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Benthic community metabolism and the role of deposit-feeding callianassid shrimp

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ABSTRACT

In temperate and tropical seas, bioturbation resulting from the burrowing and feeding activities of deposit-feeding callianassid shrimp can have an important impact on the ecosystem. In Gorda Sound, British Virgin Islands, 97 μmol $NH_4 \cdot m^{-2} \cdot d^{-1}$ and 0.2 μmol $PO_4 \cdot m^{-2} \cdot d^{-1}$ were released to the water column from burrows of callianassid shrimps (*Callianassa rathbunae* and *Calliax jonesi*). Benthic gross primary production was 288 mg $C \cdot m^{-2} \cdot d^{-1}$ and the ratio of gross production to total community 24-hr. respiration was 0.86. The flux of dissolved nutrients released from shrimp burrows could supply less than 5% of the need calculated for benthic primary production, while the net flux from the total benthic community could support 21% of the estimated demand. Stable carbon isotope measurements indicated that these callianassid shrimp derive 100% of their nutritional requirements from benthic microflora.

1. Introduction

In a review of total community metabolism for coral reef ecosystems, Kinsey (1983) concluded that the ratio of production to respiration (P/R) in high energy zones is typically greater than one and that this ratio is less than one in low energy sand flats and lagoons. The interpretation of these generalizations is that the reef proper may act as a source of organic material which may be carried downstream to the lagoon. Here it may accumulate and/or be metabolized, giving the entire ecosystem a metabolic balance (P/R = 1). In nutrient limited tropical systems, the utilization of organic matter in lagoons may in effect return inorganic nutrients to the system and thus help to sustain productivity. This paper focuses on bioturbation as a potential source of regenerated nutrients and then assesses the relative importance of this regeneration to primary production.

The amensal (indirect and negative) effects of bioturbation from callianassid ghost shrimp have been clearly established in tropical waters (Aller and Dodge, 1974; Suchanek, 1983). This group is common to many shallow bays and lagoons in temperate and tropical regions (Hailstone and Stephenson, 1961; Rodriguez, 1983;

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De Vaugelas, 1985; Riddle, 1988) and the feeding and burrowing activities of these shrimp can have dramatic effects on the habitat in which they live (Shinn, 1968; Suchanek, 1983; 1985). Measurements of sediment turnover resulting from callianassid feeding and excavation activities have shown that these shrimp move considerable amounts of sediment, up to 12 $kg \cdot m^{-2} \cdot d^{-1}$ (Aller and Dodge, 1974; Roberts *et al.,* 1981; Suchanek, 1983; Suchanek *et al.,* 1986; Suchanek and Colin, 1986; Branch and Pringle, 1987; Riddle, 1988). The resulting sediment destabilization and resuspension has been shown to kill and reduce growth in corals and sea grasses (Aller and Dodge, 1974; Suchanek, 1983).

Since these shrimp live in areas where sediment and organic matter accumulate, their activities may also stimulate organic matter decomposition and nutrient flux to the sediment surface and water column. A variety of related mechanisms are involved: resuspension and turnover of sediment through bioturbation (Branch and Pringle, 1987; Kioke and Mukai, 1983; Suchanek, 1983); aeration and ventilation of the shrimp burrow (Kioke and Mukai, 1983; Waslenchuk *et al.,* 1983; Colin *et al.,* 1986); and metabolism of organic matter by the shrimp and associated micro and macro biota (Aller *et al.,* 1983; Mukai and Kioke, 1984; Dobbs and Guckert, 1988).

Although it is clear that bioturbation can reduce seagrass productivity (Suchanek, 1983), we may speculate that nutrient regeneration could stimulate local productivity of microflora (Rodriguez, 1966) and macrophytes. Others have measured nutrient flux from callianassid mounds and measured benthic productivity on lagoon sands, but ours is the first study attempting to link these processes simultaneously at the same site.

This research took place in a shallow, back-reef environment consisting of coarse calcareous sand located in Gorda Sound near Moskito and Virgin Gorda Islands, British Virgin Islands, the Caribbean (Fig. 1). The ghost shrimp *Callianassa rathbunae* and *Calliax jonesi* dominate part of this area and were the focus of this study. The most distinguishing features of the site were the moon-scape appearance of mounds and pits created by callianassids, and the complete absence of macroalgae and seagrass (Fig. 2). Considering the shallow depth at the site (2–5 meters) and the height of the mounds (50 cm from the peak of mounds to the bottom of pits), wave action would have a continuous tendency to level the relief. One might expect considerable metabolic activity associated with maintaining such features, and that this energy must be supplied by local production or imported organic matter.

Our initial observations led to the following objectives:

1. To measure the flux of dissolved NH_4^+ and PO_4^{3-} directly attributable to callianassid-related activities;

2. To measure benthic community primary production and respiration;

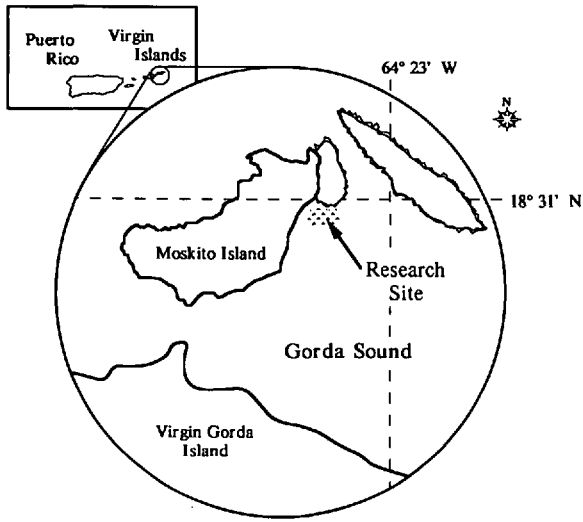

Figure 1. British Virgin Islands and Gorda Sound. Stiple indicates reef and intertidal areas, and arrow designates the subtidal research site.

