.54131	39.8048	50.56107	47.50806	80.58967	30.6211	33.06507	85.36011	23.00608
22:1w9	89.95419	61.42263	57.16041	60.48142	82.54384	68.8633	48.04765	57.62381	58.25422	69.83649	62.87602	98.56298	68.44626	86.79127	59.36058	98.95076	64.99765	41.62877	72.39514	108.2186	20.02007	15.26219	27.4085	14.44368	46.88428
22:0	598.9071	695.2603	411.4688	815.0283	1044.712	673.933	634.7684	686.4064	722.6028	583.5957	619.1672	326.7199	768.8236	572.5587	575.8664	783.1684	610.7834	292.4292	538.8285	746.1821	1281.879	595.2641	956.8314	836.5888	805.0233
23:0	426.7009	470.9003	384.5856	420.2622	586.7621	557.1024	466.7349	448.9763	471.0621	367.7972	388.2392	394.0882	430.1045	441.7132	415.4435	429.7212	527.1345	357.0781	352.7039	508.6635	475.2791	324.0675	403.7539	390.1104	363.6632
24:1	38.45628	23.90483	31.27298	30.18958	42.98869	39.41521	47.27868	26.15677	52.19135	35.72503	48.27139	24.17692	29.39223	11.09875	34.16189	44.02295	0	18.00741	29.24665	7.148888	30.08017	0	0	0	0
24:0	1012.698	1135.712	671.5119	1349.345	1792.779	1116.531	910.9076	1158.621	1163.346	1006.279	799.9088	591.9473	1238.543	916.8917	971.0452	1211.103	1023.913	466.8026	760.2294	1138.649	1829.179	1041.813	1474.811	1265.64	1258.037
25:0	122.7394	138.619	74.48169	153.2996	217.8007	206.6777	106.9127	115.8573	124.3632	122.6548	88.8569	79.34861	173.1499	118.0715	106.8291	134.8313	353.8985	58.77371	79.19319	133.472	209.1208	138.7564	191.779	157.6309	161.4437
26:0	611.8721	712.673	370.2987	732.5582	1021.679	568.7666	518.6945	563.4459	695.4153	601.0561	464.9657	398.5003	813.5595	643.6212	546.6453	628.1455	402.4803	303.0057	422.9243	833.7151	1064.25	753.48	1045.061	760.0331	840.5099
27:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28:0	367.2832	367.5074	174.6926	339.7737	509.7216	307.0783	253.0127	259.5857	417.8692	318.3914	170.4349	214.521	481.7821	414.382	247.4625	260.7031	360.5041	118.6612	178.6614	270.0040	577.5006	440.1869	534.4508	348.8384	420.1565
29:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TFA Corr total	42852.81	47986.1	33016.76	53001.32	63773.6	57450.9	52430.52	51226.08	47246.1	45559.49	44335.83	40490.8	40738.74	51492.89	45342.1	62265	45686.91	30825.64	37298.54	45862.17	62255.21	21934.48	50498.9	37670.75	38076.75

1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1
3 TFA	14 TFA	31 TFA	32 TFA	42 TFA	10 TFA	16 TFA	38 TFA	44 TFA	50 TFA	11 TFA	21 TFA	24 TFA	47 TFA	49 TFA	2 TFA	13 TFA	15 TFA	18 TFA	19 TFA	12 TFA	23 TFA	26 TFA	36 TFA	39 TFA
227.6697	126.7537	177.5773	138.6524	146.3332	181.9643	163.238	134.7505	93.54206	69.85488	187.2168	121.479	134.5816	157.0719	216.3971	162.2397	128.627	160.298	104.4992	122.8525	200.7542	189.6334	87.51366	104.0235	159.035
89.11322	53.10781	74.5505	70.76075	54.21666	36.52114	62.78676	49.74196	35.23102	37.46984	44.68587	63.28626	60.90427	54.13753	68.64169	60.49177	47.13423	50.55981	41.229	47.91702	77.86408	67.51385	35.18376	43.87886	62.1454
66.83887	30.47609	50.57309	44.9673	34.45217	22.33296	33.97779	26.52693	21.74322	9.311413	24.67355	23.97269	31.75939	27.63052	36.57821	39.57247	24.97244	32.48325	32.06935	35.52171	45.02111	43.60814	21.99923	18.89229	37.2239
0	0	13.17302	19.03241	13.36775	0	0	0	0	0	5.281112	0	0	0	4.926692	29.97666	0	29.3108	503.7594	25.73709	33.61345	509.3646	21.98761	18.44601	28.71568
122.3246	96.24354	130.9297	115.0443	110.6833	94.36212	109.721	90.52918	88.99782	66.81071	81.04617	76.74367	93.29269	85.04102	136.3415	115.2791	78.50614	107.0037	84.52332	89.79782	135.0138	119.2971	100.0929	70.79436	116.4723
588.4961	364.4078	446.2441	565.7054	371.6458	236.511	399.4709	320.515	247.2809	281.383	281.0663	324.5398	360.4738	351.0183	402.6851	427.2875	273.4636	376.988	271.0453	360.7261	486.0797	432.6542	289.0305	274.1926	417.0335
143.6151	83.46697	146.4891	135.2868	108.8364	47.36376	103.7822	79.35034	51.96399	64.54013	82.37886	79.00453	54.22467	95.34628	86.5026	82.93239	63.74434	83.22992	106.6053	74.51924	137.0535	111.5997	63.29824	68.21956	115.9876
1833.739	1386.582	1715.394	1754.819	2009.847	1101.798	1576.454	1469.064	955.8348	1327.493	998.1299	1012.329	1316.476	1177.172	1476.957	1506.147	1159.059	1381.542	1073.88	1285.651	1795.392	1330.675	1007.721	953.3414	1440.105
1587.549	1192.411	1391.737	1510.883	1197.59	747.2412	1194.491	977.1679	773.5582	959.7749	927.5238	1017.769	909.191	1144.714	1021.139	1270.99	887.3858	1053.026	835.2718	1088.808	1450.571	1195.542	1056.272	881.5887	1328.563
2040.844	1705.128	1891.959	2082.553	1660.598	1264.931	1872.042	1543.458	1013.59	1384.323	1408.611	1369.139	1329.609	1687.902	1800.974	1872.771	1317.216	1615.335	1537.113	1621.912	1994.664	2006.756	1594.131	1292.855	1931.722
95.76072	26.99413	160.2316	160.8669	151.6865	211.1169	191.5486	148.5464	165.7787	116.6721	184.7923	101.765	22.40579	162.5664	233.209	183.7416	130.1948	202.9122	1250.274	131.274	224.244	1099.746	31.83982	24.96053	195.8076
926.0742	913.6753	1183.359	1232.839	1112.313	944.6251	1188.37	943.4011	871.8991	822.4033	953.9342	640.3118	1123.613	914.0362	1186.325	1115.019	769.4048	1171.285	916.3238	847.3223	1364.151	1086.845	926.4009	621.4227	1169.553
74.91431	58.21058	83.52004	80.49047	67.04049	51.19192	67.92419	59.22404	40.08723	56.70499	50.78318	64.31878	30.87672	68.2285	87.09465	75.17542	49.90273	71.30595	56.32713	62.97469	87.78263	90.9844	56.57496	48.6085	80.17409
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
480.9813	0	0	643.5591	134.8966	0	0	0	7.852297	0	728.9619	0	22.98941	0	0	0	0	0	170.7461	0	599.6655	0	10.24121	9.905593	131.4201
459.0569	457.8779	808.4174	411.1524	1234.853	411.7886	682.6393	589.175	459.9649	498.8376	475.4774	481.7289	400.4876	625.644	745.7244	744.1508	497.0073	742.3908	423.8144	645.8698	621.1749	589.5707	425.1478	467.9886	1272.833
3938.274	4372.928	6260.079	6024.943	6995.999	5365.814	6762.478	6151.121	4583.309	5027.079	5738.624	3734.027	869.2429	5573.752	6644.283	7025.127	586.3591	4960.949	1120.928	4943.106	7012.957	6405.75	844.2391	3802.666	7338.909
312.9523	0	33.14874	52.06901	43.57811	0	227.463	43.95618	212.7923	208.7614	322.4721	121.9856	0	37.52893	40.45414	0	18.67685	906.0745	0	52.63415	294.0742	0	34.18657	147.4002	36.82509
7821.614	5994.914	8173.056	8089.377	7645.908	4904.615	7737.283	6382.209	4653.309	6069.677	4209.729	4773.495	6625.086	5815.647	6146.658	7308.626	4879.822	7677.906	10017.83	6822.457	8737.47	10785.46	5963.221	4753.615	7640.853
586.8369	420.2248	610.568	635.6611	455.5171	393.5122	600.5677	496.3895	328.2592	383.459	459.9628	387.0085	503.0079	554.7198	541.3058	498.548	360.301	372.3043	421.732	446.9295	710.095	578.8369	480.5272	381.8783	652.0116
461.68	305.6793	443.1512	456.9284	399.1629	240.833	378.6025	324.8745	221.2456	298.4038	292.1531	255.6224	331.5724	313.1536	497.7437	410.1921	252.7985	424.2503	278.5055	374.0429	452.8103	353.5997	312.5579	261.7819	411.0616
499.5571	754.6564	993.7909	1036.746	1092.87	1130.198	1292.333	1033.958	986.7851	891.1163	978.5942	612.3889	123.9657	979.3665	1260.393	1189.192	761.7657	1046.449	1048.378	803.5276	1415.37	1145.498	1052.116	612.9459	1285.241
182.002	192.4697	280.5245	248.1228	300.3361	237.2985	301.2046	240.9249	227.0349	274.3977	211.8022	165.325	109.7619	255.6165	349.0857	286.3216	199.5469	287.5441	217.1657	216.1113	346.6359	264.4765	234.4445	141.2456	316.833
833.0091	596.6137	875.7528	842.5833	770.8892	448.5944	796.2062	629.518	420.1374	588.0116	530.5596	443.0831	622.5465	543.9832	1042.567	767.9827	461.783	927.8337	572.5339	674.4884	900.769	733.8699	546.8313	431.9435	772.2728
67.73904	86.89165	121.5062	102.0199	143.7744	114.7509	156.3145	143.3687	109.9286	123.907	109.1835	51.5595	7.660462	92.92715	146.9146	163.803	94.55529	162.7132	118.3884	102.8696	161.53	132.1296	104.0819	78.56496	156.6749
381.5175	404.584	458.9864	414.8278	428.9535	232.9383	333.0503	340.7038	237.7144	304.1612	213.1198	165.8795	1320.602	253.1846	346.1783	305.7646	239.9521	333.8228	278.6172	258.2052	286.3928	240.7302	219.9899	171.4313	311.6239
1069	856.958	694.1904	488.2082	830.8698	871.5851	667.0851	664.955	505.749	512.1067	1063.438	375.6327	211.7144	629.3073	852.2442	832.3902	463.3174	742.2302	830.0388	886.7865	919.838	904.8087	1084.359	508.2602	709.4107
2053.892	1492.495	2040.617	1924.642	2205.402	1332.493	2030.194	1626.132	1144.513	1539.101	1625.606	1292.05	869.2498	1535.911	2473.592	2284.78	1183.807	2873.351	1815.851	2174.131	2213.049	2107.555	1722.759	1334.634	2053.154
2650.776	2008.015	3095.496	3634.21	3136.693	1940.554	3477.972	2692.966	1788.845	2445.034	2376.971	2419.232	570.2729	2437.143	3469.704	2900.154	1929.709	2635.54	2616.019	2904.175	3896.81	3729.35	2337.426	2175.751	3348.974
1956.78	1103.703	1819.812	1599.071	1628.315	999.733	1806.313	1416.601	889.6365	1702.011	1173.294	1418.226	1494.605	1226.557	2239.749	1485.422	980.9831	1949.117	1269.825	1507.21	1651.484	1310.859	1334.865	843.7363	1376.635
11.8606	63.39825	103.8434	69.66666	6.846418	41.94395	13.78695	92.63371	0	120.3202	68.5317	0	126.8312	46.00895	123.4973	88.70748	3.798051	18.49042	29.88442	25.01208	101.9296	5.616543	130.6018	0	64.02197
56.39797	58.82975	77.42879	83.5526	83.03528	37.48194	111.818	59.76383	47.32458	71.3304	48.83052	44.59745	4.498073	44.71247	103.6073	87.59861	38.92473	97.24813	65.84159	73.38812	107.8231	109.5006	54.09629	44.17034	78.45126
73.90643	7.698967	75.24293	40.94834	52.77295	16.56793	48.17706	21.60017	16.40175	5.665749	35.77135	25.34779	34.9651	120.8016	83.18043	87.86603	35.41882	25.68849	24.38648	58.58513	120.2507	42.73634	8.109246	32.43899	46.80728
3677.279	2490.381	3575.899	3402.864	3805.492	3750.421	3860.294	4530.968	3873.702	3973.935	3153.061	2895.288	4185.751	4300.872	4644.397	4099.806	3313.551	3737.337	3466.656	3442.04	3990.771	3292.011	3793.876	3531.879	4047.982
48.63542	106.9409	92.58179	72.17963	36.42679	16.54951	79.16618	64.71607	0	0	49.52424	33.25936	107.5621	30.1928	154.1178	0	27.45802	0	0	-11.90884	28.14957	25.34013	0	10.45866	0
930.6746	1113.241	1713.882	1206.394	1917.252	1190.916	1864.922	1686.591	1314.527	1483.73	1330.402	991.5622	99.16986	1386.018	1963.55	1734.607	1135.011	1791.473	1493.092	1254.884	1830.481	1663.673	1279.076	906.0497	1870.71
1441.631	1600.889	2288.964	1397.994	2674.764	1330.505	2484.366	2119.361	1364.978	1668.533	1430.765	1253.932	86.01794	1462.635	2871.27	2352.087	1277.011	3123.102	1725.99	1998.403	1963.909	1983.094	1485.423	1088.308	2054.42
75.01453	114.8044	134.2249	113.4122	139.6145	98.48571	116.2979	130.2296	89.71361	101.9191	92.04418	69.43078	25.69444	89.46708	150.5237	121.0884	56.19771	1011.255	112.2383	107.6018	141.8956	122.4659	104.5188	87.05665	116.7171
236.446	150.3483	225.8647	152.3429	207.463	95.24115	155.8547	106.977	60.50247	88.11588	72.58414	45.19015	393.326	75.97598	203.1697	163.6773	51.87261	183.37	108.528	136.4407	100.423	160.6153	82.77477	66.58376	137.7974
151.826	70.32226	24.46468	119.3724	155.9607	59.65891	167.5784	111.5046	74.80163	91.68758	81.63883	77.3064	23.48554	106.2239	186.9327	159.1729	62.5651	143.5425	88.97462	119.4232	163.3238	97.85341	154.0573	81.25636	117.0888
2710.279	1614.995	2701.545	2204.85	2326.566	2106.824	2421.385	2520.734	2129.119	2241.882	1984.485	1729.259	2467.653	2812.067	3148.753	2691.397	1982.038	2556.054	2173.008	2285.521	2900.961	2396.045	2454.107	2111.097	2693.102
1133.315	1602.364	1361.629	1627.302	1653.913	1437.043	1269.626	1329.264	1474.045	2635.549	1304.749	1274.351	1278.293	1424.736	1383.582	1460.059	1351.872	1438.957	1387.028	1366.608	1527.656	1400.984	1436.435	1404.065	1444.413
0	0	0	0	0	0	0	0	0	0	0	0	182.0395	0	0	0	0	0	0	0	0	0	0	0	0
374.1394	208.5912	293.3209	261.3639	205.7161	87.82946	188.1343	148.1187	81.73526	136.739	97.39153	102.1462	526.3859	101.6626	249.8836	176.1801	74.05005	232.8308	132.1255	143.95	180.0395	148.2949	132.2771	80.46995	166.6129
199.1213	178.9028	298.8458	227.9042	291.3834	119.6144	308.6459	197.267	88.61413	139.1148	111.1376	109.1634	0	85.00746	881.3656	240.9032	88.87122	445.6407	157.0044	298.0884	189.2311	347.1059	462.2027	85.73606	163.8279
204.3143	205.097	265.8981	170.0144	337.3267	116.5752	357.0604	205.1588	92.59553	153.7951	101.8426	112.2855	0	101.4141	574.965	263.8817	91.94577	643.1311	149.9463	232.0394	200.6728	224.9843	253.5333	78.92007	183.1787
102.9926	33.69794	30.81252	62.73506	29.2725	25.83235	81.76629	27.04116	12.12326	19.8058	17.51626	11.17658	45.82539	23.62535	120.9538	45.0921	15.55924	122.2221	20.54598	64.68746	47.75482	26.30782	30.69849	23.59408	28.63985
69.30553	2.216567	9.716669	36.93763	70.90638	61.46146	88.1895	35.26933	50.14246	84.27435	52.79107	29.583	58.41777	72.03651	101.2479	30.60961	53.68482	46.09889	11.53204	10.95155	8.261278	58.53568	44.79229	0	14.23319
837.5977	306.0225	671.5719	460.1562	402.7329	311.2788	539.6537	388.2012	299.4041	351.4596	428.4132	403.8287	464.102	462.2995	701.1522	664.8131	345.094	497.421	394.6315	527.3522	782.3814	626.4577	669.4215	319.0759	552.5014
384.0828	230.8103	349.2505	283.0424	269.1874	359.4891	380.6698	409.264	350.0235	437.509	336.3189	309.5769	351.4589	391.436	434.2496	317.8511	360.1755	294.8453	269.3229	285.8354	365.8746	316.0203	315.3703	265.3245	327.8304
30.09116	3.858042	6.27054	0	9.614095	4.555259	42.08529	12.52427	0	7.739472	0	69.42681	0	0	30.81697	0	0	12.21971	5.748178	11.98372	30.14749	0	0	0	22.39982
1301.033	515.3991	1087.123	778.3129	621.1613	511.9224	935.5478	626.0632	499.126	561.1303	737.9263	605.1243	725.4778	786.177	1171.029	952.4435	583.3419	793.7279	644.722	780.9628	1167.658	1632.588	991.0565	511.6961	890.6107
161.6963	55.96866	133.0502	99.87262	76.54717	62.78472	108.8892	82.5083	66.28074	74.47326	95.36637	60.48375	87.30529	92.075	136.033	95.14515	73.63996	86.53071	73.62987	82.31947	147.9837	129.8652	83.1242	69.10088	104.5132
838.1028	370.3318	631.9263	559.7321	380.6185	300.1071	559.8265	396.0087	305.8681	357.7567	463.8659	317.3715	418.9843	450.3851	854.6159	532.6824	382.1423	465.846	425.6597	450.4	798.7972	716.3642	534.6922	333.286	502.273
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1160.486	171.1424	318.9003	329.6134	181.0719	136.0748	273.2754	197.9221	153.3998	184.6917	254.2585	117.48	220.4201	208.8684	335.2791	234.4476	154.6322	272.7814	269.7368	182.8023	484.956	443.1596	270.1712	159.359	218.1505
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11.24279	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39847.84	30423.17	42678.57	40758.33	42367.14	28198.05	42724.25	35348.79	25736.12	31765.71	31208.67	26090.6	22980.68	32546.89	46371.56	41173.06	22492.47	42596.37	33947.51	35178.74	46846.82	45531.47	28769.65	24522.51	42250.23

Appendix 5. Phospholipid linked fatty acid (ng g^{1}) data from Chapter 3.

