Journal of Experimental Marine Biology and Ecology 349 (2007) 61 – 72

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Response of seagrass epiphyte loading to field manipulations of fertilization, gastropod grazing and leaf turnover rates

Bradley J. Peterson [a,*], Thomas A. Frankovich [b], Joseph C. Zieman [c]

[a] Marine Sciences Research Center, Stony Brook University, 239 Montauk Hwy, Southampton, NY 11968, United States
[b] Department of Biological Sciences, Florida International University, University Park, Miami, FL 33199, United States
[c] Department of Environmental Sciences, University of Virginia, 291 McCormick Road, P. O. Box 400123, Charlottesville, VA 22904, United States

Received 13 January 2007; received in revised form 15 March 2007; accepted 27 April 2007

Abstract

This study evaluates the bottom-up and top-down controls on epiphyte loads under low nutrient additions. Nutrients and gastropod grazers were manipulated in a field experiment conducted within a *Thalassia testudinum* meadow in Florida Bay, FL, USA. The effect of seagrass leaf turnover rate on epiphyte loading was also evaluated using novel seagrass short-shoot mimics that "grow," allowing for the manipulation of leaf turnover rates. During the summer growing season and over the course of one seagrass leaf turnover period, low-level water column nutrient additions increased total epiphyte load, epiphyte chlorophyll *a*, and epiphyte autotrophic index. *T. testudinum* leaf nutrients (N and P) and leaf productivity also increased. Epiphyte loading and *T. testudinum* shoot biomass and productivity did not respond to a 60% mean increase in gastropod abundance. Manipulations of seagrass leaf turnover rates at minimum wintertime and maximum summertime rates resulted in a 20% difference in epiphyte loading. Despite elevated grazer abundances and increased leaf turnover rates, epiphyte loads increased with nutrient addition. These results emphasize the sensitivity of *T. testudinum* and associated epiphytes to low-level nutrient addition in a nutrient-limited environment such as Florida Bay.

Keywords: Epiphytes; Florida Bay; Grazers; Leaf turnover rates; Nutrients; *Thalassia testudinum*

1. Introduction

For decades, there has been much debate whether "bottom-up" (e.g., physico-chemical resources) or "top-down" (e.g., herbivory, predation) effects control community structure. The debate is no longer about the occurrence of top-down or bottom-up control in nature. Rather, the discussion centers on the relative importance of each parameter among various ecosystems and the elucidation of the temporal and spatial variability or the relative strength of these controls within particular ecosystems (Matson and Hunter, 1992).

Seagrass meadows, and more specifically, the epiphyte communities on seagrass leaves, are ideal for investigating the roles of bottom-up and top-down control mechanisms. Examples of bottom-up controls of epiphyte loading are nutrient availability and seagrass leaf turnover rate, which determine epiphyte loads by limiting the amount of time available for accumulation. Top-down controls of epiphyte loading are achieved by grazing organisms and the higher trophic level activities, which may control the abundance of the epiphytic

* Corresponding author. Tel.: +1 631 287 8415; fax: +1 631 287 8419.
E-mail address: Bradley.Peterson@stonybrook.edu (B.J. Peterson).

0022-0981/$ - see front matter
doi:10.1016/j.jembe.2007.04.012

grazers. Consequently, the nature and quantity of epiphyte loads result from the interplay between bottom-up and top-down forces. Optimal stability and productivity of seagrass ecosystems are likely to be highly dependent on a favorable ratio of bottom-up and top-down forces in the control of epiphytes. Studies investigating the process of epiphyte accumulation on seagrass leaves have focused on fertilization (Twilley et al., 1985; Tomasko and Lapointe, 1991; Wear et al., 1999), leaf turnover rate variability (Bulthuis and Woelkerling, 1983; Borum, 1987; Frankovich and Zieman, 1994), and grazing controls (Howard, 1982; Van Montfrans et al., 1982; Hootsmans and Vermaat, 1985; Howard and Short, 1986; Jernakoff and Nielsen, 1997; Nelson, 1997).

