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Control of seagrass communities and sediment distribution by Callianassa (Crustacea, Thalassinidea) bioturbation

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ABSTRACT

Shallow tropical lagoons at St. Croix, U.S. Virgin Islands were found to have high densities of the ghost shrimp *Callianassa* spp. The ecology of four species of *Callianassa* is discussed: *C. acanthochirus*, *C. longiventris*, *C. rathbunae* and *C. quadracuta*. The first two species capture and store in their burrows drifting detritus of seagrass and algae. The latter two species build volcano-shaped mounds of ejected sediment during feeding and burrowing. Massive quantities of sediment (up to 2.59 kg/m²/day) are funneled into subsurface galleries, gleaned for organic material and sorted. Fine grains (< 1.4 mm diam.) are then pumped back up to the surface forming mounds. Coarse-grained material (\geq 1.4 mm) such as shell debris and coral fragments are not pumped back to the surface, but are stored in many deep chambers which extend > 1.5 m below the sediment surface. In cross-section, cores from high *Callianassa* mound density regions show distinct alternating coarse and fine layers. This sedimentological evidence could be used as an indicator of *Callianassa* activity when interpreting the geological record from ancient tropical lagoonal environments.

Maximum seagrass productivity and percent cover are negatively correlated (significant to $p < .01$) with *Callianassa* mound density. Experimental and control transplants of the turtle grass *Thalassia testudinum* into regions of high (16/m²) and low (1/m²) *Callianassa* mound density produced a dramatic deterioration of *Thalassia* within 2-4 months in high density *Callianassa* areas. Ejected sediment either reduces available light for photosynthesis or physically smothers *Thalassia*, thereby eliminating it from regions of abundant *Callianassa*. Because seagrass communities have such intimate energetic ties to other nearby shallow-water and deep-sea communities, the negative influence of *Callianassa* on seagrass beds is suspected to have second and third order effects on other tropical communities as well.

1. Introduction

In the past decade there has been an expanding interest in the processes that govern nearshore marine communities. One major area of nearshore research has been that of seagrass communities, which are particularly interesting for several reasons. (i) They are some of the most ubiquitous and productive communities on earth and in many parts of the world provide the nutritional base for complex trophic

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assemblages (McRoy and Helfferich, 1977; Phillips and McRoy, 1980; Ogden, 1980). (ii) It is now being recognized that seagrasses make significant contributions to detrital food chains for both shallow-water ecosystems as well as the deep-sea (Moore, 1963; Menzies *et al.*, 1967; Wood *et al.*, 1969; Fenchel, 1970; Zieman *et al.*, 1979; Wolff, 1980; Suchanek *et al.*, in prep.). (iii) The increased structural complexity created by the blades and rhizomes of seagrass beds enhances biological diversity of other infaunal or associated organisms (Jackson, 1973; Orth, 1973; Heck and Wetstone, 1977; Ogden, 1980; Stoner, 1980). (iv) Seagrass beds are also geologically important features because the blades, acting as effective "baffles," influence sedimentation rates and, together with the rhizomes, trap and bind carbonate sediments (Ginsburg and Lowenstam, 1958; Scoffin, 1970). In this way, permanent features may be formed in the geological record which can be used as indicators of ancient physical regimes and biological communities (Ginsburg and Lowenstam, 1958; Neumann *et al.*, 1970; Petta and Gerhard, 1977; Miller, 1981; Wanless, 1981).

Both biological and physical factors limit the abundance and distribution of marine plants (Southward, 1964; Dayton, 1973; Lawrence, 1975; Lubchenco, 1978) and can indirectly (via second and third order effects) influence other communities dependent upon or associated with them (Estes and Palmisano, 1974; Breen and Mann, 1976; Rosenthal *et al.*, 1974). With the present increasing awareness of how important seagrass beds are to the dynamics of nearshore communities, and the potential for second or third order effects, it is especially important to understand the mechanisms controlling seagrass distributions.

Co-occurring in and often near seagrass beds in Caribbean waters are infaunal organisms which, during the course of feeding and burrowing, continually rework vast amounts of sediment. Representatives from at least seven phyla (Cnidaria, Annelida, Mollusca, Arthropoda, Echinodermata, Hemichordata, Chordata) have been identified burrowing within sediments from shallow (1-5 m depth) Caribbean grass beds (pers. obs.). Some of the most conspicuous of these are thalassinid shrimp, holothurians, enteropneusts and polychaetes. Of these, the most active bioturbators in the Virgin Islands are the thalassinid ghost shrimp *Callianassa* spp., which create extensive regions dominated by large, volcano-shaped mounds, often in or near seagrass beds.

The negative influence of *Callianassa* on other faunal groups has been reported previously (Stevens, 1928; MacGinitie and MacGinitie, 1968). However, this report represents the first detailed analysis of amensalism by *Callianassa* on a marine plant community. Although this interaction is of a biological origin, the negative influence of *Callianassa* on seagrass beds is mediated indirectly through physical processes which are a consequence of normal burrowing or feeding activities, similar in nature to the amensal interactions between groups of deposit feeding and suspension feeding bivalves reported by Rhoads and Young (1970, 1971).