cage	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
crab	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
grazer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
nutrient	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
Component	5 plfa	9 plfa	20 plfa	37 plfa	41 plfa	17 plfa	30 plfa	33 plfa	45 plfa	46 plfa	1 plfa	7 plfa	22 plfa	27 plfa	40 plfa	6 plfa	8 plfa	25 plfa	28 plfa	48 plfa	4 plfa	29 plfa	34 plfa	35 plfa	43 plfa
12:0	7.668123	8.265578	10.81123	12.75339	12.07644	7.85118	8.656306	6.15989	51.45299	17.47422	18.95457	8.474732	21.11902	16.65122	14.43459	12.71883	17.4284	7.006668	10.04037	13.69952	11.14405	4.690435	7.762008	19.55401	19.34462
i13	7.06658	7.023316	10.69364	7.366581	7.206971	6.87646	6.255988	9.850067	5.904691	7.648534	12.25552	5.129601	13.98914	10.99519	10.1998	12.49123	11.54773	5.226137	7.531559	12.57306	12.86266	5.274383	8.304267	13.60805	16.26732
a13	0	0	0	0	0	0	0	9.073471	7.114752	0	14.65692	0	6.748193	5.761144	0	7.290385	0	0	13.46903	4.955892	6.396428	2.660993	8.034146	7.25187	8.541245
13:1	6.186431	7.686116	15.24227	7.03034	5.609394	7.385319	5.494609	5.682386	8.161135	9.692367	12.19835	0	0	0	6.169471	9.055893	0	0	4.885696	5.042672	0	0	0	0	4.299693
13:0	7.623371	8.238502	12.46513	8.498189	8.994844	8.090715	7.875183	6.131098	6.642189	10.34232	14.54575	7.596203	16.11436	15.44425	6.328113	16.46306	13.97861	8.310825	9.037647	15.39772	16.90448	8.303497	12.2691	20.14103	22.46092
i14	108.075	103.3621	56.60804	93.6201	93.09832	107.2753	83.41305	77.49328	83.03876	62.37745	106.5508	50.20367	113.1798	106.6247	46.05483	124.8658	103.6781	58.88551	82.02106	126.5023	152.6338	66.7316	111.3584	127.5047	164.9135
14:1	5.250798	4.714608	12.10634	7.08197	8.794474	10.73786	13.67859	9.672325	11.63147	25.43734	8.124329	16.67797	8.310014	10.08684	11.53765	9.967959	20.15533	8.255034	5.276373	9.019963	63.19851	6.139405	8.200985	9.801436	7.655861
14:0	318.0047	283.3898	20.01021	253.2675	257.8536	311.8092	343.1807	251.1753	16.15439	345.9956	457.3625	349.6805	362.9701	454.8133	258.392	449.2927	11.55324	305.0468	286.1904	399.2658	550.3377	264.8978	476.5099	525.8388	586.2234
i15	368.3622	334.436	184.5477	253.1499	306.2459	346.6415	289.9168	276.7516	245.0244	227.3217	331.9156	182.8036	319.985	312.0647	155.0287	449.4447	308.9107	201.4339	235.7178	385.5451	412.9842	229.0352	384.0682	412.4774	555.7034
a15	465.9839	409.533	245.9523	307.4828	357.9167	450.1059	329.1076	308.8513	289.6457	276.6753	402.8596	241.5877	383.5505	356.8222	185.0901	495.8722	365.6645	213.5077	285.8945	441.8464	511.7136	297.7874	489.0867	582.4337	716.757
15:1	16.5952	14.67366	8.556814	13.74173	13.57122	16.34139	15.78966	13.07825	10.66432	13.77189	13.96559	12.92809	12.69015	14.24915	7.731021	25.29995	17.24185	9.671833	9.972879	15.70144	15.97388	8.827475	15.0768	16.76373	30.90747
15:0	154.5132	162.7931	107.3193	126.8447	158.2268	176.8865	181.8522	147.0173	138.6649	134.0178	202.7819	125.2955	156.1185	203.4951	107.1069	246.3963	173.4245	131.7915	127.8006	182.5397	215.5496	131.4961	219.5067	248.1368	283.0562
16:4	18.99478	18.16192	17.54953	12.11351	16.28412	19.54295	12.96996	13.39575	11.45971	10.58578	20.70505	5.713159	14.26192	21.87417	13.05879	21.69538	11.09985	5.907696	8.958765	14.92705	20.87651	10.74786	18.24034	22.50721	31.34742
16:3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16:2	9.528323	15.83972	0	0	0	18.71998	0	0	15.77808	0	13.76701	0	0	129.3863	17.57902	15.37901	0	10.64496	0	0	163.1888	92.94264	157.1484	0	209.2208
i16	179.2827	180.2777	103.3681	121.927	155.3785	202.3545	144.2735	146.4916	146.8356	112.5555	191.1576	83.01828	159.5163	31.43389	88.56766	213.2183	143.6462	102.7858	114.1339	163.2232	16.86782	10.71992	10.38145	204.4839	48.80973
16:1w7	950.9197	901.678	554.1811	651.5674	725.3684	888.2367	826.4488	744.6415	683.7389	607.8029	799.3001	674.8903	678.925	779.2329	463.8381	1103.769	816.4889	560.4525	519.5098	821.7242	896.7978	533.5153	839.8893	941.9207	1504.723
16:1w9	49.70581	58.57048	27.36121	44.63772	46.90347	55.7526	47.05202	43.32657	55.59531	39.86403	50.57122	0	50.29598	39.41166	25.93203	81.55635	0	29.52412	40.64171	48.83347	49.69778	24.11767	45.74936	54.21713	70.26023
16:0	1927.252	1693.539	1499.806	1312.143	1457.255	1808.616	2057.855	1533.799	1464.315	1815.789	2039.879	1128.811	1512.619	1847.32	1367.491	1885.191	1543.629	1151.421	1205.713	1462.575	2041.021	1135.746	2153.36	2270.962	2464.849
10Me17br	110.272	104.705	57.98529	59.06512	75.85468	108.9537	77.63032	82.66942	60.66462	37.91326	91.25964	55.49914	89.39381	81.92207	38.1125	123.1952	82.07647	52.87988	54.13499	88.10805	104.2704	65.05634	0	152.8396	162.7664
i17	114.786	109.0311	67.43583	73.46801	101.213	129.5181	103.4336	99.09138	84.46347	70.7975	156.7556	58.97835	106.4345	137.7996	61.65973	143.6983	111.5117	97.1767	85.32891	99.1654	135.0814	71.93007	132.8066	157.4211	158.2068
a17	123.4482	139.9905	88.12973	90.0498	131.79	160.3491	159.1884	129.599	122.478	105.1521	113.9358	112.4312	109.9076	136.0839	75.86153	192.8175	140.1158	91.70264	82.73705	126.2896	120.5219	71.74829	99.85621	147.0664	198.0487
17:1	59.50335	52.8394	32.97766	29.28012	49.1867	54.23622	45.28346	45.92471	37.42267	51.64139	37.28102	43.25645	44.12978	64.42452	21.49011	58.8034	63.62357	25.92194	49.13262	45.90715	59.91671	31.09091	43.30474	62.64156	87.08217
17:0	176.3541	163.9601	116.0059	121.3062	140.5203	206.5293	170.4495	136.0647	136.7664	136.8629	279.4905	110.9811	166.7396	278.6427	137.7267	230.8081	176.9573	167.8881	179.4671	202.0522	219.8712	125.8602	247.3826	260.3003	256.3826
18:4	10.8427	14.88541	10.3093	14.78377	16.38256	19.12672	19.09479	19.48866	13.64365	15.10436	11.99496	9.511492	9.248553	19.02882	10.42291	18.59622	12.17851	22.8955	25.86187	12.26913	12.72366	7.761706	0	10.41031	21.23621
18:3	53.10402	60.42	40.40893	75.11211	61.35416	77.02399	60.04055	61.17797	59.37603	58.00429	03.5847	39.95694	54.25783	78.0824	63.87571	76.3728	57.82617	52.53031	43.92178	65.27117	69.2501	49.49333	72.35064	89.88764	54.09032
18:2	145.7187	185.2368	144.1867	227.7932	214.6353	213.3208	220.0771	190.1103	573.2904	250.1414	195.3056	71.56952	138.3863	197.0563	277.5416	183.6111	120.5736	95.10397	167.8263	153.0362	187.6619	103.7242	177.0935	164.7009	328.5003
18:1w9c	784.4086	695.6954	642.1466	578.4634	560.3354	727.7371	775.8868	510.4441	648.4569	640.3844	692.2555	302.2303	535.4667	651.9167	576.0095	592.4751	469.8146	297.7662	464.0373	510.1913	630.7752	298.511	475.8597	753.4982	843.5836
18:1w9t	923.4046	854.9744	674.8669	609.2195	737.4417	880.7965	809.1077	089.3713	620.5459	794.9342	888.7218	489.6817	787.8725	729.8088	517.9206	891.9747	632.5486	432.1283	464.7512	694.7129	925.7735	460.3137	828.2706	1253.791	1333.962
18:0	712.8332	449.4537	763.6063	349.0799	374.1867	477.0255	632.2712	340.3463	485.6654	1204.347	655.1442	378.0323	468.4728	545.1056	799.5732	471.7102	653.5593	366.2612	392.5334	434.1306	519.9075	281.0299	610.6486	616.0208	521.1022
i19	44.40573	19.7641	21.34465	0	33.09669	0	31.01972	0	0	54.68658	23.12197	0	13.04361	40.45369	28.0404	49.5215	0	0	0	4.833238	36.83703	10.92725	77.41826	52.00074	7.508529
a19	30.93681	28.87655	16.84203	20.4985	22.55859	31.70947	20.84394	21.65801	30.33507	15.60361	47.47248	13.48612	30.47712	45.05609	19.17232	32.7036	21.67003	24.60227	27.62523	33.70454	36.45966	17.37708	29.06566	39.15602	41.32631
19:1	0	23.23334	12.95016	20.48174	12.21682	31.43464	21.3859	22.73457	63.19827	13.84742	46.99651	15.59548	21.13506	15.67042	45.23134	61.94898	24.87722	10.07319	14.20009	0	0	0	0	10.25782	36.08018
19:0	43.93212	57.8018	43.95153	63.08945	64.72786	58.30163	65.52556	63.17004	64.86845	62.17992	91.27833	36.12799	68.69403	104.2445	57.20849	93.33036	51.30231	71.97218	49.22057	143.0397	95.35748	74.90313	153.213	100.7291	147.7506
20:5w6	9.88942	0	14.78281	23.79276	8.149514	0	13.45541	14.73973	0	36.81192	11.01904	0	20.081	43.30442	13.24491	18.308	8.829259	19.10475	15.8921	0	20.50284	16.91695	33.7476	22.04547	0
20:4w6	12.36781	24.14588	0	0	20.2478	15.03146	0	0	20.11038	0	18.45044	6.136116	28.99067	23.64869	14.34282	30.06551	14.46255	10.1935	17.16703	21.97232	0	0	0	0	0
20:5w3	150.3253	209.0473	152.9618	172.6805	182.7342	295.2556	222.567	190.5146	247.0093	165.4272	344.2469	181.2732	169.1063	396.5519	148.2257	385.0679	224.4786	196.8684	233.5982	258.5365	206.7908	98.08005	150.9331	221.6725	425.2439
20:3	14.63772	21.08599	17.16784	14.93313	14.20663	29.92187	19.9371	17.14107	20.29744	17.96194	753.9461	11.86601	4.643793	26.62109	312.0044	12.01715	13.40689	9.519459	12.24586	7.472351	19.26735	9.379414	11.5158	17.94372	32.99905
20:2	19.98973	30.98758	26.08592	22.34417	21.91046	52.02772	27.75898	28.09373	41.14757	32.11689	71.13593	29.03957	28.63549	58.90679	37.03682	71.5549	42.0471	29.90817	51.34686	28.09764	0	19.47032	29.35554	26.22022	20.35324
20:1w7	24.26563	29.83449	22.47917	23.29186	21.65686	39.20608	32.25416	32.52952	35.52085	24.55235	9.480435	28.82754	42.75148	9.599046	26.51374	60.74355	40.41833	68.49767	5.663912	43.245	189.2903	32.39364	62.33689	84.11952	7.969951
20:0	69.85434	78.26143	60.20383	75.7234	82.9002	77.49034	84.21322	73.54202	78.82352	76.14946	113.4851	47.94642	80.19186	111.052	57.94291	86.79156	73.47388	77.99581	59.98557	114.8872	112.0428	78.22582	156.0993	115.1562	139.8132
21:0	277.3148	250.772	229.7239	393.5079	212.7116	281.6539	240.3077	231.7931	225.5078	227.2769	217.9211	227.8107	245.1852	237.976	237.4645	234.579	286.5862	238.3932	226.8977	266.3459	348.123	217.9823	316.1829	364.4285	527.233
22:6w6	8.258918	7.320803	10.30157	9.418606	0	0	8.328196	0	0	0	0	0	0	0	38.82711	0	0	0	0	0	0	0	0	0	0
22:6w3	29.93373	39.79559	24.71301	27.22864	27.47798	51.39802	35.17011	35.63348	54.76297	27.19839	73.24949	27.36574	35.46773	86.42731	32.89422	75.65626	44.16099	51.04219	58.1322	59.8173	60.45635	44.56579	42.46234	89.82016	89.98279
*22:5w6	21.02993	40.31352	31.33083	27.22875	23.3324	161.4929	41.45735	39.42361	100.6727	31.02271	271.9721	52.93913	68.73942	375.9868	79.14253	221.3281	67.41121	114.9318	154.8119	116.574	0	49.90529	72.84647	180.7312	0
22:5w3	20.61845	36.86287	28.00648	25.73789	18.21441	93.66989	38.3354	34.85607	75.22249	29.17563	225.2369	61.67548	62.90161	261.8374	89.53086	171.5176	69.12929	118.6481	147.7688	119.3959	65.19818	47.20604	63.13498	115.6902	108.1149
22:2	11.74916	3.574086	9.253346	7.735564	4.808738	23.83705	7.771697	8.330591	7.999198	7.309076	44.54971	5.322877	8.285841	52.23615	11.98289	26.46526	0	17.34512	22.38324	15.70985	7.404915	5.906485	10.90631	17.22961	14.72781
22:1w9	14.73367	8.730166	8.117472	4.843	8.63869	12.96693	9.864863	9.418535	13.3901	10.58329	27.96007	9.950106	15.99654	24.80467	4.972755	16.20533	0	14.35561	18.20131	16.29044	20.02007	15.28219	27.4085	14.44368	21.96059
22:0	50.51636	60.73659	41.26489	61.69381	60.06563	62.02145	69.66418	61.34079	61.78506	48.04655	87.86138	33.14435	82.31915	73.49489	39.35752	73.59679	58.78774	41.99278	52.60037	72.44127	89.60026	47.82021	109.0029	89.50697	87.3917
23:0	149.7987	172.9976	164.7422	132.4215	184.3364	233.8299	184.6437	169.1473	186.6669	127.0573	172.4846	151.635	148.9075	191.9258	133.5752	149.9977	209.6789	179.6056	151.2591	182.8635	155.5697	126.7174	137.3653	142.1733	134.7488
24:1	0	0	6.702486	0	5.72089	6.908864	7.879286	6.175286	10.54333	11.16948	11.50045	0	0	11.09875	6.177708	8.629618	0	5.014096	7.504638	7.148688					
24:0	60.75706	78.67878	61.89759	94.92581	93.20835	88.38989	92.31731	102.0724	89.17326	72.59516	102.0772	53.98155	89.85502	107.784	56.74682	127.1999	91.5621	63.4212	65.22874	126.1394	113.767	84.59159	153.1796	111.4007	120.0133
25:0	6.889053	10.11191	7.872015	11.31602	11.78992	88.38989	10.83905	10.4326	15.12128	9.339992	11.10834	5.548349	11.87438	12.76486	0	16.01386	9.849679	7.70923	6.882189	16.32515	12.95012	7.290679	17.16272	14.18891	14.75118
20:0	30.12112	48.56099	36.77622	50.37336	56.19758	9.709102	54.49078	48.1372	49.6216	41.24705	59.64313	33.45817	65.65	68.96801	34.73317	85.37629	58.4315	40.87013	42.52334	87.56743	105.5574	49.6995	115.3972	101.1129	114.6032
27:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28:0	9.743524	17.97754	13.78679	21.42215	22.79558	17.97457	17.98713	17.33121	20.36537	15.57049	21.99794	8.761156	22.27208	29.94674	14.23748	46.67229	16.45527	13.25685	12.86761	42.3109	25.28275	12.202	34.7388	16.34215	23.85948
29:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32:0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
corr total	8386.857	7783.003	6089.355	6100.993	6762.71	8609.189	8229.611	8607.441	7053.094	7766.99	10160.31	5123.291	7132.911	9040.7	6417.149	9754.624	6885.228	5369.281	5962.064	7634.089	9153.509	4989.167	8693.113	10370.06	11894.99

