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Remote underwater video reveals grazing preferences and drift export in multispecies seagrass beds

Chen-Lu Lee [a], Yen-Hsun Huang [a], Chien-Hsun Chen [b], Hsing-Juh Lin [a,c,*]

[a] Department of Life Sciences and Research Center for Global Change Biology, National Chung Hsing University, Taichung 402, Taiwan
[b] Taiwan Ocean Research Institute, National Applied Research Laboratories, Kaohsiung 852, Taiwan
[c] Biodiversity Research Center, Academia Sinica, Taipei 115, Taiwan

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ABSTRACT

The leaf tethering method has frequently been applied in the quantification of herbivory in seagrass beds. The major limitation of this method is the inability to differentiate between biomass that is consumed versus exported as drift, particularly from thin-leaved seagrass species, due to leaf damage caused by grazers. The loss of leaf biomass to herbivory and the export of four tropical seagrass species (*Thalassia hemprichii* (TH), *Cymodocea rotundata* (CR), *Cymodocea serrulata* (CS), and *Halodule uninervis* (HU)) by drift were quantified using the tethering method with remote underwater video (RUV) in multispecies seagrass beds at Dongsha Island in the South China Sea. The diversity of grazers, and the forage preferences for each of the four seagrass species were also recorded. Most seagrass herbivory (>75%) was due to parrotfish (*Leptoscarus vaigiensis* and *Calotomus spinidens*); both juvenile and adult parrotfish preferred the fast-growing HU, but adult parrotfish apparently fed more on the more nutrient-rich TH and CS than the juveniles. The thin-leaved HU had higher relative biomass loss to grazing (74%) and drifting (13%) per day than the other species. Collectively our estimates suggest that 16% and 2% of daily production of local seagrass beds were lost due to grazing and drift export, respectively. Compared to the total loss of biomass due to grazing, the total loss due to drifting biomass was minor.

1. Introduction

Herbivory is a critical process controlling the abundance of seagrass and the transfer of energy from leaf production to higher trophic levels, but grazers generally remove a small proportion of seagrass leaf production (Chiu et al., 2013; Huang et al., 2015). Seagrasses are not preferred by many grazers because their cellulose-rich leaves are difficult to digest (Thayer et al., 1984; Duarte, 1990). Certain grazers, such as green turtles, dugongs, sea urchins, and some herbivorous fish, can directly consume seagrasses and act as important grazers in seagrass ecosystems (Heck and Valentine, 2006; Aragones et al., 2006).

Various approaches have been applied to quantify the loss of seagrass biomass to grazing. Early studies often used indirect estimation methods either by counting grazing marks on leaves, comparing leaf biomass at grazed and ungrazed sites, or conducting laboratory ingestion studies. These indirect methods tend to underestimate the actual amount of herbivory (Heck and Valentine, 2006). Direct estimation methods, such as the leaf tethering method, have been used to track grazing activities and quantify the rate of biomass loss in seagrass beds and coral reefs (Hay, 1981; Lewis and Wainwright, 1985; Kirsch et al., 2002; Tomas et al., 2005; Unsworth et al., 2007; Chiu et al., 2013). By marking ungrazed seagrasses in situ, the biomass lost to grazing can be estimated more accurately by comparing leaves pre- and post-grazing during a specific time period. Furthermore, the loss of seagrass biomass can be analyzed relative to the overall leaf production, and the size and shape of the bite marks themselves can be used to identify the predominant grazing fauna (Lee et al., 2015).

It has been argued that the tethering method is not suitable for thin-leaved seagrass species (e.g., *Halodule*, *Syringodium*, and *Zostera* spp.) as the leaves may be easily damaged and inadvertently drift during grazing (Hemminga and Nieuwenhuize, 1990; Hemminga and Duarte, 2000). First, simply quantifying the loss of leaf biomass would overestimate the amount of grazing as it is difficult to identify whether the part that is drifting was truly consumed by a grazer or is just detritus from the seagrass meadow. Second, drifting leaves could result in “missing” or unobserved bite marks (Unsworth et al., 2007; Pinna et al., 2009). Third, high intensity grazing events in seagrass beds may damage existing bite marks, making them difficult to identify. Briefly, the fate of biomass lost from the tethering method is often unknown.

Remote underwater video (RUV) is a useful tool for recording the activity of aquatic animals in situ over relatively long temporal scales, and it allows for direct observation without interference by observers. Previous studies have used RUV to record fish communities and behavior in coral reefs (Harvey et al., 2004; Jan et al., 2007; Luo et al., 2009) and to

* Corresponding author at: Department of Life Sciences and Research Center for Global Change Biology, National Chung Hsing University, Taichung 402, Taiwan.
E-mail address: hjlin@dragon.nchu.edu.tw (H.-J. Lin).

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study food selection by herbivorous fish for different macroalgae in coral reefs (Mantyka and Bellwood, 2007a, 2007b; Fox and Bellwood, 2008; Rasher et al., 2013; Loffler et al., 2015), which can reveal the preferences and functional roles of different herbivorous fishes. The main goal of the present study was to quantify the loss of seagrass biomass due to drift versus grazing, and how this varies between seagrass species in multispecies seagrass beds of Dongsha Island in the South China Sea.

