

Seagrass Ecosystem Energy Fluxes: A Global Collaborative Survey



Seagrasses are essential coastal habitats that support diverse and productive food webs. However, identifying factors that structure seagrass food webs and drive the flow of energy within them remain a key frontier in a rapidly changing world. Here, we propose a collaborative survey coordinated by the [Smithsonian Institution's MarineGEO program](#) and using standardized approaches to characterize the rich flora and fauna of seagrass beds around the world. We will use these data to construct simple food webs, apply a novel framework to estimate energy fluxes among trophic levels, and associate these with hypothesized abiotic and biotic drivers, especially biodiversity. The proposed work will lead to one or more peer-reviewed manuscripts (including all participants as co-authors, to be submitted within one year of fieldwork) that will strongly enhance and generalize our understanding of seagrass ecosystem dynamics.

Introduction

Seagrasses are important foundation species worldwide, supporting abundant and diverse communities of micro- and macroalgae, small invertebrate grazers, fishes, and other larger consumers (1). Herbivorous grazers in particular play critical roles in seagrass food webs: facilitating seagrass growth by removing fouling epiphytes (2), and serving as the central link that shunts that primary production to higher trophic levels (3). This trophic transfer is especially important as seagrass habitats are critical foraging grounds for many juvenile fishes and invertebrates (4) and are therefore substantial contributors to global fisheries production (5).

All living systems are supported by the accumulation and transfer of energy, yet few studies have attempted to quantify the movement of energy within seagrass food webs. Instead, focus has centered on the standing stock or production of particular groups (6, 7). Evidence shows, however, that seagrass beds are generally highly productive and export substantial quantities of animal biomass (8), implying considerable internal accumulation as well. In southern Australia, for example, 7-58% of invertebrate production (< 0.125 mm) was consumed by fishes in or near seagrass beds (9–11), and 51-75% in a similar study conducted along the Swedish west coast (12). Yet, these studies were conducted decades ago, and we have little understanding of their generality. The [Smithsonian Institution's MarineGEO program](#) proposes a general test of these processes across geography to illuminate the potential responses of seagrass systems to climate warming, eutrophication, exploitation, and habitat fragmentation, which are substantially altering structure and functioning of seagrass systems worldwide (13).

The proposed study involves a broad comparative sampling of seagrass ecological structure and environmental parameters using a standardized set of protocols, to which we will apply a new framework that estimates the fluxes of energy through food webs (14). We will then relate these values to properties of the community and ecosystem. The framework requires information only on

the composition, biomass, size structure, and general trophic relationships of the community, which is then combined with generalized equations for metabolic losses and assimilation efficiencies to estimate fluxes between trophic groups. This method is a key conceptual advancement, as it allows us to explore not just the stocks of biomass present within an ecosystem—an historical focus throughout much of ecology—but, through general principles, to estimate the movement of energy within the system.

Hypotheses

We will test the following questions:

- (1) **Does the structure of seagrass food webs change predictably across the world's environments and geography?**
 - a. We hypothesize that trophic transfer is rapid in relatively oligotrophic tropical areas, and biomass is likely to be concentrated at higher levels. In contrast, in heavily impacted or exploited areas, removal of larger predators may lead to proliferation of smaller predators, reduced herbivores, and accumulation of algae. Thus, the length of the food chain, itself modulated by a number of factors, may result in different allocation of biomass among trophic levels (13).
 - b. We hypothesize that sparse or patchy habitat (as characterized by quadrat surveys) and position within the bed (edge vs. exterior) may reduce diversity and food web complexity through various mechanisms (reviewed in 15).
- (2) **How does energy move between adjacent trophic levels, and how do this flux change with biotic and abiotic properties across seagrass ecosystems?**
 - a. We hypothesize that higher diversity within a trophic level enhances resource capture, leading to higher fluxes to that level (14, 16).
 - b. We hypothesize that higher temperatures will drive both direct effects (higher metabolic rates (17)) and indirect effects (e.g., by changing resources) on standing stocks and energy fluxes, as predicted by metabolic theory. Computing fluxes that are both temperature-dependent and independent and comparing them will allow us to disentangle these direct and indirect effects. For example, a strong divergence in fluxes obtained with and without adjusting for temperature effects would indicate strong control by individual metabolic rates, rather than other ecological processes, such as accumulation of biomass (18).
 - c. We hypothesize that low salinity and dissolved oxygen (stress) will reduce fluxes by reducing foraging (19).
 - d. We hypothesize that Increasing habitat heterogeneity will increase fluxes to herbivores by providing more substrate/resources, and/or reduce fluxes to predators by reducing foraging efficiency (15).