1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
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1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1
3 plfa	14 plfa	31 plfa	32 plfa	42 plfa	10 plfa	16 plfa	38 plfa	44 plfa	50 plfa	11 plfa	21 plfa	24 plfa	47 plfa	49 plfa	2 plfa	13 plfa	15 plfa	18 plfa	19 plfa	12 plfa	23 plfa	26 plfa	36 plfa	39 plfa
5.563103	3.55548	4.511014	21.07123	9.367141	19.09031	1	9.762699	7.518698	9.655851	11.29858	15.29305	14.26471	30.76668	16.38299	14.99725	5.144028	16.81626	8.183261	5.916856	20.39858	6.60277	9.40859	7.133839	12.46746
4.68214	2.121785	5.006233	13.56143	8.10526	9.341827	3.713997	8.220623	6.960371	6.5446	6.698412	20.97064	10.82744	6.521059	8.812396	11.40612	3.988458	9.148587	3.864336	6.025548	14.06006	3.53528	6.657402	10.66865	8.638
4.578971	0	4.459155	7.525886	6.921316	4.541463	0	0	4.118064	9.311413	0	0	4.349609	0	0	11.40155	0	5.793014	4.351608	9.032955	7.239836	3.700907	4.197814	0	4.444953
0	0	0	5.903531	0	0	0	0	0	0	5.281112	0	0	0	4.928692	9.995548	0	9.433531	503.7594	6.425772	10.09087	476.6484	6.711868	6.918795	5.735509
7.414877	5.973346	8.297273	18.68899	12.2986	10.23802	6.574546	6.944213	5.851	8.876122	8.415914	9.359694	10.29761	7.045002	10.77412	15.3413	4.490201	15.83587	11.21424	11.13243	17.96508	11.38864	11.26622	7.242903	12.83543
79.73619	47.04166	63.74438	165.3941	101.5271	70.49718	28.57313	87.63266	57.9208	70.72106	71.45235	83.79441	82.17465	82.60273	84.66291	139.7869	41.7871	103.2605	52.23102	93.76825	129.0486	53.41888	78.35287	61.98252	94.03922
7.394636	4.187932	6.220779	30.68646	9.536403	5.115419	3.671377	6.838011	4.37225	5.286241	14.93518	13.42301	0	30.26135	7.663942	12.12475	6.529907	9.379852	6.826267	6.609122	9.05297	7.067828	19.18227	17.81055	10.4412
235.8047	202.4072	242.115	496.633	567.2116	229.4383	152.305	263.8457	165.6884	287.7434	205.548	256.7438	206.1874	255.3787	234.6357	427.2258	148.4645	371.5128	296.0231	342.7509	368.3372	271.4366	287.8101	215.7632	295.1764
266.2957	181.287	226.1903	428.3634	352.9567	206.3231	99.18067	265.411	174.3015	221.806	257.8173	287.0654	19.89746	313.2665	20.81003	449.6618	157.2116	303.4751	178.6249	336.1769	405.1512	183.1052	308.8882	246.1269	323.2983
378.4974	228.5028	286.6655	581.6779	444.1008	291.1763	123.9202	355.7265	46.33663	270.1724	353.6788	345.8312	0	398.0899	338.032	655.2843	175.4901	440.2616	506.5737	463.8279	574.7799	508.9212	394.8305	308.2314	415.5445
10.99977	8.373326	10.69334	19.34115	17.89831	15.11615	6.447429	15.56236	6.787406	10.49193	12.80053	12.887	0	14.14356	0	20.12842	6.149025	16.68765	1116.579	15.25606	22.87944	1079.828	14.68805	9.003193	15.57189
136.7254	103.481	131.9344	246.983	208.6064	115.1778	72.44303	146.7164	95.66719	125.071	140.9483	133.1783	233.7496	138.4848	15.61073	208.3036	77.00473	223.9102	185.3616	204.8064	208.6565	184.3129	158.8067	122.8462	172.2346
13.91542	8.327278	12.03908	20.94971	18.58104	12.27704	6.457845	16.50094	6.054403	13.67467	0	24.94967	0	16.13766	15.82379	21.02533	7.893165	20.11576	19.86625	19.14386	23.99472	20.54295	14.88621	13.12881	17.61041
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.648396	0	0	163.9854	134.8966	0	0	0	7.852297	0	728.9619	0	2.154087	0	0	0	0	0	170.7461	0	183.2853	0	10.24121	9.905593	131.4201
126.8426	12.24487	115.072	30.95878	30.04757	98.84994	50.60428	133.6291	67.37733	107.8043	79.71061	122.8555	5.525005	149.113	126.1567	213.6442	82.63802	233.9118	19.94581	204.7423	41.21723	16.72889	26.73985	118.4939	27.22428
535.7645	42.15727	545.4191	1023.785	1035.137	544.9313	303.5509	779.7284	302.1831	582.5585	1026.442	605.9361	60.12062	675.5847	644.1468	1169.286	308.9626	76.52807	886.438	913.2697	1023.702	905.6108	628.724	597.3508	776.4478
32.845	0	33.14874	52.06901	43.57811	0	17.42387	43.95618	105.6912	30.79866	322.4721	34.62892	0	37.52893	40.45414	0	18.67685	906.0745	0	52.63415	64.4384	0	34.18657	25.30986	36.82509
1416.888	931.9348	1182.432	2012.237	1895.977	957.9889	594.837	1437.277	860.5815	1483.058	99.23047	1415.343	945.8199	1319.289	1469.697	2084.883	745.7688	2381.041	5913.715	2265.001	2063.874	5502.693	1602.922	1238.144	1545.836
95.07141	57.69719	74.19981	117.8198	99.75747	76.1008	32.41338	77.65174	42.89578	63.30649	71.02818	60.76921	58.07427	93.59217	0	143.1968	47.21609	11.61975	61.42954	111.8675	166.1375	66.76734	92.60827	69.90408	104.702
89.47399	63.05291	79.69244	129.0745	125.7650	69.71849	42.33937	95.34077	46.05746	72.97671	100.7467	79.34096	67.56968	91.70614	128.2029	158.5078	54.84406	147.8147	65.30736	138.5607	145.2504	63.38072	109.5858	81.47805	109.7919
56.70767	57.74794	88.43748	161.3893	146.0554	96.48756	44.25905	111.0205	50.57086	96.69407	26.11183	89.09068	4.295601	113.4617	113.7243	168.2447	49.34342	12.46334	161.1212	153.6525	169.6993	159.8607	130.8672	85.00805	141.5673
29.83461	23.79067	33.5249	23.94148	54.71556	29.4559	24.35536	36.56988	30.06712	44.785	0	28.44717	11.86716	46.14792	61.48419	65.56846	21.80626	19.78886	38.53797	52.11976	68.82812	39.20907	39.63588	24.58044	48.61141
150.1281	96.72723	121.8275	189.9557	208.037	99.31918	80.84295	147.0415	88.41854	147.0761	134.1702	126.2135	91.36827	112.6345	210.3442	240.6125	72.76329	280.7404	171.8003	265.7439	241.2258	179.1347	161.1619	116.474	169.0935
4.008969	5.607226	8.839377	12.63439	16.06254	8.845196	5.12243	13.8024	7.429004	9.255221	9.565195	0	7.660462	10.51491	12.76456	13.6822	5.434674	22.86026	14.41624	16.16591	14.03251	13.01148	12.93967	7.781467	12.88751
3.79713	34.6604	49.79389	84.21432	88.60085	41.57856	34.99819	58.50123	34.31163	52.21625	23.16457	30.25412	134.1943	49.64574	56.73936	23.38218	26.1694	54.20058	46.81905	34.65115	25.17658	28.32703	33.10526	8.079577	26.23547
44.67987	132.118	105.1409	20.4699	204.0638	137.4208	44.725	122.2251	67.84915	101.6793	26.5662	98.08235	6.817526	106.086	156.3947	14.44038	63.69978	96.20935	275.9958	282.419	238.6833	244.5579	274.2828	149.8663	141.3984
123.6788	230.3189	355.5221	537.4688	568.9546	264.8455	217.3944	395.9367	232.6801	379.0145	360.8633	380.7802	71.6199	357.6727	594.2488	751.8334	171.3718	1045.097	645.903	904.4686	660.302	645.0022	447.9198	377.7453	491.5806
363.0915	324.221	567.7611	982.0278	898.9873	434.6005	281.5697	656.396	253.6281	585.0509	548.9324	663.6627	58.54895	616.346	624.1865	1046.894	275.0411	824.4762	1006.814	1055.004	1143.97	1020.23	806.5658	584.8811	748.7357
14.22067	237.4406	325.2717	464.5301	530.6809	248.414	231.7667	397.1851	173.0704	792.1453	305.4067	641.7539	226.1641	386.3458	544.0221	532.0761	200.254	662.0415	581.722	650.6022	451.3735	380.7177	537.9322	275.966	384.2656
11.8606	8.580691	40.56988	49.4563	6.846418	0	13.76696	0	0	37.97441	0	0	32.4503	0	0	0	3.796051	18.49042	29.88442	25.01208	7.007172	5.616543	31.63352	0	7.742308
7.37319	15.21525	16.90885	29.40877	32.84605	12.04605	13.18293	23.77409	10.64276	21.5823	17.47769	13.74036	4.498073	17.90225	34.77599	34.08841	9.634537	38.74892	29.93296	33.02783	35.08551	36.41885	21.26153	16.06005	25.1525
7.158483	7.698967	7.705445	0	32.83095	0	0	0	0	5.665749	6.989586	0	0	91.65137	27.12378	63.57156	9.183533	0	5.314042	39.12307	64.46145	0	8.109246	13.50033	0
103.052	108.0249	115.2217	150.8893	122.8367	45.8896	74.12075	80.44288	55.86543	65.33682	70.23269	102.6479	71.34104	44.10044	74.54352	206.6253	43.757	97.95352	86.01943	104.8825	87.36105	86.54292	87.85578	100.0497	100.1911
8.206806	13.13753	10.50586	0	0	0	0	14.17621	0	0	5.412784	14.74501	21.46606	9.313794	20.25655	0	5.537262	0	0	11.90884	0	0	0	10.45866	0
5.086223	0	6.21743	0	0	15.06153	0	0	85.16323	9.948855	7.021417	0	4.026784	7.101514	12.9256	14.29979	0	0	12.34722	20.38012	27.69162	34.22286	32.20819	0	23.35942
125.703	105.983	145.9711	232.8827	263.3858	121.0397	95.72337	206.1986	21.41952	158.957	163.2233	153.0977	3.686344	151.6442	302.4253	329.3844	54.52865	462.275	220.6544	311.8473	236.5121	283.5054	165.8881	125.8392	190.9307
10.92072	28.4177	13.66224	21.84546	28.70323	11.66007	8.117426	17.49737	0	11.26531	10.63959	13.50258	5.227386	11.52445	8.421354	24.64155	5.638528	694.9537	21.98116	28.07959	23.84949	28.10636	19.10486	20.18756	16.97739
23.23895	0	17.46091	30.60233	51.79247	17.28309	9.167602	15.56621	3.735791	23.64709	15.54662	8.334351	43.66427	17.70986	29.8868	37.72355	6.821833	40.73189	33.70003	30.13185	17.26204	46.12264	27.26844	25.60423	22.82332
31.81341	4.557439	24.46468	41.00629	70.24839	24.32351	2.552807	34.40218	14.64604	20.71197	17.48273	21.55622	4.139077	38.51203	32.88557	63.02348	10.13881	46.25683	39.24459	56.32145	42.21729	5.220631	54.35744	27.7747	32.24048
67.72756	80.24244	88.19571	123.9513	137.5165	60.69753	52.49068	83.90719	45.59795	59.79533	73.69374	60.99927	68.55517	55.84049	92.38993	184.149	46.80299	106.7592	101.9239	110.7003	108.0745	103.5534	106.2192	86.94504	95.74925
139.5019	205.1862	207.3872	475.0002	447.7982	239.5072	211.6047	221.5441	248.0623	239.5953	217.4581	212.3918	214.7348	237.458	282.3546	294.8564	225.312	299.3752	303.7152	261.076	401.0963	312.8562	277.2437	313.2682	288.1346
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
69.83938	33.44663	39.27128	71.91421	62.52859	21.09924	23.83871	38.59113	10.74186	30.50903	21.84305	26.19202	102.1784	22.28449	59.92939	57.22552	5.948431	78.41795	40.61723	53.00667	43.70238	49.04507	31.93793	22.95365	37.10605
56.70201	0	62.87136	89.73221	117.9334	34.58361	61.2415	58.1701	14.63326	37.70381	26.36983	30.14236	0	0	355.2132	91.21151	9.335406	0	53.31282	159.2838	56.06173	126.8285	122.542	23.96106	0
51.30189	48.46125	45.84442	70.02531	133.7654	32.87489	75.48623	55.87599	10.08693	38.29955	21.33451	30.94911	0	16.51862	194.431	90.659	6.873626	309.7218	48.33873	108.3597	49.44753	79.29822	66.4	21.00673	40.05772
6.605282	11.79129	8.413344	11.51116	14.47157	4.395536	6.628729	4.385385	0	0	5.515015	0	45.82539	23.62535	49.6241	36.02412	0	63.64815	0	14.30814	4.965681	11.92864	4.584698	9.085465	3.727244
8.384346	2.216567	9.718669	24.9942	36.27418	2.675695	27.69321	0	0	10.92308	5.660881	0	23.95006	0	13.27083	17.7522	2.573875	7.633246	3.657677	10.95155	6.261278	18.52442	12.10142	0	4.029808
61.39492	16.54987	58.34295	31.7571	73.17395	42.93455	21.92119	56.69013	27.84872	49.21298	57.25361	53.07031	47.04729	42.16803	57.40981	112.2021	30.2061	68.51534	86.50249	90.85082	72.66572	66.14484	78.55644	51.69794	60.84141
146.1494	127.2415	136.8938	133.4519	139.6842	166.4481	123.6045	181.046	141.9852	191.9443	139.3645	136.913	123.1742	144.1372	127.5368	135.0386	138.9016	131.9787	125.462	128.0353	147.84	126.0198	134.2498	126.3288	133.9124
6.768776	3.856042	6.27054	0	9.614095	4.555259	3.686752	0	0	7.739472	0	0	0	0	0	0	0	12.21971	5.748178	11.98372	4.780751	0	0	0	5.688517
82.07384	63.57635	80.02132	108.808	109.7135	61.39819	51.24106	70.5573	38.15582	59.36327	71.98246	83.91026	65.48833	63.63751	81.57986	130.7372	43.64022	85.73369	88.39834	126.0976	98.73621	93.18503	108.7376	72.46249	91.00971
10.21636	6.568104	9.469976	13.5506	10.89172	8.081688	5.70537	10.44292	4.671262	7.207667	10.44301	0	9.187292	8.944522	9.885406	14.19455	4.606952	9.838315	10.36312	15.57908	13.38653	13.67787	12.56593	9.854026	11.69198
81.60942	40.68256	58.86499	85.84123	71.11911	38.96301	33.86392	44.30849	24.53924	36.25411	46.67401	39.49379	40.32606	36.83359	47.75494	75.79439	24.37766	47.65109	56.74186	86.84237	74.75803	62.57285	52.91417	41.58364	53.99147
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16.78251	14.67158	16.31632	26.39959	15.25009	10.24397	17.36908	14.80012	7.212006	11.38707	17.17976	0	12.0696	9.737174	19.34097	28.7178	0	16.86694	21.42058	37.0596	30.11898	30.02121	22.9858	15.59905	16.03846
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11.24279	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4926.13	3470.369	5366.831	9003.078	8979.817	4559.887	2987.373	6379.058	3205.916	6144.129	5482.297	6069.389	2798.779	6029.478	8897.942	9842.186	3024.236	10543.62	13722.73	9914.131	9441.812	13066.18	6962.263	5305.252	6926.059

Appendix 6. Daytime (light) DO fluxes from Chapter 4.

tank	cosm	nutrients	crab	richness	DO (mg/L) T1	DO (mg/L) T2	DO (mg/L) T3	DO (mg/L) T4	DO (mM) T1	DO(mM) T2	DO (mM)) T3	DO (mM) T4	Tl (min)	T2 (min)	T3 (min)	T4 (min)	T1 (hr)	T2 (hr)	T3 (hr)	T4 (hr)
10	5	1	1	0	9.31	13.56	14.61	18.27	0.29094	0.42375	0.45656	0.57094	0	74	145	206	0.00	1.23	2.42	3.43
12	6	1	1	0	10.33	12.49	14.61	18.31	0.32281	0.39031	0.45656	0.57219	0	70	150	213	0.00	1.17	2.50	3.55
14	3	1	1	0	10.8	13.34	18.5	19.3	0.3375	0.41688	0.57813	0.60313	0	72	154	207	0.00	1.20	2.57	3.45
10	6	1	1	1	9.16	10	10.96	11.93	0.28625	0.3125	0.3425	0.37281	0	74	148	205	0.00	1.23	2.47	3.42
11	6	1	1	1	8.61	9.29	10.74	11.43	0.26906	0.29031	0.33563	0.35719	0	68	154	219	0.00	1.13	2.57	3.65
12	3	1	1	1	7.27	7.99	8.6	9.33	0.22719	0.24969	0.26875	0.29156	0	73	155	211	0.00	1.22	2.58	3.52
8	3	1	1	3	8.71	9.69	11.05	12.65	0.27219	0.30281	0.34531	0.39531	0	71	147	204	0.00	1.18	2.45	3.40
10	7	1	1	3	9.46	10.61	12.51	13.41	0.29563	0.33156	0.39094	0.41906	0	74	145	206	0.00	1.23	2.42	3.43
11	4	1	1	3	7.82	8.74	9.74	10.79	0.24438	0.27313	0.30438	0.33719	0	67	153	218	0.00	1.12	2.55	3.63
9	4	1	1	5	8.8	10.53	12.93	14.07	0.275	0.32906	0.40406	0.43969	0	74	148	205	0.00	1.23	2.47	3.42
11	5	1	1	5	7.68	9.08	10.05	11.12	0.24	0.28375	0.31406	0.3475	0	71	153	215	0.00	1.18	2.55	3.58
14	2	1	1	5	9.51	10.55	12.25	13.08	0.29719	0.32969	0.38281	0.40875	0	70	151	207	0.00	1.17	2.52	3.45
8	4	1	0	0	12.46	17.4	20.12	22.47	0.38938	0.54375	0.62875	0.70219	0	71	146	204	0.00	1.18	2.43	3.40
12	1	1	0	0	7.8	10.75	13.56	15.94	0.24375	0.33594	0.42375	0.49813	0	72	154	211	0.00	1.20	2.57	3.52
14	4	1	0	0	12.8	14.87	17.08	16.22	0.4	0.46469	0.53375	0.50688	0	71	153	210	0.00	1.18	2.55	3.50
8	6	1	0	1	8.53	11.24	12.66	13.41	0.26656	0.35125	0.39563	0.41906	0	72	146	204	0.00	1.20	2.43	3.40
9	6	1	0	1	9.87	11.5	15.61	15.56	0.30844	0.35938	0.48781	0.48625	0	74	148	205	0.00	1.23	2.47	3.42
12	2	1	0	1	10.08	12.25	14.3	15.06	0.315	0.38281	0.44688	0.47063	0	71	154	216	0.00	1.18	2.57	3.60
9	2	1	0	3	8.52	10.02	11.07	12	0.26625	0.31313	0.34594	0.375	0	72	148	205	0.00	1.20	2.47	3.42
11	7	1	0	3	7.15	7.85	9.83	10.6	0.22344	0.24531	0.30719	0.33125	0	71	153	216	0.00	1.18	2.55	3.60
12	5	1	0	3	9.04	10.55	11.29	12.09	0.2825	0.32969	0.35281	0.37781	0	72	154	209	0.00	1.20	2.57	3.48
9	5	1	0	5	8.35	9.64	10.9	12.6	0.26094	0.30125	0.34063	0.39375	0	74	148	205	0.00	1.23	2.47	3.42
10	8	1	0	5	9.38	12.19	13.47	14.07	0.29313	0.38094	0.42094	0.43969	0	74	146	203	0.00	1.23	2.43	3.38
12	7	1	0	5	8.8	9.59	11.08	11.31	0.275	0.29969	0.34625	0.35344	0	69	150	205	0.00	1.15	2.50	3.42
8	8	0	1	0	12.91	17.34	21.65	19.51	0.40344	0.54188	0.67656	0.60969	0	70	147	204	0.00	1.17	2.45	3.40
10	1	0	1	0	9.9	11.56	12.21	16.47	0.30938	0.36125	0.38156	0.51469	0	74	146	204	0.00	1.23	2.43	3.40
14	8	0	1	0	9.2	9.74	11.64	12.63	0.2875	0.30438	0.36375	0.39469	0	71	152	208	0.00	1.18	2.53	3.47
8	5	0	1	1	7.03	7.82	8.33	9.22	0.21969	0.24438	0.26031	0.28813	0	71	147	204	0.00	1.18	2.45	3.40
9	7	0	1	1	8.07	8.64	10.2	11.51	0.25219	0.27	0.31875	0.35969	0	73	147	204	0.00	1.22	2.45	3.40
10	4	0	1	1	8.34	9.54	10.37	10.96	0.26063	0.29813	0.32406	0.3425	0	74	148	204	0.00	1.23	2.47	3.40
9	8	0	1	3	8.15	8.92	10.59	11.67	0.25469	0.27875	0.33094	0.36469	0	74	148	205	0.00	1.23	2.47	3.42
11	2	0	1	3	11.28	12.74	13.67	14.9	0.3525	0.39813	0.42719	0.46563	0	69	153	220	0.00	1.15	2.55	3.67
12	4	0	1	3	8.85	9.06	9.76	11.3	0.27656	0.28313	0.305	0.35313	0	71	152	214	0.00	1.18	2.53	3.57
9	3	0	1	5	7.65	8.15	9.55	11.05	0.23906	0.25469	0.29844	0.34531	0	74	148	205	0.00	1.23	2.47	3.42
10	2	0	1	5	7.91	8.69	9.56	10.55	0.24719	0.27156	0.29875	0.32969	0	73	147	205	0.00	1.22	2.45	3.42
11	3	0	1	5	7.57	8.12	9.56	10.08	0.23656	0.25375	0.29875	0.315	0	71	153	217	0.00	1.18	2.55	3.62
8	2	0	0	0	15.51	17.94	20.18	24.94	0.48469	0.56063	0.63063	0.77938	0	71	145	202	0.00	1.18	2.42	3.37
9	1	0	0	0	9.8	11.37	13.87	16.88	0.30625	0.35531	0.43344	0.5275	0	75	148	205	0.00	1.25	2.47	3.42
14	1	0	0	0	9.5	10.97	12.56	14.37	0.29688	0.34281	0.3925	0.44906	0	72	154	207	0.00	1.20	2.57	3.45
8	1	0	0	1	8.8	10.84	11.67	13.21	0.275	0.33875	0.36469	0.41281	0	71	138	195	0.00	1.18	2.30	3.25
12	8	0	0	1	9.4	10.84	12.75	13.86	0.29375	0.33875	0.39844	0.43313	0	71	151	213	0.00	1.18	2.52	3.55
14	7	0	0	1	9.8	11.77	12.27	13.32	0.30625	0.36781	0.38344	0.41625	0	72	153	205	0.00	1.20	2.55	3.42
8	7	0	0	3	7.5	9.52	9.6	9.99	0.23438	0.2975	0.3	0.31219	0	71	147	204	0.00	1.18	2.45	3.40
11	1	0	0	3	7.23	8.29	8.99	9.75	0.22594	0.25906	0.28094	0.30469	0	71	153	217	0.00	1.18	2.55	3.62
14	5	0	0	3	8.65	9.98	10.6	11.61	0.27031	0.31188	0.33125	0.36281	0	72	154	206	0.00	1.20	2.57	3.43

10	3	0	0	5	8.04	9.6	10.05	10.53	0.25125	0.3	0.31406	0.32906	0	73	146	204	0.00	1.22	2.43	3.40
11	8	0	0	5	7.72	8.3	9.97	11.17	0.24125	0.25938	0.31156	0.34906	0	71	154	218	0.00	1.18	2.57	3.63
14	6	0	0	5	7.74	9.26	9.87	10.79	0.24188	0.28938	0.30844	0.33719	0	71	153	208	0.00	1.18	2.55	3.47

Appendix 7. Nitetime (dark) DO fluxes from Chapter 4.

tank	cosm	nutrients	crab	richness	DO (mg/L) T1	DO (mg/L) T2	DO (mg/L) T3	DO (mg/L) T4	DO (mM) T1	DO(mM) T2	DO (mM)) T3	DO (mM) T4	TI (min)	T2 (min)	T3 (min)	T4 (min)	TI (hr)	T2 (hr)	T3 (hr)	T4 (hr)
10	5	+	+	0	5.2	3.89	3.47	2.67	0.1625	0.12156	0.10844	0.08344	0	57	114	170	0.00	0.95	1.90	2.83
12	6	+	+	0	5.14	3.8	3.08	2.2	0.16063	0.11875	0.09625	0.06875	0	59	127	186	0.00	0.98	2.12	3.10
14	3	+	+	0	5.08	4.31	4.26	2.35	0.15875	0.13469	0.13313	0.07344	0	60	135	194	0.00	1.00	2.25	3.23
10	6	+	+	1	4.94	4.18	3.63	3.02	0.15438	0.13063	0.11344	0.09438	0	55	114	170	0.00	0.92	1.90	2.83
11	6	+	+	1	9.39	8.07	7.1	6.38	0.29344	0.25219	0.22188	0.19938	0	61	126	185	0.00	1.02	2.10	3.08
12	3	+	+	1	5.75	4.99	4.27	3.69	0.17969	0.15594	0.13344	0.11531	0	58	127	188	0.00	0.97	2.12	3.13
8	3	+	+	3	7.59	6.69	5.84	4.77	0.23719	0.20906	0.1825	0.14906	0	57	111	169	0.00	0.95	1.85	2.82
10	7	+	+	3	5.62	4.87	4.32	3.87	0.17563	0.15219	0.135	0.12094	0	57	114	170	0.00	0.95	1.90	2.83
11	4	+	+	3	6.23	5.33	4.78	4.15	0.19469	0.16656	0.14938	0.12969	0	64	124	189	0.00	1.07	2.07	3.15
9	4	+	+	5	5.56	4.91	4.43	3.84	0.17375	0.15344	0.13844	0.12	0	58	113	170	0.00	0.97	1.88	2.83
11	5	+	+	5	5.95	5.09	4.35	3.73	0.18594	0.15906	0.13594	0.11656	0	59	126	185	0.00	0.98	2.10	3.08
14	2	+	+	5	5.91	5.19	3.11	3.84	0.18469	0.16219	0.09719	0.12	0	58	127	180	0.00	0.97	2.12	3.00
8	4	+	-	0	8.29	7.07	6.09	5.16	0.25906	0.22094	0.19031	0.16125	0	61	113	171	0.00	1.02	1.88	2.85
12	1	+	-	0	5.24	4.33	3.07	2.14	0.16375	0.13531	0.09594	0.06688	0	58	126	187	0.00	0.97	2.10	3.12
14	4	+	-	0	5.64	4.48	3.37	2.25	0.17625	0.14	0.10531	0.07031	0	58	128	191	0.00	0.97	2.13	3.18
8	6	+	-	1	7.32	6.31	5.42	4.6	0.22875	0.19719	0.16938	0.14375	0	61	113	172	0.00	1.02	1.88	2.87
9	6	+	-	1	7.17	6.33	5.71	4.9	0.22406	0.19781	0.17844	0.15313	0	57	112	169	0.00	0.95	1.87	2.82
12	2	+	-	1	5.07	4.1	3.07	2.42	0.15844	0.12813	0.09594	0.07563	0	57	117	174	0.00	0.95	1.95	2.90
9	2	+	-	3	5.31	4.67	4.2	3.65	0.16594	0.14594	0.13125	0.11406	0	57	112	169	0.00	0.95	1.87	2.82
11	7	+	-	3	5.58	4.81	4.06	3.64	0.17438	0.15031	0.12688	0.11375	0	58	126	185	0.00	0.97	2.10	3.08
12	5	+	-	3	5.04	4.18	3.53	2.88	0.1575	0.13063	0.11031	0.09	0	57	111	171	0.00	0.95	1.85	2.85
9	5	+	-	5	5.48	4.73	4.09	3.37	0.17125	0.14781	0.12781	0.10531	0	54	112	167	0.00	0.90	1.87	2.78
10	8	+	-	5	4.96	4.82	3.45	2.91	0.155	0.15063	0.10781	0.09094	0	55	114	170	0.00	0.92	1.90	2.83
12	7	+	-	5	5.88	5.16	4.45	3.87	0.18375	0.16125	0.13906	0.12094	0	59	130	190	0.00	0.98	2.17	3.17
8	8	-	+	0	6.95	6.23	5.62	4.91	0.21719	0.19469	0.17563	0.15344	0	59	112	170	0.00	0.98	1.87	2.83
10	1	-	+	0	5.31	4.78	4.32	3.82	0.16594	0.14938	0.135	0.11938	0	56	114	170	0.00	0.93	1.90	2.83
14	8	-	+	0	7.61	7.26	6.65	6.41	0.23781	0.22688	0.20781	0.20031	0	59	128	193	0.00	0.98	2.13	3.22
8	5	-	+	1	7.81	7.53	7.19	6.92	0.24406	0.23531	0.22469	0.21625	0	58	112	169	0.00	0.97	1.87	2.82
9	7	-	+	1	5.11	4.59	4.07	3.71	0.15969	0.14344	0.12719	0.11594	0	54	113	168	0.00	0.90	1.88	2.80
10	4	-	+	1	5.22	4.79	4.28	3.89	0.16313	0.14969	0.13375	0.12156	0	55	114	170	0.00	0.92	1.90	2.83
9	8	-	+	3	5.98	5.46	5.07	4.66	0.18688	0.17063	0.15844	0.14563	0	57	112	170	0.00	0.95	1.87	2.83
11	2	-	+	3	6.4	5.62	4.79	4.1	0.2	0.17563	0.14969	0.12813	0	63	123	188	0.00	1.05	2.05	3.13
12	4	-	+	3	6.4	5.81	5.54	5.19	0.2	0.18156	0.17313	0.16219	0	58	128	186	0.00	0.97	2.13	3.10
9	3	-	+	5	5.56	5.17	4.78	4.41	0.17375	0.16156	0.14938	0.13781	0	55	112	167	0.00	0.92	1.87	2.78
10	2	-	+	5	4.87	4.29	3.69	3.14	0.15219	0.13406	0.11531	0.09813	0	52	111	166	0.00	0.87	1.85	2.77
11	3	-	+	5	6	5.22	4.64	4.13	0.1875	0.16313	0.145	0.12906	0	59	126	185	0.00	0.98	2.10	3.08
8	2	-	-	0	9.52	8.46	7.49	7.17	0.2975	0.26438	0.23406	0.22406	0	61	112	170	0.00	1.02	1.87	2.83
9	1	-	-	0	5.07	4.23	3.49	2.99	0.15844	0.13219	0.10906	0.09344	0	55	112	168	0.00	0.92	1.87	2.80
14	1	-	-	0	5	3.94	3.05	2.19	0.15625	0.12313	0.09531	0.06844	0	60	129	194	0.00	1.00	2.15	3.23
8	1	-	-	1	6.64	6.04	5.42	4.76	0.2075	0.18875	0.16938	0.14875	0	58	111	169	0.00	0.97	1.85	2.82
12	8	-	-	1	6	5.26	4.7	4.22	0.1875	0.16438	0.14688	0.13188	0	58	127	187	0.00	0.97	2.12	3.12
14	7	-	-	1	6.65	6.08	5.35	4.31	0.20781	0.19	0.16719	0.13469	0	59	115	181	0.00	0.98	1.92	3.02
8	7	-	-	3	7.45	6.97	6.54	6.16	0.23281	0.21781	0.20438	0.1925	0	57	112	169	0.00	0.95	1.87	2.82
11	1	-	-	3	6.22	5.56	5.02	4.5	0.19438	0.17375	0.15688	0.14063	0	60	126	186	0.00	1.00	2.10	3.10
14	5	-	-	3	6.09	5.56	4.86	4.49	0.19031	0.17375	0.15188	0.14031	0	60	129	195	0.00	1.00	2.15	3.25