2. Materials and methods

2.1. Study site

Dongsha Island (20°43′N, 116°42′E) is a 1.74-km^2 coral island on the eastern side of an atoll (Fig. 1a) in the South China Sea. Although the island is dominated by a tropical climate and water temperatures around the island average 28 °C, the intense northeast monsoons from October to early March can markedly decrease water temperatures to 19 °C. A semi-enclosed lagoon (0.64 km^2) occupies the central part of the island (Fig. 1b), and the depth of the surrounding water is less than 5 m. Around the entire island, large seagrass beds (11.85 km^2) extend from the intertidal to the subtidal zones, and the level of grazing on seagrasses was 3.6× higher in the subtidal zone than in the intertidal zone and 2.6× higher in the warm season than in the cool season (Lee et al., 2015). The subtidal zone on the northern coast of Dongsha Island was selected as the experimental site to examine the preferences of herbivores for different seagrass species and to quantify biomass drift and consumption via RUV in the summer, from June to August, of 2011.

2.2. Studied seagrass species

Four of the most abundant seagrass species were selected to represent the multispecies seagrass beds around Dongsha Island (Lin et al., 2005): *Thalassia hemprichii* (TH), *Cymodocea rotundata* (CR), *C. serrulata* (CS), and *Halodule uninervis* (HU). These species account for more than 90% of the total coverage of the seagrass beds around the island.

2.3. Studied leaf features

Seagrass leaf production was quantified using the leaf marking method (Zieman, 1974); three 10 × 10-cm quadrats for each of the seagrass species were randomly deployed in the seagrass beds and each shoot was marked through the sheath with a needle (8–25 TH shoots, 9–20 CR shoots, 6–16 CS shoots or 17–25 HU shoots in each of the respective quadrats). Damaged or withered leaves were excluded from this process, and the marked seagrass shoots were retrieved after settling for five days. The epiphytes on the leaves were scraped off with razors in the laboratory, and the newly grown leaves were dried overnight at 60 °C and weighed to calculate the leaf production per shoot per day. For comparison across species, the specific growth rate was calculated by dividing leaf production per shoot by leaf biomass per shoot (Cebrián and Duarte, 1998), and the total leaf production per unit area was calculated by summing the average leaf production of the different seagrass species per unit area of the seagrass beds.

To determine the nutrient content of each seagrass species, three shoots per species during the study period were collected, and the epiphytes on the leaves were carefully scraped off with razors. The recovered seagrass leaves were dried for 48 h at 60 °C and ground to a fine powder. An Elementar Vario EL III CHN-O-S-Rapid Analyzer (Elementar Analysensysteme GmbH Co., Hanau, Germany) was used to determine the carbon (C) and nitrogen (N) content. The leaf samples were further analyzed to determine crude fiber content using the gravimetric method. The anthrone method was also used to determine the total sugar and starch content of the seagrass leaves (Yemm and Willis, 1954).

2.4. Seagrass tethering experiments

The tethering quadrat method of a previous study (Lee et al., 2015) was modified to quantify herbivory in the seagrass beds. Only the ungrazed shoots of four seagrass species were collected; damaged, withered, or small shoots (shoot height < 3 cm) were excluded from the study. Before deployment, epiphytes were carefully removed using a razor blade. All of the leaves on the ungrazed shoots were recorded with a digital camera, and the leaf area was analyzed using Image-Pro Plus software (Media Cybernetics Inc., Silver Springs, MD, version 4.5) following the methods of Unsworth et al. (2007).

Five quadrats (50 × 50 cm each) were deployed as the tethering plots, and each plot was divided into 25 10 × 10-cm squares (Fig. 2). Each of the 4 seagrass species was planted into 6 squares, which were randomly selected within each plot. In total, seagrass shoots were planted in 24 squares (4 seagrass species × 6 squares) of each plot, and the central square in each plot was used to anchor the plot in the sediment using plastic ropes attached to wire stakes. The combination of these squares constituted the main "tethering plot" for the tethering experiment. The density of each of the seagrass species within each plot was the same as the natural density in the seagrass beds described for the leaf marking method. The tethering plots were set in bare sand at a distance of 3–8 m from the edge of seagrass beds dominated by the four target species. All seagrass shoots were left in situ and retrieved after one day of deployment, and this procedure was repeated for two additional days ($n = 3$). Each deployment was done with a new random distribution of the 4 species among the squares, and in a new place at least 5 m away from the previous plot. In total, we created 15 replicates (5 quadrats × 3 deployments) of the seagrass beds during the study

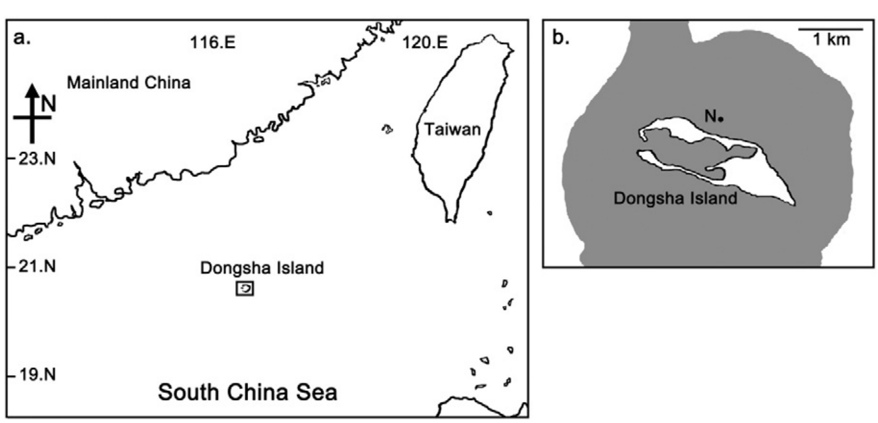

Fig. 1. Maps showing Dongsha Island's location within the South China Sea (a) and the seagrass beds surrounding Dongsha Island (shaded area) and the location of experimental site (b).