3. To determine what percentage of community primary production could be supported by ghost shrimp-related nutrient regeneration; and
4. To assess the relative importance of on-site production to that of imported organic matter for ghost shrimp nutrition.

All of our studies took place in the field so as to perturb the natural system as little as possible. We refer to "shrimp-related" effects because flux measurements *in situ* include a suite of processes taking place in the shrimp burrows, in addition to the shrimp's own metabolic activities.

2. Methods

a. Ghost shrimp habitat survey. Surveys were made in July and August 1985 through 1988 by counting the number of mounds and pits created by callianassids within a 1 m^2 quadrat dropped repeatedly in a haphazard manner. A one-way ANOVA indicated there was no significant difference between these years and all data were pooled to estimate mounds and pits per m^2.

Callianassids were captured for identification and observation using a SCUBA tank driven airlift system with a fine mesh bag at its upper end. Because of the extensive burrow system into which shrimp could flee as the air lift tube descended into the sediment, very few shrimp were captured and these data were not indicative of population density. Two species were recovered, *Callianassa rathbunae* and *Calliax jonesi,* but several other species occur in comparable habitats and may have been

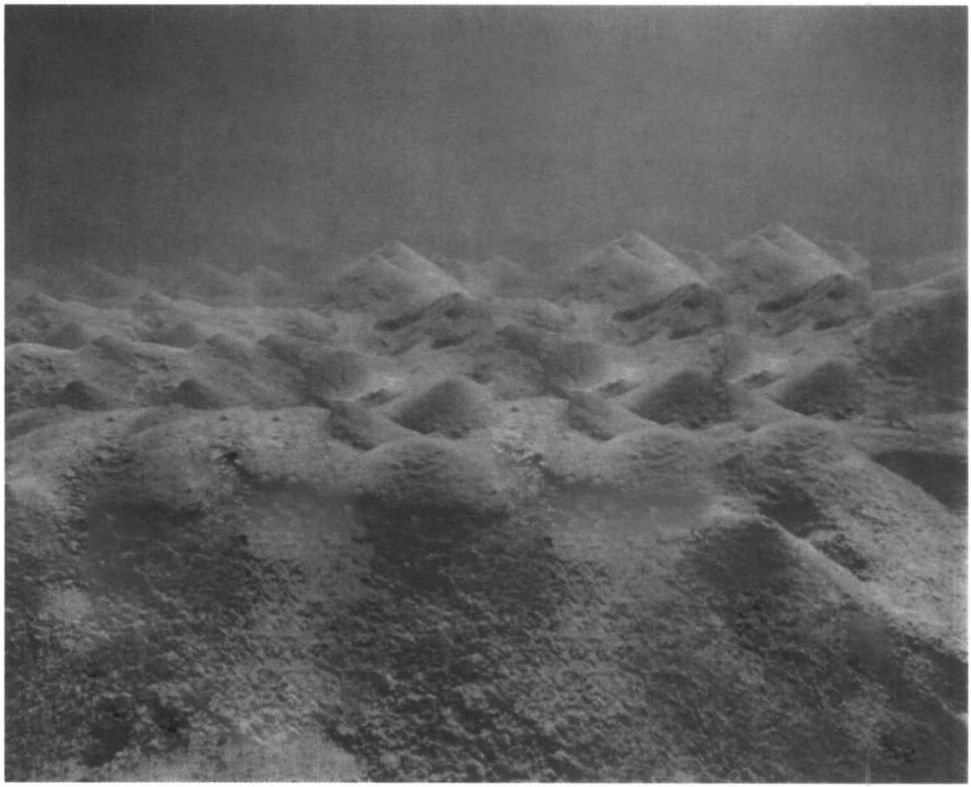

Figure 2. Mounds and pits resulting from the feeding and burrowing activities of callianassid shrimp.

present (Heard, 1989; Suchaneck, 1985). We were not able to differentiate between the burrows of *C. rathbunae* and *C. jonesi* and thus cannot attribute metabolic data below to either one or the other species.

b. Shrimp burrow flux measurements. To determine the water pumping or flushing rate by the shrimp *in situ,* 15 cm diameter plastic funnels were placed over the mounds. The funnels were pressed gently onto the sediment until sand rose to fill the neck of the funnel. A wire bracket was placed over the funnel with one end extending into the sand to hold the funnel in place. The funnel was then left undisturbed for 24 hours to enable the sediment to restabilize and to allow the shrimp to reconstruct the burrow connection to the apex of the mound. Funnels were deployed on up to 45 nearby mounds at a time. These funnels were then monitored for activity over specific intervals of time throughout the day and night. Water and sediment expelled from shrimp burrows were collected in 200 ml Nasco Whirl-pak™ bags attached to the funnels and held tight with a rubber "O" ring. Trial measurements were made to determine the general rate of sediment and water flux so as to adjust the measure-

ment period (3 hours, approximately) and avoid the collection bags becoming completely filled. The volumes of water and sediment were measured, and water samples were analyzed for NH_4 and PO_4. Not all mounds were active (releasing water or sediment), and the percent activity was used to normalize the fluxes according to the number of mounds and % activity $\cdot$ m^{-2}.

c. Community metabolism assessment. Oxygen production and respiration, and nutrient flux (NH_4, PO_4) were measured for the total community in two types of benthic enclosures. Incubations on the intact benthic community employed stainless steel rings which consisted of a circular band of metal 20 cm in height enclosing 1.4 m^2. These were placed firmly into the sediment and sampled at different times over the next few days. Clear and opaque plastic sheets were pulled taut over the rings, secured with surgical tubing, and the enclosed community was incubated for about 3 hours. Although this method has the advantage of measuring rates on the natural community, there is the chance that some shrimp burrows inside a ring were connected to either pits or mounds outside the ring. Measured rates of change would thus be confounded by any water exchanged from outside the ring. Sufficiently large chambers would minimize this effect, and we believe the 1.4 m^2 area was adequate, but we also used complete enclosures (barrels) which avoid this limitation for comparison.