10	3	-	-	5	5.09	4.49	4.08	3.67	0.15906	0.14031	0.1275	0.11469	0	56	114	169	0.00	0.93	1.90	2.82
11	8	-	-	5	10.17	9.27	8.57	8.11	0.31781	0.28969	0.26781	0.25344	0	60	125	184	0.00	1.00	2.08	3.07
14	6	-	-	5	6.7	6.27	5.71	5.36	0.20938	0.19594	0.17844	0.1675	0	58	127	190	0.00	0.97	2.12	3.17

Appendix 8. Day and night NH_4 fluxes from Chapter 4.

Light	Tank	cosm	nutrients	crab	richness	NH4 time 1	NH4 Time 2	NH4 Time 3	NH4 Time 4	T1 (hr)	T2 (hr)	T3 (hr)	T4 (hr)
Day	8	2	0	0	0	31.27	1.22	1.23	1.04	0.00	1.18	2.42	3.37
Day	9	1	0	0	0	4.02	3.81	3.37	3.70	0.00	1.25	2.47	3.42
Day	14	1	0	0	0	2.98	2.93	2.82	2.35	0.00	1.20	2.57	3.45
Day	8	1	0	0	1	3.99	3.41	2.75	2.83	0.00	1.18	2.30	3.25
Day	12	8	0	0	1	5.56	6.36	6.04	6.64	0.00	1.18	2.52	3.55
Day	14	7	0	0	1	3.94	3.35	3.06	2.34	0.00	1.20	2.55	3.42
Day	8	7	0	0	3	5.94	6.03	5.71	5.45	0.00	1.18	2.45	3.40
Day	11	1	0	0	3	8.52	8.15	8.22	8.27	0.00	1.18	2.55	3.62
Day	14	5	0	0	3	5.18	4.40	4.11	3.50	0.00	1.20	2.57	3.43
Day	10	3	0	0	5	7.72	7.68	7.92	7.50	0.00	1.22	2.43	3.40
Day	11	8	0	0	5	8.01	8.14	8.22	7.32	0.00	1.18	2.57	3.63
Day	14	6	0	0	5	6.35	6.38	5.80	5.22	0.00	1.18	2.55	3.47
Day	8	8	0	1	0	2.98	2.20	1.56	1.48	0.00	1.17	2.45	3.40
Day	10	1	0	1	0	3.07	2.49	1.91	1.56	0.00	1.23	2.43	3.40
Day	14	8	0	1	0	3.15	2.40	2.10	1.40	0.00	1.18	2.53	3.47
Day	8	5	0	1	1	4.27	3.72	3.23	3.37	0.00	1.18	2.45	3.40
Day	9	7	0	1	1	7.10	6.74	6.31	6.22	0.00	1.22	2.45	3.40
Day	10	4	0	1	1	7.31	7.27	6.83	6.40	0.00	1.23	2.47	3.40
Day	9	8	0	1	3	6.12	5.61	4.94	4.57	0.00	1.23	2.47	3.42
Day	11	2	0	1	3	3.34	2.54	2.23	2.25	0.00	1.15	2.55	3.67
Day	12	4	0	1	3	6.43	5.92	5.38	4.63	0.00	1.18	2.53	3.57
Day	9	3	0	1	5	6.59	6.54		6.19	0.00	1.23	2.47	3.42
Day	10	2	0	1	5	10.28	11.17	10.61	11.31	0.00	1.22	2.45	3.42
Day	11	3	0	1	5	6.83	6.56	7.08	5.68	0.00	1.18	2.55	3.62
Day	8	4	1	0	0	10.36	10.30	10.48	32.55	0.00	1.18	2.43	3.40
Day	12	1	1	0	0	14.62	16.02	20.49	23.93	0.00	1.20	2.57	3.52
Day	14	4	1	0	0	13.47	14.81	17.01	15.66	0.00	1.18	2.55	3.50
Day	8	6	1	0	1	32.36	31.17	33.10	30.01	0.00	1.20	2.43	3.40
Day	9	6	1	0	1	39.03	48.57	43.14	38.78	0.00	1.23	2.47	3.42
Day	12	2	1	0	1	11.53	19.20	22.02	24.71	0.00	1.18	2.57	3.60
Day	9	2	1	0	3	16.77	29.18	31.48	36.23	0.00	1.20	2.47	3.42
Day	11	7	1	0	3	19.44	21.95	27.32	31.13	0.00	1.18	2.55	3.60
Day	12	5	1	0	3	16.44	22.94	21.91	25.00	0.00	1.20	2.57	3.48
Day	9	5	1	0	5	30.77	46.41	49.08	74.84	0.00	1.23	2.47	3.42
Day	10	8	1	0	5	20.84	27.81	34.76	49.20	0.00	1.23	2.43	3.38
Day	12	7	1	0	5	18.34	22.21	25.95	28.13	0.00	1.15	2.50	3.42
Day	10	5	1	1	0	2.82	1.71	2.52	5.12	0.00	1.23	2.42	3.43
Day	12	6	1	1	0	13.07	13.70	37.61	57.27	0.00	1.17	2.50	3.55
Day	14	3	1	1	0	13.35	19.74	22.45	21.26	0.00	1.20	2.57	3.45
Day	10	6	1	1	1	15.71	19.20	20.43	19.96	0.00	1.23	2.47	3.42
Day	11	6	1	1	1	25.14	28.94	30.81	35.62	0.00	1.13	2.57	3.65
Day	12	3	1	1	1	24.63	28.01	32.23	32.66	0.00	1.22	2.58	3.52
Day	8	3	1	1	3	1.51	33.32	36.96	39.52	0.00	1.18	2.45	3.40
Day	10	7	1	1	3	27.28	36.50	37.92	42.83	0.00	1.23	2.42	3.43
Day	11	4	1	1	3	22.14	53.07	43.88	55.53	0.00	1.12	2.55	3.63
Day	9	4	1	1	5	17.66	20.16	22.75	29.05	0.00	1.23	2.47	3.42
Day	11	5	1	1	5	17.94	20.87	23.17	27.09	0.00	1.18	2.55	3.58
Day	14	2	1	1	5	18.33	21.26	24.86	25.82	0.00	1.17	2.52	3.45

Night	8	2	0	0	0	1.77	0.58	0.65	0.50	0.00	1.02	1.87	2.83
Night	9	1	0	0	0	3.77	3.40	2.88	2.61	0.00	0.92	1.87	2.80
Night	14	1	0	0	0	2.05	1.93	1.65	1.27	0.00	1.00	2.15	3.23
Night	8	1	0	0	1	4.22	3.84	3.34	2.96	0.00	0.97	1.85	2.82
Night	12	8	0	0	1	3.06	3.17	2.73	2.74	0.00	0.97	2.12	3.12
Night	14	7	0	0	1	1.38	2.31	1.96	1.75	0.00	0.98	1.92	3.02
Night	8	7	0	0	3	5.71	5.74	5.51	5.15	0.00	0.95	1.87	2.82
Night	11	1	0	0	3	6.28	7.12	5.40	5.01	0.00	1.00	2.10	3.10
Night	14	5	0	0	3	2.00	3.18	2.72	2.83	0.00	1.00	2.15	3.25
Night	10	3	0	0	5	8.71	8.78	9.09	8.74	0.00	0.93	1.90	2.82
Night	11	8	0	0	5	6.15	4.97	4.84	4.51	0.00	1.00	2.08	3.07
Night	14	6	0	0	5	4.05	3.98	3.96	3.80	0.00	0.97	2.12	3.17
Night	8	8	0	1	0	30.08	1.15	0.61	0.53	0.00	0.98	1.87	2.83
Night	10	1	0	1	0	3.99	3.17	2.94	2.17	0.00	0.93	1.90	2.83
Night	14	8	0	1	0	1.33	0.94	0.89	0.71	0.00	0.98	2.13	3.22
Night	8	5	0	1	1	2.80	2.75	2.32	2.09	0.00	0.97	1.87	2.82
Night	9	7	0	1	1	7.43	7.73	7.70	6.71	0.00	0.90	1.88	2.80
Night	10	4	0	1	1	8.23	7.61	7.54	7.35	0.00	0.92	1.90	2.83
Night	9	8	0	1	3	6.01	5.92	5.73	5.11	0.00	0.95	1.87	2.83
Night	11	2	0	1	3	3.51	2.50	1.50	1.38	0.00	1.05	2.05	3.13
Night	12	4	0	1	3	2.87	2.80	2.49	2.52	0.00	0.97	2.13	3.10
Night	9	3	0	1	5	6.32	7.04	6.49	5.70	0.00	0.92	1.87	2.78
Night	10	2	0	1	5	9.80	10.37	10.54	10.39	0.00	0.87	1.85	2.77
Night	11	3	0	1	5	4.82	4.90	4.76	4.62	0.00	0.98	2.10	3.08
Night	8	4	1	0	0	14.79	14.52	14.68	15.20	0.00	1.02	1.88	2.85
Night	12	1	1	0	0	8.49	11.10	7.82	8.84	0.00	0.97	2.10	3.12
Night	14	4	1	0	0	11.96	13.11	14.94	14.62	0.00	0.97	2.13	3.18
Night	8	6	1	0	1	2.09	32.07	34.88	36.19	0.00	1.02	1.88	2.87
Night	9	6	1	0	1	30.88	32.38	40.71	42.24	0.00	0.95	1.87	2.82
Night	12	2	1	0	1	11.18	12.32	15.30	16.24	0.00	0.95	1.95	2.90
Night	9	2	1	0	3	23.08	22.73	30.22	29.31	0.00	0.95	1.87	2.82
Night	11	7	1	0	3	16.68	20.33	24.59	24.50	0.00	0.97	2.10	3.08
Night	12	5	1	0	3	14.41	14.84	18.74	18.36	0.00	0.95	1.85	2.85
Night	9	5	1	0	5	29.94	34.26	39.46	42.92	0.00	0.90	1.87	2.78
Night	10	8	1	0	5	25.32	27.01	30.00	33.12	0.00	0.92	1.90	2.83
Night	12	7	1	0	5	14.71	17.65	18.76	20.51	0.00	0.98	2.17	3.17
Night	10	5	1	1	0	27.33	40.52	42.87	53.23	0.00	0.95	1.90	2.83
Night	12	6	1	1	0	10.99	8.73	10.11	10.50	0.00	0.98	2.12	3.10
Night	14	3	1	1	0	10.14	8.31	11.42	9.30	0.00	1.00	2.25	3.23
Night	10	6	1	1	1	21.69	27.15	32.28	33.15	0.00	0.92	1.90	2.83
Night	11	6	1	1	1	37.74	39.88	42.27	44.30	0.00	1.02	2.10	3.08
Night	12	3	1	1	1	20.08	24.21	25.95	31.30	0.00	0.97	2.12	3.13
Night	8	3	1	1	3	28.82	29.94	35.98	35.70	0.00	0.95	1.85	2.82
Night	10	7	1	1	3	32.73	35.64	41.76	43.85	0.00	0.95	1.90	2.83
Night	11	4	1	1	3	21.06	23.15	23.93	26.07	0.00	1.07	2.07	3.15
Night	9	4	1	1	5	18.48	19.14	22.47	25.74	0.00	0.97	1.88	2.83
Night	11	5	1	1	5	16.56	19.43	18.04	19.35	0.00	0.98	2.10	3.08
Night	14	2	1	1	5	17.61	20.37	16.90	21.83	0.00	0.97	2.12	3.00

Appendix 9. Day and night NO_x fluxes from Chapter 4.

Light	Tank	cosm	nutrients	crab	richness	NOx time 1	NOx Time 2	NOx Time 3	NOx Time 4	NO2 time 1	NO2 time 2	NO2 time 3	NO2 time 4	NO3 time 1	NO3 time 2	NO3 time 3
day	8	2	-	-	0	18.46	0.04	0.03	0.00	0.46	0.03	0.04	0.01	18.00	0.01	-0.01
day	9	1	-	-	0	0.55	0.44	0.32	0.41	0.18	0.14	0.10	0.13	0.38	0.29	0.22
day	14	1	-	-	0	0.82	0.91	0.59	0.46	0.21	0.21	0.25	0.19	0.61	0.70	0.34
day	8	1	-	-	1	0.46	0.42	0.27	0.23	0.22	0.23	0.15	0.15	0.24	0.19	0.12
day	12	8	-	-	1	0.87	0.88	0.65	0.56	0.43	0.44	0.30	0.33	0.44	0.44	0.35
day	14	7	-	-	1	0.95	1.42	0.65	0.45	0.33	0.30	0.36	0.24	0.62	1.12	0.29
day	8	7	-	-	3	0.47	0.46	0.45	0.40	0.24	0.24	0.24	0.21	0.23	0.23	0.21
day	11	1	-	-	3	1.48	1.45	1.10	1.04	0.61	0.56	0.52	0.47	0.87	0.88	0.59
day	14	5	-	-	3	1.29	1.37	0.87	0.80	0.41	0.38	0.42	0.38	0.88	0.99	0.45
day	10	3	-	-	5	0.86	0.62	0.58	0.52	0.32	0.26	0.26	0.22	0.55	0.36	0.32
day	11	8	-	-	5	1.14	1.13	0.93	0.77	0.50	0.46	0.44	0.39	0.64	0.67	0.49
day	14	6	-	-	5	1.25	1.49	0.92	0.89	0.44	0.41	0.43	0.40	0.82	1.08	0.49
day	8	8	-	+	0	0.47	0.23	0.14	0.06	0.16	0.12	0.12	0.07	0.31	0.10	0.01
day	10	1	-	+	0	0.45	0.32	0.22	0.19	0.19	0.19	0.09	0.10	0.26	0.13	0.13
day	14	8	-	+	0	0.86	1.08	0.61	0.45	0.28	0.26	0.28	0.21	0.59	0.82	0.33
day	8	5	-	+	1	0.63	0.37	0.32	0.29	0.20	0.17	0.17	0.19	0.43	0.20	0.15
day	9	7	-	+	1	1.01	0.58	0.54	0.48	0.36	0.28	0.25	0.22	0.64	0.30	0.29
day	10	4	-	+	1	0.80	0.68	0.59	0.50	0.29	0.29	0.30	0.24	0.51	0.39	0.30
day	9	8	-	+	3	0.89	0.57	0.53	0.45	0.31	0.28	0.23	0.21	0.58	0.28	0.30
day	11	2	-	+	3	0.73	0.59	0.41	0.27	0.34	0.25	0.21	0.13	0.39	0.33	0.20
day	12	4	-	+	3	1.26	1.10	0.94	0.60	0.56	0.47	0.47	0.39	0.70	0.64	0.48
day	9	3	-	+	5	1.02	0.65		0.62	0.36	0.30		0.27	0.67	0.35	
day	10	2	-	+	5	0.87	0.72	0.65	0.64	0.30	0.30	0.27	0.24	0.57	0.42	0.37
day	11	3	-	+	5	1.42	1.31	1.07	0.92	0.58	0.52	0.52	0.44	0.84	0.79	0.55
day	8	4	+	-	0	14.92	17.77	20.57	39.64	1.33	1.54	1.78	4.12	13.59	16.23	18.79
day	12	1	+	-	0	8.16	8.75	13.93	17.66	0.85	1.16	1.50	1.98	7.32	7.59	12.43
day	14	4	+	-	0	11.29	15.09	17.95	17.03	0.82	1.09	2.10	1.57	10.47	14.00	15.85
day	8	6	+	-	1	23.31	24.17	31.22	30.58	0.68	0.74	0.84	0.91	22.63	23.43	30.38
day	9	6	+	-	1	27.30	35.84	33.52	32.00	0.72	0.82	0.91	1.00	26.56	35.02	32.61
day	12	2	+	-	1	5.09	10.63	12.78	16.84	0.57	0.62	0.66	0.71	4.52	10.01	12.12
day	9	2	+	-	3	7.36	17.20	18.60	22.74	0.42	0.47	0.53	0.55	6.93	16.73	18.07
day	11	7	+	-	3	9.70	11.98	20.82	20.68	0.78	0.82	0.85	0.95	8.91	11.16	19.97
day	12	5	+	-	3	7.20	13.34	13.84	18.41	0.70	0.87	0.83	0.77	6.50	12.47	13.01
day	9	5	+	-	5	16.98	29.63	31.87	48.35	0.58	0.77	0.96	1.18	16.40	28.86	30.91
day	10	8	+	-	5	9.21	14.66	20.45	32.01	0.66	0.75	0.89	1.14	8.54	13.91	19.56
day	12	7	+	-	5	8.41	10.75	14.65	17.27	0.77	0.90	0.98	1.04	7.63	9.85	13.67
day	10	5	+	+	0	29.25	52.79	87.86	92.88	0.74	1.27	1.43	1.49	28.51	51.53	86.43
day	12	6	+	+	0	7.76	9.07	28.93	43.54	0.71	0.69	0.62	0.73	7.05	8.38	28.31
day	14	3	+	+	0	7.25	13.67	16.60	15.58	0.45	0.64	0.56	0.59	6.80	13.03	16.04
day	10	6	+	+	1	8.96	10.50	12.69	12.66	0.54	0.45	0.45	0.44	6.42	10.05	12.24
day	11	6	+	+	1	18.31	22.57	23.78	27.20	0.77	0.80	0.83	0.80	17.54	21.77	22.95
day	12	3	+	+	1	15.11	18.35	23.07	24.14	0.77	0.82	0.81	0.82	14.34	17.53	22.26
day	8	3	+	+	3	0.39	20.84	27.11	31.15	0.02	0.47	0.52	0.59	0.37	20.37	26.59
day	10	7	+	+	3	13.43	21.54	23.60	27.41	0.42	0.47	0.49	0.51	13.01	21.07	23.11
day	11	4	+	+	3	13.60	40.85	30.96	41.03	0.73	0.75	0.80	0.79	12.87	40.10	30.16
day	9	4	+	+	5	8.73	10.50	13.20	18.64	0.36	0.41	0.41	0.46	8.36	10.09	12.79
day	11	5	+	+	5	10.27	13.88	15.25	19.56	0.62	0.66	0.67	0.60	9.65	13.22	14.58
day	14	2	+	+	5	12.79	16.61	20.20	21.85	0.61	0.72	0.73	0.70	12.18	15.89	19.47