Mounds built by *Callianassa* in tropical carbonate sediments have also been reported earlier, but because of the inherent difficulty in capturing these active burrowers the identification of the mound/burrow inhabitants has now rested for nearly 15 years on a single specimen which died and decayed before identification beyond the generic level was possible (Shinn, 1968). Subsequent studies (Bathurst, 1971; Clifton and Hunter, 1973; Aller and Dodge, 1974) have assumed the accuracy of this early report and no further taxonomic work has been attempted. The purpose of this paper is three-fold. First, I report on the identification of several species of *Callianassa* from St. Croix, at least two of which build mounds (*C. rathbunae* and *C. quadracuta*) and at least two others (*C. acanthochirus* and *C. longiventris*) which build no mounds, but capture detrital seagrass and algae drifting past their burrow openings (Suchanek, in prep.). Second, I elucidate the mechanisms involved in the limitation of seagrass beds by *Callianassa* spp. and the sedimentological consequences of this bioturbation. Finally, I discuss the potential influence of these processes on associated nearby communities.

2. Methods

Data on *Callianassa*, seagrass and algal distributions were collected from January 1979-April 1981 in Tague Bay on the north shore of St. Croix, U.S. Virgin Islands (17°46'N; 64°36'W), Figure 1. Comparative data were also collected in another shallow (5 m depth) lagoon at Great Pond Bay (see Fig. 1 and Roberts *et al.*, 1982 for details of study site) on the south shore (17°43'N; 64°39'W) and from Salt River Canyon (17°47'N; 64°45'W) to depths of 40 m during NOAA's NULS-1 "Hydrolab" Mission #80-5 (Fig. 1).

Long term estimates of *Callianassa* abundance in Tague Bay were determined using SCUBA on three permanently established grids (A, B, C). Each grid was 10 m on a side and delineated by lines extending in from each meter interval, forming 100 1.0 m² quadrats in each grid (see Fig. 2 for locations). Grid A was chosen to represent the highest density of *Callianassa* mounds (up to 16/m²), grid B represents an intermediate density (to 7/m²) and grid C the lowest (maximum density of 2/m²). This same grid technique was also used on a short-term basis to determine *Callianassa* densities at Salt River Canyon.

A more extensive survey of the distribution and abundance of *Callianassa* mounds and percent cover of seagrass and algae was determined by SCUBA using a 1 m × 1 m quadrat with lines strung at 25 cm intervals in both directions, yielding 25 regularly spaced points at the intersections. Replicate haphazard tosses of this quadrat were made at 30 locations in Tague Bay lagoon, 25 of those along 5 prescribed transects (T1-T5), 400 m apart, running in a north-south direction from the bank-barrier reef to shore, at 100 m intervals (see Fig. 2). The abundance of mounds/m² for each toss was recorded as was the number of points/25 lying over

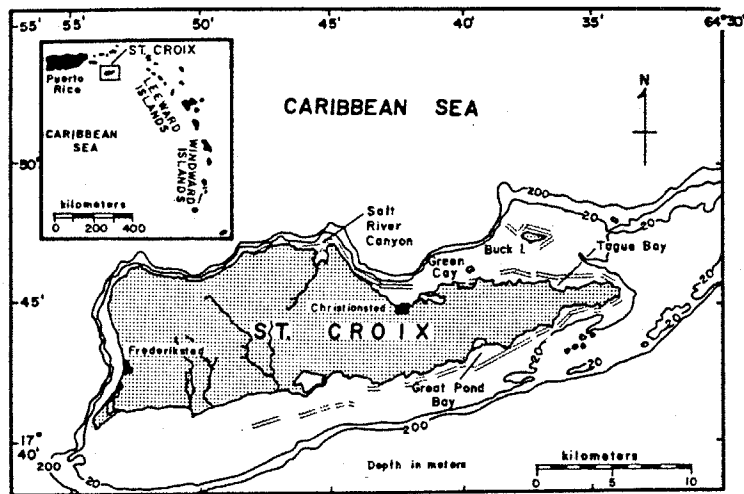


Figure 1. Location map for study sites on St. Croix, U.S. Virgin Islands.

seagrass, algae or sand. Mounds were recorded in the count if half or more fell within the quadrat area. Mounds and sediment ejection heights were measured with a meter stick. Mound ejection frequencies and durations were recorded over 60 and 90 minute observation intervals.

Ejecta from mounds were captured in six replicated sets of sediment collection traps for 12-24 hour periods. Each trap, consisting of a plastic bucket with a 4 cm hole cut in the bottom, was placed over the top-dead-center of a flattened *Callianassa* mound and secured in place with wire stakes. Gauze mesh was fitted over the top to prevent influx or eflux of sediment. Using SCUBA, ejected sediments were collected *in situ* by sealing in a plastic bag and later washed, dried and weighed on an analytical balance. Grain size analyses were performed on sediments using the methods of Folk (1974).

The nature of sediment sorting performed by *Callianassa* was examined by seeding *Callianassa* burrows with a mixture of pre-weighed sediment samples (500 g each and uniquely painted for ease of identification) from 7 pre-sorted ϕ sizes: -2.0, -1.0, 0.0, 1.0, 2.0, 3.0, 4.0 ϕ . Subsequent collection and grain size analysis of ejected sediments in collection traps (see above) allowed a determination of the propensity of *Callianassa* to sort and/or pump specific grain sizes from its burrow.

High-density fiberglass resin (Dynatron Bondo™) was used to cast burrow shapes. Resin was poured underwater using SCUBA and allowed to harden for 24-48 hours. Subsequent extraction of casts was facilitated by air-lifting equipment.

