Journal of Experimental Marine Biology and Ecology 448 (2013) 220–227

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Recurring nocturnal benthic emergence along the coral reef–seagrass interface in the Florida Keys National Marine Sanctuary: Evidence of a possible novel prey escape response

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ARTICLE INFO

Article history:
Received 2 January 2013
Received in revised form 19 July 2013
Accepted 22 July 2013
Available online August 15 2013

Keywords:
Behavior
Macroinvertebrate
Plankton
Predation
Settlement

ABSTRACT

Using multiple sampling techniques we documented the nightly occurrence of benthic macroinvertebrates in the water column, and quantified the intensity of their emergence from and re-settlement back to the benthos, along the seagrass–coral reef interface at two widely separated locations in the Florida Keys National Marine Sanctuary (FLKNMS). Plankton collections consistently documented dramatic increases in benthic invertebrate abundance in the water column after sunset. Subsequent collections using emergence traps showed that the density of benthic invertebrates, emerging from the seagrass habitats was great (often >1000 individuals/m^2). Settlement traps further revealed that emigrant invertebrates were dispersed by currents and did not necessarily resettle in the same intensity back to the emergence site. Our results show that the nocturnal emergence of benthic invertebrates is widespread and persistent temporally. As a result, we hypothesize that the diurnal emergence of these organisms probably reduces the intensity of food web interactions between benthic organisms and demersal reef fishes that enter nearby seagrass habitats to feed at night. These results further illustrate a need to conduct more studies after sunset in order to develop a better understanding what role diurnal shifts in predator and prey occupancy patterns play in determining the intensity of the transfer of energy and nutrients across adjacent trophic levels in marine food webs.

1. Introduction

Predator-induced nocturnal emigrations of planktonic organisms from deeper water to shallow water (in freshwater and marine ecosystems) and macroinvertebrates from the benthos into the water column of freshwater ecosystems are known to have profound impacts on the structure of freshwater and some marine planktonic communities (Kohler, 1985; Palmer et al., 1996; Sih and Wooster, 1994). Similar diurnal shifts in habitat occupancy patterns, documented in a number of unrelated studies, are displayed by a diverse array of benthic marine invertebrates, including seagrass meiofauna (Walters and Bell, 1986), bivalves (e.g. Olivier et al., 1996), gastropods (Martel and Chia, 1991), polychaetes (see e.g. references in Caspers, 1984; Gaston and Hall, 2000) and crustaceans (e.g. Blackmon and Eggleston, 2001; Forward and Rittschof, 2000; Robertson and Klumpp, 1983). Collectively, these seemingly disparate observations suggest that nocturnal invertebrate movement plays an important role in determining the structure of marine benthic communities and, by extension, the intensity of trophic interactions on a daily basis.

Based primarily on sampling conducted during daylight, we know that seagrass habitats, found along the margins of every continent except Antarctica, are sites of extraordinary macroinvertebrate abundance (e.g. Douglass et al., 2010; Valentine and Heck, 1993). Circumstances may change at night, however, as large numbers of bottom-feeding predators come to prey on organisms hiding within the structure these habitats provide (summarized in Heck and Orth, 2006). Given the emerging recognition that vulnerable organisms frequently utilize a number of behaviorally-mediated responses to reduce encounter rates with predators (e.g., Burkholder et al., 2013), and that these responses can be of equal or greater importance than density-mediated interactions in determining community structure (Preisser et al., 2005; Robertson and Klumpp, 1983; Walters and Bell, 1986), we hypothesized that the influx of nocturnally active predators triggers the nightly evacuation of seagrass habitats by vulnerable prey organisms (i.e. benthic macroinvertebrates). Supporting evidence for this hypothesis comes from a limited number of studies conducted in temperate locations which have quantitatively shown that macroinvertebrates and meiofauna can be dramatically more abundant in waters overlying seagrasses at night than during the day (i.e., Robertson and Klumpp, 1983; Walters and Bell, 1986). How widespread such nocturnal emigrations might be, especially in tropical environments where predation is known to be extraordinary (e.g. Steneck and Sala, 2005; Valentine et al., 2008), remains unknown.

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http://dx.doi.org/10.1016/j.jembe.2013.07.012

Here, we report on the findings of an initial mensurative study (sensu Hurlbert, 1984), designed to determine if there was support for our hypothesis, conducted along the seagrass–coral reef interface at two sites in the Florida Keys National Marine Sanctuary. The goals of this study were to determine if: 1) macroinvertebrate composition and abundance in the overlying water column change diurnally regardless of location or sample date; 2) the source of the emergent organisms was the reefs or seagrasses adjacent to the reefs; 3) the intensity of benthic emergence and re-settlement varies either with distance from the reef, or sample date; 4) macroinvertebrate re-settlement patterns are similar to the emergence patterns and 5) emergence intensity is related to infaunal density.