night	8	2	-	-	0	0.33	0.05	0.15	0.06	0.16	0.07	0.05	0.00	0.18	-0.02	0.10
night	9	1	-	-	0	0.45	0.39	0.27	0.21	0.19	0.15	0.12	0.09	0.26	0.24	0.15
night	14	1	-	-	0	0.49	0.90	0.23	0.13	0.19	0.22	0.15	0.10	0.30	0.68	0.07
night	8	1	-	-	1	0.58	0.54	0.41	0.32	0.27	0.38	0.20	0.18	0.31	0.16	0.21
night	12	8	-	-	1	0.55	0.51	0.40	0.32	0.37	0.40	0.29	0.26	0.18	0.11	0.10
night	14	7	-	-	1	0.82	1.29	0.40	0.30	0.26	0.32	0.26	0.22	0.56	0.98	0.14
night	8	7	-	-	3	0.66	0.58	0.52	0.48	0.36	0.29	0.27	0.29	0.31	0.29	0.24
night	11	1	-	-	3	0.76	0.69	0.59	0.55	0.45	0.71	0.40	0.36	0.31	-0.02	0.19
night	14	5	-	-	3	0.60	1.30	0.55	0.47	0.40	0.36	0.35	0.32	0.20	0.94	0.21
night	10	3	-	-	5	0.97	0.91	0.81	0.75	0.48	0.44	0.46	0.47	0.49	0.47	0.36
night	11	8	-	-	5	0.35	0.37	0.24	0.25	0.18	0.26	0.19	0.18	0.17	0.12	0.05
night	14	6	-	-	5	0.93	1.52	0.57	0.49	0.37	0.43	0.35	0.33	0.56	1.10	0.22
night	8	8	-	+	0	31.56	0.09	0.03	-0.04	1.23	0.10	0.03	0.04	30.33	-0.01	0.00
night	10	1	-	+	0	0.54	0.47	0.28	0.20	0.27	0.22	0.21	0.12	0.27	0.25	0.07
night	14	8	-	+	0	0.65	1.03	0.25	0.21	0.19	0.23	0.17	0.17	0.46	0.80	0.07
night	8	5	-	+	1	0.44	0.35	0.31	0.27	0.21	0.21	0.17	0.16	0.23	0.14	0.14
night	9	7	-	+	1	0.88	0.80	0.75	0.64	0.39	0.37	0.42	0.31	0.49	0.43	0.33
night	10	4	-	+	1	0.91	0.84	0.75	0.67	0.45	0.41	0.47	0.34	0.46	0.43	0.28
night	9	8	-	+	3	0.79	0.74	0.68	0.61	0.37	0.34	0.33	0.29	0.42	0.40	0.36
night	11	2	-	+	3	0.28	0.28	0.13	0.07	0.20	0.23	0.14	0.09	0.09	0.06	0.00
night	12	4	-	+	3	0.64	0.63	0.51	0.45	0.43	0.46	0.35	0.32	0.21	0.17	0.16
night	9	3	-	+	5	0.82	0.78	0.70	0.63	0.35	0.40	0.45	0.27	0.47	0.38	0.25
night	10	2	-	+	5	0.97	0.91	0.83	0.78	0.45	0.44	0.42	0.37	0.52	0.47	0.41
night	11	3	-	+	5	0.78	0.64	0.55	0.48	0.46	0.47	0.37	0.33	0.33	0.17	0.18
night	8	4	+	-	0	30.31	31.03	32.21	34.06	4.03	4.32	4.68	4.86	26.29	26.71	27.53
night	12	1	+	-	0	7.11	9.08	7.40	8.56	0.98	0.99	0.86	0.94	6.13	8.09	6.53
night	14	4	+	-	0	8.70	14.47	11.59	13.09	0.92	0.86	0.95	1.04	7.78	13.61	10.64
night	8	6	+	-	1	0.20	33.41	34.66	36.88	0.12	1.06	1.17	1.15	0.08	32.35	33.49
night	9	6	+	-	1	29.34	28.47	33.60	34.55	0.95	1.06	1.15	1.13	28.39	27.41	32.45
night	12	2	+	-	1	6.09	7.07	9.07	10.05	0.68	0.66	0.63	0.70	5.41	6.41	8.43
night	9	2	+	-	3	9.30	10.59	17.10	15.17	0.57	0.64	0.65	0.58	8.73	9.95	16.45
night	11	7	+	-	3	9.12	11.52	12.73	13.67	0.75	0.75	0.85	0.77	8.37	10.77	11.88
night	12	5	+	-	3	10.10	10.07	12.64	12.55	0.79	0.70	0.71	0.72	9.31	9.37	11.93
night	9	5	+	-	5	19.51	21.08	23.85	26.49	0.98	1.09	1.21	1.19	18.53	19.99	22.64
night	10	8	+	-	5	12.36	12.37	14.28	17.10	0.83	0.84	1.19	0.92	11.53	11.53	13.09
night	12	7	+	-	5	9.56	12.48	13.17	14.56	0.81	0.79	0.84	0.84	8.76	11.69	12.33
night	10	5	+	+	0	29.34	26.09	26.15	32.09	0.83	0.82	0.88	0.96	28.51	25.27	25.27
night	12	6	+	+	0	9.79	5.39	6.82	6.62	0.53	0.40	0.37	0.36	9.26	4.98	6.45
night	14	3	+	+	0	4.77	5.97	6.36	5.79	0.56	0.35	0.39	0.32	4.21	5.62	5.97
night	10	6	+	+	1	12.90	16.47	19.41	21.27	0.61	0.64	0.68	0.73	12.29	15.83	18.73
night	11	6	+	+	1	44.79	47.22	44.91	46.47	1.01	1.02	0.95	0.97	43.78	46.20	43.96
night	12	3	+	+	1	16.26	19.32	21.03	26.13	0.75	0.70	0.71	0.76	15.51	18.62	20.32
night	8	3	+	+	3	26.77	28.30	32.69	32.57	0.66	0.73	0.78	0.73	26.11	27.57	31.91
night	10	7	+	+	3	18.95	20.32	23.72	25.22	0.64	0.65	0.72	0.69	18.31	19.67	23.00
night	11	4	+	+	3	12.97	15.38	13.77	15.72	0.71	0.73	0.57	0.60	12.26	14.65	13.20
night	9	4	+	+	5	9.99	10.48	12.23	14.60	0.54	0.58	0.69	0.55	9.45	9.90	11.54
night	11	5	+	+	5	10.66	11.11	11.15	12.34	0.62	0.74	0.57	0.53	10.04	10.37	10.58
night	14	2	+	+	5	11.57	18.74	14.16	15.81	0.57	0.55	0.98	0.58	11.00	18.20	13.18

NO3 time 4	T1 (hr)	T2 (hr)	T3 (hr)	T4 (hr)
-0.01	0.00	1.18	2.42	3.37
0.28	0.00	1.25	2.47	3.42
0.27	0.00	1.20	2.57	3.45
0.08	0.00	1.18	2.30	3.25
0.23	0.00	1.18	2.52	3.55
0.20	0.00	1.20	2.55	3.42
0.19	0.00	1.18	2.45	3.40
0.57	0.00	1.18	2.55	3.62
0.41	0.00	1.20	2.57	3.43
0.29	0.00	1.22	2.43	3.40
0.37	0.00	1.18	2.57	3.63
0.49	0.00	1.18	2.55	3.47
0.00	0.00	1.17	2.45	3.40
0.09	0.00	1.23	2.43	3.40
0.24	0.00	1.18	2.53	3.47
0.10	0.00	1.18	2.45	3.40
0.26	0.00	1.22	2.45	3.40
0.26	0.00	1.23	2.47	3.40
0.24	0.00	1.23	2.47	3.42
0.15	0.00	1.15	2.55	3.67
0.41	0.00	1.18	2.53	3.57
0.35	0.00	1.23	2.47	3.42
0.40	0.00	1.22	2.45	3.42
0.48	0.00	1.18	2.55	3.62
35.52	0.00	1.18	2.43	3.40
15.68	0.00	1.20	2.57	3.52
15.46	0.00	1.18	2.55	3.50
29.67	0.00	1.20	2.43	3.40
31.00	0.00	1.23	2.47	3.42
16.13	0.00	1.18	2.57	3.60
22.19	0.00	1.20	2.47	3.42
19.73	0.00	1.18	2.55	3.60
17.64	0.00	1.20	2.57	3.48
47.17	0.00	1.23	2.47	3.42
30.87	0.00	1.23	2.43	3.38
16.23	0.00	1.15	2.50	3.42
91.40	0.00	1.23	2.42	3.43
42.81	0.00	1.17	2.50	3.55
14.99	0.00	1.20	2.57	3.45
12.22	0.00	1.23	2.47	3.42
26.40	0.00	1.13	2.57	3.65
23.32	0.00	1.22	2.58	3.52
30.56	0.00	1.18	2.45	3.40
26.90	0.00	1.23	2.42	3.43
40.24	0.00	1.12	2.55	3.63
18.18	0.00	1.23	2.47	3.42
18.96	0.00	1.18	2.55	3.58
21.15	0.00	1.17	2.52	3.45

0.07	0.00	1.02	1.87	2.83
0.12	0.00	0.92	1.87	2.80
0.03	0.00	1.00	2.15	3.23
0.14	0.00	0.97	1.85	2.82
0.07	0.00	0.97	2.12	3.12
0.08	0.00	0.98	1.92	3.02
0.20	0.00	0.95	1.87	2.82
0.20	0.00	1.00	2.10	3.10
0.14	0.00	1.00	2.15	3.25
0.28	0.00	0.93	1.90	2.82
0.08	0.00	1.00	2.08	3.07
0.16	0.00	0.97	2.12	3.17
-0.08	0.00	0.98	1.87	2.83
0.09	0.00	0.93	1.90	2.83
0.04	0.00	0.98	2.13	3.22
0.11	0.00	0.97	1.87	2.82
0.33	0.00	0.90	1.88	2.80
0.33	0.00	0.92	1.90	2.83
0.32	0.00	0.95	1.87	2.83
-0.02	0.00	1.05	2.05	3.13
0.14	0.00	0.97	2.13	3.10
0.36	0.00	0.92	1.87	2.78
0.41	0.00	0.87	1.85	2.77
0.15	0.00	0.98	2.10	3.08
29.20	0.00	1.02	1.88	2.85
7.63	0.00	0.97	2.10	3.12
12.05	0.00	0.97	2.13	3.18
35.73	0.00	1.02	1.88	2.87
33.42	0.00	0.95	1.87	2.82
9.35	0.00	0.95	1.95	2.90
14.59	0.00	0.95	1.87	2.82
12.90	0.00	0.97	2.10	3.08
11.83	0.00	0.95	1.85	2.85
25.30	0.00	0.90	1.87	2.78
16.18	0.00	0.92	1.90	2.83
13.72	0.00	0.98	2.17	3.17
31.13	0.00	0.95	1.90	2.83
6.26	0.00	0.98	2.12	3.10
5.47	0.00	1.00	2.25	3.23
20.54	0.00	0.92	1.90	2.83
45.50	0.00	1.02	2.10	3.08
25.37	0.00	0.97	2.12	3.13
31.84	0.00	0.95	1.85	2.82
24.53	0.00	0.95	1.90	2.83
15.12	0.00	1.07	2.07	3.15
14.05	0.00	0.97	1.88	2.83
11.81	0.00	0.98	2.10	3.08
15.23	0.00	0.97	2.12	3.00

Appendix 10. Day and night PO_4^{-3} fluxes from Chapter 4.

time	tank	cosm	nutrients	crab	richness	PO4 time 1	PO4 time 2	PO4 time 3	PO4 time 4	T1 (hr)	T2 (hr)	T3 (hr)	T4 (hr)
day	8	2	-	-	0	2.09	0.32	0.21	0.28	0.000	1.183	2.417	3.367
day	9	1	-	-	0	0.62	0.52	0.44	0.42	0.000	1.250	2.467	3.417
day	14	1	-	-	0	0.60	0.32	0.45	0.41	0.000	1.200	2.567	3.450
day	8	1	-	-	1	0.42	0.41	0.34	0.39	0.000	1.183	2.300	3.250
day	12	8	-	-	1	0.66	0.86	0.87	0.75	0.000	1.183	2.517	3.550
day	14	7	-	-	1	0.43	0.46	0.47	0.48	0.000	1.200	2.550	3.417
day	8	7	-	-	3	0.42	0.54	0.51	0.54	0.000	1.183	2.450	3.400
day	11	1	-	-	3	0.79	0.86	0.72	0.94	0.000	1.183	2.550	3.617
day	14	5	-	-	3	0.57	0.66	0.59	0.53	0.000	1.200	2.567	3.433
day	10	3	-	-	5	0.66	0.45	0.63	0.53	0.000	1.217	2.433	3.400
day	11	8	-	-	5	0.68	0.72	0.72	0.70	0.000	1.183	2.567	3.633
day	14	6	-	-	5	0.55	0.49	0.42	0.39	0.000	1.183	2.550	3.467
day	8	8	-	+	0	0.35	0.44	0.49	0.37	0.000	1.167	2.450	3.400
day	10	1	-	+	0	0.48	0.51	0.42	0.42	0.000	1.233	2.433	3.400
day	14	8	-	+	0	0.52	0.44	0.37	0.32	0.000	1.183	2.533	3.467
day	8	5	-	+	1	0.32	0.29	0.29	0.31	0.000	1.183	2.450	3.400
day	9	7	-	+	1	0.62	0.51	0.58	0.56	0.000	1.217	2.450	3.400
day	10	4	-	+	1	0.60	0.49	0.55	0.60	0.000	1.233	2.467	3.400
day	9	8	-	+	3	0.52	0.60	0.53	0.40	0.000	1.233	2.467	3.417
day	11	2	-	+	3	0.56	0.59	0.66	0.66	0.000	1.150	2.550	3.667
day	12	4	-	+	3	0.76	0.68	0.52	0.56	0.000	1.183	2.533	3.567
day	9	3	-	+	5	0.56	0.52		0.47	0.000	1.233	2.467	3.417
day	10	2	-	+	5	0.74	0.79	0.65	0.84	0.000	1.217	2.450	3.417
day	11	3	-	+	5	0.65	0.79	0.79	0.77	0.000	1.183	2.550	3.617
day	8	4	+	-	0	1.13	0.89	1.28	2.61	0.000	1.183	2.433	3.400
day	12	1	+	-	0	1.53	1.56	1.95	2.34	0.000	1.200	2.567	3.517
day	14	4	+	-	0	1.45	1.88	2.75	2.15	0.000	1.183	2.550	3.500
day	8	6	+	-	1	2.66	2.56	3.62	3.07	0.000	1.200	2.433	3.400
day	9	6	+	-	1	2.36	2.73	3.20	2.36	0.000	1.233	2.467	3.417
day	12	2	+	-	1	1.27	1.84	1.53	2.28	0.000	1.183	2.567	3.600
day	9	2	+	-	3	0.96	1.39	1.92	2.33	0.000	1.200	2.467	3.417
day	11	7	+	-	3	1.27	1.93	2.18	2.88	0.000	1.183	2.550	3.600
day	12	5	+	-	3	1.04	2.17	2.04	2.57	0.000	1.200	2.567	3.483
day	9	5	+	-	5	1.49	2.76	3.60	5.72	0.000	1.233	2.467	3.417
day	10	8	+	-	5	1.66	1.82	2.48	3.47	0.000	1.233	2.433	3.383
day	12	7	+	-	5	1.62	1.53	1.84	2.53	0.000	1.150	2.500	3.417
day	10	5	+	+	0	0.68	0.43	0.55	1.81	0.000	1.233	2.417	3.433
day	12	6	+	+	0	1.41	1.69	2.42	4.30	0.000	1.167	2.500	3.550
day	14	3	+	+	0	1.32	1.98	1.97	1.92	0.000	1.200	2.567	3.450
day	10	6	+	+	1	1.33	1.42	1.44	1.46	0.000	1.233	2.467	3.417
day	11	6	+	+	1	1.36	2.03	2.14	2.55	0.000	1.133	2.567	3.650
day	12	3	+	+	1	1.90	2.31	1.83	2.17	0.000	1.217	2.583	3.517
day	8	3	+	+	3	0.23	2.55	3.08	3.57	0.000	1.183	2.450	3.400
day	10	7	+	+	3	1.36	2.54	2.69	3.16	0.000	1.233	2.417	3.433
day	11	4	+	+	3	1.76	4.62	3.39	4.78	0.000	1.117	2.550	3.633
day	9	4	+	+	5	1.01	1.19	1.43	1.88	0.000	1.233	2.467	3.417
day	11	5	+	+	5	1.31	1.88	2.47	2.74	0.000	1.183	2.550	3.583

day	14	2	+	+	5	1.32	2.11	2.34	2.39	0.000	1.167	2.517	3.450
night	8	2	-	-	0	0.30	0.21	0.16	0.07	0.000	1.017	1.867	2.833
night	9	1	-	-	0	0.33	0.40	0.34	0.32	0.000	0.917	1.867	2.800
night	14	1	-	-	0	0.39	0.40	0.27	0.24	0.000	1.000	2.150	3.233
night	8	1	-	-	1	0.45	0.55	0.44	0.33	0.000	0.967	1.850	2.817
night	12	8	-	-	1	0.46	0.58	0.40	0.46	0.000	0.967	2.117	3.117
night	14	7	-	-	1	0.38	0.89	0.27	0.23	0.000	0.983	1.917	3.017
night	8	7	-	-	3	0.52	0.39	0.37	0.34	0.000	0.950	1.867	2.817
night	11	1	-	-	3	0.65	2.39	0.56	0.52	0.000	1.000	2.100	3.100
night	14	5	-	-	3	0.30	0.70	0.37	0.36	0.000	1.000	2.150	3.250
night	10	3	-	-	5	0.76	0.53	0.64	1.44	0.000	0.933	1.900	2.817
night	11	8	-	-	5	0.44	0.65	0.40	0.37	0.000	1.000	2.083	3.067
night	14	6	-	-	5	0.34	0.52	0.28	0.23	0.000	0.967	2.117	3.167
night	8	8	-	+	0	2.50	0.35	0.16	0.11	0.000	0.983	1.867	2.833
night	10	1	-	+	0	0.48	0.56	0.90	0.48	0.000	0.933	1.900	2.833
night	14	8	-	+	0	0.23	0.39	0.26	0.16	0.000	0.983	2.133	3.217
night	8	5	-	+	1	0.27	0.39	0.15	0.17	0.000	0.967	1.867	2.817
night	9	7	-	+	1	0.56	0.61	0.70	0.57	0.000	0.900	1.883	2.800
night	10	4	-	+	1	0.58	0.46	0.58	0.71	0.000	0.917	1.900	2.833
night	9	8	-	+	3	0.42	0.46	0.40	0.33	0.000	0.950	1.867	2.833
night	11	2	-	+	3	0.37	0.54	0.42	0.39	0.000	1.050	2.050	3.133
night	12	4	-	+	3	0.24	0.39	0.21	0.16	0.000	0.967	2.133	3.100
night	9	3	-	+	5	0.42	0.54	0.53	0.37	0.000	0.917	1.867	2.783
night	10	2	-	+	5	0.69	0.78	0.67	0.76	0.000	0.867	1.850	2.767
night	11	3	-	+	5	0.60	0.69	0.83	0.55	0.000	0.983	2.100	3.083
night	8	4	+	-	0	1.76	1.96	1.58	1.39	0.000	1.017	1.883	2.850
night	12	1	+	-	0	1.21	1.11	0.78	1.00	0.000	0.967	2.100	3.117
night	14	4	+	-	0	1.65	1.24	1.47	1.49	0.000	0.967	2.133	3.183
night	8	6	+	-	1	0.25	2.77	3.71	3.56	0.000	1.017	1.883	2.867
night	9	6	+	-	1	2.37	2.26	3.10	2.81	0.000	0.950	1.867	2.817
night	12	2	+	-	1	1.16	0.84	1.04	1.31	0.000	0.950	1.950	2.900
night	9	2	+	-	3	0.96	1.27	2.05	1.61	0.000	0.950	1.867	2.817
night	11	7	+	-	3	1.76	1.26	1.99	1.81	0.000	0.967	2.100	3.083
night	12	5	+	-	3	1.27	1.13	1.52	1.61	0.000	0.950	1.850	2.850
night	9	5	+	-	5	1.60	2.24	2.20	2.21	0.000	0.900	1.867	2.783
night	10	8	+	-	5	1.72	1.71	1.80	2.00	0.000	0.917	1.900	2.833
night	12	7	+	-	5	1.36	1.33	1.53	1.47	0.000	0.983	2.167	3.167
night	10	5	+	+	0	1.68	1.95	2.19	2.76	0.000	0.950	1.900	2.833
night	12	6	+	+	0	1.39	0.80	0.88	0.84	0.000	0.983	2.117	3.100
night	14	3	+	+	0	1.22	0.63	0.98	0.71	0.000	1.000	2.250	3.233
night	10	6	+	+	1	1.26	1.49	2.91	1.46	0.000	0.917	1.900	2.833
night	11	6	+	+	1	3.09	4.04	3.16	3.28	0.000	1.017	2.100	3.083
night	12	3	+	+	1	1.54	3.26	1.67	3.23	0.000	0.967	2.117	3.133
night	8	3	+	+	3	1.86	2.74	3.26	2.58	0.000	0.950	1.850	2.817
night	10	7	+	+	3	1.99	2.19	2.40	2.60	0.000	0.950	1.900	2.833
night	11	4	+	+	3	3.09	1.85	1.36	1.44	0.000	1.067	2.067	3.150
night	9	4	+	+	5	0.83	1.10	1.56	0.98	0.000	0.967	1.883	2.833
night	11	5	+	+	5	1.25	1.91	1.07	1.52	0.000	0.983	2.100	3.083
night	14	2	+	+	5	1.55	1.24	1.59	1.75	0.000	0.967	2.117	3.000

Appendix 11. Total fatty acid (ng g^{-1}) data from Chapter 5.