To assess the influence of *Callianassa* on the health and distribution of seagrass communities, 6 healthy plugs of the seagrass *Thalassia testudinum* (using 20 cm

diameter cores, 30-40 cm deep) were transplanted from the Blowout³ region in Tague Bay to areas of high and low *Callianassa* densities in October 1980. Three experimental replicates were transplanted to a region adjacent to grid A (max. mound density = 16/m²) and three control replicates were transplanted back into an area in the Blowout region near grid C with a maximum of 2 mounds/m². Densities of shoots and blades and relative health of these transplants were monitored through March 1981. Biomass estimates for seagrass and algae were obtained by washing in distilled water, decalcifying with 5% HCl and drying samples at 105°C for 24 hrs before weighing.

To evaluate differences in behavior and sediment processing abilities, live *C. rathbunae* and *C. quadracuta* were held in separate sediment-filled aquaria supplied with running seawater.

3. Results

The most dominant marine plants found in both Tague Bay and Great Pond Bay are the turtle grass *Thalassia testudinum* and the manatee grass *Syringodium filiforme* with other seagrasses (*Halodule wrightii* and *Halophila engelmannii*) and algae (*Halimeda* spp., *Penicillus* spp. and *Dictyota* spp.) playing only a minor role in space occupation of sandy substrates. Survey results of *Callianassa* distribution and densities in relation to seagrass and algal cover are shown in Figures 2 and 3. A gradient is present in Tague Bay from dense *Thalassia* cover in the eastern portion (especially in the Blowout region near grid C), through a transition zone of mixed *Thalassia* and *Syringodium* cover, through scattered grass and algae to areas of very low seagrass or algal cover with mostly sand (up to 96% near grid A) in some western sectors. A reverse gradient of *Callianassa* mound densities is found moving from east to west with the lowest number of mounds in the eastern portion and the highest being found close to the reef in the central and western sectors (Fig. 3). Long-term monitoring of the three fixed grids (A, B, C) for 1.5 yrs reveals this same trend with average mound densities (pooled for all dates) for grid A of $6.3 \pm 0.9/\text{m}^2$, grid B with $1.7 \pm 0.6/\text{m}^2$ and grid C at $0.1 \pm 0.1/\text{m}^2$.

To evaluate mound-building *Callianassa* distribution in deep habitats, mound densities were monitored at Salt River Canyon. Average densities per m² were 1.3 ± 1.2 at 20 m, 0.4 ± 0.6 at 25 m, 0.8 ± 1.0 at 35 m and 2.4 ± 1.4 at 40 m depth. Mounds at this highest density were observed to extend down well beyond 50 m depth.

Although *Callianassa* are inherently extremely difficult to capture (Shinn, 1968), air-lifting with SCUBA enabled the capture and identification of several individuals of two species of *Callianassa* from the sandy region near grid A. *Callianassa rath-*

3. Blowouts are large, fluted erosional scours in sandy substrates (Wanless, 1981). In Tague Bay, the Blowout region is a former erosional scar created in the early 1950's which has since been re-colonized by seagrasses (see Fig. 2).

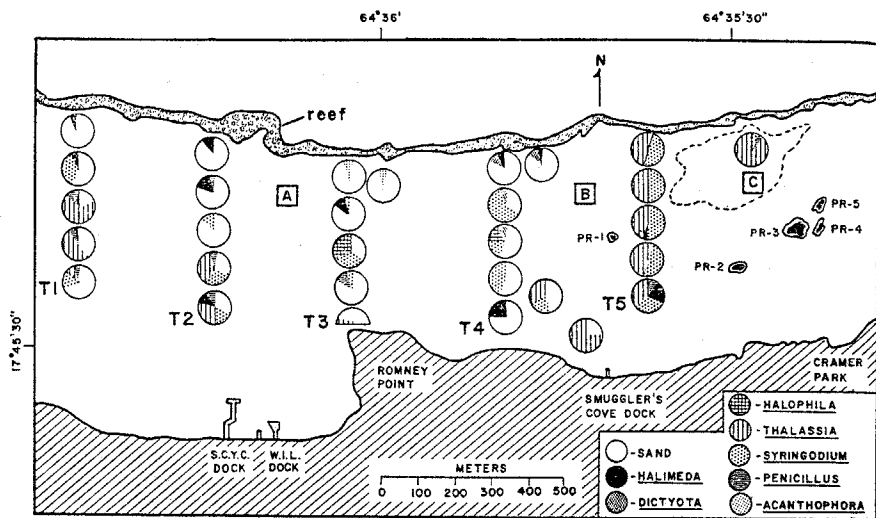


Figure 2. Pie-diagrams for the percentage of seagrass, algae and sand in Tague Bay. A,B,C represent permanently established 10 m × 10 m sampling grids. Transects are marked T1-T5, with 5 sample sites running north/south along each transect. Note: five other misc. sampling sites are located outside the major transect lines. Patch reefs are marked PR1-PR5. The Blowout region is delineated by a dotted line.