2. Methods and materials

2.1. Description of the study sites

The protective boundaries of the Florida Keys National Marine Sanctuary (FKNMS) were established in 1990 because of the importance of the largest living coral reefs in the continental United States (see Fig. 1). Within the FKNMS there are 19 Sanctuary Preservation Areas (SPAs), designated in 1997, where the removal of marine life, or damaging of existing habitat, is prohibited by law. For this reason, and the fact that these sites had been protected from fishing for over 5 years at the time this study began, we anticipated that predator assemblages would be representative of times before intense fishing pressure altered the food web structure (cf. Halpern, 2003; Halpern and Warner, 2002).

Because replication is a central tenet of the scientific method, and to ensure independence between replicate locations, we conducted this study in two, haphazardly selected, and widely separated SPAs. One was located in the upper (Key Largo Dry Rocks reef) Florida Keys reef tract and the other was located in the middle Florida Keys (Newfound Harbor reef) (Fig. 1. Key Largo Dry Rocks SPA (latitude 25°07.59, longitude 80°17.91) encloses both coral and seagrass habitats within an approximate 16-ha area (total SPA area). On the leeward side of this reef is a large contiguous seagrass bed wherein this study was conducted. The second site, Newfound Harbor SPA (Fig. 1; latitude 24° 37.00, longitude 81° 23.86), encloses similar habitats within an approximate 40-ha SPA area. Sampling at this reef was conducted in a large seagrass bed located on the northwest side of the reef.

2.2. Documentation of diurnal shifts in the abundance of benthic macroinvertebrates in the water column at Dry Rocks reef and Newfound Harbor

Replicate plankton tows were made during daylight and nighttime hours at 2 distances from the reefs to document diurnal shifts in the abundance and composition of emergent benthic macroinvertebrates in the water column at each site. Plankton tows were made, with the aid of SCUBA, between the hours of 10:00 and 11:00 am each day and 9:30–10:30 pm each night during the first and last quarter lunar phases, to control for the effects of variation in moonlight on emergence intensity (cf. Alldredge and King, 1980). These collections were replicated over three consecutive days and nights in May and September of 2002 at Key Largo Dry Rocks (hereafter referred to as Dry Rocks) and in May and

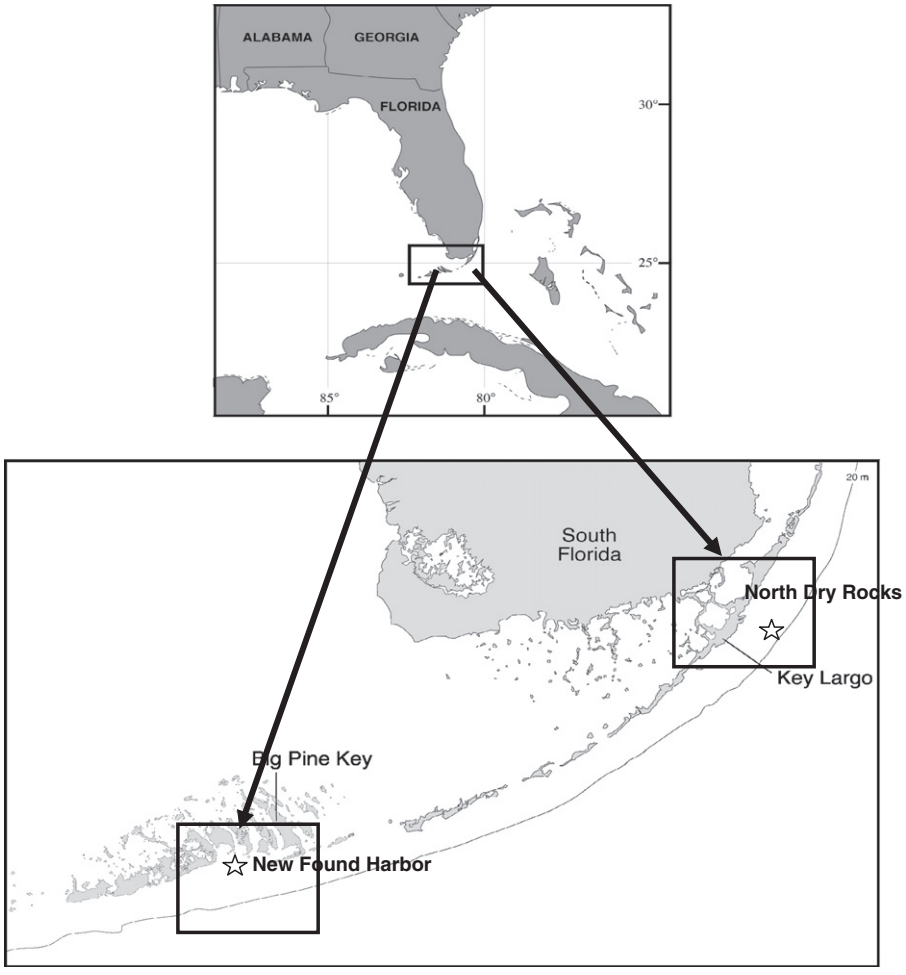

Fig. 1. Location of the two sites used in this study.