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Lucinid Clam Influence on the Biogeochemistry of the Seagrass *Thalassia testudinum* Sediments

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ABSTRACT: Lucinid bivalves dominate the infauna of tropical seagrass sediments. While the effect of seagrass on lucinids has been studied, the reverse effect has largely been ignored. Lucinids can alter porewater chemistry (i.e., increase porewater nutrients by suspension feeding and decrease porewater sulfides by oxygen introduction and bacterial oxidation), which can potentially change seagrass productivity and growth morphology. To observe correlations between porewater chemistry and lucinid presence, a field survey and laboratory microcosm experiment were conducted. Survey sampling sites with lucinids had significantly lower sulfide and higher ammonium concentrations than sampling sites without lucinids. There was no difference in phosphate concentration among sampling sites. Both lucinid species used in the microcosm experiment (*Ctena orbiculata* and *Lucinesca nassula*) significantly lowered sulfide concentrations in the sediment porewater. Microcosm and field survey results were incorporated into a sulfide budget. In seagrass sediments, lucinids remove 2–16% of the total sulfide produced. Sulfide is a major stressor to both plants and animals in Florida Bay sediments; this removal may be important to maintaining seagrass productivity and health. Oxygen introduction into sediments by *C. orbiculata* was estimated in a dye experiment. *C. orbiculata* were added to small tubes containing sieved mud and incubated in a bath of seawater with a Rhodamine WT. Rhodamine WT accumulation in the sediment was measured. A first order estimate showed that oxygen introduction can account for less than 5% of *C. orbiculata* sulfide removal.

Introduction

Bivalves belonging to the family Lucinidae are the most abundant and diverse of the infaunal mollusks living within the sediments of tropical seagrass meadows. These sediments are also the primary habitat for shallow water lucinid bivalves (Moore 1968; Barnes 1996; Jackson 1972, 1973). The association between lucinid bivalves and seagrasses is strong enough that the shells of dead lucinid bivalves are used to age seagrass meadows and to locate relic seagrass meadows (Barnes 1996; Jackson 1972, 1973; Bretsky 1976, 1978).

Lucinids are unique bivalves. Compared to other bivalves, they have unusual gills, mantile placations, reduced labial palps, and lack an inhalant siphon. They filter the water column by building hollow tubes to the sediment–water interface and using ciliary currents to bring the water into their bodies (Allen 1958; Jackson 1972; Taylor and Glover 2000). Lucinids also have a symbiosis. All species of lucinids analyzed to date harbor chemoautotrophic-endosymbiotic bacteria living within their gills. While each lucinid species harbors only one bacterial species, there is a diversity of bacterial species among lucinids. All bacteria found in lucinid bivalves are confined to the gamma subdivision of Protobacteria (Durand and Gros 1996; Durand et al. 1996). These bacteria enzymatically oxidize sulfides, which are found in abundance in the sediment, to provide energy that is used to fix dissolved carbon dioxide into sugars. Lucinids have a reduced filtering capacity and a reduced digestive system, so these sugars are an important food source for not only the bacteria but also for the bivalve (Distel and Felbeck 1987; Cary et al. 1989; Le Pennec et al. 1995; Talyor and Glover 2000).

The positive influence of seagrass on lucinid bivalves is often credited with the close association of the two (Jackson 1972, 1973; Bretsky 1976, 1978; Barnes 1996). Seagrasses provide an ideal habitat for lucinid bivalves. The dense root and rhizome mat created by the grass protects the bivalves from encountering predators (Barnes 1996; Barnes and Hickman 1999; Jackson 1972). For most relatively immobile mollusks, seagrass sediments are harsh environments, because they are relatively reduced and rich in sulfide, which is toxic to most animals (Hemminga and Duarte 2001). Lucinids, unlike most animals, thrive in sulfide rich sediments, so competition from other bivalves is reduced (Cavanaugh 1983; Barnes 1996; Barnes and Hickman 1999). The goal of this investigation is to demonstrate that not only do seagrasses positively affect lucinids, but these bivalves can potentially positively affect seagrasses by altering porewater biogeochemistry.

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Seagrass vegetated sediments typically have high sulfide concentrations. Sulfides accumulate as a standing stock in seagrass vegetated sediments as an end product of microbial decomposition (Fenchel and Riedel 1970; Fenchel et al. 1998) and exit the system by reaction with oxygen to form sulfate ions, by bonding to hydrogen ions and diffusing into the water column as a gas, or by adsorbing to heavy metals such as iron or manganese. The latter reaction is not significant because tropical carbonate sediments, such as those in Florida Bay, tend to be very low in these heavy metals (Carlson et al. 1994; Duarte et al. 1995; Erskine and Koch 2000; Chambers et al. 2001).