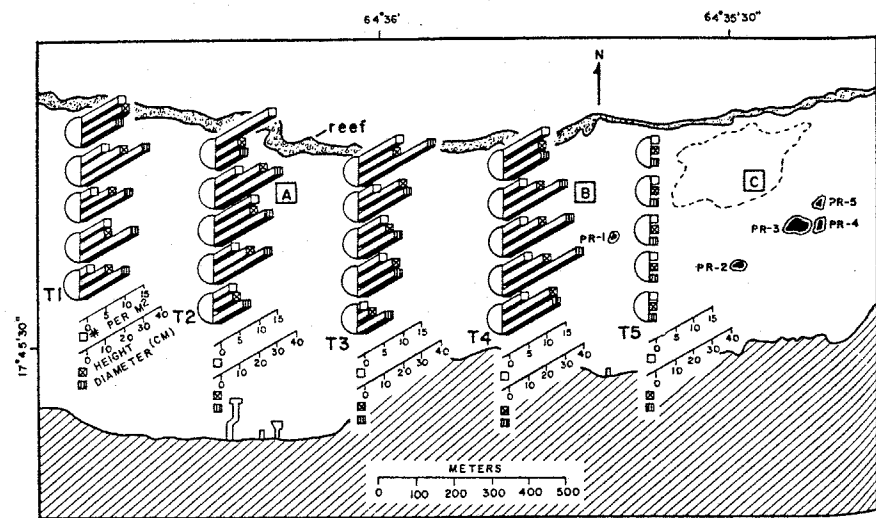


Figure 3. Abundance, height and diameter of *Callianassa* mounds in Tague Bay. See Figure 2 for other details.

Table 1. Bioturbation statistics from sandy versus grassy bottoms.

	Sandy bottom (at or near area A) <i>Callianassa rathbunae</i>		Grass beds (at or near area C) <i>Callianassa</i> spp.		Sig. levels
	(n)	$\bar{X} \pm \text{S.E. (range)}$	(n)	$\bar{X} \pm \text{S.E. (range)}$	
Mound density #/m ²	Oct. '79 (100)	4.98 ± 1.93 (1-11)	(100)	0.14 ± 0.35 (0-1)	***
	Dec. '79 (100)	6.20 ± 2.72 (1-15)	(100)	0.04 ± 0.20 (0-1)	***
	Mar. '80 (100)	6.88 ± 2.68 (2-16)	(100)	0.02 ± 0.20 (0-2)	***
	Apr. '81 (100)	7.03 ± 2.72 (1-14)	— no data —		
Mound height (cm)	(22)	19.1 ± 3.98 (10.3-26.7)	(5)	5.46 ± 1.68 (3.2-6.1)	***
# Ejections per mound per hour	(24)	6.9 ± 4.3 (2-20)	(10)	3.1 ± 2.0 (1-7)	*
Ejection height (cm)	(13)	3.0 ± 1.7 (1.0-5.5)	(6)	1.5 ± 0.6 (1.0-2.0)	ns
Ejection duration (sec)	(17)	3.9 ± 2.0 (1-8)	(9)	6.7 ± 2.6 (3-10)	**
Dry weight sediment ejected g/mound/day	(62)	369 ± 175 (0-1571)	(24)	158 ± 127 (4-468)	***
Mean size ejected sediments (φ)	(11)	1.58 ± 0.49 (0.66-2.29)	(11)	1.96 ± 0.61 (0.81-2.63)	ns
Average total sediment processed (kg/m ² /day)		2.59		0.004	

Significance Levels:
 ns = not significant
 *** = p < .001
 ** = p < .01
 * = p < .05

bunae Schmitt, 1935, the larger of the two species, is responsible for the major mound-building activity within Tague Bay, Great Pond Bay and Salt River Canyon. Sex, body length (rostrum to telson), female reproductive status and capture dates of individuals were as follows: ♂ 32 mm, ♀ 65 mm (ovigerous)—26 July 1979; ♀ 56 mm (nonovigerous)—2 August 1979. Several individuals of *Callianassa quadracuta* Biffar, 1970, which builds smaller mounds, were also obtained: ♂ 31 mm, ♂ 42 mm, ♀ 39 mm (ovigerous)—26 July 1979.

In other areas of Tague Bay and Salt River Canyon two other non-mound-building species were found. *Callianassa acanthochirus* (Stimpson, 1866) was found at the perimeter of patch reefs in Tague Bay and *Callianassa longiventris* A. Milne-Edwards, 1870 was found in thick *Thalassia* stands in Tague Bay and in sandy areas in Salt River Canyon. Rather than being deposit feeders (as are the mound-

builders), both of these species capture detrital seagrass and algae drifting past their burrow openings (Suchanek, in prep.).

In comparing open sandy regions with grass beds, there are important differences which may be a result of different mound-building *Callianassa* species being found in each habitat. Table 1 lists critical statistics for *Callianassa* mounds and activity patterns for both sandy and grassy bottoms in Tague Bay. Using a Student's *t*-test for differences between means (Sokal and Rohlf, 1969), highly significant ($p < .001$) differences were found between sandy and grassy areas for mound densities, mound heights and dry weight of sediment ejected per mound each day. Other significant differences ($p < .01$ and $p < .05$) were found for mound ejection durations and ejection rates, respectively. Neither the mean grain size of ejected sediments nor the ejection heights were significantly different at $p < .05$. Calculated estimates for the total potential amount of sediment processed per m^2 per day for sandy areas ranged from 0.37 to 25.14 kg with a mean value of 2.59 $kg/m^2/day$; for grassy areas, values ranged from 0.00 to 0.94 kg with a mean of 0.004 $kg/m^2/day$. Table 1 shows sandy bottom areas being dominated by *C. rathbunae* although other *Callianassa* (certainly *C. quadracuta*) are present as well. Typical *C. rathbunae* mounds were less often found in grassbeds where smaller mounds were more common. These smaller mounds may have been created by small *C. rathbunae* or *C. quadracuta* or even some other, as yet unidentified, *Callianassa*. The differences seen in Table 1 may therefore represent basic differences between two (or even more) *Callianassa* species.