In order to enclose a complete ghost shrimp burrow system with its associated community, as well as to create control systems without shrimp, six 470 L Nalgene plastic food processing barrels were placed in the substrate. The barrels measured 0.9 m deep and 0.8 m in diameter with a flange at the top; they were closed at the bottom thus isolating the sediment and associated community inside. During the summers of 1986 and 1987, sand was excavated and the barrels were buried with the top extending from 20 cm to 40 cm above the normal bottom. The same sand was put back into the barrel. Callianassids were collected and put into three of the barrels (two barrels with one shrimp each and one with two shrimp); the other three barrels were left as controls. Upon being placed in the barrels the shrimp began digging and within minutes disappeared below the surface. The shrimp were allowed to adapt and reconstruct the burrow system for one year before measurements were made. Thereafter the presence of shrimp was confirmed by active pits and mounds within the barrels. Each year three weeks before incubations were begun, all epibiota attached to the barrels was scraped off and removed from inside the barrel. Every week thereafter during the measurement period the surfaces were scoured again. Plastic sheets were used to cover the barrels as described for the rings and similar flux measurements conducted.

The flexible plastic sheets allowed wave action to mix the water inside the chambers. This was confirmed by observing the dispersal of rhodamine dye throughout the chamber and analyzing samples with a fluorometer. Water was collected for

nutrient and oxygen analysis through a plastic tube attached to a nipple fitted through the plastic cover. Dark chambers had aluminum foil wrapped around the tube and nipple to prevent light leakage. A cascade system, which avoided bubble contamination of oxygen samples, was used to fill five 60 ml BOD bottles for each sample.

Water samples from the benthic incubations were fixed in the field for O_2 analysis. Triplicate oxygen samples were titrated using the Winkler method and a microburette (Strickland and Parsons, 1972) or a computer-driven automatic titrator detecting the end-point spectrophotometrically. Samples from funnels and chambers were held in a cool, light tight container in the field, and aliquots were removed for NH_4 and PO_4 on land within 30 minutes of collection. Some water samples were frozen and returned for organic phosphorus analysis by autoanalyzer after oxidation by ultraviolet irradiation (Armstrong *et al.,* 1966). Triplicate 5 ml samples for ammonium and phosphate analyses were analyzed colorimetrically on a spectrophotometer according to Strickland and Parsons (1972). Chlorophyll *a* in sediment samples was determined by spectrophotometric analysis of acetone extracts of 1 cm^3 sediment samples, using the trichromatic equations in Strickland and Parsons (1972). The incubation volume of barrels and rings was determined after the final incubation each year by manually leveling the sediment and directly measuring its distance below the rim of the chamber where the plastic cover had been attached.

d. Stable carbon isotope analysis. The analysis of stable isotopes has been useful in determining food web connections when two or more potential food sources have different ratios of ^{12}C to ^{13}C (Peterson *et al.,* 1985; Rounick and Winterbourn, 1986). Our callianassid habitat survey indicated the two most likely sources of food were blades of sea grass, *Thalassia testinudium,* in various stages of decomposition which had drifted from nearby sea grass beds and microflora on the sediment surface. Qualitative microscopic evaluation of the microflora revealed blue-green algae, *Oscillatoria* and *Spirulina,* pennate diatoms, and benthic foraminifera with symbiotic algae.

In 1987 and 1988 samples of *T. testinudium* blades, sediment microflora and callianassids were collected, dried and sealed for transport. *Thalassia* blades and fragments were divided into aliquots of approximately equal volumes for analysis. Sediments were tested to determine appropriate levels of acidification to remove $CaCO_3$ from micro algae. Samples were pretreated in 1N reagent grade HCl heated to 40–50°C for one hour, allowed to cool to room temperature overnight, centrifuged, washed four times in distilled H_2O to neutrality, and then freeze dried and held for analysis.

For combustion, the sample was put into an inner quartz tube and weighed. Cupric oxide wire pieces and a piece of silver foil (0.05 mm thick) were added. This tube was then inserted into the outer quartz tube along with copper metal granules. This outer

Table 1. Summary of flux data presented in Figure 3. The third column presents the medians converted to daily rates. Initial measurements of ammonium and phosphate were below our level of detection therefore these rates are based on final concentrations only.

	Median ($hour^{-1}$)	Quartiles: (Lower, Upper)	Median (day^{-1})	Number
H_2O ($L \cdot m^{-2}$)	0.26	(0.17, 0.39)	6.2	535
Sediment ($g \cdot m^{-2}$)	12.14	(0.00, 33.45)	291.3	501
NH_4 ($\mu mol \cdot m^{-2}$)	4.1	(2.7, 6.3)	97.4	201
PO_4 ($\mu mol \cdot m^{-2}$)	0.01	(0.00, 0.07)	0.2	201

tube was evacuated overnight to remove air and water, sealed, preheated to 50°C for ½ hour and then elevated to 850°C for two hours. After combustion and cooling, the outer tube was placed in a vacuum line and cracked to introduce all the gas into a glass tube. N_2, CO_2, and H_2O were separated cryogenically. During collection, the combusted tube was heated to 120°C. All gases were collected in a 6-mm glass tube with a Toepler pump, and the amount of each gas was measured manometrically.