Lucinids can further increase the rate of sulfide removal by two methods: bacterial oxidation and oxygen introduction. Since the bacteria living within the gills of the bivalve enzymatically oxidize sulfide to elemental sulfur or to sulfate in order to create sugars (Distel and Feldbeck 1987), they remove a finite amount of the available sulfide. Lucinids can also reduce sulfide levels by oxygen introduction. Sulfides and oxygen cannot coexist for very long. Oxygen will spontaneously react with sulfide to produce sulfate until one of those reactants is no longer available. Paradoxically, these bivalves require both oxygen and sulfides to survive. Lucinids obtain oxygen from the water column using ciliary currents to transport water through hollow tubes (Allen 1958; Jackson 1972). Not all oxygen brought into the tubes reaches the bivalves' body. Bacterial symbionts consume oxygen for sulfide oxidation (Duplessis et al. 2004), and some oxygen will naturally diffuse through the tube walls into the sediments, where it may encounter and react with sulfide. Oxygen introduced by bivalve activity can also be consumed in reactions such as mineralization or nitrification.

The process of bringing water column water into the lucinid's body is also used as a feeding mechanism. While the bivalves get sugars from their endosymbiotic bacteria, they still require other nutrition, which they obtain from organic material suspended in the water column (i.e., suspension feeding; Distel and Felbeck 1987). Other suspension feeders living in seagrass meadows have been shown to increase nutrients in the interstitial water of the sediments (Reusch et al. 1994; Peterson and Heck 1999, 2001a,b). Suspension feeding bivalves transfer planktonic production in the water column to the sediments by means of fecal and pseudofecal production. Nutrient pools in the sediment can be increased by means of bivalve activity.

These biochemical changes (i.e., increased nutrients and decreased sulfides) have the potential to increase seagrass productivity. Seagrasses tend to be nutrient limited, and in Florida Bay, phosphorous is typically the limiting nutrient (Fourqurean et al. 1992). *Thalassia testudinum*, the most abundant seagrass in Florida Bay, is more efficient at gaining nutrients from the sediment porewater as opposed to the water column (Zieman 1982; McGlathery 2001). An addition of these nutrients or a transfer of these nutrients from the water column to the sediments should stimulate seagrass productivity. This increase should allow the seagrasses to allocate more resources to aboveground as opposed to belowground production, increasing the aboveground to belowground biomass (Hemminga and Duarte 2001).

Sulfide is toxic to seagrasses and other plants (Carlson et al. 1994; Koch and Erskine 2001; Borum et al. 2005). Seagrasses have mechanisms for surviving in sulfide rich marine sediments. An end product of photosynthesis is oxygen gas, which can diffuse from the leaves through lacunae to the roots. Some of that oxygen escapes through the roots into the sediments where it reacts with and reduces the amount of toxic sulfide in close proximity to the seagrass tissue (Pederson et al. 1998). Although seagrasses have this mechanism, sulfide at high but natural levels, can reduce photosynthetic capacity and even induce die-off (Goodman et al. 1995; Koch and Erskine 2001; Pederson et al. 2003). Reducing the ambient sulfide levels further by means of bivalve activity reduces this toxic stress on the seagrasses. Lower sulfide levels also allow the seagrass to allocate more resources to aboveground as opposed to belowground biomass, since they do not need excess belowground surface areas from which to introduce oxygen (Fig. 1).

Study Site

Florida Bay is a shallow, triangular embayment of approximately 2,000 km^2. It is bordered by the southern tip of the Florida peninsula on the north, by the Florida Keys on the south and east, and is open to the Gulf of Mexico on the west. The bay contains numerous mangrove islands and meandering mud banks subdividing the bay into many distinct basins. The sediment typically consists of carbonate muds. The most common benthic cover is seagrass. Three species of seagrasses are found in Florida Bay: *Halodule wrightii*, *Syringodium filiforme*, and *T. testudinum*. *T. testudinum* is the most abundant (Zieman 1982).