When held in captivity and allowed to occupy a 1 m high sand-filled vertical aquarium, one ♀ *C. rathbunae* took nearly 20 hrs to initiate burrowing but then constructed an extensive burrow system with a 15 cm high mound of ejected sediment and within three days had produced a second mound of equal size. A ♂ *C. quadracuta* on the other hand, initiated burrowing within one minute, but eventually produced only a single, small (1-2 cm high) mound after a comparable three day period.

Resin casts of *C. rathbunae* burrows revealed an architecturally complex series of chambers which extended greater than 1.5 m below the sediment surface. Figure 4 shows the relationship between chambers and interconnecting tunnels which lead to mounds and valleys on the surface. Two or three mound connections were found for each burrow complex, but it is not known how many individuals occupy each burrow. Also found in nearly all lower chambers were many pockets of coarse-grained sediments. Vertical distances between lower chambers (and therefore between pockets of coarse-grained sediments) were found to be 8.7 ± 0.8 cm (range = 8-11 cm).

It is clear that *Callianassa* is modifying the grain size distribution within sediments, potentially altering the sedimentary column in a way which might be recognizable in the geological record. To more accurately evaluate what influence *Callianassa*

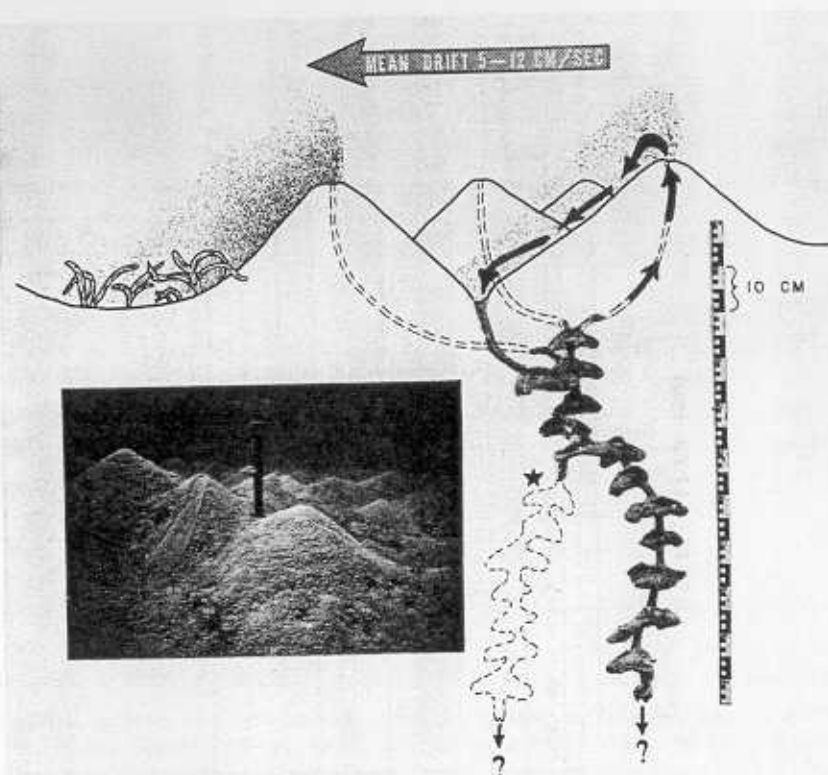


Figure 4. Diagrammatic cross-sectional view of *Callianassa rathbunae* mounds, a valley and associated burrow complex and galleries. Darker subsurface chambers represent an extracted resin cast. Gallery at star represents additional speculated chambers not discovered by resin casting. Dark arrows show route of sediment being cycled into burrow complex and some finer particles being pumped back out through mounds. Seagrass on left is being smothered by fine-grained sediment. Inset is a photograph of *C. rathbunae* mounds in Tague Bay with diver's knife for scale; handle of knife = 15 cm.

has upon these sediments, replicate cores were taken in high, low and no mound density regions in Tague Bay. Figure 5 (data from C. A. Wilson, unpublished) shows the mean grain size \pm SE and distribution of sediment types within cores from each of these areas. Cores from sandy and grassy blowout regions (without *Callianassa* mounds) near Green Cay (Fig. 1) are also shown for comparison. For areas with high *Callianassa* mound density, layers of coarse-grained debris made up of coral and shell fragments and polychaete tubes are found at fairly regularly spaced intervals. The vertical distribution of these pockets closely approximates both the thickness and distance between burrow chambers found by resin casting (Fig. 4). This

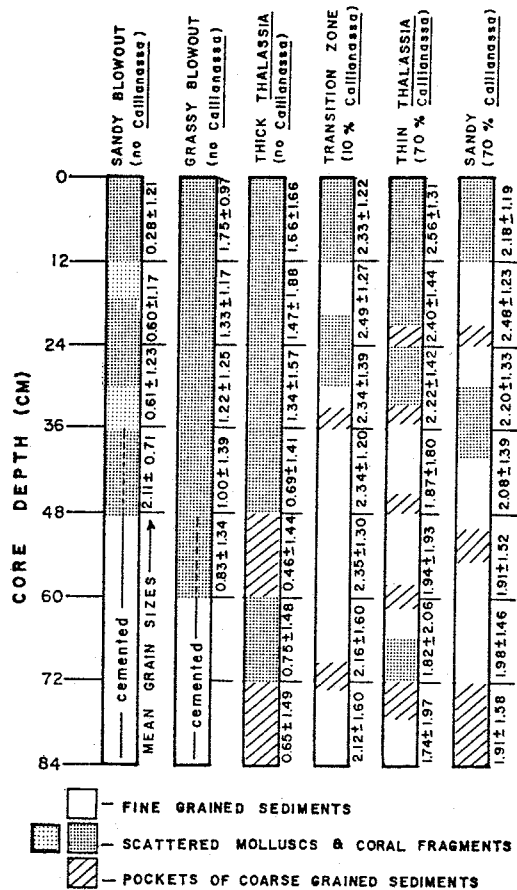


Figure 5. Grain size \pm SE of sediments from various levels in cores taken from a sandy blowout at Green Cay with no *Callianassa* and several regions in Tague Bay with varying densities of *Callianassa*. (Data from C. A. Wilson, unpublished)