Isotope ratio measurements were performed with a Nuclide RMS 6-60 dual-collecting mass spectrometer and a Varian MAT 250 triple-collecting mass spectrometer. The results are presented in the conventional notation

$$\delta^{13}C_{PDB} = \frac{[^{13}C/^{12}C]\text{sample} - [^{13}C/^{12}C]_{PDB}\text{standard}}{[^{13}C/^{12}C]_{PDB}\text{standard}} \times 1000.$$

3. Results

a. Habitat. The area inhabited by callianassids was located between a shallow *Thalassia testudinum* bed at the edge of Moskito Island to the west, a very shallow reef flat to the south and south-east behind Calcahoun Reef, and a sloping sand bottom to the south-east and north inhabited by *T. testudinum* and *Syringodium filiforme.* The depth of the area studied ranged from 2 to 5 meters and water temperature ranged from 29 to 32°C. The density of callianassid mounds averaged $4.4 \cdot m^{-2}$ and mean pit density was $4.8 \cdot m^{-2}$ ($N = 105$).

b. Ghost shrimp activity. The percentage of active mounds (mounds from which water and/or sediment was released during 1 to 7 hour measurement period) was 60%. This value was used to adjust fluxes of water, sediment, NH_4 and PO_4 measured per mound to a m^2 basis. Fluxes of water and sediment from shrimp mounds during the months of July and August 1986, 1987 and 1988 around the diel cycle showed that neither mound activity nor expelled volume was related to time of day nor were these activities significantly different from one year to the next (Kruskal-Wallis $p < 0.05$). None of the flux data were normally distributed as determined by Lillifords test of normality (Wilkinson, 1987). Water flux from the mounds (Table 1, Fig. 3a) tended

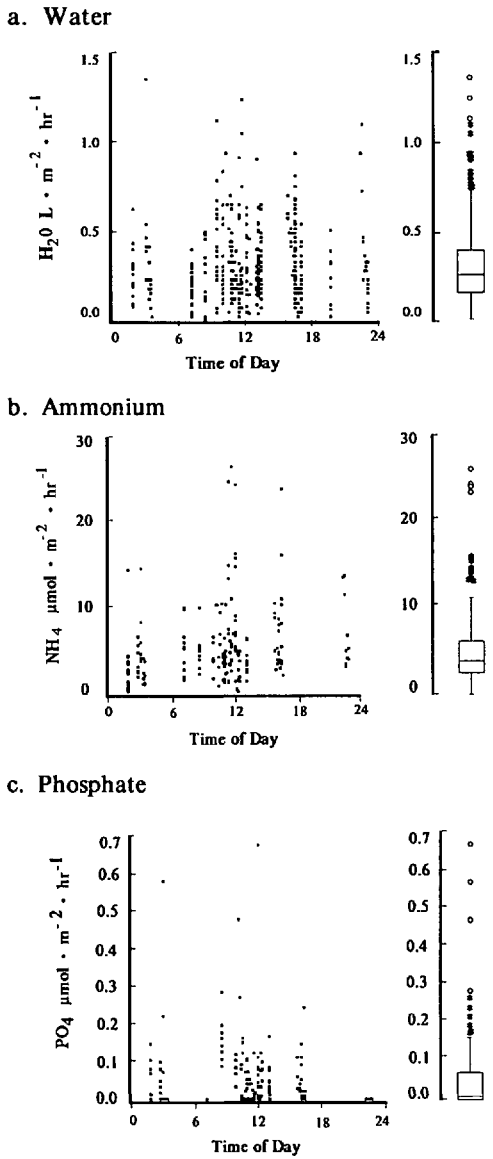

Figure 3. Material fluxes from shrimp burrows: (a) water, (b) ammonium, and (c) Phosphate. Each panel contains a scatter plot of all data through time-of-day (left) and a non-parametric Box and Whisker plot (right). The box represents the median and the upper and lower quartiles (25th & 75th %-ile); whiskers extend to include the range of data up to 1.5 times the upper interquartile distance; asterisks and open dots show data exceeding 1.5 and 3 times the interquartile, respectively (Data Desk, 1988).

to be skewed around the median of 6.24 $L \cdot m^{-2} \cdot d^{-1}$, with more extreme values extending above than below. Median sediment flux was 291 $g \cdot m^{-2} \cdot d^{-1}$.

c. Flux of chemical species.

i. Shrimp mounds. Neither the mass of NH_4 nor PO_4 ejected from shrimp mounds appeared to vary consistently over a diel cycle, although all rates were highly variable (Fig. 3b, c; Table 1). These data were also strongly skewed with median values for ammonium of 97.4 $\mu mol \cdot m^{-2} \cdot d^{-1}$ and phosphate of 0.24 $\mu mol \cdot m^{-2} \cdot d^{-1}$. Thus, the water flowing out of the burrows has a ratio of dissolved N:P of 400:1. Since PO_4 was undetectable in our measurements of ambient water, these data suggest excretion of both N and P by the burrow comunity. However, phosphorus in burrow waters is seriously depleted relative to nitrogen in comparison to the Redfield Ratio of 16N:1P (Redfield *et al.,* 1963) that is typically assumed to support planktonic primary production. This is in sharp contrast to flux ratios in rich temperate sediments where N losses to denitrification typically lowers the benthic flux ratios to 4–8N:1P (Nixon, 1981).

ii. Incubation chambers. As were the data from ghost shrimp mounds, measured fluxes of NH_4 and O_2 within the incubation chambers were highly variable (Fig. 4). These data were normally distributed so parametric statistics were used. NH_4 and O_2 fluxes were not significantly different between barrels with and without shrimp, suggesting shrimp-related flux was small compared to other benthic processes, or that other compensatory changes occurred in the community in the absence of shrimp.