nutrient	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
crab	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
richness	0	0	0	1	1	1	3	3	3	5	5	5	0	0	0	1	1	1	3	3	3	6	6	5	0	0	0
Componen	8-2 fame	9-1 fame	14-1 fame	8-1fame	12-8 fame	14-7 fame	8-7 fame	11-1 fame	14-5 fame	10-3 fame	11-8 fame	14-6 fame	8-8 fame	10-1 fame	14-8 fame	8-5 fame	9-7 fame	10-4 fame	9-8 fame	11-2 fame	12-4 fame	9-3 fame	10-2 fame	11-3 fame	8-4 fame	12-1 fame	14-4 fame
12:0	4.70	65.83	103.47	137.58	61.24	128.45	75.57	179.47	54.29	239.68	145.60	86.70	41.46	62.36	82.38	64.40	109.22	134.08	171.63	108.06	117.37	169.26	45.14	166.65	22.17	57.67	40.96
i13	4.56	25.39	30.51	73.93	25.79	59.07	27.10	47.89	16.44	122.27	48.48	26.12	23.55	23.95	24.48	17.11	43.35	58.85	52.33	41.17	36.37	65.87	24.09	54.12	17.75	26.70	21.28
a13	3.16	19.66	13.50	23.58	22.15	24.87	23.26	22.72	6.57	42.75	15.35	28.61	20.70	13.37	21.10	17.26	16.99	26.98	30.21	18.02	15.92	30.00	7.99	22.68	0.00	12.35	0.00
13:1	4.94	26.14	17.13	0.00	0.00	0.00	4.41	15.00	0.00	35.16	41.02	31.16	4.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	36.63	21.93	29.58	0.00	0.00	0.00
13:0	5.63	75.36	76.99	83.15	78.34	121.84	68.08	241.66	50.28	178.11	92.89	57.38	37.34	79.99	76.83	47.78	123.86	133.08	239.45	74.47	121.85	134.25	39.40	166.47	21.31	57.73	45.15
i14	21.15	184.74	188.94	432.45	223.86	370.09	178.84	305.66	102.48	974.30	286.17	171.64	170.29	158.68	218.65	180.80	337.25	521.30	349.40	290.30	228.39	626.71	185.61	378.68	66.27	158.93	129.20
14:1	5.08	61.53	44.94	0.00	0.00	0.00	49.96	72.42	24.50	127.61	61.08	43.46	34.23	49.47	52.26	0.00	0.00	0.00	75.05	56.43	49.11	80.38	26.31	82.22	18.50	32.79	34.65
14:0	284.21	3803.24	2216.55	2279.27	1173.86	2802.82	1275.23	1852.97	894.06	4356.35	2128.73	1254.95	1439.94	1967.99	1976.24	938.72	2094.18	2305.45	2282.64	2319.34	1725.36	2399.51	945.17	2128.55	869.06	1291.24	1113.67
i15	130.66	832.49	906.12	1607.34	885.29	1379.31	558.71	1027.62	416.85	2206.00	980.47	580.56	673.29	661.47	211.91	536.32	1274.18	1499.50	1244.89	1007.06	812.35	1334.19	552.18	1198.18	449.67	749.43	711.09
a15	93.72	663.87	600.38	1139.19	832.94	1009.26	489.41	1029.41	400.30	1682.04	780.27	521.56	508.06	632.38	788.84	450.70	1097.41	1363.99	1035.84	851.92	775.71	1311.51	464.62	1161.48	228.37	541.36	469.90
15:1	3.74	265.35	149.75	0.00	0.00	0.00	26.99	351.37	96.21	364.23	210.93	127.43	25.90	275.74	252.72	0.00	0.00	0.00	529.02	218.39	281.93	328.91	33.13	291.17	19.36	36.57	90.03
15:0	175.27	2011.07	1310.67	1334.20	2034.78	2179.96	1174.37	3383.73	816.34	2182.00	1461.83	1009.89	923.43	1637.70	1917.03	753.88	2364.16	1961.22	4454.75	1361.18	2162.65	2329.84	559.87	2003.17	526.47	990.78	626.62
16:4	12.39	65.87	65.32	71.89	45.80	69.70	51.45	82.71	39.17	160.36	80.23	46.21	58.06	56.22	74.96	25.98	67.62	73.30	92.40	73.70	68.47	101.33	46.45	101.18	38.55	54.14	52.34
16:3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1029.27	0.00
16:2	0.00	0.00	0.00	67.83	86.86	95.57	0.00	0.00	0.00	13.32	965.26	9.45	591.15	0.00	0.00	9.32	95.88	111.96	8.52	0.00	0.00	1090.86	0.00	0.00	0.00	32.73	0.00
i16	67.37	1682.55	402.58	505.87	354.60	448.97	260.96	672.23	215.33	2329.04	951.28	300.99	571.12	810.01	409.04	206.79	438.81	511.85	820.41	499.54	372.81	871.05	240.73	795.25	38.81	734.55	396.99
16:1w7	1894.35	17218.57	7928.66	0.00	0.00	0.00	6721.54	1149.77	3861.17	16428.72	8273.75	6763.82	7597.02	10430.70	13248.24	0.00	0.00	12.04	10460.19	10711.30	7888.32	11191.50	2421.72	9191.01	5229.71	616.35	5667.06
16:1w9	70.59	0.00	2178.43	0.00	29.86	7.69	47.54	7474.17	22.46	1474.37	751.80	288.02	56.62	879.02	59.92	0.00	0.00	0.00	605.89	596.52	49.68	95.05	1295.51	848.09	375.56	5081.44	555.70
16:0	1932.78	14763.51	10226.90	11839.78	6074.43	12915.30	6050.15	8975.27	4267.93	18150.81	9937.18	7145.59	7055.94	9208.66	9762.28	5096.10	10793.23	11553.86	9962.79	10440.54	7327.57	11806.15	3961.97	10164.51	5172.85	12078.93	7511.13
10Me17br	54.15	258.83	305.79	235.74	308.41	255.46	142.47	372.24	146.07	69.45	268.70	189.18	144.45	224.26	329.77	136.86	326.48	374.92	504.14	232.81	76.37	351.93	127.79	397.05	126.10	69.41	198.88
i17	57.30	307.31	299.18	283.19	285.86	461.16	170.36	368.32	145.36	622.92	394.47	193.05	200.46	251.55	239.15	177.56	384.06	444.17	410.40	266.62	267.05	430.42	147.94	361.20	189.42	239.84	239.86
a17	113.48	1073.60	784.98	5.77	220.11	37.44	854.47	1798.39	448.81	1042.23	839.72	577.62	472.84	1067.75	1128.81	36.89	30.65	17.01	2676.59	691.00	1171.39	1222.26	261.63	1084.19	294.71	433.02	337.87
17:1	46.90	397.11	272.88	96.24	86.63	91.85	174.98	472.83	104.92	588.34	358.82	157.70	234.33	379.98	383.09	53.73	88.34	121.09	513.33	298.30	291.86	484.89	172.17	397.44	136.09	155.14	159.30
17:0	134.13	922.88	673.92	863.22	626.16	933.18	451.94	973.75	310.25	1068.01	800.14	486.22	492.52	696.75	690.84	369.95	933.33	992.20	1036.70	635.38	658.37	1040.66	328.28	839.02	387.52	658.14	491.01
18:4	25.96	305.74	130.94	114.08	61.87	112.16	106.60	120.45	74.84	199.15	139.29	94.16	115.29	147.77	163.49	19.25	114.91	87.73	149.80	182.97	106.80	207.03	43.96	150.11	21.69	22.94	21.99
18:3	23.39	1883.88	115.69	2228.36	1311.74	2637.12	49.61	689.89	331.17	1047.42	899.70	46.51	72.75	72.44	85.85	1547.27	4076.35	3365.56	652.17	91.28	65.15	1128.80	54.51	86.24	76.88	106.30	127.52
18:2	341.59	2354.06	2836.91	730.56	607.91	848.04	911.46	1761.93	655.25	2877.99	1744.57	1365.47	1302.12	1705.00	2281.88	460.56	629.89	751.20	1449.66	2091.39	1190.70	3074.90	685.83	1820.39	1251.07	1960.04	1617.23
18:1w9c	222.12	1508.22	1260.33	402.50	257.63	468.40	726.09	1154.34	481.83	2399.12	1366.51	1058.75	652.63	900.18	986.24	253.22	406.37	462.86	900.36	1178.50	730.80	1614.30	464.54	1134.98	685.25	1444.70	1119.19
18:1w9t	376.94	2569.82	2351.37	94.65	75.50	115.17	1258.88	2533.34	919.67	4267.13	2514.98	1520.81	1493.22	2056.62	2220.62	95.02	84.74	119.60	2626.49	2235.34	1638.97	3073.23	1199.21	2660.39	1424.84	2383.38	2253.25
18:0	510.25	2111.16	1535.17	2247.74	1373.39	2256.97	1137.75	1899.25	849.14	2563.40	1791.04	1218.37	1068.75	1247.94	1317.73	1261.93	2011.82	2032.83	1692.17	1630.55	1149.58	2068.31	680.55	1621.95	1010.05	1513.99	1175.47
10Me19br	0.00	0.00	0.00	16.58	25.41	28.90	19.95	30.29	10.96	67.69	18.67	12.30	0.00	0.00	8.85	4.89	27.71	37.32	43.53	13.95	26.03	30.33	5.09	30.03	0.00	0.00	10.29
i19	7.64	74.35	33.57	86.75	85.89	128.98	5.69	46.19	28.84	127.05	73.48	67.92	40.56	60.96	51.06	66.73	111.35	105.78	51.40	22.24	34.06	97.43	17.92	78.24	34.74	28.76	32.87
a19	7.15	71.00	34.08	88.34	82.36	122.17	32.88	106.84	23.27	73.58	63.23	40.55	19.86	40.87	66.82	57.19	112.96	106.06	72.55	25.46	39.80	88.41	19.25	53.23	13.41	30.90	25.02
19:1	40.30	199.67	115.24	169.37	114.74	176.43	9.98	214.07	86.09	135.53	164.73	122.46	92.44	79.77	89.54	52.94	116.93	164.83	186.02	154.67	146.82	180.35	50.97	169.59	112.64	156.34	150.35
19:0	2222.30	2992.91	2952.84	2948.65	2777.77	3156.37	2028.35	3505.82	2231.67	3413.38	3107.79	3030.65	2455.98	2348.83	2699.78	2431.37	3121.53	3202.06	2810.94	3065.38	2248.74	3431.84	978.96	3456.37	2865.07	2989.92	2569.55
20:5w6	10.40	0.00	54.83	532.90	426.20	550.34	150.09	153.75	89.76	67.54	64.10	152.65	96.55	45.43	103.27	403.07	459.85	607.40	145.41	51.06	189.53	112.80	33.59	139.20	20.20	168.95	60.85
20:4w6	192.08	1585.15	887.07	56.36	39.04	47.71	506.57	1100.60	325.00	1513.40	1046.34	907.22	606.59	846.74	873.79	45.87	37.10	56.49	1018.81	852.74	665.25	1222.31	322.67	1214.20	834.55	910.32	694.37
20:5w3	24.75	7.25	2279.22	2.91	0.00	0.00	1220.48	2347.90	971.82	3910.59	3463.77	2558.02	1360.58	2188.51	1811.98	0.00	0.00	0.00	2085.02	1694.77	1515.99	3434.92	928.11	2781.12	1507.45	1688.54	1433.98
20:3	65.24	648.10	99.44	0.00	0.00	0.00	244.18	265.03	143.24	207.84	112.69	74.78	68.15	94.65	84.32	0.00	0.00	0.00	200.69	226.97	224.36	162.81	41.25	119.63	234.64	92.21	258.11
20:2	3.52	171.94	89.69	304.98	191.31	331.78	46.20	98.55	39.90	158.88	110.57	69.26	47.58	64.72	69.52	156.47	320.68	363.99	96.98	86.58	63.46	129.69	37.41	114.74	47.18	101.65	70.57
20:1w7	55.49	487.51	311.68	288.79	127.34	252.75	206.81	412.46	169.38	389.68	428.12	211.15	167.75	229.79	176.23	94.92	211.94	229.57	56.34	199.66	300.11	372.55	133.76	291.29	254.55	216.17	231.43
20:0	1762.57	2892.02	2972.53	3213.00	3035.46	3405.31	2005.59	3855.88	2180.99	3389.52	3067.36	3056.07	2520.50	2285.54	2926.09	2292.38	3326.28	3875.63	3416.97	2743.86	2650.26	3962.36	977.17	3854.97	2192.94	3014.77	2424.33
21:0	512.02	1136.35	1981.63	2192.52	1784.08	1889.65	1956.31	2178.06	1881.71	2133.49	2268.23	2309.63	1096.90	1102.46	1978.27	1960.65	2004.24	2118.38	2022.05	1957.65	1983.79	1979.99	1969.95	2427.91	1001.72	2016.22	1907.10
22:6w6	3.69	0.00	0.00	318.89	99.88	462.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	111.66	0.00	357.16	554.92	485.81	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22:6w3	27.23	531.29	253.34	1015.82	655.45	1097.81	61.67	138.28	50.27	220.86	145.71	92.23	98.09	232.31	123.71	567.05	893.36	1023.25	119.32	152.32	82.60	175.96	74.44	186.81	94.47	148.85	109.05
*22:5w6	12.12	327.97	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	26.02	14.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	47.33	195.53	23.15
22:5w3	26.01	174.75	101.90	5.36	0.00	0.00	18.35	0.00	0.00	208.59	115.54	60.50	33.36	51.61	81.04	0.00	0.00	0.00	0.00	0.00	0.00	306.90	84.57	90.69	100.06	107.67	74.43
22:2	5.08	26.48	38.03	0.00	0.00	0.00	25.32	47.04	14.94	69.09	64.83	5.35	5.52	109.00	13.61	0.00	0.00	0.00	38.01	4.61	18.66	60.35	16.33	27.40	3.48	25.54	34.82
22:1w9	42.04	143.77	69.97	110.19	53.76	79.11	44.21	157.10	37.32	126.00	93.41	40.99	47.45	50.56	88.14	59.18	80.49	62.80	129.45	50.49	42.05	92.08	17.14	69.30	46.56	41.93	63.97
22:0	177.74	771.15	894.27	1477.61	820.47	1251.56	534.34	1055.17	423.54	1413.01	845.38	744.42	655.54	624.48	686.65	573.45	1080.24	1334.51	919.10	720.27	695.19	1169.65	348.97	1101.68	345.94	916.11	590.48
23:0	328.78	457.99	533.91	948.79	815.12	881.33	520.38	630.44	549.29	707.27	521.61	308.54	433.88	452.91	450.07	744.85	849.92	844.44	670.81	718.60	617.43	443.17	211.76	430.40	410.09	512.12	435.48
24:1	15.01	55.60	57.57	55.88	33.30	53.91	16.74	33.86	10.91	102.37	42.51	31.68	28.72	33.21	33.31	36.83	53.02	61.81	26.74	26.26	25.81	36.65	24.78	41.53	27.89	41.68	35.47
24:0	330.25	1421.69	1432.77	2051.16	1208.75	2005.93	1006.14	1469.19	658.97	2274.63	1054.81	896.86	1213.37	1044.96	1213.17	836.71	1481.90	1496.51	1271.39	1035.43	1097.96	1622.47	501.63	1663.07	594.39	1622.05	830.96
25:0	31.92	209.14	16.58	185.71	133.56	190.06	6.37	156.02	69.88	156.53	88.50	83.36	6.55	8.01	108.92	114.17	168.24	172.89	6.57	6.12	124.51	146.36	47.93	159.87	3.76	6.46	85.92
26:0	208.24	637.95	795.12	1002.81	692.21	914.99	350.60	792.74	319.17	961.08	535.68	608.74	542.37	578.60	657.50	446.87	746.57	824.18	464.23	530.38	517.01	732.37	332.89	757.45	303.34	632.75	456.84
27:0	20.78	59.86	81.74	4.70	52.53	63.44	21.33	69.11	24.13	55.25	39.84	34.53	38.23	42.53	61.70	34.57	56.93	71.76	36.85	41.92	39.93	43.55	19.58	50.57	23.38	48.77	34.80
28:0	169.52	503.93	638.80	504.72	388.13	394.47	154.93	585.26	147.47	355.52	379.00	324.72	276.46	320.94	498.55	226.96	399.17	512.30	249.91	285.36	250.18	322.23	112.00	337.49	188.56	428.78	253.75
29:0	8.87	0.00	30.97	66.15	54.62	55.71	0.00	60.12	18.12	38.17	50.39	36.16	0.00	23.53	28.91	31.51	53.18	71.58	76.26	28.48	30.19	31.81	12.75	38.44	0.00	26.36	25.65
30:0	181.81	477.68	604.61	425.77	354.67	331.79	168.78	539.63	130.27	206.02	385.86	304.42	205.76	242.92	471.11	190.60	313.22	483.91	229.91	190.59	212.62	232.38	79.49	264.54	132.89	477.03	232.98
31:0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
32:0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total	8287.37	63933.80	45948.50	35668.85	22794.30	38369.88	27719.79	48907.88	19545.72	80661.07	47717.10	31901.69	31722.87	43069.68	46429.23	17123.58	35222.85	37308.36	52940.78	44600.44	35721.58	59386.07	18300.54	48916.09	23669.37	41602.97	30937.33
Sat FA's	4176.08	27834.26	20638.52	24503.59	15126.94	26546.48	12475.58	22233.32	9033.84	34218.56	19736.57	14292.32	13997.65	17989.38	19548.74	10994.62	22729.25	24079.36	23094.33	19408.08	16238.17	24250.88	8015.62	21463.35	9601.69	20707.71	13515.27
Mono Unsa	2777.50	22923.29	14757.96	1216.60	788.75	1245.30	9288.14	14040.74	5816.44	26428.17	14307.66	9417.44	10434.46	15364.99	17590.20	655.86	1041.83	1234.59	16198.88	15725.87	11444.47	17566.52	5861.17	15006.69	8330.97	11205.50	10270.40
Polyunsat	773.46	8082.47	6952.39	5449.94	3526.04	6252.41	3391.98	6806.14	2735.36	10655.02	8952.58	5481.82	4445.78	5770.07	5781.88	3601.99	7250.57	6926.69	6055.76	5508.39	4181.99	11208.56	2349.12	6831.71	4277.45	6664.70	4578.41
Br FA's	560.34	5093.79	3599.63	4498.71	3352.57	4325.68	2564.10	5827.69	1960.09	9369.31	4720.29	2710.10	2844.98	3945.24	3508.42	1871.11	4201.20	5067.73	7591.80	3958.09	3858.95	6360.11	2074.63	5814.34	1459.26	3025.05	2573.25
Sum	7910.78	63933.80	45948.50	35668.85	22794.30	38369.88	27719.79	48907.88	19545.72	80661.07	47717.10	31901.69	31722.87	43089.68	46429.23	17123.58	35222.85	37308.36	52940.78	44600.44	35721.58	59386.07	18300.54	48918.09	23669.37	41802.97	30937.33
Scsatfa	2731.93	23753.06	16143.67	18784.94	11422.00	21338.52	10233.09	17606.06	7242.29	26738.36	16357.22	11259.11	11059.37	15103.39	15822.32	8534.76	18429.80	19112.72	19840.12	16569.51	13270.65	19950.07	6560.38	17090.24	8009.43	18548.48	11003.89
Lcsatfa	1067.55	4081.20	4494.86	5718.66	3704.94	5207.96	2242.49	4727.23	1791.54	5460.21	3379.35	3033.22	2938.28	2885.99	3726.42	2459.86	4299.45	4966.64	3254.21	2838.57	2967.52	4300.80	1455.24	4373.12	1592.26	4159.23	2611.38
pfa/tfa	0.11	0.09	0.21	0.22	0.17	0.15	0.14	0.08	0.11	0.13	0.12	0.10	0.14	0.12	0.12	0.21	0.15	0.13	0.09	0.09	0.11	0.15	0.40	0.10	0.14	0.13	0.13