Sunset Cove is located in the northeastern part of Florida Bay very close to the main line of the keys, adjacent to Key Largo (25°05′30″N, 80°27′20″W). Maximum water depth is no more than 2 m. Sunset Cove is characterized by patches of hard bottom and patches of relatively dense *T. testudinum* (742 shoots m^{-2}) with low densities of *H. wrightii* (95 shoots

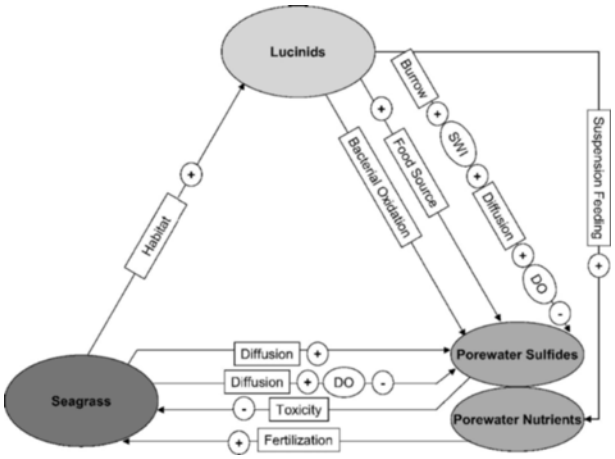

Fig. 1. Conceptual model describing the interactions in seagrass vegetated sediments. The rectangular boxes describe processes. The ovals describe standing stocks. Pluses and minuses describe increases or decreases, respectively, in the standing stocks symbol following. The model describes the following interactions: the presence of seagrass increases lucinid survival, which increases porewater nutrients and decreases porewater sulfides. Both increased nutrients and decreased sulfides increase the standing stock of seagrass. The following is an example of how to read this diagram using the outside connection between lucinids and porewater sulfides. Lucinid bivalves create burrows, which increase the sediment water interface. The increase sediment water interface allows for a greater diffusion and a larger introduction of dissolved oxygen into the sediments. Dissolved oxygen will react with porewater sulfides and decrease the ambient pool. DO = dissolved oxygen; SWI = sediment water interface.

m^{-2}) in a very thin sediment layer (10–50 cm; Reynolds unpublished data).

Rabbit Key Basin is located within the western central portion of Florida Bay (24°58′63″N, 80°50′36″W). It is further from inhabited land influence than Sunset Cove. Maximum water depth is again no more than 2 m. The bottom is carpeted by dense *T. testudinum* (1146 shoots m^{-2}; Reynolds unpublished data).

Methods

Survey

Approximately biweekly, during the spring and summer of 2003 (March until August), at both Sunset Cove and Rabbit Key Basin, twelve 20-ml porewater samples were collected at a depth of 15 cm using a sampling probe (Berg and McGlathery 2001). Each porewater sampling site was marked with a numbered flag. The sample was filtered through a 0.45-μm Millipore filter, and one 5-ml subsample was fixed with 5-ml zinc acetate for sulfide analysis. Samples were transported on ice to laboratory facilities where they were analyzed for sulfide, ammonium, and phosphate concentrations. Sulfide concentration was analyzed using the method of Cline (1969). Sulfides were converted to zinc sulfide with zinc acetate. The zinc sulfide then reacted with a dimethyl solution producing a blue color, which was analyzed spectrophotometrically. Ammonium concentration was also determined spectrophotometrically using a method based on the formation of a blue color (indophenol) by the reaction of hypochlorite and phenol in the presence of ammonium (Strickland and Parsons 1972). Phosphate was determined spectrophotometrically by reacting a composite reagent containing molybdic acid and ascorbic acid, and trivalent antimony reacts with phosphate to produce a blue color (Stainton et al. 1974). Directly around each flag-marked porewater sampling site, one core (diameter = 7.6 cm, depth = bedrock or 50 cm maximum) was taken. The 12 cores were sieved in 5-cm segments through a 1-mm mesh. All seagrass tissue was discarded, but all live bivalves were kept, identified, and measured.

Once during the sampling period, three smaller sediment cores were taken with a 60 cc syringe. These sediment samples were weighed, then dried at 60°C, and reweighed. These data were used to calculate sediment water content. The water content of the sediment was determined as the mass of water lost by drying divided by the mass of the total wet sample.

Sulfide Microcosm Experiment

Fifteen tubes (diameter = 3.8 cm, depth = 10 cm, capped at one end) were filled with coarsely sieved (1 cm) sediment from Rabbit Key Basin. These tubes were placed into a tank of seawater continuously bubbled with air and maintained at a temperature of approximately 28°C using aquarium heaters. After a settling period of at least 24 h, the tubes were carefully removed from the water bath, and a 2-ml sample of the porewater was taken from a depth of 10 cm using a sampling probe (Berg and McGlathery 2000). Removing the tubes assured that water column water was not introduced into the sample. In the lab, samples were filtered through a 0.45-μm Millipore filter and analyzed for sulfides using the method of Cline (1969). Following initial sampling, the tubes were carefully returned to the seawater bath. The tubes were randomly assigned to one of three treatment groups: control, *Ctena orbiculata*, or *Lucinesca nassula*. Control tubes were not manipulated. One live *C. orbiculata* or one live *L. nassula* was added to their respective tubes and allowed to burrow. After an incubation period of 3 d, porewater was sampled and analyzed for sulfide concentration using the method described previously. The sediment used in the experiment was analyzed for water content.