Apparent daytime production measured in the morning, mid-day and in the afternoon, showed no systematic pattern. Dark ammonium flux and respiration were similar throughout the day and night. Rates of production and respiration were greater in barrels than in rings (Fig. 4, Table 2). Gross production was calculated as the sum of the apparent daytime production rate plus the average dark respiration rate (Table 4). The ratio of 12-h P_{gross} to 24-h Respiration was 0.86 and 1.07 for the rings and barrels, respectively. This expression of P:R quantifies the balance of photosynthesis and respiration for the total community on a 24 hr basis, indicating the tendency for net autotrophy or heterotrophy on the days measured.

Even though the barrels were cleaned weekly during the measurement period, it is possible that surface microflora and fauna are the reason for the higher rates of production and respiration. Rings were removed between experiments and thus were not subject to as much fouling. Since the rings more closely represent the natural system, we have chosen to focus on data from the rings. Consequently, ring data indicate that local benthic production could supply about 86% of the energy requirements of the community, although there is considerable variation around this mean value.

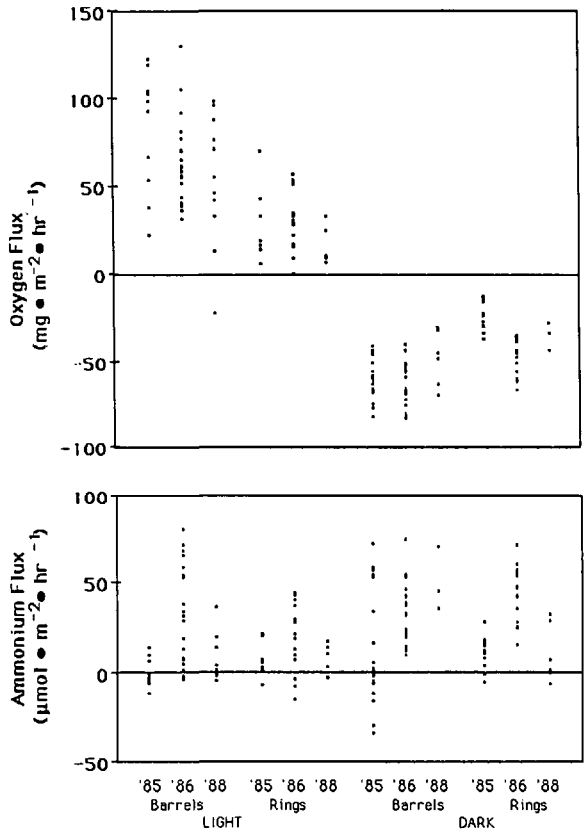

Figure 4. Rates of oxygen and ammonium flux measured in light and opaque incubation chambers. Two types of chambers (barrels and rings) were used during August of 1985, 1986, and 1988.

Table 2. Measured metabolic rates in enclosures (Mean + s.d.)

		Oxygen ($mg\ O_2 \cdot m^{-2} \cdot hr^{-1}$)		Ammonium ($\mu mol\ NH_4 \cdot m^{-2} \cdot hr^{-1}$)	
		Light†	Dark	Light	Dark
Rings	'85	26 ± 22	−24 ± 8	7 ± 10	10 ± 9
	'86	29 ± 17	−47 ± 10	20 ± 19	44 ± 15
	'88	16 ± 11	−34 ± 8	9 ± 7	50 ± 18
Barrels	'85	73 ± 38	−59 ± 12	−5 ± 21	11 ± 30
	'86	63 ± 23	−61 ± 12	28 ± 27	32 ± 15
	'88	56 ± 36	−48 ± 16	6 ± 12	11 ± 16

†O_2 changes in light enclosures are Apparent Daytime Net Production.

Table 3. Pigment concentration in enclosures (Mean + s.d.)

	Chl a ($\mu g \cdot g$ sediment^{-1})	Phaeo ($\mu g \cdot g$ Sediment^{-1})
Rings	2.04 ± 0.27	1.19 ± 0.22
Barrels	1.30 ± 0.54	1.37 ± 0.37

Ammonium generally increased in all enclosures, both light and dark (Fig. 4, Table 2). Phosphate concentrations in barrels and rings remained at the limit of detection and thus fluxes were not calculated. This is noteworthy in view of the readily detectable ammonium changes seen in light and dark barrels and rings.

d. Chlorophyll and stable carbon isotopes. Microalgal pigments were detected 10 cm down into the sediments. Chlorophyll *a* decreased to half of the surface value by 5 cm depth, while phaeopigment varied over similar ranges throughout the 10 cm surface layer. Pigment levels in the rings, which represented essentially natural conditions, were compared with samples from the experimental barrels (Table 3).

Average concentrations in the top centimeter of sediment suggested that chlorophyll *a* was significantly different between rings and barrels (*t*-test) but phaeopigments were not. There was no significant difference in pigment level between barrels with and without shrimp. As mentioned above, it is likely that microalgal growth on the barrel's surface may account for their higher productivity despite lower sediment chlorophyll concentration.