evidence strongly suggests that these coarse-grained sediment pockets or lenses are an artifact of sorting by *Callianassa* during the normal course of bioturbation.

Sediments pumped from *Callianassa* mounds and captured in collection buckets were analyzed for day/night activity trends and grain size distribution patterns. Chi square analysis showed no significant differences at $p < .05$ ($n=24$) between rates of sediment pumped during daylight and night hours. For all samples, however, grain size distribution of ejected sediments was skewed toward the finer particles with *Callianassa* rarely pumping sediments larger than 1.0-1.4 mm (-1.0 to 0.0ϕ). Figure 6a is a comparison of grain size distributions for naturally occurring sediments collected as grab samples ($n=8$) of material sliding into *Callianassa* valleys

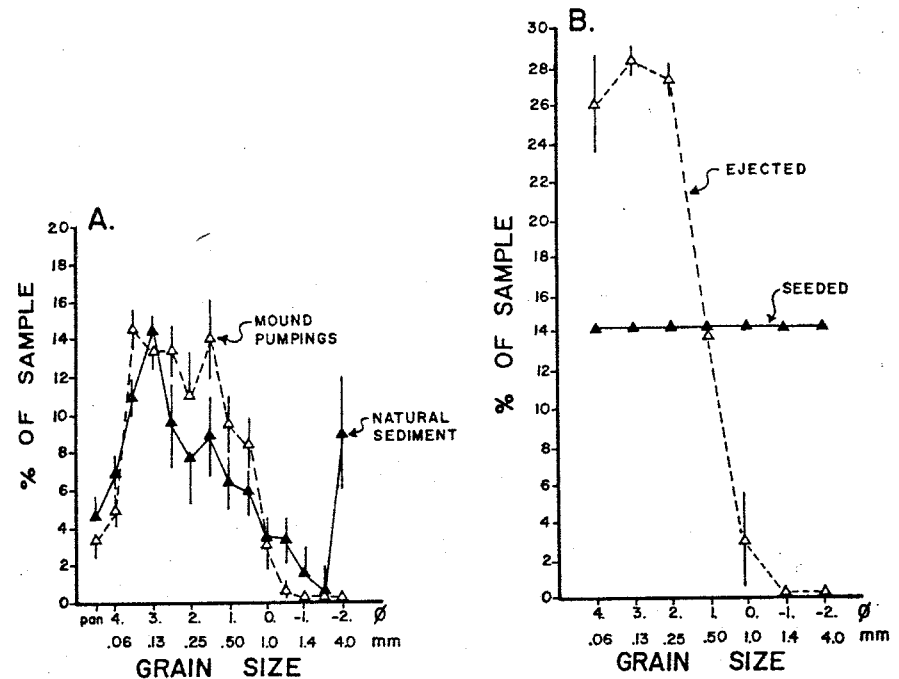


Figure 6(A). Mean grain size distribution of naturally occurring sediment, (i.e., taken from valleys before *Callianassa* sorting) versus sediment pumped from mounds into collection buckets (i.e., after *Callianassa* sorting) from grid A region, Tague Bay. (B) Mean grain size distribution of equally sorted, labeled sediments from 7 pre-designated ϕ sizes seeded into *Callianassa* valleys. Ejected sediments are those pumped back out of mounds into collection buckets, showing selective sorting of fine-grained sediments.

(i.e., pre-sorted) versus sediments sorted by *Callianassa* and pumped out from mounds into collection buckets ($n=12$). Clearly those larger particles which were composed of shell fragments and coral debris (> 1.4 mm) were not able to be pumped by *Callianassa*.

To evaluate the actual potential to pump sediments of any grain size, a mixture of pre-weighed, painted sediments from a range of 7 ϕ sizes (see Methods) was seeded into *Callianassa* valleys. Sediment collection traps were then fitted over nearby mounds to retrieve these sediments. Sorting and processing by *Callianassa* started almost immediately and seeded sediments began to reappear from mounds on the surface within 1-2 hrs. Figure 6b shows that *Callianassa* preferentially pumped experimentally seeded sediments < 1.4 mm to the surface and selectively stored those sediments ≥ 1.4 mm. Further, the grain size most chosen for pumping was approximately 3.0ϕ ($= 0.13$ mm).

Figure 4 demonstrates the route of recycled sediments from a burrow complex, out of a mound, down the mound slope and back into a valley (heavy arrows) in a high *Callianassa* mound density region. Residence time of sediments remaining on the surface range from one to several weeks or more depending on the angle of slope, distance from mound to valley, mean current drift and frequency of valley openings (pers. obs.). During this time, diatoms, filamentous algae and organic detritus accumulate on the grains which can be gleaned by *Callianassa* when sediments are later reprocessed.

