

Ammonium Excretion by Benthic Invertebrates and Sediment-Water Nitrogen Flux in the Gulf of Mexico Near the Mississippi River Outflow

WAYNE S. GARDNER
*National Oceanic and Atmospheric Administration
Great Lakes Environmental Research Laboratory
2205 Commonwealth Boulevard
Ann Arbor, Michigan 48105*

ELVA ESCOBAR BRIONES
*Laboratorio de Ecología del Bentos
Instituto de Ciencias del Mar y Limnología
Universidad Nacional Autónoma de México
Apartado Postal 70-305
México 04510, D.F.*

ELIZABETH CRUZ KAEGI
GILBERT T. ROWE
*Texas A&M University
Department of Oceanography
College Station, Texas 77843*

ABSTRACT: Benthic macroinvertebrate biomass and ammonium excretion rates were measured at four stations in the Gulf of Mexico near the Mississippi River mouth. Calculated areal excretion rates were then compared to sediment-water nitrogen fluxes measured in benthic bottom lander chambers at similar stations to estimate the potential importance of macroinvertebrate excretion to sediment nitrogen mineralization. Excretion rates for individual crustaceans (amphipods and decapods) was 2–21 nmoles NH_4^+ (mg dry weight) $^{-1}$ h $^{-1}$. The mean excretion rates for the polychaetes, *Paraprionospio pinnata* [6–12 nmoles NH_4^+ (mg dry weight) $^{-1}$ h $^{-1}$] and *Magelona* sp. [27–53 nmoles NH_4^+ (mg dry weight) $^{-1}$ h $^{-1}$], were comparable or higher than previous measurements for similar size benthic or pelagic invertebrates incubated at the same temperature ($22 \pm 1^\circ\text{C}$). Although the relatively high rates of excretion by these selective feeders may have been partially caused by experimental handling effects (e.g., removal from sediment substrates), they probably reflected the availability of nitrogen-rich food supplies in the Mississippi River plume. When the measured weight-specific rates were extrapolated to total areal biomass, areal macroinvertebrate excretion estimates ranged from 7 $\mu\text{mole NH}_4^+ \text{m}^{-2} \text{h}^{-1}$ at a 40-m deep station near the river mouth to 18 $\mu\text{mole NH}_4^+ \text{m}^{-2} \text{h}^{-1}$ at a shallower (28-m deep) station further from the river mouth. The net flux of ammonium and nitrate from the sediments to the water measured in bottom lander chambers in the same region were 15–53 $\mu\text{mole NH}_4^+ \text{m}^{-2} \text{h}^{-1}$ and –25–21 $\mu\text{mole NO}_3^- \text{m}^{-2} \text{h}^{-1}$. These results suggest that excretion of NH_4^+ by macroinvertebrates could be a potentially important component of benthic nitrogen regeneration in the Mississippi River plume-Gulf shelf region.

Introduction

Recycling of organic materials by bacterial mineralization and invertebrate excretion is an important mechanism supplying nutrients to phytoplankton in estuarine and coastal ecosystems (Rowe et al. 1975; Harrison 1978; Hopkinson and Wetzel 1982). In these shallow ecosystems, significant quantities of organic material settle to the sedi-

ments and provide substrates for heterotrophic energy transformations and nutrient regeneration (Zeitschel 1979). Deposited organic matter supports microflora and meiobenthic and macrobenthic communities. The pathways of energy and nutrient flow through these benthic compartments are complex and incompletely understood (Nixon 1981). Similarly, specific information on marine

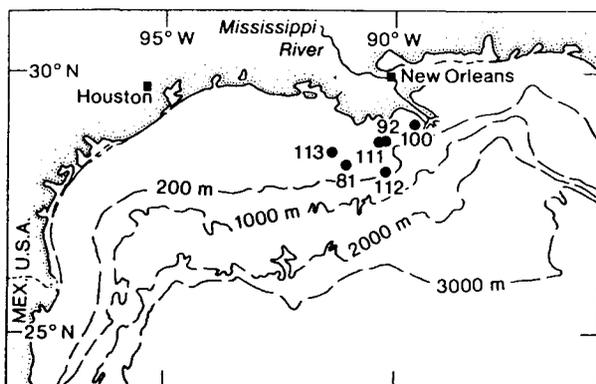


Fig. 1. Map of sampling sites.

macrobenthic process rates is very limited, except for growth and respiration studies (Lopez et al. 1989). Metabolic rates (e.g., respiration and ammonium excretion) of invertebrates can be measured to help explain benthic structure and function, but only minimal information is available about these processes in the Gulf of Mexico. Respiration rates have been measured for macrocrustacea obtained from trawls in the inner and mid-continental shelf of the western Gulf of Mexico (Sanchez et al. 1991; Rosas et al. 1992a, b), and ammonium excretion rates have been reported for some macrocrustaceans on the Cuban continental shelf (Zuniga et al. 1984).