Stable carbon isotope ratios (Table 4) indicate benthic microflora ($\delta^{13}C = -19$) was the source of carbon for callianassids ($\delta^{13}C = -20$), and that carbon fixed by seagrass *T. testudinum* ($\delta^{13}C = -6$) did not contribute substantially to the nutrition of these ghost shrimp.

4. Discussion

a. The callianassid community. Generalizing about callianassid communities is difficult due to large differences in sediment type, species composition, shrimp density,

Table 4. Stable carbon isotope ratios for ghost shrimp, seagrass and microalgae. Seagrass values represent composite samples of many blade fragments in various stages of degradation.

Sample	$\delta^{13}C_{PDB}$ Mean	Range	Number
Calliax jonesi and *Callianassa rathbunae*	−19.17	18.19–23.32	3
Thalassia testudinum	−6.25	6.10–6.39	4
Microalgae	−19.93	16.80–20.57	4

size and behavior. In addition, there are no quantitative data relating the surface evidence of shrimp (pits and mounds) to the number of shrimp per square meter for subtidal habitats. Suchanek *et al.* (1986) measured mound densities greater than 30 m^{-2} in Enewetak Lagoon. Mean mound densities per square meter from 0.1–16 in St. Croix (Suchanek, 1983; Roberts *et al.*, 1981) and 4–7 in French Polynesia (De Vaugelas, 1985) are similar to the 4.5 m^{-2} we observed. None of these data were correlated to numbers of shrimp, although various researchers have implied that there may be one mound per shrimp. Estimates of shrimp density in intertidal habitats are 250 to 500 m^{-2} for *Callianassa australiensis* along the east coast of Australia (Hailstone and Stephenson, 1961), 20 m^{-2} for *C. japonica* at Yamada Bay, Honshu, Japan (Kioke and Mukai, 1983) and up to 8 m^{-2} on the coast of Sao Paulo, Brazil (Rodriguez, 1983). Our collections, while not quantitative, lead us to believe that densities may approximate 4 m^{-2}.

The volume of water expelled from ghost shrimp mounds measured in Enewetak Lagoon was 2.2 $L \cdot mound^{-1} \cdot d^{-1}$ (Colin *et al.*, 1986) and 0.8 $L \cdot mound^{-1} \cdot d^{-1}$ for intertidal ghost shrimp in Japan (Kioke and Mukai, 1983), both considerably lower than our $6L \cdot m^{-2} \cdot d^{-1}$. Other researchers who have measured rates of irrigation or sediment ejection have implied that all mounds are irregularly or generally active during most of the time (Walsenchuk *et al.*, 1983; Colin *et al.*, 1986; Roberts *et al.*, 1981), although Suchanek (1985) indicates that the shrimp may alternate locations of incurrent and excurrent openings as food becomes depleted. In contrast, about 40% of the mounds on which we placed funnels and collecting bags in Gorda Sound did not flush during the period of investigation which ranged from 1 to 7 hours. Although it is possible that placement of the funnel disturbed the shrimp and caused them to create or move to another mound, 3–4 hour underwater observations of undisturbed mounds in Gorda Sound indicated many were indeed inactive for extended periods.

b. Total community metabolism.

i. Production and respiration. The estimates of gross production fall within the wide range of values measured in other tropical lagoons (Table 5). The productivity (P_{gross} = 265 mg $C \cdot m^{-2} \cdot d^{-1}$) indicates substantial microfloral activity in spite of substantial bioturbation. Branch and Pringle (1987) observed no difference in diatom densities in cages with and without *Callianassa kraussi* in South Africa. Based on finding viable diatoms 10 to 40 cm into the sediments they suggest that burial may be compensated by nutrient enrichment at depth and thus permit higher production. Sundback and Graneli (1988) and Gargas and Gargas (1982) have shown that some benthic diatoms are remarkably hardy, remaining viable after four months of darkness in the lab. Some microalgae can survive up to three years in darkness (Anita, 1976). Consequently rapid sediment turnover does not necessarily eliminate a substantial standing crop of benthic microflora nor productivity. We frequently observed distinct brown patches on ejected sediments on the upper slopes of shrimp

Table 5. Comparison of benthic gross production and P:R in tropical lagoons.

Location	Production (Gross) (mg C · m^{-2} · d^{-1})	P:R	Researcher
BVI Back Reef Sediments (rings)	265	0.86	This Study
Enewetak Lagoon Sediment	23	0.95	Harrison, Pers. Comm.
French Polynesia Lagoon Sediment	1–3000	1.5–3.0	Sournia, 1976
Great Barrier Reef Multiple Sites Sediment	1000		Kinsey, 1983
South Africa Langebaan Lagoon Sediment	173–639		Fielding *et al.*, 1988
Belize (Carrie Bow Cay) Lagoon Sand	23–32	0.87–0.77	Hargraves, 1982

mounds indicating microflora blooms possibly from recently recycled microalgae. Overall, however, the production to respiration ratio (P_{gross}:R_{24h} = 0.86) was less than one, so that some additional energy appears to be imported to this system. The rates of change in light and dark incubations show substantial variability, and conclusions about the exact P:R are tentative.

ii. Potential contribution of shrimp-related nutrient regeneration to benthic productivity. Estimating the potential contribution of callianassid-related ammonium and phosphate flux from the sediments to benthic productivity requires knowledge of microfloral nutrient requirements. The Redfield ratio (C:N:P = 106:16:1) predicts that photosynthetic fixation of 106 atoms of carbon would require 16 atoms of nitrogen and 1 atom of phosphorus. Under conditions of nutrient depletion these ratios in diatoms can change, with N:P > 30:1 when phytoplankton are deprived of P and N:P < 10:1 when deprived of N (Redfield *et al.*, 1963; Atkinson and Smith, 1983). This suggests that greater rates of diatom production could be supported by a given nitrogen flux than generally predicted from Redfield ratios.