Sediments that are not pumped back out via mounds (i.e., those ≥ 1.4 mm) appear to be stored in the deep chambers found by resin casting. This could occur either because of an inability of shell and coral fragments to physically fit through the restricted aperture leading to mound openings, or the inability of *Callianassa* pleopods to create a current sufficient to move these heavier objects. Or, it is possible that *Callianassa* is actively attempting to enhance smaller particles being recycled through the environment to increase or optimize the surface area to volume ratio in order to obtain the maximum organic content from any given volume of processed particles. Many deep chambers were found partially filled with these coarse-grained sediments and it is speculated that when enough chambers have been sufficiently filled, the entire lower complex is sealed off and another series of chambers is formed for the deposit of discarded rubble and shell fragments. Figure 4 shows the blind end of a resin-filled tunnel (at star) leading to one of these speculated older, or perhaps newer, galleries (dashed lines).

The pumping of fine-grained sediments by *Callianassa* can significantly enhance sediment movements in shallow lagoons like Tague Bay. We have already reported on the influence of *Callianassa* pumping on sediment transport in Great Pond Bay (Roberts *et al.*, 1982) and it appears that the same processes apply in Tague Bay as well. Massive quantities of sediment are moved across Tague Bay each year, enhanced by the bioturbation of *Callianassa*. In Great Pond Bay both percent cover and the productivity of seagrass and algae are negatively correlated with the density of *Callianassa* mounds. Figure 7 compares the maximum productivity of seagrass and algae from Great Pond Bay as well as the maximum percent cover from both Tague Bay and Great Pond Bay as a function of the density of *Callianassa* mounds. Using a Spearman Rank Correlation test (Sokal and Rohlf, 1969), negative correlations with mound density are significant to at least $p < .01$ for all three parameters in Figure 7. These results indicate strongly that where mound-building *Callianassa* occur in high densities, not only is biologically enhanced sediment transport high, but seagrass and algal beds are sparse as well.

The potential negative influence of *Callianassa* bioturbation on seagrass stands was studied experimentally by transplanting replicated plugs of *Thalassia testudinum* from a healthy bed in Tague Bay to nearby areas with high (area A) and low (area C) *Callianassa* mound densities (see Methods). Within two weeks the health of

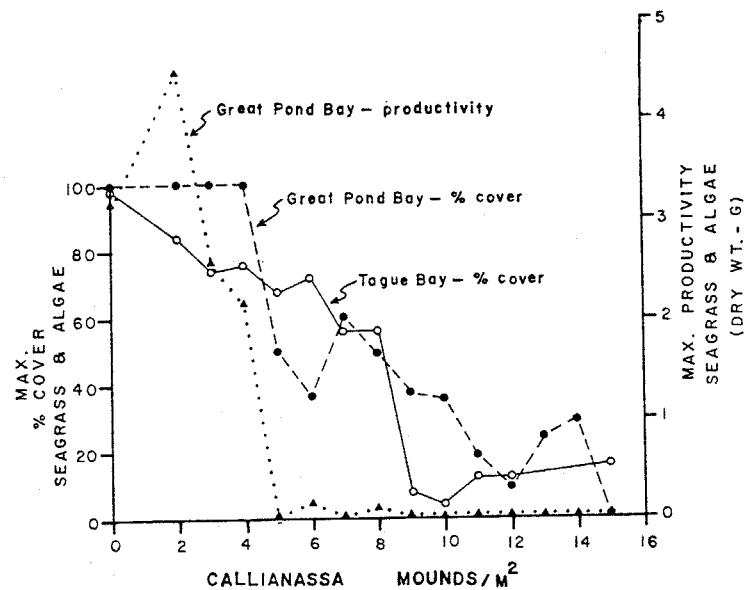


Figure 7. Maximum percent cover of seagrasses and algae from Tague Bay and Great Pond Bay versus *Callianassa* mound density. Associated levels of productivity from Great Pond Bay are included for reference.

Thalassia plants in high mound density areas was beginning to decline; blades became silted over and were rapidly being colonized by blue-green algae. At the end of one month, blades were physically deteriorating and continued to do so through the last observation period some 6 months later. Figure 8 demonstrates the dramatic difference between the number of blades and shoots for both experimental and control transplants. At the 6 month observation period, many of the remaining *Thalassia* blades in high mound density areas were completely buried and/or in poor condition. Those in the area with virtually no mounds (near grid C) were lush and healthy. This evidence indicates strongly that *Callianassa* has a dramatically negative effect on, and therefore has the ability to control, seagrass distribution and abundance in shallow lagoons. This negative effect appears to stem from the pumping of fine-grained sediments which can either reduce the available light needed for photosynthesis or physically smother the plants.

4. Discussion

Callianassa rathbunae and *C. quadricata*, the mound-builders, selectively sort natural sediments pulled into subsurface chambers, pumping the fines (< 1.4 mm) up out of mounds. These grains, during a residence time of days to weeks on the

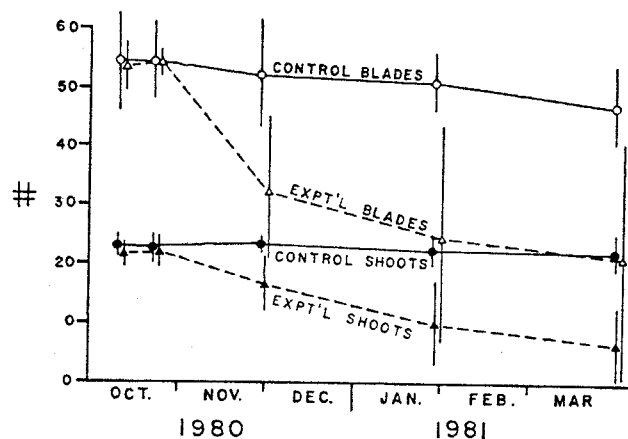


Figure 8. Mean number of blades and shoots \pm 1 SE error bars from transplanted *Thalassia testudinum* plugs over time. Experimental plugs were transplanted into a high density *Callianassa* mound region (near grid A). Control transplants were placed in a low density *Callianassa* mound region (near grid C).

