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Accelerated Decomposition of *Caulerpa paspaloides* Due to Influence of Grazing by *Oxynoe azuropunctata*

Bradley J. Peterson
Dauphin Island Sea Lab

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Marine Mammal Research Program, Texas
A&M University at Galveston.

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- D. FERTL, A. J. SCHIRO, S. COLLIER, AND G. A. J. WORTHY, (DF, AJS, SC) *Marine Mammal Research Program, Texas A&M University, 4700 Avenue U, Building 303, Galveston, Texas 77551; and (GAJW) Physiological Ecology and Bioenergetics Laboratory, Texas A&M University, 5001 Avenue U, Suite 105, Galveston, Texas 77551. Present address (DF): Minerals Management Service, U.S. Dept. of the Interior, 1201 Elmwood Park Boulevard, New Orleans, Louisiana 70123.*

ACCELERATED DECOMPOSITION OF *CAULERPA PASPALOIDES* DUE TO INFLUENCE OF GRAZING BY *OXYNOE AZUROPUNCTATA*.—Over the past two decades research on the decomposition of plant matter has revealed the importance of plant detritus to aquatic ecosystems (Knauer and Ayers, 1977; Thayer et al., 1977; Godshalk and Wetzel, 1978). These studies investigated primarily decomposition of vascular macrophytes, such as seagrasses, marsh grasses, and mangroves, whose biomass is generally not grazed directly but instead consumed as detritus (Odum et al., 1972; Mann, 1973). Few quantitative analyses of macroalgal decomposition have been performed. Presumably, this is because macroalgae are heavily consumed by herbivores, whereas vascular plants are consumed more frequently by detritivores (Paine and Vadas, 1969; Hunter, 1976; Tenore, 1977; Hanson, 1982; Rice, 1982; Luning, 1990; Mathieson and Nienhuis, 1991).

However, marine rhizophytic siphonous green macroalgae (Order Caulerpales) have evolved mechanisms to escape or deter herbivores. These algae use either calcification or toxicity, making them logical candidates for studies of decomposition and detritus formation. In addition, these algae, which are often the dominant macroalgae of tropical soft-bottom environments, have the ability to grow from unstable sediments by root-like rhizoids that anchor the plants and stabilize sediments (Williams, 1984). Consequently, rhizophytic macroalgae have an important ecological role as an early colonizing species of seagrass beds (Den Hartog, 1977). Several authors suggest that nitrogen accumulation in the sediments is the rate-limiting step in seagrass bed succession (McRoy and Lloyd, 1981; Kenworthy et al., 1982). Nutrient cycling in seagrass beds is characterized by detritus decomposition processes (Klug, 1980). Therefore, an important input to the nutrient pool accumulating in the sediments may be from decomposition of rhizophytic algae.

Despite their adaptations, siphonous green macroalgae are consumed by a few opisthobranch molluscs (Taylor, 1967; Trench, 1973). These ascoglossans demonstrate great feeding specificity (Kay, 1968). For example, *Oxynoe azuropunctata* shows extreme trophic specificity, exhibiting near exclusive food preference for the siphonales algae, *Caulerpa paspaloides*. The purpose of this experiment was to determine

Fig. 1. Percent biomass of *Caulerpa paspaloides* remaining as a function of time. Samples with *Oxynoe azuropunctata* present or absent are compared.

if the grazing influence of *O. azuropunctata* significantly increases the decomposition rates of *C. paspaloides*.

Methods.—Both *Oxynoe azuropunctata* and *Caulerpa paspaloides* were collected at Lake Surprise, Key Largo, FL. Lake Surprise is a shallow-water (0.5–1.5 m) tidal basin with sediments composed of organic detritus, calcareous silt, and shell chaff (Clark and DeFreese, 1987). Salinity varies between 35 and 37 ppt and temperatures have been recorded as low as 12 C in Feb. and as high as 35 C in Sept. (Jensen and Clark, 1983). Large quantities of detrital organic material are added to sediments by well-established assemblages of siphonlean algae and *Thalassia testudinum*. *Caulerpa paspaloides* dominates in discrete communities between the mangrove fringes and *Thalassia* beds.

Litter bag experiment: Freshly collected *C. paspaloides* weighing 20 g wet weight, with epiphytes removed, was rinsed briefly with reagent-grade water and placed in numbered 7 × 18 cm litter bags of 0.3-mm nylon mesh. Control treatments contained only *C. paspaloides*; experimental treatments also contained two individuals of *O. azuropunctata*. Experimental densities were chosen to reflect those occurring naturally in Lake Surprise. Four replicate series of three bags per treatment were anchored and suspended in the water column in a 200-gallon flow-through seawater system.