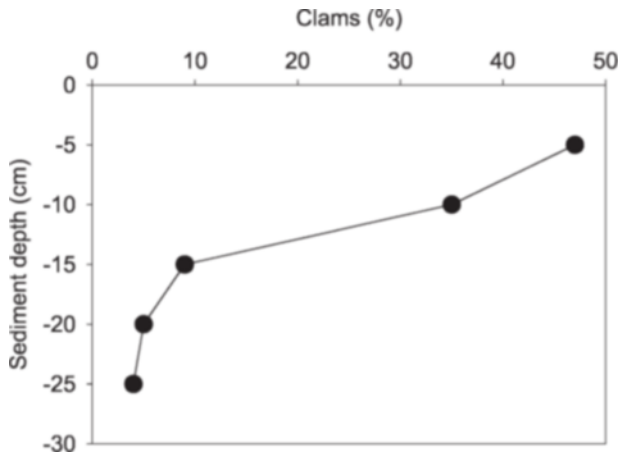

Fig. 2. Lucinid depth distribution. The × axis describes the percentage of lucinids (*Ctena orbiculata* and *Lucinesca nassula*) found at the sediment depth represented on the y axis. n = 75.

The change in sulfide concentration was calculated as the initial sulfide concentration of each tube subtracted from the final concentration. The mean rate of concentration change was calculated as the quotient of the mean change and the incubation period. The actual consumption rate of each lucinid bivalve was determined by subtracting the mean sulfide change in the control tubes from the mean change in the lucinid experiment tubes.

The effect of the bivalves on a 1 × 1 × 0.15 m block of natural sediment was estimated for the two surveyed basins: Rabbit Key Basin and Sunset Cove. The depth of 15 cm was chosen because 90% of the lucinids found were at that depth or shallower (Fig. 2). This estimate was based on several assumptions. Sulfide production was assumed to be spatially homogenous. Lucinid consumption rates of sulfide were assumed to be constant with time and with various conditions (i.e., various water column nutrient levels, various porewater sulfide levels) and similar to those consumption rates measured in the microcosm experiment. To put these rates in perspective they were compared with published rates of sulfide production through sulfate reduction (Pollard and Moriarty 1991; Holmer and Nielson 1997).

Oxygen Transport Dye Experiment

Eight tubes (diameter = 2.5 cm, depth = 15 cm, capped at one end) were filled with coarsely sieved (1 cm) sediment. These tubes were placed in a tub containing seawater continuously bubbled with air and maintained at a temperature of approximately 28°C using aquarium heaters. After a settling period of approximately 24 h, the tubes were randomly assigned to one of two treatment groups: control or *C. orbiculata*. Controls were not manipulated. In the *C. orbiculata* tubes, one live *C. orbiculata* was placed on the surface and allowed to burrow and acclimate for 24 h. Concentrated Rhodamine WT dye (200 ml) was added to the water column, resulting in a water column with a concentration of 3% Rhodamine WT.

After 5 d of incubation, the tubes were removed, covered with parafilm, and frozen. Once completely frozen, the tubes were segmented into 2-cm sections. The sediment from each section was allowed to thaw and placed into a centrifuge tube and centrifuged on the highest setting for 10 min. The resulting supernatant was pulled off with a syringe, filtered through a 0.45-µm Millipore filter, and analyzed spectrophotometrically for Rhodamine WT concentration.

The amount of Rhodamine WT introduced to the sediment by one *C. orbiculata* was determined by subtracting the bulk amount of Rhodamine WT found in the control tubes from the bulk amount of Rhodamine WT found in the lucinid tubes. The bulk amount of Rhodamine WT was calculated by multiplying the measured porewater concentration of dye by the volume of porewater present. The amount of water column intrusion due to the bivalve activity was determined by dividing the amount of Rhodamine WT added to the sediments by the experimental water column concentration. Results were depth integrated to estimate a total amount of introduced water due to one bivalve.

Using the assumption that lucinids react similarly in the natural environment, the results were scaled up to a 1-m^2 area within a natural basin (Sunset Cove) in Florida Bay. Depth of influence was estimated to 15 cm. This assumption was supported by the field survey data as well as the dye experiment data. The total water column intrusion was determined by multiplying the water column intrusion of one experimental *C. orbiculata* by the density of *C. orbiculata* in Sunset Cove determined in the field survey. The amount of oxygen introduction was determined by multiplying the average water column dissolved oxygen concentration by the volume of water column water introduced. It was assumed that all of this oxygen chemically reacted with the sulfide in the sediment, and the amount of sulfide used in this reaction was determined stoichiometrically. Since the sediment characteristics of Sunset Cove are known, a concentration change was also determined.