surface, likely renew their organic load in the form of diatoms, filamentous algae and detritus, are subsequently gleaned by *Callianassa* and later recycled again. Coarser sediments such as shell debris and coral fragments are selectively sorted out and stored in deep chambers, creating predictable bedding features in high density *Callianassa* regions. Although most studies on bioturbation have shown effects restricted to the upper 20-30 cm of sediment (Rhoads, 1967; Rhoads and Young, 1970; Myers, 1977), *Callianassa rathbunae* here joins the ranks of a few other thalassinid shrimp known to produce deep burrows (1-3 m in depth) and significant bioturbation (Shinn, 1968; Pemberton *et al.*, 1976; Ott *et al.*, 1976).

While organisms both create and destroy sedimentary structures, most sedimentologists favor the idea that physical factors produce laminated sediments, whereas biological processes like bioturbation tend to homogenize them (Moore and Scruton, 1957; Toots, 1961; Warme, 1965; Berger and Heath, 1968; Wanless, 1981). The idea that biological processes produce small-scale, laminar features of widespread lateral extent has not been generally recognized. Rhoads and Stanley (1965) do describe such bedding with limited local extent by the polychaete *Clymenella*. The evidence presented here shows that *Callianassa* is capable of producing regularly-spaced, distinct, alternating laminations of thinner coarse beds and thicker fine-grained layers. In regions where mound-building *Callianassa* are in high densities, this bedding covers a broad lateral region. Classic dogma would incorrectly interpret these coarse-grained layers as physically-generated storm or high current "lag" deposits when, in fact, they were not associated with such events. Perhaps a reason-

able criterion for recognition would be their association with super- or subadjacent, homogeneous fine-grained beds rather than medium-sized, cross-bedded sands often found in association with storm lags.

Because shallow tropical lagoons in both Caribbean and Pacific waters have abundant *Callianassa* populations (Suchanek and Colin, in prep.), care is needed when interpreting the origin of sedimentological features in these regions. Therefore these deposits can be used not only as important indicators of bioturbation, but may also indicate the absence of significant seagrass beds in the sedimentary record.

The results presented here indicate strongly that where mound-building *Callianassa* occur in high densities, biologically enhanced sediment transport is high, and seagrass and algal beds are sparse. The negative correlation between grassbed productivity and *Callianassa* mound density that we have reported for the south shore of St. Croix at Great Pond Bay (Roberts *et al.*, 1982) has been confirmed here on the north shore at Tague Bay. Further, the experimental transplant results at Tague Bay provide evidence for causality by showing that *Callianassa* bioturbation has a negative influence on the health and standing crop of the turtle grass *Thalassia testudinum*. While it is conceivable that a healthy stand of *Thalassia* with its complex rhizome mat could potentially inhibit invasion by *Callianassa*, many grassbed regions in Tague Bay and Great Pond Bay appear to have been invaded successfully. This evidence together with the results of the transplant experiments indicate strongly that once *Callianassa* invade a grassbed region, they can and do severely limit or even eliminate seagrasses and algae.

At this point in time it is unclear what limits *Callianassa* abundance, and more in-depth studies are needed to determine what factors ultimately control these influential bioturbators. Over many hundreds of hours of observation (both day and night) I have never seen a *Callianassa* naturally occurring out of its burrow. However, when a *Callianassa* is exposed by human excavation or disturbance it is preyed upon immediately by predatory fish such as the blue-head wrasse *Thalassoma bifasciatum* (Bloch) (pers. obs.). Through gut content analysis, J. E. Randall (pers. comm.) has also found at least one natural predator on *Callianassa*, the bone fish *Albula glossodonta* (Forsskal). This specimen was collected in mid-afternoon at Enewetak Atoll lagoon with approximately 25% of the gut contents composed of callianassid shrimp (fish std. length = 530 mm, 2.22 kg).

In local regions whenever *Callianassa* does limit or eliminate seagrass beds it also affects the extremely complex assemblage of other populations which are either directly or indirectly dependent upon the grassbeds (Ogden, 1980). Because of the tight energetic ties to both coral reefs and mangroves, reduction or elimination of seagrass beds by *Callianassa* has a profound influence on nearshore community structure. For instance, direct herbivores on seagrass blades such as urchins, fish, and turtles and their associated predators would necessarily shift to lower abundances, migrate or be eliminated completely. Those micro- or macro-invertebrates

and fish using the seagrass beds for substrate, protection or nursery grounds would be significantly affected as well. Because organic detritus would no longer be trapped by seagrass blades, those deposit or suspension feeders (so characteristic of grassbeds) that are dependent upon this source of energy would also be equally affected. Lastly, the contribution made by seagrass beds to nearby shallow and distant deep-sea detrital food chains would be severely limited. In short, bioturbation by *Callianassa* has a direct effect on seagrass beds but may indirectly influence a multitude of faunal relationships both within the grassbeds and in nearby communities such as coral reefs, mangroves and the deep-sea.

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