One replicate series of litter bags was sampled at 48-hr intervals for 10 d, starting on day

4. Once samples of *C. paspaloides* were collected, the specimens of *O. azuropunctata* and any egg masses were removed, and final shell lengths and dry weights were determined. Control and experimental litter bags were dried to constant weight. The initial algae dry weights were derived from wet weight/dry weight regression curves and used to determine the percent change in dry weight of *C. paspaloides*.

Results.—One-half of the original plant matter in the control bags was decomposed after 10 d. Experimental treatment bags exhibited significantly less percent biomass of *Caulerpa* than the control bags on day 6 (Kruskal-Wallis one-way ANOVA on ranks, $P = 0.02$) and day 8 (Kruskal-Wallis one-way ANOVA on ranks, $P = 0.02$) (Fig. 1). More than 60% of the plant matter was decomposed by day 6 and more than 90% was decomposed by day 8. Data after day 8 were discarded due to the death of all grazing organisms. Qualitatively, after day 4, the appearance of the algae in the control treatments was distinctive from the algae in the experimental treatments. The plant matter in experimental bags lost green pigmentation and disintegrated into a mulch, while that in the control bags remained pigmented and displayed little visibly detectable deterioration from day 0 to day 10.

Discussion.—If nutrient accumulation is the rate-limiting step in seagrass bed succession, then the role of marine rhizophytic siphonous green macroalgae and their rapid decomposi-

tion is significant in their position as early colonizers of seagrass beds. When *Caulerpa* begins to decompose *in situ*, the thallus and rhizoids remain intact after death. This allows approximately 20% of *Caulerpa*'s biomass to be incorporated into the sediments (Williams, 1984). Therefore, the below-ground biomass of *Caulerpa* may represent an important source of nutrient input to the sediments.

In this experiment, *Caulerpa* decomposed rapidly, especially in comparison to rates reported for vascular macrophytes (Heald and Odum, 1970; Harrison and Mann, 1975; Hunter, 1976; Godshalk and Wetzel, 1978). Even in the absence of grazing, one-half of the initial *Caulerpa* decomposed in 8 d. Williams (1984) found that rates of decomposition of *Caulerpa* declined after the first 14 d and that 25% of plant matter remained after 28 d. By contrast, *Thalassia testudinum*, a late-stage seagrass species in the Caribbean, loses an equal amount of matter only after 120–180 d (Odum et al., 1972).

Numerous studies over the past two decades have revealed the importance of herbivory in regulating the structure and function of marine algal communities (Ogden and Lobel, 1978; Birkeland et al., 1985; Morrison, 1988; Horn 1989). Herbivores reduce algal standing crops and areal rates of productivity and alter the composition of the community. As a result, marine plants have evolved several mechanisms to escape, tolerate, or deter herbivores (Hay and Fenical, 1988). To minimize the effect of grazing, *Caulerpa* has evolved the production of unpalatable chemicals (Lobban et al., 1985). *Caulerpa*'s chemical defense, however, does not entirely remove the influence of grazers. Virtually all siphonaceous algae inhabiting the coastal waters of Florida support at least one ascoglossan species (Jensen, 1980).

In this study, the influence of grazing on *Caulerpa* significantly increased its decomposition rate. The grazing influence of *Oxynoe* accelerated the decomposition rate of *Caulerpa* by a factor of four. The fourfold acceleration in decomposition rates of *Caulerpa* resulting from grazers may significantly influence seagrass bed succession. Assuming the early colonizer seagrass species *Halodule wrightii* decomposes as slowly as other vascular macrophytes, *Caulerpa*'s decomposition would supply nutrients to the sediments much more rapidly. Therefore, where present, ascoglossans may act as catalysts for seagrass succession by accelerating sediment nutrient accumulation. Based on this study, the logical future direction is to conduct a field manipulation, testing whether

the addition of ascoglossans to stands of rhizophytic macroalgae increases the sediment nutrient content.

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- BRADLEY J. PETERSON, *University of South Alabama, Dauphin Island Sea Lab, P.O. Box 369–370, Dauphin Island, Alabama 36528. Present address: Department of Biological Sciences, Florida International University, Miami, Florida 33199.*