Results

Survey

In Sunset Cove, the lucinid population is dominated by *C. orbiculata* (80 m^{-2} SE = 13, n = 83). In Rabbit Key Basin, two species of lucinid bivalves

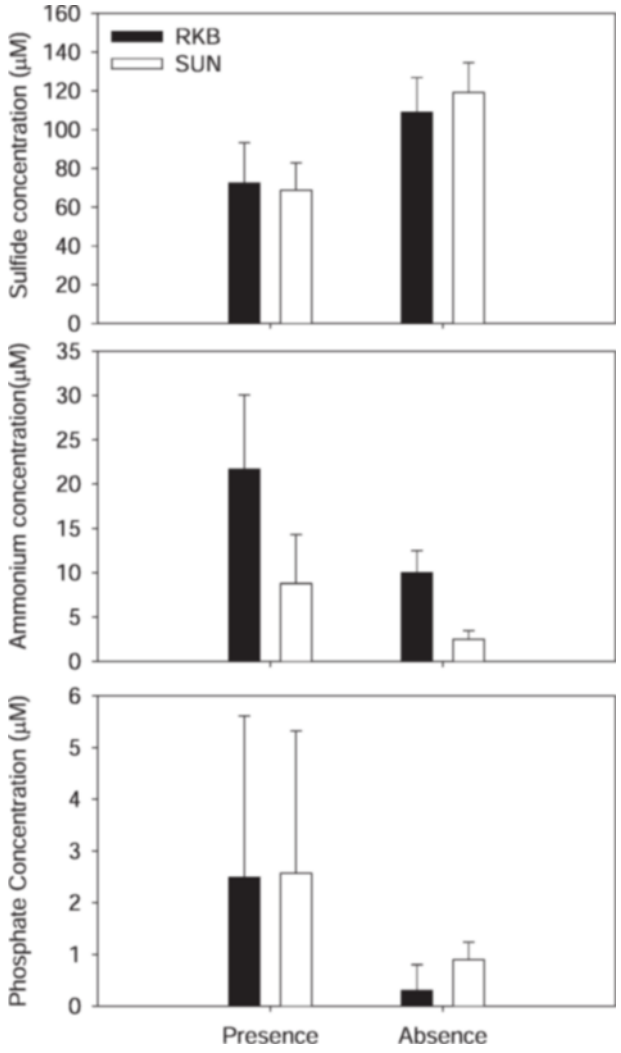

Fig. 3. Lucinid influence on porewater: Survey results. The bar graphs display the results from a 2003 survey of two Florida Bay basins: Rabbit Key Basin and Sunset Cove. The bars marked presence reflect porewater concentrations in cores that contained lucinids, and the bars marked absence reflect porewater concentrations in cores without lucinids. Error bars represent standard errors.

dominate the population: *C. orbiculata* (25 m^{-2} SE = 12, n = 56) and *L. nassula* (30 m^{-2} SE = 10, n = 56). A third species, *Anodontia alba*, is found rarely. All lucinid bivalves were found between 0 and 25 cm sediment depth, with most individuals burrowing to a depth of 5 to 10 cm (Fig. 2).

The difference in porewater sulfide, ammonium, and phosphate concentrations between cores where bivalves were found or not found was analyzed using a *t*-test. Sulfide concentration was lower in cores with Lucinids as opposed to cores without lucinids (Sunset Cove $p < 0.05$; Rabbit Key Basin $p < 0.1$). Ammonium concentration was higher in cores with