The data on population body sizes collected during this study allows us to answer additional questions:

(3) **How does the size distribution of prey change in response to predation pressure and other factors?**

- a. We hypothesize that epifauna will be smaller, on average, in the tropics based on a seminal early study reported increasing body size with increasing latitude (20). The study attributed this trend to (weak) effects of predators selecting for larger individuals in the tropics. A later experiment confirmed that predator access led to smaller body sizes, on average, but the same amount of total biomass, leading the author to conclude that epifaunal communities are primarily resource-limited (21).
- b. Thus, we also hypothesize that this trend is driven by higher predation pressure in the tropics, which we can measure using simple [predation assays](#) conducted at the same time as the ecological sampling.

We can increase the scope and power of this third hypothesis by drawing on existing data from the [Zostera Experimental Network](#), which deployed observational and experimental surveys of size-structured epifaunal abundance, biomass, and predation pressure in eelgrass beds at 50+ sites from 2011-2014.

Methods

Smithsonian MarineGEO commits to provide: coordination in the form of participant recruitment, planning fieldwork with each participant, standardized protocols and templates, data management, data synthesis, and lead writing of the publications. Each partner commits to: conducting the required field work, processing the samples collected, submitting the data in standard format to MarineGEO, and contributing to data interpretation and manuscript preparation. MarineGEO further commits to preparing the first manuscript for peer-reviewed publication, with all co-authors, *within one year of completion of fieldwork*.

In this project, we propose to use the regular ecological surveys coordinated by the Smithsonian Institution's MarineGEO program to apply this energy-flux framework in seagrass ecosystems at a global scale, quantifying for the first time how seagrass food webs and energy fluxes vary across a range of biotic and abiotic conditions. We will use MarineGEO's existing standardized [survey design](#) to gather the necessary data, including: quantification of [seagrass cover and density](#), and measures of [fouling epiphyte loads](#), [predation](#), and environmental conditions. These methods are designed to be as similar as possible to those of [SeagrassNet](#) and [Seagrass-Watch](#), and should produce data that are comparable in most respects.

Each partner site will further quantify seagrass fauna as follows: herbivorous grazers and macroalgae with [grab-samples](#), and meso- and larger predators through traps, [seines](#), trawls, and [visual surveys](#). We encourage participants to characterize as much of the community as possible given the uniqueness of each site, with the aim of understanding links from epiphytes to herbivores and herbivores to mesopredators at every site.

All materials are open-source, and we encourage participation by anyone with the capacity to complete the proposed work. We are happy to work with partners who may face site-specific difficulties in collecting or processing the field samples.

Data on species' interactions will be sourced from the scientific literature, from online databases such as FishBase, and expert (participant) opinion to construct simplified food webs for each site (e.g., 20). Trophic data for species missing from these resources can be inferred or empirically imputed from taxonomy or phylogeny.

A Worked Example

To show how these concepts and methods can be applied to observational data, we provide an example from a dataset sampled through time (rather than space as in the proposed project) from the Chesapeake Bay, USA. Using these data, collected using similar methods as above, we construct a simple species-interaction matrix based on known trophic positions from the literature, and compute the fluxes of energy first to herbivores and then to small mesopredators, such as crabs and fishes.