Ammonium. Using these data we can calculate possible diatom productivity supported by ammonium released from callianassid burrows. Assuming a C:N of 6.6:1, the median flux of 97 μmol N · m^{-2} · d^{-1} (Table 1) could support a productivity of 7.7 mg C · m^{-2} · d^{-1}. Considering the measured primary productivity rate of 265 mg C · m^{-2} · d^{-1} in the rings, shrimp-related ammonium contribution could account for less than 3%. Even if all mounds were active, this would increase the estimated ammonium flux by 40% to give only a 7% contribution by shrimp-related activities. In order to assess the relative contribution of the shrimp themselves through ammonium excretion, we may use the excretion rates measured by Mukai and Kioke (1984)

for another species of callianassid and apply them to the shrimp in Gorda Sound. Assuming one shrimp per mound (average dry weight = 0.3 g) and 4.4 mounds · m^{-2}, we calculate 23.6 μmol NH_4 · m^{-2} · d^{-1} which is only 24% of the flux we measured from the shrimp mounds. Harrison (1981) also found that shrimp metabolism directly contributes less than 10% of the observed total nitrogen flux. Although the species and ecosystems are different, these calculations suggest that shrimp excretion may contribute insignificant ammonium to benthic production. This is supported by our observation that there was no detectable difference in NH_4 or O_2 flux between barrels with and without shrimp.

Phosphate. Bluegreen algae were also an important component of the microflora in this study site. Element ratios are much more variable for this group than in diatoms. Entsch *et al.* (1983) measured C:N:P in benthic bluegreens from the Great Barrier Reef and found 290:42:1 and 420:70:1. Considering the fact that bluegreen algae are important nitrogen fixers in coral reef sediments (Larkum *et al.*, 1988), these algae seem particularly well adapted to survive in a nutrient depleted system, possibly giving them a selective advantage over diatoms.

Since phosphorus is more likely to be the limiting nutrient we can calculate the predicted production of bluegreen algae using the 400:1 ratio of C:P in a tropical lagoon from Entsch *et al.* (1983). With our median flux of 0.24 μmol P · m^{-2} · d^{-1} (Table 1) we calculate 1.15 mg C · m^{-2} · d^{-1} could be fixed. These values indicate that the measured flux of inorganic phosphate could support 0.4% of the observed productivity, 265 mg C · m^{-2} · d^{-1}. Selected samples of burrow water analyzed for organic phosphorus indicate it is unlikely that DOP fluxes would change our conclusions. Consequently, we conclude that the flux of dissolved phosphorus from shrimp mounds is even more limiting than ammonium in supporting primary production, and both are minor contributions to community primary productivity.

Fluxes per square meter. The mean NH_4 rate per m^2 for rings in the dark was 8 times the flux measured directly from the mounds (752 vs. 97 μmol · m^{-2} · d^{-1}; Table 6). This flux (752 μmol · m^{-2} · d^{-1}) represents a productivity of about 60 mg C · m^{-2} · d^{-1}, assuming a C:N of 6.6:1. This flux accounts for only 22% of the measured primary productivity rate of 265 mg C · m^{-2} · d^{-1} in the rings. These observations must be viewed in light of some additional considerations.

Other forms of nitrogen and phosphorus were not measured, such as nitrate, nitrite and organic nitrogen and phosphorus. The diffusion of nitrate and ammonium from sediments was calculated from interstitial concentrations in a Puerto Rican lagoon inhabited by *Callianassa* by Corredor and Morell (1989). Their estimates indicate that nitrate (0.510 μmol · m^{-2} · hr^{-1}) may be as important as ammonium (0.858 μmol · m^{-2} · hr^{-1}), although their sediments were much richer organically than those of this study. If rates were comparable at our site, the nitrogen flux would increase from 97 to 162 μmol · m^{-2} · d^{-1}, which increases the contribution of N required for observed productivity to 35%. In contrast, studies in Enewetak Lagoon

Table 6. Comparison of benthic and shrimp-related ammonium flux in various shallow temperate and tropical systems.

Location	Organism/ System	Concentration μmol $NH_4 \cdot L^{-1}$ (range)	Rate μmol $NH_4 \cdot m^{-2} \cdot d^{-1}$ (range)	Researchers
British Virgin Islands (Back reef)	Ambient Water	0.00		This Study
	Callianassid Flush	15.60 (2–44)	97.4 (4.8–663.8)	
	Sediment Flux (Dark rings)		752 (−125 to +1696)	
Bermuda (Pond)	C. spp.	30 (15–64)		Waslenchuk *et al.*, 1983
	Sediment Pore Water	300–900		
	Pond Water	4.5 (0.6–11.6)		
Japan (Intertidal/ aquarium)	*C. japonica* burrow	11.9, 59.2		Kioke & Mukai, 1983
	Aquarium water	1.24, 3.44		
Japan (Intertidal/ aquarium)	*C. japonica* enrichment in aquarium		118 (.3 g shrimp, 20 m^{-2})	Mukai & Kioke, 1984
St. Croix (Back reef)	Sediment efflux		71.00	Williams *et al.*, 1985
Puerto Rico (Lagoon)	Calculation of sediment efflux in *Callianassa* ssp. bed from pore water concentration	20.6 (diffusion only)	Corredor & Morell, 1989	
Enewetak Lagoon (Lagoon)	Sediment efflux	131	Harrison, Pers. Comm.	

by Harrison (Univ. Hawaii, pers. comm.) indicate that nitrate is unimportant as compared to ammonium. There is relatively little information on organic phosphorus in tropical benthic systems but it would have to be two orders of magnitude greater than the measured phosphate flux to be important, which seems unlikely.