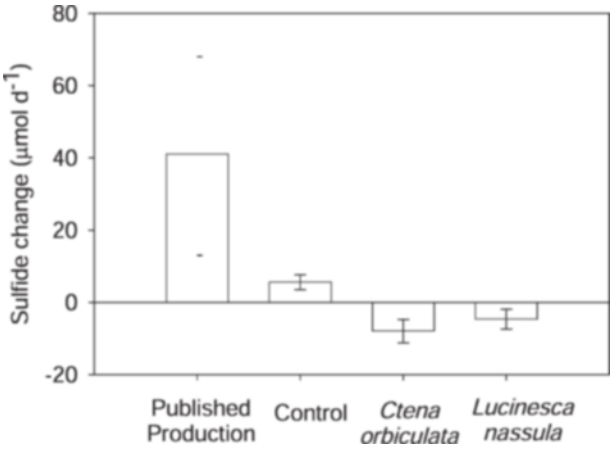

Fig. 4. Lucinid influence on porewater sulfide concentration: Microcosm experiment results. The chart describes the sulfide change in small tubes incubated under one of the following treatments: control, +1 *Ctena orbiculata*, or +1 *Lucinesca nassula*. The first bar represents published sulfide production rates for *Thalassia testudinum* sediments scaled down to the size of the experimental tubes. Decreases in both lucinid tubes are significantly different from the control increases, but the changes in the *C. orbiculata* and *L. nassula* tubes were not different from each other. The error bars represent standard error. The symbols around the published sulfide production bar represent the range of values.

lucinids as opposed to cores without lucinids (Sunset Cove and Rabbit Key Basin $p < 0.1$), and there was no correlation between lucinid bivalve presence and phosphate concentration (Fig. 3).

Sulfide Mesocosm Experiment

Sulfide concentration increased in the experimental control tubes, while the sulfide concentration in each of the lucinid tubes decreased (Fig. 4). Decreases in both lucinid tubes are significantly different from control tubes ($p < 0.05$), but the changes in the *C. orbiculata* and *L. nassula* tubes were not different from one another. The sediment volume of the experimental tubes was 115 ml. Using a sediment wet density of 1.4 g ml^{-1} (Teeter 2002), the weight of the sediment was calculated to be 215 g, and using the water content of the sediment (70%, SE = 0.5, n = 4), the weight of the porewater was 149 g. Using a seawater density of 1.02 g ml^{-1}, the volume of the porewater in each tube was 137 ml. Molar amount of change was determined by multiplying the concentration change by the volume of porewater. Consumption rate was calculated as the increase in control tubes subtracted from the decrease in the *C. orbiculata* and the *L. nassula* tubes. Mean daily consumption of sulfide for one *C. orbiculata* was 23 μmol. Mean daily consumption for one *L. nassula* was 18 μmol.

In Sunset Cove (*C. orbiculata* density of 80 m^{-2}) total lucinid consumption is 1.9 mmol m^{-2} d^{-1}. In

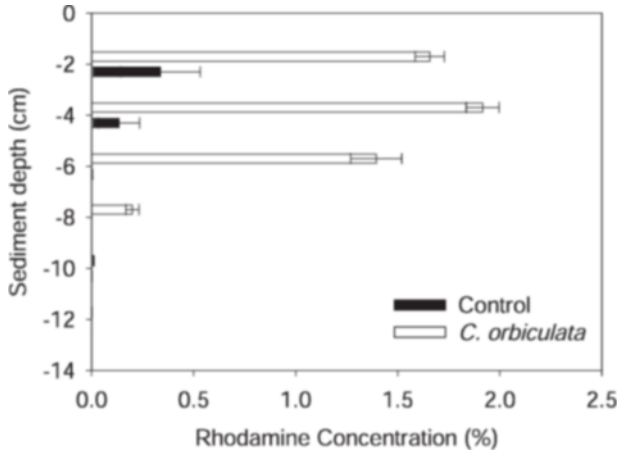

Fig. 5. Porewater and water column interactions via *Ctena orbiculata*: Dye experiment results. The chart describes the Rhodamine WT concentration change of tubes containing either 0 or 1 *C. orbiculata*. All tubes were incubated for 5 d in a bath of seawater with a 3% Rhodamine WT concentration. At a depth of 9 cm, the difference between the control and *C. orbiculata* tubes becomes insignificant. Error bars represent standard error.

Rabbit Key Basin (*C. orbiculata* density 26 m^{-2} and *L. nassula* density 28 m^{-2}) total lucinid consumption is 1.1 mmol m^{-2} d^{-1}. The range of sulfate reduction, determined from a literature review, was 12–60 mmol m^{-2} d^{-1} (Pollard and Moriarty 1991; Holmer and Nielson 1997). These sulfide production rates were used for both Sunset Cove and Rabbit Key Basin (ambient sulfide concentration 102 and 104 μM, respectively) and resulted in an estimate of 11–59 mmol m^{-2} d^{-1} of sulfide that is removed from the system. That means that sulfide removal due to lucinid activity is between 2% and 16% of the total sulfide removal in both systems.

Oxygen Transport Dye Experiment

In the experiment, one *C. orbiculata* introduced 0.7 μl of Rhodamine WT per day. Since the Rhodamine WT concentration in the water column was 2.8%, bivalves introduced water at a rate of 2.3 ml d^{-1} (Fig. 5).