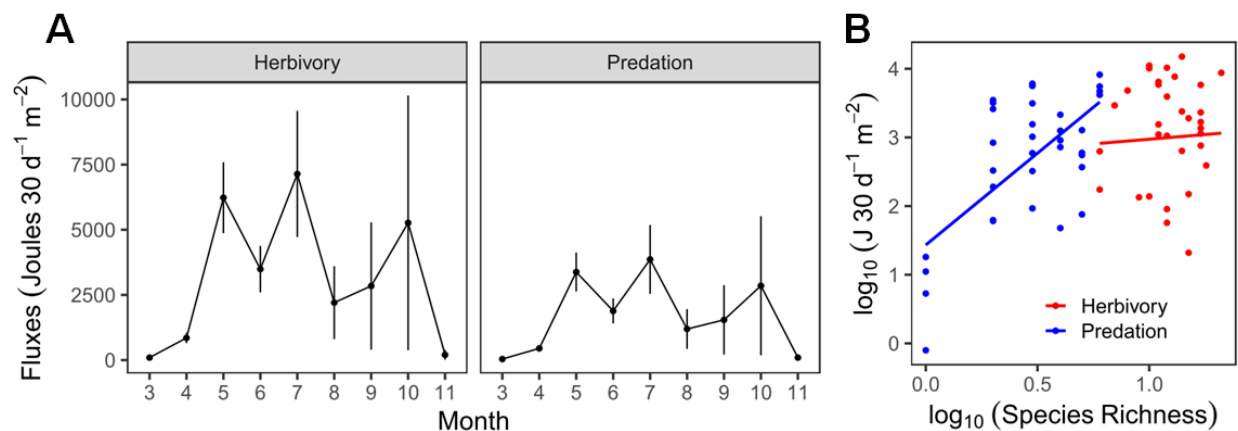


Figure 1. (A) Estimated energy fluxes for herbivores (left panel) and predators (right panel) through time (March-November) across all years of the survey in Chesapeake Bay, USA. Bars are ± 2 standard errors of the mean. **(B)** Log-transformed energy flux as a function of log-transformed consumer richness (herbivores for herbivory, red; predators for predation, blue). Lines are predicted fits from linear regression.

We show that, unsurprisingly, fluxes from both groups increase through the summer and decrease into the fall (Fig. 1A). As such, fluxes appear to be most strongly related to mean monthly temperature, but after accounting for this effect, there was a significant and strong effect of predator richness on fluxes from herbivores (Fig. 1B).

A full work-up, including data processing and a description of the statistical tests and extensions to the proposed work, can be found [here](#)

Timeline and Products

March-May 2019: Interested parties contact Smithsonian to indicate participation; Smithsonian works with partners to review site selection and survey methods.

May-August 2019: Participants conduct observational surveys at their sites.

September 2019-February 2020: Smithsonian works with partners on literature review to construct food web matrices; partners work on post-processing of epifauna samples

February-March 2020: Participants complete post-processing of epifaunal samples and submit data to Smithsonian; Smithsonian begins processing data; Smithsonian and partners begin collaborative analysis

March-May 2020: Smithsonian and partners write and submit Manuscript #1 relating estimated fluxes to biotic/abiotic conditions globally.

May-September 2020: Smithsonian and partners write and submit Manuscript #2 reporting spatial gradients in epifaunal size structure and relationship to biotic/abiotic variables (e.g., predation).

Prior to initiation of the project, we will distribute and discuss an agreement between Smithsonian and participants detailing guidelines for authorship, ethics, and responsibilities of each party associated with the project. All participants who were instrumental in conducting the proposed work (including idea generation, providing required data, and assisting in manuscript preparation and submission) will be co-authors on both publications.

The project will be led by Jon Lefcheck, Marine GEO Coordinating Scientist. Jon will also lead coordination, analysis, and writing of the manuscripts, and we anticipate that he will be primary author on these manuscripts. Smithsonian is happy to work with individuals or groups to pursue additional questions related to the data, which will be made freely available to all partners after curation (March 2020).

How to Join

Interested participants should contact the MarineGEO Coordinating Scientist, Jon Lefcheck, at LefcheckJ@si.edu. Questions, comments, or suggestions are also welcome.

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