Bulthuis and Woelkerling (1983) discussed the importance of leaf productivity as a mechanism ameliorating or exacerbating the effects of epiphyte loading. Higher rates of leaf productivity reduce the mean epiphyte load per short-shoot by producing new epiphyte-free leaf biomass. Older leaf material is subject to greater time periods for epiphyte settlement and growth; therefore, leaf longevity is a contributing factor to epiphyte loading. Due to a lack of direct measurements of leaf longevity, leaf turnover periods (biomass divided by productivity) have been used to infer the amount of time available for epiphyte accumulation (Frankovich and Zieman, 1994).

Observations of greater epiphyte loads in areas of increased nutrient availability (Cambridge and McComb, 1984; Borum, 1985; Tomasko and Lapointe, 1991) suggested significant nutrient control of epiphyte accumulations. This idea was further supported by experimental studies showing increased epiphyte loads under nutrient fertilization (Twilley et al., 1985; Tomasko and Lapointe, 1991). These experimental studies were conducted in artificial ponds, microcosms, and aquaria, and, with the exception of Tomasko and Lapointe (1991), were without grazing organisms. Later fertilization studies indicated that even under highly nutrient-enriched conditions, epiphyte loads did not change when grazers were present at or above mean natural abundances (Williams and Ruckelshaus, 1993; Lin et al., 1996; Wear et al., 1999; Heck et al., 2000). These observed relationships were predicted much earlier in a hypothetical model constructed by Orth and Van Montfrans (1984) that suggested reduced epiphyte loads would occur under the influence of grazing pressure.

Neckles et al. (1993) investigated the interactive effects of nutrient fertilization and grazing pressure on a seagrass community. In microcosm experiments, it was demonstrated that grazer effects on epiphyte loads were stronger than that of fertilization. The experiments showed also that the strength of these controls, and of the interaction between the two, varied seasonally. These bottom-up and top-down control mechanisms in a seagrass ecosystem were experimentally tested in the field by Heck et al. (2000) who manipulated nutrients and the density of pinfish (a predator of mesograzers) in expectation of finding evidence of a "trophic cascade" (Carpenter et al., 1985). While there were few nutrient effects, pinfish treatments significantly lowered *both* epiphyte biomass and mesograzer density due to their omnivorous feeding and were unable to reduce mesograzers enough to allow epiphyte accumulation (Heck et al., 2000).

The present study investigates the role of gastropod grazers under enriched and ambient nutrient conditions and the effect of seagrass leaf turnover rate on epiphyte loads in a robust seagrass community in Florida Bay. Unique because of its use of seagrass short-shoot mimics to manipulate seagrass "leaf" productivities in an experimental setting, this investigation is the first to manipulate leaf turnover rates. This has not been attempted before because the productivity of natural seagrass short-shoots cannot be manipulated without altering environmental conditions. Utilizing seagrass short-shoot mimics that "grow" allowing for the manipulation of leaf turnover rates, this investigation reports the results of two experiments quantifying the effects of nutrient availability, grazing pressure, and substratum turnover rate manipulations on epiphyte loading and *Thalassia testudinum* productivity.

2. Materials and methods

2.1. Nutrient and grazer manipulative field experiment

The experiments were conducted in eastern Rabbit Key Basin, Florida Bay, Florida U.S.A. (Fig. 1). Seasonal water temperatures and salinities in Florida Bay range from 15–32 °C and 27–43 ppt, respectively (Boyer et al., 1999). The study area is characterized by dense *T. testudinum* beds (mean annual short-shoot density = 1280 ss m^{-2}, mean above-ground biomass = 100 g m^{-2} (Frankovich and Zieman, 1994). The seagrass meadows also contain a robust epiphyte grazing community which includes gastropods (Frankovich and Zieman, 2005b), pinfish *Lagodon rhomboides* (Thayer and Chester, 1989), and caridean and penaeid shrimp (Robblee and Daniels, 2003).

The main effects of grazing pressure (+G) and nutrient manipulation (+N) on *T. testudinum* productivity and its associated epiphyte load were tested using a two-factor (fertilization and grazer addition) factorial design