In a 1 × 1 × 0.12 m block of Sunset Cove sediment (*C. orbiculata* density = 80 individuals m^{-2}), bivalves introduce 180 ml of water into the sediments. Assuming an average dissolved oxygen concentration of 6.0 mg l^{-1}, lucinid activity in Sunset Cove can add an increase in dissolved oxygen of 35 μmol d^{-1}. Using natural Sunset Cove sediment characteristics, that results in an 0.21-μM increase in sediment dissolved oxygen per day. Assuming that all of the introduced oxygen reacts with sulfide and converts it to sulfate, sulfide concentration will decrease 0.11 μM d^{-1}.

Discussion

Survey

Sediment sulfide concentration was lower in areas that were in close proximity to lucinids, suggesting that bivalve activity reduces porewater sulfides. There are problems affecting the observation of sulfide removal. Sulfide is a very transient molecule. Measuring the ambient pool might not accurately depict alterations made by lucinids. Accurately measuring sulfide oxidation would reveal a better understanding of lucinid effect on porewater sulfide. Measuring sulfide pools is much easier and less time consuming than measuring sulfide oxidation. Despite the complications with these measurements and the problems associated with surveying a complex system, it is apparent that the presence and activity of lucinids is correlated to some extent with decreased sulfide concentrations in the sediment (Fig. 3). Altering the sulfide levels even to a small degree in the systems has many implications for the seagrasses in these sediments.

In both systems, the presence of lucinids was weakly associated with increased ammonium concentrations in the sediment (Fig. 3). The alterations in porewater ammonium concentration appear somewhat less than the increases found with mussels in seagrass beds (Reusch et al. 1994; Peterson and Heck 2001a,b). A possible explanation for this discrepancy is that lucinids rely to some degree on the bacteria living in their gills for food and have a reduced filtering capacity (Cary et al. 1989; Le Pennec et al. 1995). The small changes can still be detected since ammonium is relatively labile in the sediments of Florida Bay. Florida Bay is typically considered phosphorous limited (Fourqurean et al. 1992), so nitrogen additions are not taken up quickly. Lucinids and seagrass exist in other systems that are not phosphorous limited, and in other areas of the world, this interaction between lucinids and sediment ammonium levels might be more significant. This nitrogen addition might be underestimated. Nitrogen addition is occurring in close proximity to oxygen introduction (via diffusion through hollow tubes). Some of the ammonium might be nitrified to nitrate. Nitrate was not measured in this survey, since nitrate is typically considered below the detection level in Florida Bay sediments.

While this study found no evidence of lucinid influence on sediment porewater phosphate concentrations, in phosphorous limited systems, an addition of phosphate will be immediately taken up by plants and bacteria in the sediments. The carbonate muds of these systems are able to sorb phosphate and remove it from the porewater pool. It is not unexpected that slight phosphate additions

to the sediment due to suspension feeding are difficult to detect, especially since lucinid suspension feeders have a reduced filtering capacity and presumably introduce only a small amount of phosphorous to the sediments.

Sulfide Mesocosm Experiment

The microcosm experiment data show that the bivalves *C. orbiculata* and *L. nassula* do have the potential to considerably alter the sulfide concentration of sediment porewater in controlled conditions (Fig. 4). Scaling these results up assumes that lucinids act similarly in the manipulated sediment conditions of the microcosms and in the natural environment. These are bold assumptions, but the results of the survey support and help to validate the results of the microcosm experiment.

While lucinid activity is certainly not the only method for removing toxic sulfide from the environment, it does appear to be important. These bivalves may be more important to total sulfide removal than the 2–16% calculated, since sulfide production was most likely overestimated. This overestimate is supported by the controls from the microcosm experiment. Without bivalves, sulfide accumulated at a rate of 2 mmol m^{-2} d^{-1}. While acknowledging that this is a conservative estimate of sulfide production, using this value as the sulfide production rate, bivalves remove a liberal estimate of 16–32% of the total sulfide removed from the system.

Without sulfide removal by lucinid bivalves, sulfide would either accumulate or be removed by another process. The latter appears unlikely to compensate for lucinid sulfide removal since in the laboratory microcosm experiment, sulfide accumulated in the sediments. High sulfide accumulation has been linked to seagrass decline (Carlson et al. 1994; Koch and Erskine 2001; Borum et al. 2005). Removal by bivalves potentially has a positive effect on seagrass productivity and health.

These bivalves are not only important in reducing the total amount of sulfide; the specific location of these two species makes them even more beneficial to seagrasses. The average depth of these bivalves is 7–9 cm. This depth is above the bulk of the rhizosphere, closer to the basal meristem area of *T. testudinum* where sulfide intrusion into the tissues is most detrimental and most likely to initially induce die-off (Borum et al. 2005).