Although it is not the goal of this paper to develop a mass balance for productivity and nutrients in this system, some speculation on other possible sources of nitrogen and phosphorus seems appropriate. Ammonium fluxes measured in our dark rings

exceeded those from the mounds by a factor of eight, suggesting an additional contribution from interstitial sediments. This may be due largely to bacterial regeneration and meiofaunal excretion. Gray (1985) measured ammonium excretion rates of individual meiofauna collected from Great Barrier Reef sediments and then predicted benthic rates based on total standing stocks. Rates as high as 880 μmol $NH_4 \cdot m^{-2} \cdot hr^{-1}$ were predicted.

Regarding our observation that NH_4 flux in the rings could account for only 22% of the measured productivity, it would seem that nitrogen fixation by blue-green algae and ammonium uptake by microflora at the sediment surface may be important. Larkum *et al.* (1988) working on hard and sand substrates on the Great Barrier Reef hypothesized that disturbance and early successional stages may enhance nitrogen fixation as cyanophytes opportunistically develop on newly exposed surfaces. It is also likely that diatoms, bluegreen algae and foraminifera with autotrophic symbionts sequester nutrients excreted by meiofauna before they can reach the water column above even in the dark. Sundbach and Graneli (1988) described such a filter effect for the microphytobenthos in the northeast Atlantic, where increasing light was correlated with decreasing nutrient flux from a soft substrate. Atkinson (1981) has shown there was no release of phosphorus from reef sediments in the presence of algae. And some of our enclosure data showed a tendency for O_2 rates to vary inversely with NH_4. Thus, it is likely that ammonium fluxes measured in chambers are underestimates due to simultaneous microbial uptake of nutrients.

The high adsorption affinity of PO_4 in carbonate sands (Gulbrandsen and Robertson, 1973; DeKanel and Morse, 1978; Rosenfeld, 1979; Krom and Berner, 1980) and the relative amount of measured P to N suggest phosphate may be even more difficult to measure. The relatively few measurements of PO_4 flux and stoichiometry in tropical sediments make speculation on the PO_4 question difficult (Entsch *et al.*, 1983; Powell *et al.*, 1989). Very low concentrations of dissolved inorganic phosphorus do not mean that it is not available to primary producers. Entsch *et al.* (1983) posed the question: "Is it possible that the bulk of P absorbed for algal production is to be found as an integral part of the matrix of the reef?" They showed high concentrations of phosphorus (mean ranges 260–470 ppm by weight) in carbonate sediments after treatment with HCl at 80°C and suggest, as does Smith (1987), that adsorbed phosphorus as apatite may be the source of phosphate for microflora. Craven and Hayasaka (1982) have shown that bacteria in association with *Zostera* can release organic acids which alter the pH in their immediate vicinity and thus increase the solubility of phosphorus. Smith and Gerace (1990) have suggested this might be taking place in *Thalassia* beds where phosphate is a limiting nutrient. Were such a process to occur in benthic microflora, the appropriate measurement to address the question of how bioturbation affects primary production would be to measure the phosphorus in fine particles ejected from the shrimp mounds rather than dissolved phosphate. *Callianassa* has been shown to sort sediments effectively, depositing

larger particles in deep chambers and cycling the smaller ones (Suchanek, 1983; Tudhope and Scoffin, 1984). The greater relative surface area of these fine particles would further increase the potential availability of phosphorous.

Thus it would appear from our data and these speculations that callianassids may not have a significant effect on productivity through dissolved phosphate flux to the water column in tropical systems. However, by turning over sediments containing microalgae, and thus exposing them to nutrients in and bound to the sediments, these ghost shrimp may have a positive effect on benthic productivity.

c. Source of ghost shrimp nutrition. Our final question was whether or not callianassids in Gorda Sound were dependent on drift sea grass or on the resident microflora. The data (Table 2) leave little doubt that *Callianassa rathbunae* and *Calliax jonesi* at our site totally depend on microflora for their energy, either directly or indirectly through an intermediate trophic level such as protozoa feeding on diatoms and bluegreen algae. The fact that some species of *Callianassa* have been observed to feed on drift *Thalassia* and that detritus accumulates in ghost shrimp pits has led some researchers to conclude that *Callianassa* are dependent on external sources of food, particularly since there is little "apparent" evidence of production in the ghost shrimp community (Rodrigues, 1966; Ott *et al.,* 1976). Branch and Pringle (1987) have suggested that *Callianassa* may use detritus as a substrate on which to cultivate microbiota as a source of food. It is inappropriate to generalize from one species to another and possibly even one site to another, since it is probable that many callianassids are opportunistic detritivores. But this study clearly shows that *Callianassa rathbunae* and *Calliax jonesi* can satisfy their nutritional requirement with benthic microflora as the primary source of fixed carbon.

5. Conclusions

We conclude that primary production in this highly disturbed system is generally comparable to that of other Caribbean lagoons, even those not affected by bioturbation. Local production accounts for approximately 86% of the community's energy requirements. *Callianassa rathbunae* and *Calliax jonesi* derive 100% of their nutrition from benthic microflora, either directly or indirectly, rather than drift sea grass. Callianassid-related dissolved nutrient flux only accounts for less than 5% of this system's nutrient requirement. A thorough investigation of the relationship between microflora and sediment-bound phosphorus could greatly improve our understanding of productivity and nutrient dynamics in tropical systems.

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