1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
1	1	1	3	3	3	5	5	5	0	0	0	1	1	1	3	3	3	5	5	5
8-6 fame	9-6 fame	12-2 fame	9-2 fame	11-7 fame	12-5 fame	9-5 fame	10-8 fame	12-7 fame	10-5 fame	12-6 fame	14-3 fame	10-6 fame	11-6 fame	12-3 fame	8-3 fame	10-7 fame	11-4 fame	9-4 fame	11-5 fame	14-2 fame
27.74	28.28	15.88	195.70	118.56	67.74	138.33	107.15	58.83	60.49	52.19	37.03	131.89	17.41	84.18	70.29	119.50	127.77	210.20	162.42	84.51
11.04	18.75	12.84	96.97	39.48	30.72	48.93	42.32	24.69	38.54	23.54	23.01	78.46	26.02	41.85	39.56	58.96	64.40	87.85	78.01	37.64
0.00	17.70	17.37	32.42	12.67	11.86	14.27	13.33	0.00	10.44	10.95	0.00	22.67	0.00	13.94	29.30	20.44	17.66	29.17	25.02	13.34
0.00	0.00	0.00	4.84	0.00	0.00	25.66	15.66	20.57	0.00	4.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	31.43	22.25	25.02
25.06	42.47	31.90	121.13	99.04	50.48	107.80	75.46	55.69	45.29	32.98	36.68	100.57	33.69	74.32	50.92	72.66	100.33	128.18	119.78	75.73
82.83	75.28	104.67	678.89	215.91	189.44	337.97	237.44	133.67	207.00	145.02	123.80	508.19	85.11	342.70	232.92	405.03	318.07	560.39	474.50	224.58
0.00	0.00	0.00	116.67	70.43	38.27	83.95	59.68	38.94	41.95	21.53	26.11	0.00	0.00	0.00	44.55	74.44	85.68	103.67	89.53	55.43
675.28	605.35	676.12	2526.03	1736.18	1411.97	2218.25	1891.37	910.21	1256.63	957.49	838.55	2340.93	422.58	1476.59	1508.24	1783.34	1617.85	2654.48	2442.45	1347.60
407.43	362.33	458.38	1791.26	875.65	769.69	1108.87	926.36	555.07	972.49	682.20	669.18	1653.58	418.94	1232.58	978.45	1565.64	1128.92	1988.88	1694.34	1036.95
236.23	325.70	382.86	1364.44	675.81	449.36	951.89	686.54	409.72	693.07	518.33	471.88	1323.60	428.67	1065.19	609.04	1183.27	946.58	1745.39	1336.13	849.72
0.00	0.00	0.00	265.86	140.49	17.94	192.89	128.77	100.05	33.58	80.06	21.45	0.00	0.00	0.00	113.74	193.30	211.00	259.01	251.28	139.93
300.36	778.79	419.01	1676.94	1083.26	572.64	1442.32	1009.28	912.20	873.55	695.24	558.82	1708.65	408.53	1256.86	989.78	1147.94	1410.39	1610.88	1633.15	1061.04
16.60	16.43	19.01	134.12	75.79	47.62	90.52	73.74	46.82	18.43	47.79	52.72	81.69	23.07	89.41	73.30	113.02	80.47	150.07	129.15	80.90
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	24.74	34.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	269.89	301.64	78.86	38.73	125.38	41.60	0.00	7.94	13.51	1219.25	0.00
130.62	163.82	167.60	574.03	418.46	283.29	522.82	458.31	234.60	630.50	279.53	245.71	116.21	182.63	429.86	362.86	600.25	465.28	856.62	1100.25	457.76
0.00	0.00	0.00	1041.74	8372.14	5361.79	9243.20	8773.94	3903.53	686.57	547.85	4311.07	0.00	0.00	0.00	5897.64	882.30	6951.39	11541.83	11766.96	6521.27
0.00	0.00	4.92	10074.86	0.00	398.98	85.95	356.41	254.21	6988.53	4731.45	402.63	50.48	0.00	7.49	1573.69	8479.12	941.86	1872.55	1131.23	395.42
4585.31	3726.52	3504.93	12716.94	9620.73	9450.44	11291.24	8442.82	5360.45	10926.25	8694.74	5657.91	12530.39	2795.91	8344.91	8279.54	11617.41	8569.66	13231.52	12471.19	7489.93
94.39	162.00	150.09	114.96	219.70	155.49	271.19	271.70	171.36	211.24	177.27	144.64	251.28	72.25	279.90	154.56	258.84	285.68	517.00	123.43	322.74
142.28	158.97	147.89	174.94	347.72	53.86	413.71	289.56	203.19	254.99	253.09	185.44	477.09	147.62	337.34	260.71	432.83	297.20	566.74	484.85	315.14
80.86	116.38	110.78	815.61	636.83	292.23	340.79	546.38	559.05	402.49	309.64	267.16	4.10	131.16	196.88	419.05	551.71	753.56	644.06	854.23	631.95
36.81	60.21	41.37	379.59	216.12	106.12	127.27	189.04	177.30	229.64	148.00	159.79	83.06	43.62	101.40	273.78	312.60	367.78	549.46	425.87	238.91
257.16	336.31	294.30	1051.52	744.89	517.31	819.14	657.70	446.40	653.07	616.53	391.41	1007.39	279.43	728.12	582.01	672.91	708.44	964.59	940.40	652.96
56.29	35.40	47.62	119.27	124.61	124.17	177.46	115.04	75.25	81.77	58.13	63.97	118.89	30.15	73.45	82.27	89.25	105.99	152.32	135.42	27.63
934.86	765.03	766.32	176.08	125.50	72.83	83.26	83.02	50.99	132.93	128.06	83.04	3792.33	545.44	1877.02	594.42	177.00	105.01	159.73	145.20	80.59
371.60	271.09	359.04	2665.03	2016.15	2657.66	2750.89	1751.53	1154.70	2077.86	1719.64	1380.60	1175.99	359.19	778.62	1319.74	2496.32	1622.61	2683.97	2280.86	1445.32
174.65	190.78	197.44	1518.06	1456.46	1838.40	1855.45	966.90	891.01	1052.09	781.94	840.82	346.09	180.12	329.15	783.99	1504.17	1063.78	1531.45	1519.51	858.93
72.54	47.66	97.38	3954.44	2686.24	1712.88	2965.32	2326.88	1524.56	2893.43	1791.83	1706.97	87.24	72.22	66.54	2233.31	3495.74	2794.90	4442.51	3881.77	2369.50
1288.98	1149.03	1164.11	2509.65	1796.26	1558.16	1906.55	1392.26	1015.66	1424.39	1544.96	975.90	2204.38	898.45	1657.10	1727.91	1931.08	1631.07	1922.42	1742.74	1302.86
9.16	3.42	3.54	30.41	30.04	8.25	5.81	16.90	16.68	0.00	0.00	9.42	27.41	3.76	21.12	32.22	21.12	39.53	41.07	40.31	36.16
43.34	56.25	83.35	82.46	24.22	55.32	99.07	64.37	46.66	65.77	32.41	39.59	95.97	64.17	95.81	34.95	81.06	43.63	83.87	99.92	30.37
28.43	65.29	24.92	56.29	48.24	23.97	63.95	51.08	32.98	28.11	22.90	14.69	90.98	37.96	68.50	40.84	49.63	40.93	46.00	73.84	32.56
61.01	74.63	47.72	169.08	195.89	105.44	149.16	105.41	100.12	124.59	101.32	109.36	179.55	47.46	191.06	132.14	193.64	157.59	142.73	252.07	149.16
2837.97	2735.84	2491.77	2744.30	2619.92	2138.04	3319.82	3039.57	2773.44	2247.18	2415.45	2310.55	3022.45	2760.65	3038.26	2461.47	2807.33	2740.23	3582.76	3232.78	3083.40
86.39	96.42	118.52	115.80	67.20	65.43	73.44	71.11	34.02	70.56	93.73	69.53	357.06	146.85	264.94	61.92	587.03	130.70	232.12	174.95	108.40
17.22	17.40	23.70	1254.97	1399.67	987.24	1545.99	1208.86	642.02	716.59	765.84	537.30	0.00	21.07	42.13	797.99	961.79	989.88	1389.35	1492.80	735.10
0.00	0.00	0.00	2295.96	3223.60	1685.36	4182.14	3057.51	1467.89	1302.23	1354.65	881.37	0.00	0.00	0.00	1403.27	2051.15	2012.37	3040.46	2866.47	1610.78
0.00	0.00	0.00	492.56	610.16	290.76	140.62	99.63	57.98	78.15	78.32	159.58	0.00	0.00	0.00	72.50	117.77	209.09	129.02	109.10	74.07
298.96	157.05	138.63	96.75	108.78	92.19	112.23	99.06	44.12	67.35	80.39	41.37	279.20	113.26	228.99	59.36	142.90	90.29	116.63	104.15	89.11
78.27	318.76	257.82	421.34	561.89	166.28	542.80	434.14	284.13	206.02	139.82	141.77	214.49	51.94	176.65	281.59	312.80	333.42	362.49	319.41	336.63
2279.36	2378.14	2060.85	3358.15	2500.12	2015.53	3446.23	2950.46	2311.13	2513.75	2792.21	2332.88	3246.80	2677.53	3374.10	2606.40	4063.72	2984.07	4907.19	3510.79	3284.65
1986.56	1927.47	1925.04	2049.51	1969.21	1895.21	1904.52	1930.65	2228.50	1019.99	1961.23	1925.96	2014.37	1906.33	2064.73	1921.83	2301.05	2074.00	2137.17	2288.70	2283.40
633.79	269.78	262.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	435.42	180.46	348.30	0.00	30.39	0.00	0.00	0.00	0.00
535.31	421.73	495.58	172.09	171.23	97.27	156.45	154.97	62.48	62.66	92.45	69.10	1015.70	402.72	779.67	112.86	243.64	114.64	143.83	165.87	95.81
0.00	0.00	0.00	0.00	383.23	15.39	0.00	0.00	0.00	107.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	107.09	138.91	0.00	136.20	116.11	55.16	43.72	168.67	43.30	6.75	0.00	0.00	52.30	82.24	0.00	112.96	94.08	97.19
0.00	0.00	0.00	42.38	28.81	71.63	61.69	34.83	6.64	5.14	28.25	3.52	0.00	0.00	0.00	6.41	25.58	32.03	27.84	22.27	33.31
36.67	37.20	51.02	125.87	94.77	55.28	167.62	70.59	51.69	37.19	26.08	40.87	49.88	37.25	59.27	37.57	41.21	95.76	70.95	70.71	48.64
402.80	388.75	371.48	1729.87	657.15	494.27	1054.19	713.77	444.90	910.04	864.40	656.39	1336.22	524.94	1125.15	891.57	1317.45	825.51	1689.32	1099.03	866.92
730.29	772.09	682.74	837.18	606.38	533.54	419.07	577.62	531.63	462.83	541.53	434.13	862.07	779.26	907.64	703.79	825.48	720.62	812.37	398.44	593.34
10.06	24.18	20.62	92.70	37.88	15.09	47.62	44.40	5.07	29.50	32.83	24.07	36.18	29.58	39.95	30.68	48.29	20.33	61.75	47.01	37.02
526.93	599.83	526.56	2509.97	993.29	669.96	1353.22	1138.22	652.76	1450.23	1506.07	1026.24	1848.75	752.72	1559.74	1332.12	1852.03	1193.31	2454.61	1661.91	1235.34
77.36	105.25	100.65	198.91	7.12	62.84	132.33	111.32	82.08	6.67	128.11	94.93	169.09	105.20	164.79	111.37	141.34	8.21	229.84	122.12	124.12
351.25	388.62	308.58	1352.92	594.50	375.60	976.27	636.45	470.64	903.07	775.70	547.94	1151.84	384.42	883.64	730.50	919.63	636.27	1456.72	651.02	627.81
18.15	39.19	27.29	82.60	47.79	25.98	41.58	35.30	30.71	71.46	60.28	45.42	57.76	26.89	68.71	41.67	58.07	42.10	81.16	34.31	41.75
113.18	255.41	193.05	625.20	304.22	172.90	317.51	258.43	191.97	634.32	446.34	321.30	431.42	169.96	483.10	318.18	540.57	262.36	718.67	241.64	280.96
0.00	39.15	26.55	0.00	0.00	22.94	31.12	27.02	23.77	18.41	70.74	20.74	52.04	23.19	61.74	36.56	59.02	41.76	69.73	24.82	30.62
90.71	229.00	186.72	143.20	230.40	128.00	234.62	194.37	144.73	626.11	403.09	251.25	330.09	154.22	428.57	232.98	291.67	205.91	596.70	181.88	221.93
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
13324.72	13079.35	12485.17	58980.83	43882.06	33928.46	51240.60	40725.46	24237.76	40480.76	32596.28	25127.00	38645.84	10869.17	28112.61	36278.75	50409.11	40300.94	64665.78	58650.83	35077.18
8740.27	8712.94	7837.03	27440.77	18033.39	15581.02	22064.46	16690.92	10801.03	19859.99	16848.86	11460.51	25401.41	6977.54	18387.50	16903.64	22524.61	17380.97	27997.11	23528.86	15433.97
409.01	753.44	718.29	18155.05	13832.31	9816.42	15486.89	13561.82	7351.18	12321.09	8406.74	7764.91	1046.96	462.20	971.51	11502.59	15537.62	13029.50	20969.83	19777.59	11176.07
2848.82	2065.08	2265.57	7672.12	8471.64	6207.54	9509.88	6865.42	3697.87	4785.05	4885.80	3687.05	7341.90	1840.95	4607.93	4678.05	7118.09	5501.02	8351.81	8959.57	4478.21
1266.62	1547.90	1664.27	5712.89	3644.72	2323.48	4179.26	3607.30	2387.68	3514.64	2454.88	2194.52	4856.55	1588.49	4145.66	3194.47	5228.79	4389.46	7347.03	6364.81	3988.92
13324.72	13079.35	12485.17	58980.83	43882.06	33928.46	51240.60	40725.46	24237.76	40480.76	32596.28	25127.00	38645.84	10869.17	28112.61	36278.75	50409.11	40300.94	64665.78	58650.83	35077.18
7159.89	6067.75	6096.25	20798.11	15198.92	13628.76	17923.63	13576.04	8759.46	15239.67	12594.13	8496.30	20024.19	4855.99	13622.07	13208.68	17344.83	14165.53	20720.37	19512.13	12014.53
1580.38	2045.19	1740.78	6642.67	2834.47	1952.26	4140.83	3114.88	2041.57	4620.32	4254.74	2964.21	5377.22	2121.55	4765.43	3694.96	5179.78	3215.43	7275.74	4016.73	3419.45
0.18	0.17	0.18	0.17	0.13	0.10	0.16	0.13	0.16	0.19	0.18	0.15	0.14	0.18	0.16	0.20	0.17	0.16	0.15	0.13	0.12

Appendix 12. Phospholipid linked fatty acid (ng g $^{-1}$) data from Chapter 5.

nutrient	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
crab	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
richness	0	0	0	1	1	1	3	3	3	5	5	5	0	0	0	1	1	1	3	3	3	5	5
component	8-2 plfa	9-1 plfa	14-1 plfa	8-1 plfa	12-8 plfa	14-7 plfa	8-7 plfa	11-1 plfa	14-5 plfa	10-3 fame	11-8 fame	14-6 fame	8-8 plfa	10-1 plfa	14-8 plfa	8-5 plfa	9-7 plfa	10-4 plfa	9-8 plfa	11-2 plfa	12-4 plfa	9-3 fame	10-2 fame
12:0	0.00	0.00	7.70	6.32	0.00	10.69	3.69	5.68	6.48	0.00	6.08	6.17	4.16	0.00	9.63	0.00	0.00	0.00	4.87	4.02	4.23	15.75	8.26
i13	0.00	0.00	2.86	8.04	0.00	5.69	5.60	4.76	2.77	0.00	4.79	4.11	3.57	0.00	0.00	0.00	0.00	0.00	3.39	2.89	3.05	12.79	7.64
a13	0.00	0.00	0.00	2.01	0.00	3.28	3.31	0.00	6.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.34	0.00	0.00	8.24	0.00
13:1	0.00	0.00	0.00	0.00	0.00	0.00	4.41	0.00	0.00	0.00	9.39	4.53	4.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.76	4.26
13:0	0.97	5.00	5.23	8.48	3.94	6.18	4.60	4.83	3.12	7.41	6.03	4.70	6.44	4.69	7.82	7.99	3.78	10.52	7.41	4.08	5.03	9.89	9.22
i14	3.22	16.21	40.49	94.88	35.70	63.02	34.99	35.40	16.20	150.57	44.16	27.95	27.54	0.00	28.84	24.37	45.41	44.10	40.73	38.05	33.90	94.13	86.31
14:1	0.00	0.00	4.83	0.00	0.00	0.00	6.38	5.41	0.00	7.58	0.00	4.79	4.97	0.00	0.00	0.00	0.00	0.00	3.35	3.00	0.00	9.10	6.63
14:0	28.61	197.32	399.71	371.19	162.22	291.19	163.39	156.67	101.62	483.23	245.81	143.99	154.58	147.94	156.12	120.56	212.70	158.29	197.97	198.52	169.29	339.42	373.55
i15	27.05	118.52	243.47	472.51	191.94	292.14	133.50	137.09	76.61	432.57	169.23	96.73	153.79	125.28	153.30	138.18	259.05	228.03	178.57	140.64	140.43	290.26	270.37
a15	16.79	73.92	152.50	317.56	162.77	210.31	102.40	141.21	74.22	285.86	121.48	75.26	106.05	104.92	118.88	106.74	207.38	190.66	180.11	106.77	127.76	282.09	209.46
15:1	0.00	10.44	20.18	0.00	0.00	0.00	14.37	18.12	7.41	7.27	12.52	7.07	13.38	16.85	13.67	0.00	0.00	0.00	24.39	12.31	17.30	31.98	23.27
15:0	18.24	114.14	223.39	229.54	184.05	190.53	119.77	148.32	66.35	242.79	127.87	85.98	104.90	154.89	144.02	91.33	195.64	132.57	222.86	95.62	136.31	260.60	187.50
16:4	2.21	12.19	20.14	20.26	8.41	10.97	12.16	10.33	6.32	31.41	11.60	7.20	13.16	11.73	17.36	4.67	9.51	7.95	12.13	11.24	12.17	20.87	22.87
16:3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16:2	0.00	0.00	0.00	17.62	13.51	11.30	0.00	0.00	0.00	13.32	16.53	9.45	0.00	0.00	0.00	9.32	12.34	9.78	8.52	0.00	0.00	40.91	0.00
i16	16.81	66.86	127.10	161.69	87.98	108.55	60.85	69.12	37.74	177.53	69.91	48.16	75.40	76.24	78.92	65.88	107.05	98.54	90.17	60.79	70.99	130.58	114.21
16:1w7	22.15	945.12	170.77	0.00	0.00	0.00	562.65	578.98	343.74	244.24	120.46	70.50	790.09	120.92	780.13	0.00	0.00	12.04	94.87	86.64	560.33	1166.28	175.84
16:1w9	0.00	0.00	1751.14	0.00	0.00	7.69	47.54	54.55	22.46	1474.37	751.80	32.33	56.62	879.02	59.92	0.00	0.00	0.00	605.89	598.52	49.68	95.05	1120.38
16:0	290.22	1418.88	2295.55	2563.18	1141.07	1909.79	948.37	878.28	554.16	2740.55	1450.03	932.59	1203.87	1367.50	1176.42	1065.71	1723.82	1473.93	1007.11	1099.98	853.15	2058.67	1743.95
10Me17br	13.89	47.32	88.02	83.12	52.13	46.71	34.31	42.75	23.90	11.14	50.04	29.27	47.29	53.00	52.65	41.57	65.66	60.98	68.01	32.21	44.54	78.79	66.23
i17	15.80	56.22	93.86	4.57	67.47	88.96	41.13	47.43	28.34	144.94	68.18	38.06	55.37	62.91	62.28	50.44	82.35	70.67	69.77	38.91	49.07	99.74	79.70
a17	11.95	82.56	143.56	5.77	54.41	5.67	75.32	115.54	31.84	125.01	73.63	43.54	63.59	122.22	97.35	36.89	3.36	5.12	146.34	46.65	82.79	145.84	96.55
17:1	5.53	28.87	43.31	29.57	18.05	20.07	28.25	31.62	8.10	31.57	30.65	14.49	40.61	48.05	31.85	24.13	20.07	19.37	37.87	23.76	27.26	70.83	73.19
17:0	23.73	105.92	153.88	210.70	106.62	145.32	84.67	91.96	45.64	9.27	123.47	80.45	96.46	123.96	101.06	83.60	145.05	130.57	112.52	70.26	84.64	207.48	147.72
18:4	2.07	21.77	23.17	20.44	9.61	16.71	9.80	9.21	5.16	16.35	11.03	7.97	11.46	14.82	12.24	3.82	13.09	12.00	9.60	9.91	8.07	19.54	13.22
18:3	13.17	34.39	40.96	398.82	181.59	229.97	19.92	24.12	7.19	96.63	23.94	12.31	31.01	32.55	29.96	237.34	252.61	247.52	23.42	22.73	19.69	50.73	38.77
18:2	39.98	240.28	968.67	149.12	109.70	132.80	162.01	185.81	76.12	412.58	213.41	154.34	203.07	291.87	860.89	88.81	94.81	97.37	149.99	193.61	145.67	416.94	276.75
18:1w9c	37.26	200.72	356.78	78.61	43.12	55.76	123.18	143.09	60.92	378.30	213.76	149.47	146.18	185.00	254.24	37.62	52.89	52.61	130.09	142.85	111.54	336.58	229.19
18:1w9t	96.01	575.35	745.02	6.45	16.97	21.06	395.54	413.37	154.71	1076.81	512.50	262.69	485.00	557.67	490.03	21.48	19.66	25.95	439.75	338.40	329.40	884.46	679.29
18:0	87.17	292.28	394.86	576.54	296.63	428.68	231.29	194.09	143.88	451.42	326.31	221.40	209.43	256.32	296.30	307.29	376.95	343.76	234.06	206.60	188.85	398.49	314.26
10Me19br	0.00	0.00	0.00	16.58	5.07	6.02	19.95	30.29	10.96	46.50	18.67	12.30	0.00	0.00	8.85	4.89	4.91	5.45	43.63	13.95	26.03	30.33	5.09
i19	0.00	9.73	8.89	29.22	33.16	28.42	5.69	5.66	4.89	31.51	0.00	0.00	5.90	5.80	9.12	21.06	34.42	22.12	4.68	6.21	5.19	12.45	0.00
a19	2.08	5.70	9.24	8.82	5.27	7.03	5.65	4.10	3.96	16.47	9.07	6.58	6.02	7.72	31.44	12.38	5.91	5.79	4.83	2.91	4.53	16.54	10.21
19:1	4.05	13.19	0.00	0.00	0.00	0.00	9.98	12.82	5.87	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.77	7.62	10.56	47.30	24.19
19:0	10.17	77.49	113.64	60.00	48.38	49.33	43.24	40.34	22.55	89.65	55.84	45.05	31.78	40.29	110.30	27.15	43.02	39.62	52.04	34.44	28.56	82.55	73.95
20:5w6	0.99	0.00	0.00	309.75	180.23	277.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	235.04	221.24	246.74	0.00	0.00	0.00	0.00	0.00
20:4w6	0.00	0.00	19.13	56.36	39.04	47.71	0.00	0.00	0.00	14.14	13.45	39.19	9.70	6.12	9.54	45.87	37.10	56.49	0.00	0.00	0.00	23.29	13.14
20:5w3	20.78	7.25	466.67	2.91	0.00	0.00	11.99	20.10	9.21	296.66	262.15	259.69	173.41	0.00	7.21	0.00	0.00	0.00	13.63	7.80	24.14	449.84	273.62
20:3	39.39	494.38	20.49	0.00	0.00	0.00	195.69	234.29	95.45	26.15	14.53	5.11	12.18	15.02	0.00	0.00	0.00	0.00	157.95	146.29	159.94	25.50	14.26
20:2	0.00	13.89	18.75	99.91	37.13	69.36	7.74	8.27	3.64	13.99	10.19	4.44	6.38	13.73	6.62	47.04	60.39	46.00	8.56	5.86	5.67	10.12	20.83
20:1w7	2.39	64.82	72.06	222.13	81.63	167.37	44.64	51.53	19.38	66.56	60.04	32.55	35.01	55.50	0.00	64.57	139.35	131.84	56.34	37.61	38.13	93.77	49.07
20:0	18.33	45.50	153.76	124.45	74.36	99.20	62.16	46.07	35.98	131.53	94.93	68.57	56.10	72.77	57.22	52.47	82.85	83.56	51.52	36.38	47.14	124.72	113.20
21:0	170.67	757.56	360.30	416.48	369.87	391.74	355.69	396.01	342.13	426.70	453.65	461.93	731.27	734.97	359.69	372.41	380.69	402.37	367.65	355.94	360.69	396.00	393.99
22:6w6	3.69	0.00	0.00	0.00	75.25	7.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	103.87	103.40	89.23	0.00	0.00	0.00	0.00	0.00
22:6w3	0.00	70.35	56.98	583.46	191.72	467.15	14.46	17.07	5.43	25.88	18.59	10.92	17.87	29.41	15.70	247.31	258.96	278.82	15.16	15.15	12.13	28.94	29.19
*22:5w6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.10	14.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22:5w3	3.60	0.00	25.95	5.36	0.00	0.00	18.35	0.00	0.00	32.25	20.24	9.04	0.00	0.00	10.58	0.00	0.00	0.00	0.00	0.00	0.00	105.81	19.48
22:2	1.87	4.70	13.84	0.00	0.00	0.00	9.44	6.08	0.00	43.06	13.42	5.35	5.52	18.28	0.00	0.00	0.00	0.00	6.35	4.61	5.54	27.32	7.89
22:1w9	2.19	12.86	16.39	59.92	18.65	27.34	7.53	5.91	6.26	20.26	10.51	7.38	3.53	15.91	11.40	29.09	28.45	24.83	28.21	4.20	5.89	22.91	9.35
22:0	14.10	61.73	131.05	161.99	78.79	126.85	44.34	42.25	29.87	129.96	79.19	58.85	47.84	68.35	55.16	70.72	99.57	106.57	47.42	46.44	47.68	86.27	78.24
23:0	130.66	169.95	215.27	477.98	378.26	379.24	268.04	187.25	245.69	156.15	117.20	109.90	160.84	202.75	183.60	389.58	362.97	390.52	251.41	275.97	263.19	126.15	130.51
24:1	3.15	7.21	15.07	23.29	13.02	14.77	3.61	0.00	0.00	15.04	9.75	5.58	4.78	5.72	7.18	16.57	17.09	17.08	0.00	0.00	2.96	0.00	8.52
24:0	25.86	92.66	205.01	193.93	66.91	152.10	77.45	57.69	44.32	199.43	99.49	76.35	84.26	95.44	93.47	73.21	112.84	122.52	57.17	56.69	71.96	106.22	107.87
25:0	2.12	5.69	16.58	45.49	10.22	33.23	6.37	6.81	5.74	14.13	9.89	9.18	6.55	8.01	7.55	28.75	32.57	37.97	6.57	6.12	8.47	10.66	10.89
26:0	13.25	35.05	99.80	179.57	66.03	126.20	70.99	71.41	33.21	160.93	85.61	81.50	47.99	64.95	41.67	69.53	119.73	125.11	28.52	41.62	52.25	91.02	141.96
27:0	0.88	0.00	5.68	4.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.19
28:0	4.16	9.63	37.60	15.83	19.31	18.28	8.40	10.21	9.32	27.30	25.56	21.10	11.05	14.93	10.10	10.65	17.56	20.33	8.06	9.64	13.51	26.13	25.19
29:0	0.00	0.00	5.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30:0	3.59	0.00	24.36	9.12	10.25	8.56	10.22	0.00	7.59	0.00	23.48	17.51	7.33	10.50	0.00	0.00	9.21	12.80	0.00	0.00	10.60	18.75	19.05
31:0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
32:0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total	921.00	5573.13	9783.01	7845.12	3899.56	5898.03	4005.90	4132.22	2206.56	10232.93	5600.41	3238.12	4597.47	5197.44	5373.95	3648.19	5205.97	4781.99	4610.76	3998.47	3800.19	8804.06	7248.83
Sat FA's	512.90	2338.32	4005.74	4576.36	2166.03	3447.60	1773.56	1668.21	1051.20	4466.42	2610.79	1739.77	1984.87	2317.29	2099.31	1929.35	3049.41	2674.93	1934.54	1839.59	1545.88	3629.36	3171.86
Mono Unsat	172.73	1858.56	3195.54	419.97	191.44	314.05	1248.08	1315.41	828.85	3321.98	1731.39	591.39	1584.33	1884.63	1648.44	193.47	277.60	283.71	1436.52	1252.89	1173.05	2753.01	2403.18
Polyunsat	127.76	899.20	1673.74	1644.02	846.19	1270.58	461.56	515.27	208.52	1022.42	629.09	525.00	483.76	437.44	984.57	1022.98	1063.48	1091.89	405.31	417.00	393.00	1219.81	728.02
Br FA's	107.61	477.04	907.99	1204.77	695.90	865.78	522.70	633.33	317.99	1422.11	629.15	381.98	544.52	558.08	641.64	502.39	815.50	731.46	834.38	489.88	566.26	1201.88	945.77
Sum	921.00	5573.13	9783.01	7845.12	3899.56	5898.03	4005.90	4132.22	2206.56	10232.93	5600.41	3238.12	4597.47	5197.44	5373.95	3648.19	5205.97	4781.99	4610.76	3999.47	3800.19	8804.06	7248.83
Scsatfa	448.93	2133.54	3480.31	3985.94	1894.52	2962.39	1555.78	1479.83	921.16	3934.87	2287.58	1475.29	1779.84	2055.11	1891.36	1676.49	2657.94	2249.64	1786.81	1679.07	1441.51	3290.30	2784.46
Lcsatfa	63.97	204.78	525.43	610.42	271.51	465.22	217.78	188.37	130.05	531.75	323.22	264.49	205.03	262.18	207.94	252.86	391.48	425.29	147.73	160.52	204.37	339.05	387.40