Oxygen Transport Dye Experiment

The depth integrated bulk calculation estimates that one *C. orbiculata* introduces 0.4 μmol O_2 d^{-1} into the sediment (Fig. 6). The microcosm experiment showed that one *C. orbiculata* can remove

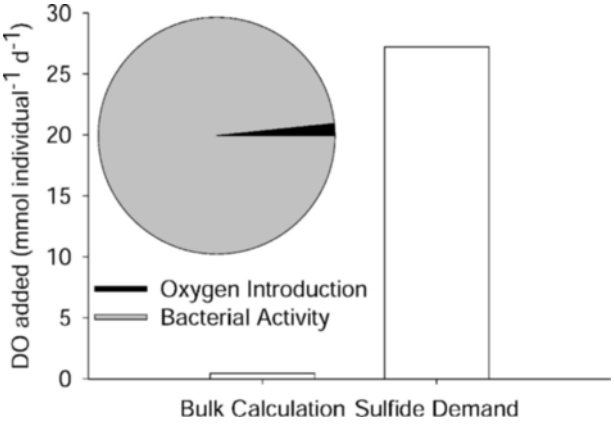

Fig. 6. Oxygen introduction estimates. The figure shows the estimates of oxygen introduction via *Ctena orbiculata* burrows. The second bar shows the amount of introduced oxygen needed to remove 13.6 μmol of sulfide. This value was estimated as potential sulfide removal due to lucinid activity using a microcosm experiment. The pie chart displays the percentage of sulfide removal due to bacterial activity in the lucinid's gills as opposed to oxygen introduction via burrows.

14 μmol of sulfide per day. If all of that sulfide was removed by oxygen, one *C. orbiculata* individual would need to add 28 μmol O_2 d^{-1} in addition to the oxygen that it introduces for its own respiration and that oxygen which is consumed by bacterial endosymbionts. The estimate of *C. orbiculata* oxygen introduction projects a much smaller oxygen introduction. This estimate of oxygen introduction suggest that oxygen introduction can only remove about 1.5% of the sulfide removed by lucinid activity. One must assume that most of the sulfide removal is achieved by means of bacterial oxidation or by another method (Fig. 6).

The calculation is subject to some measurement errors. The approach used Rhodamine WT diffusion to approximate dissolved oxygen diffusion. The diffusivities of the two compounds are not equal. Rhodamine WT diffusivity is 2.3×10^{-6} cm^2 s^{-1} (Glud and Fenchel 1999), and oxygen diffusivity is approximately 1.9×10^{-5} cm^2 s^{-1}. Since the diffusivity of oxygen is over 8 times larger than the diffusivity of Rhodamine WT, oxygen diffusion should be considerably larger than that of Rhodamine WT.

The sulfide removal achieved by lucinid burrows might be underestimated for other reasons as well. This study only addresses sulfide removal by oxygen introduced into the sediments. Sulfide will be diffusing out of the sediments into the bivalve tube as well. From the bivalve tube, the sulfide can diffuse into the water column. When the bivalve tubes contain dissolved oxygen, that sulfide can also react to form sulfate.

While this oxygen introduction via lucinid burrows is small and may not be the predominant method for sulfide removal, it may still be important. Oxygen typically enters the sediment by means of diffusion from the overlying water column. That oxygen is depleted in the top few millimeters of sediment by bacterial respiration (Hemminga and Duarte 2001). *C. orbiculata* burrows to an average depth of 7.5 cm (Fig. 2). These bivalves are introducing oxygen in small amounts to a deeper depth. This creates or enhances a sediment complex that while mostly anoxic has small transient patches of oxygenated sediment.

Small oxygenated zones can have a large effect on the sediment environment. Microbes are much more efficient decomposers when they use oxygen as opposed to sulfate as a terminal electron acceptor (Alongi 1998). More energy is produced, and more of the available carbon is assimilated. While seagrass meadows are some of the most productive systems in the world, most of the production is passed to higher trophic levels only via the detrital food web (Zieman 1982). More efficient assimilation by bacteria will result in more efficient transfer of energy up the food chain.

Sulfide dynamics in seagrass systems are highly studied (Carlson et al. 1994; Koch and Erskine 2001; Borum et al. 2005), but most studies of sulfide dynamics do not incorporate lucinid sulfide removal. This study demonstrates that these lucinids remove a significant amount of sulfide from these sediments, and in order to get the full and accurate understanding of sulfide dynamics, the activities of these bivalves must be considered.

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