ng/g dry weight

0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
5	0	0	0	1	1	1	3	3	3	5	5	5	0	0	0	1	1	1	3	3	3	5	5	5
11-3 fame	8-4 plfa	12-1 plfa	14-4 plfa	8-6 plfa	9-6 plfa	12-2 plfa	9-2 plfa	11-7 plfa	12-5 plfa	9-5 fame	10-8 fame	12-7 fame	10-5 plfa	12-6 plfa	14-3 plfa	10-6 plfa	11-6 plfa	12-3 plfa	8-3 plfa	10-7 fame	11-4 plfa	9-4 fame	11-5 fame	14-2 fame
11.33	4.19	0.00	0.00	0.00	0.00	0.00	8.09	5.93	3.70	9.32	5.90	4.88	5.03	7.25	0.00	5.81	0.00	11.95	6.40	6.07	10.67	9.82	13.15	4.85
6.44	0.00	0.00	0.00	0.00	0.00	0.00	8.73	4.18	5.07	6.23	4.49	6.70	4.47	3.99	0.00	3.45	0.00	3.53	6.99	5.01	8.65	7.76	8.81	4.06
2.20	0.00	0.00	0.00	0.00	0.00	0.00	3.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3.28	0.00	0.00	0.00	0.00	0.00	0.00	4.64	0.00	0.00	6.79	0.00	0.00	0.00	4.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.60	5.61
10.16	4.45	6.88	0.00	4.72	9.43	4.73	10.06	6.57	3.36	9.62	5.86	4.55	4.84	4.06	0.00	6.06	9.94	4.83	6.54	6.21	9.10	9.83	9.82	5.28
55.07	0.00	21.52	0.00	7.95	7.53	13.53	107.42	33.68	24.72	66.43	42.97	26.15	35.69	38.22	0.00	66.80	14.13	53.20	62.83	72.96	66.67	90.89	84.10	34.94
6.56	0.00	0.00	0.00	0.00	0.00	0.00	7.93	6.46	0.00	6.84	4.73	5.70	6.71	0.00	0.00	0.00	0.00	0.00	6.54	6.09	5.44	7.61	8.21	5.80
213.66	75.29	156.72	112.45	84.84	66.44	72.36	416.28	225.80	133.67	366.20	253.05	149.76	191.25	186.86	93.97	253.51	60.74	192.86	295.28	273.08	241.01	360.32	342.70	167.44
181.64	72.72	129.37	94.08	72.28	69.05	88.89	406.04	136.51	88.80	232.10	162.16	117.27	237.75	166.29	111.36	311.13	89.01	254.89	267.80	336.46	216.56	365.41	317.98	166.34
151.43	33.91	90.79	61.00	40.66	58.97	70.87	207.70	103.19	53.05	185.70	114.14	82.15	161.04	141.06	72.58	200.80	87.15	205.99	164.86	241.52	179.15	316.08	230.91	128.27
17.69	3.07	7.42	5.81	0.00	0.00	0.00	33.61	14.89	4.21	21.89	10.79	8.69	15.45	11.65	6.42	0.00	0.00	0.00	18.13	26.93	19.19	24.70	19.79	9.16
134.12	48.40	90.78	61.09	38.89	92.16	48.58	234.15	124.89	50.94	215.53	115.67	102.53	126.47	109.53	64.40	173.62	46.34	136.09	182.87	171.35	154.40	213.33	178.56	98.19
15.06	6.73	11.66	8.85	3.55	0.00	4.82	28.74	12.39	6.54	16.03	12.91	8.17	18.43	11.27	10.23	12.63	3.51	10.93	20.72	24.38	14.83	29.75	22.02	11.21
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	32.73	0.00	0.00	0.00	8.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.50	16.37	8.86	7.06	11.84	0.00	0.00	7.94	13.61	0.00	0.00
80.43	38.81	62.54	47.50	33.03	42.34	41.16	56.13	71.56	37.27	105.81	78.87	58.58	99.58	90.98	49.91	102.36	47.10	106.39	103.17	127.07	90.71	166.01	126.64	74.04
82.53	533.89	104.28	602.06	0.00	0.00	0.00	185.65	1179.69	79.72	1144.73	851.57	460.82	148.58	111.73	522.28	0.00	0.00	0.00	160.28	172.93	125.95	164.86	152.65	605.77
846.09	44.62	749.06	59.77	0.00	0.00	4.92	1459.01	0.00	398.96	85.95	81.12	42.13	1163.05	845.21	0.00	9.33	0.00	7.49	1203.03	1263.73	941.86	1353.50	1131.23	51.30
1099.83	643.58	1734.35	1078.83	760.08	694.65	684.89	2308.68	1427.52	970.33	2099.22	1313.78	963.81	2298.42	1466.96	1133.20	2053.49	542.87	1646.01	1816.56	2262.52	1493.18	2360.34	2050.78	1041.86
51.28	30.35	48.20	32.89	25.17	34.66	29.95	64.22	4.23	22.48	6.37	52.17	37.86	61.07	49.29	31.42	44.51	38.22	63.49	56.90	8.87	69.53	103.81	70.79	47.27
67.19	34.06	51.95	37.26	33.52	39.94	34.76	105.12	58.30	30.60	85.17	66.66	46.97	74.18	60.72	40.29	93.18	37.72	77.88	77.25	92.05	74.99	128.19	105.23	58.81
66.85	28.82	49.83	35.47	20.59	31.32	27.67	117.24	92.12	20.18	132.97	60.27	63.16	71.15	85.91	33.82	4.10	34.54	5.65	70.12	88.34	96.21	102.68	86.81	50.27
33.74	10.47	21.16	18.88	16.94	17.04	13.71	67.68	29.67	7.70	40.27	22.20	16.44	51.31	0.00	22.32	15.29	11.11	16.05	47.13	28.30	44.82	68.31	54.22	23.43
104.47	67.92	90.93	68.11	47.86	63.37	56.21	183.18	112.07	60.27	155.95	114.18	83.37	128.12	104.32	67.58	149.73	49.57	128.01	129.99	7.62	128.77	183.28	158.94	91.03
9.97	6.74	10.46	8.00	6.35	0.00	8.71	14.89	12.72	8.42	21.75	10.94	8.61	14.28	8.94	8.25	19.27	6.13	13.06	11.64	11.42	10.20	13.72	11.20	6.16
20.85	22.09	32.52	30.10	143.00	134.26	134.63	92.08	25.94	13.60	41.24	24.98	17.97	63.22	67.49	25.99	257.36	102.87	245.98	58.99	86.63	39.55	64.46	50.40	19.12
184.50	201.80	309.18	207.21	48.30	54.21	57.49	543.43	261.06	222.56	491.26	222.36	182.10	564.95	389.30	222.18	138.91	56.70	129.46	259.38	585.64	258.36	492.94	343.00	160.70
157.00	118.50	218.89	206.09	26.99	30.30	26.70	406.92	217.73	168.41	390.77	165.09	156.52	293.40	223.65	187.47	48.57	33.58	45.26	220.95	395.60	243.15	337.22	264.31	119.00
394.73	343.25	608.54	415.99	12.33	9.39	13.99	1168.65	534.26	236.57	772.78	467.35	350.75	1008.91	572.76	409.68	26.36	18.30	17.54	850.53	1005.47	730.61	1050.44	833.36	392.35
229.93	196.56	216.35	164.94	278.04	243.34	227.45	436.17	236.21	242.20	386.72	266.98	205.35	295.30	248.87	154.21	407.86	196.23	340.08	387.58	381.68	352.97	407.01	347.97	203.97
5.25	0.00	0.00	10.29	9.16	3.42	3.64	30.41	18.32	8.25	5.81	3.31	18.68	0.00	0.00	9.42	4.18	3.76	4.90	3.27	5.70	27.18	7.97	5.31	18.28
6.88	4.32	0.00	8.23	9.04	18.50	13.58	10.70	5.78	4.46	21.48	12.44	0.00	8.94	10.37	6.85	19.60	11.16	27.04	4.93	18.91	9.29	0.00	16.74	0.00
5.24	0.00	6.09	0.00	0.00	13.52	5.83	7.66	5.79	0.00	12.30	7.61	6.14	7.55	9.26	0.00	4.65	18.96	6.39	7.53	10.07	4.72	10.82	9.70	5.99
0.00	6.18	11.28	8.95	0.00	0.00	0.00	23.35	12.89	8.56	0.00	28.31	0.00	0.00	24.02	8.42	0.00	0.00	0.00	0.00	0.00	15.70	0.00	0.00	0.00
49.78	41.90	29.69	49.51	20.45	30.11	22.33	83.28	36.80	16.40	70.14	77.86	30.70	29.55	29.24	30.99	58.12	21.28	46.88	26.94	39.26	80.35	68.48	44.94	34.89
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	39.90	0.00	0.00	0.00	0.00	3.82	0.00	0.00	0.00
26.21	0.00	12.71	0.00	17.22	17.40	23.70	0.00	0.00	0.00	15.36	15.68	0.00	6.30	6.95	0.00	0.00	21.07	42.13	8.75	44.45	6.71	36.17	38.95	18.81
147.90	97.48	140.50	4.83	0.00	0.00	0.00	11.44	8.06	5.64	460.94	266.26	199.89	194.22	218.11	4.49	0.00	0.00	0.00	173.97	296.93	14.55	232.59	171.48	157.51
8.66	175.27	14.20	195.02	0.00	0.00	0.00	389.85	499.93	206.77	23.69	9.91	8.32	20.12	3.96	118.70	0.00	0.00	0.00	13.18	14.15	179.14	14.63	9.94	8.07
10.35	4.24	13.18	8.16	55.88	31.84	31.65	14.05	10.42	6.41	13.70	17.41	5.71	13.50	8.37	6.35	54.75	19.67	46.23	13.83	10.85	9.13	10.01	5.66	3.43
49.30	46.15	33.97	42.57	78.27	66.55	64.73	112.03	89.70	18.28	89.71	57.30	38.30	82.35	33.64	37.61	118.66	51.94	91.64	56.75	52.32	69.82	67.81	64.68	32.37
74.17	28.22	49.88	37.02	35.80	48.20	39.11	79.19	45.94	36.54	115.41	103.67	45.70	63.07	50.01	35.90	98.19	37.03	83.96	66.26	85.04	66.26	136.73	84.19	58.76
485.58	667.81	368.59	346.74	377.72	366.11	355.65	372.64	358.04	344.58	380.90	388.13	445.70	662.10	356.59	350.16	382.52	362.10	392.18	349.42	418.37	377.09	427.43	457.74	455.68
0.00	0.00	0.00	0.00	110.93	63.87	68.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	82.43	43.83	81.17	0.00	30.39	0.00	0.00	0.00	0.00
58.37	0.00	25.67	14.46	167.55	131.18	155.90	33.41	23.82	11.07	26.37	16.34	11.49	0.00	29.66	12.52	257.28	127.18	243.74	25.42	123.63	15.68	17.23	16.52	11.12
0.00	0.00	20.18	23.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
15.45	14.86	32.56	12.28	0.00	0.00	0.00	0.00	0.00	0.00	25.99	15.53	10.77	0.00	88.55	9.84	6.75	0.00	0.00	11.87	28.04	0.00	15.83	15.60	19.07
4.65	3.48	7.14	6.01	0.00	0.00	0.00	3.96	6.58	9.25	11.44	6.06	6.64	5.14	15.16	3.52	0.00	0.00	0.00	6.41	7.60	5.99	6.62	5.88	8.63
19.13	4.27	6.50	3.71	16.09	10.67	22.46	19.10	15.07	5.08	44.08	9.40	6.81	4.55	4.69	0.00	25.21	10.80	21.57	8.61	7.44	16.76	10.41	11.48	0.00
73.99	35.77	67.71	42.90	49.78	45.10	47.89	90.77	46.74	39.49	96.73	66.36	45.85	81.48	57.28	50.43	125.19	42.51	108.19	72.31	9.83	61.86	125.54	86.45	60.11
109.41	169.65	181.44	160.27	364.86	368.06	346.56	298.84	242.08	237.23	126.73	121.52	119.29	197.80	164.17	149.88	361.00	357.02	424.01	293.89	351.65	320.62	158.88	125.33	113.10
6.17	5.52	4.96	4.04	10.05	6.11	20.62	8.78	3.67	0.00	8.47	7.95	5.07	4.86	5.00	3.56	13.56	8.63	11.74	4.91	0.00	5.12	7.36	7.76	6.10
105.21	61.50	87.18	54.28	52.60	50.03	50.88	110.77	59.36	55.86	101.61	94.17	52.96	96.02	89.79	64.36	140.21	43.31	114.24	109.01	132.68	76.84	166.11	112.92	78.28
14.08	3.76	6.48	4.97	25.60	21.00	35.22	9.16	7.12	5.52	13.89	11.86	9.61	6.67	6.96	5.71	33.00	14.36	19.07	8.54	9.27	8.21	18.42	10.70	10.75
95.63	47.98	50.81	59.76	108.43	33.97	42.33	151.56	76.40	78.32	142.16	79.41	84.02	89.32	66.11	60.24	241.08	32.55	146.48	129.15	136.12	98.97	140.32	120.34	81.25
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
32.30	7.11	11.54	8.25	10.52	12.79	14.68	17.26	12.35	10.34	26.70	21.75	14.33	15.65	12.84	11.54	18.05	13.30	18.38	11.66	22.24	16.14	46.64	23.74	22.03
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
26.90	0.00	10.08	8.62	10.58	8.24	16.08	10.34	10.69	6.67	19.61	15.12	11.93	13.64	9.64	9.09	10.46	6.94	9.68	0.00	0.00	18.08	36.76	17.84	19.15
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4753.62	3278.11	5317.80	3873.67	2406.52	2235.47	2280.67	9799.60	5649.24	3373.22	6244.59	5293.36	3768.74	7773.09	6706.92	3704.41	5598.87	1962.74	4622.07	7159.40	8638.62	6285.78	9429.04	7781.35	4169.16
2151.69	1385.52	2526.79	1663.40	1451.94	1341.53	1300.92	3985.43	2351.65	1660.68	3626.16	2384.09	1733.16	3362.32	2375.96	1714.74	3617.06	1060.75	2777.89	3165.90	3400.64	2668.21	4079.95	3473.90	1684.18
1417.43	1115.10	1666.03	1365.88	161.89	142.07	157.13	3497.54	2104.03	927.58	2611.26	1685.79	1113.23	2759.20	1836.60	1195.77	256.99	134.35	211.28	2674.86	2968.72	2218.13	3112.22	2553.26	1250.89
501.99	632.70	682.66	517.88	541.59	432.84	493.05	1131.64	660.90	490.17	1147.79	618.36	459.66	900.15	840.25	436.23	878.07	385.92	824.54	603.95	1264.49	565.90	947.47	690.97	441.83
662.81	242.79	460.30	326.70	261.31	319.24	328.78	1184.78	632.66	294.79	860.36	605.09	462.69	761.42	658.11	356.86	844.75	381.72	808.36	824.69	1004.97	833.54	1289.41	1063.21	682.28
4753.62	3276.11	5317.80	3673.67	2406.62	2235.47	2280.67	9799.60	5649.24	3373.22	6244.59	5293.36	3768.74	7773.09	5708.92	3704.41	5598.87	1962.74	4622.07	7159.40	8638.82	6285.78	9429.04	7761.35	4159.16
1803.49	1229.40	2295.01	1465.42	1194.43	1169.39	1093.93	3595.59	2138.98	1464.47	3224.45	2095.42	1614.26	3049.43	2127.86	1513.37	3049.08	905.88	2369.83	2625.22	3090.62	2390.10	3543.93	3101.92	1612.82
346.10	166.13	233.77	177.98	257.51	172.14	206.99	389.84	212.68	196.20	400.70	288.67	218.90	302.88	248.10	201.37	567.99	155.07	418.06	330.69	310.12	276.11	536.02	371.96	271.67

VITA

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Born November 1979 in New Jersey. Attended Pitman High School and graduated in 1997. Graduated *magna cum laude* from Bryn Mawr College in 2001, earning an A.B. in Biology (with honors) with a concentration in Environmental Science and a minor in English. Entered the School of Marine Science graduate program at the College of William and Mary in 2002.