As the primary excretory product of protein catabolism, ammonium accounts for most of the nitrogen excreted by invertebrates (see summaries by Quetin et al. 1980 and Le Borgne 1986). Records on nitrogen excretion rates are very limited for polychaete worms and crustacea that are dominant components of benthic communities in coastal marine environments such as the Mississippi River plume-Gulf shelf region (Gottleson 1976). Information on ammonium excretion rates of these benthic invertebrates is needed both to help understand the life strategies of the animals and to estimate the importance of benthos excretion to the recycling of nitrogen in the Gulf shelf ecosystem.

In this paper, we report ammonium excretion rates for benthic macroinvertebrates and compare estimated areal excretion rates to sediment-water bottom lander flux measurements to estimate the potential importance of macrobenthos excretion to benthic nitrogen regeneration in the Mississippi River plume-Gulf shelf region.

Methods

Macroinvertebrates for excretion measurements were collected during July 1990 from three locations off the coast of Louisiana near the Mississippi River outflow (stations: 100, depth 40 m; 111, depth

28 m; 113, depth 39 m) as part of a research cruise on the Texas A&M RV *Gyre*. A few epifaunal specimens were also collected by trawl from 100 m depth at station 112 (Fig. 1).

Benthic samples for infaunal specimens were collected by a GOMEX box core (Boland and Rowe 1991) or by a Van Veen Grab (station 113). Superficial sediment was sieved through 250- μ m mesh to collect the animals. Epifaunal specimens from site 112 were collected from a 30-min trawl, sorted immediately after the capture, and placed in containers with seawater. Animals were transferred to containers of filtered (0.2- μ m pore size) seawater (FSW), rinsed in a second container of FSW, and then transferred to measured volumes of FSW (usually 5.0 ml for small animals) in glass vials, or plastic zip-lock bags for the large animals. The initial samples for ammonium analysis (1.0 ml each) were taken from the respective vials within 3 min before sample injection, and the injection time was recorded. Because the ratio of water volume to animal size was relatively low for some of the large animals collected by trawl from station 112, water samples from these experiments were diluted 100 times before analysis. Initial analyses for the respective animals in each group were completed within 60–80 min after the animals were removed from the sediments and placed in the incubation vessels. Approximately 2 h after the “initial” sample in a given set was analyzed, the sampling-analysis sequence was repeated, with exact injection times recorded, to provide final “2-h” measurements for excretion rate determinations. Incubations were conducted at room temperature (20–23°C), which was slightly lower than the bottom sediment temperatures (23–25°C). After incubations and final analyses, the animals were placed in aluminum foil packets, frozen, and returned to the laboratory for biomass determination. The samples were transferred to tared aluminum vials, dried at 65°C for 12–18 h, or until constant dry weight was achieved, and weighed on a Sartorius model 1712MP8 analytical balance (0.01 mg accuracy).

Ammonium was measured by high performance cation exchange liquid chromatography with fluorometric detection after post-column reaction with o-phthalaldehyde/2-mercaptoethanol reagent (Gardner and St. John 1991).

Biomass-specific ammonium excretion rates were determined as

$$E = (C_f - C_i) \times V \times DW^{-1} \times (T_f - T_i)^{-1}$$

where E is excretion rate [nmole NH_4^+ ($\text{mg dry weight})^{-1} \text{ h}^{-1}$], C_i and C_f are the initial and final concentrations of ammonium ($\mu\text{M NH}_4^+ = \text{nmole NH}_4^+ \text{ ml}^{-1}$) in the incubation water, V = incubation volume (ml), DW is animal biomass expressed as dry weight (mg), and T_i and T_f are the beginning

and final incubation times (h). Note, because the animals were not axenic, these measurements may include some mineralization of organic nitrogen by microbes associated with the animals in addition to the direct metabolic excretion of ammonium by the animals.

Macrofauna for biomass determinations were collected with a GOMEX box corer (Boland and Rowe 1991). Macrofauna were separated from the sediments and small organisms using a 250- μm mesh sieve and were preserved in 10% buffered formalin. Further separation and identification was done in the laboratory with a dissecting microscope. The wet preserved weight was measured directly and the organic carbon content was assumed to be 4.3% of wet preserved weight (Rowe 1983).

Benthic chamber experiments were conducted using a "benthic lander" (Smith et al. 1976; Smith and Baldwin 1983; Pomeroy et al. 1991) that placed two incubation chambers over the sediment-water interface. Each chamber enclosed a volume of 7.0 l over an area of 906 cm^2 . The enclosed water was mixed by a stirring bar that was in turn powered by an oil-filled electric motor rotating a small magnet outside the chamber. An acoustic command system, including a Benthos model 210 acoustic commandable transponder and a modified Williams Timed Release, was used to initiate multiple burn-wire release latches, lower the chamber after the lander hit the bottom, take a sequence of syringe samples, and drop the anchor weights. One-way valves on the top of each chamber allowed water to escape as the chambers sunk into the bottom. The open bottom rim of each chamber had a sharp edge to allow sediment penetration. After the lander reached the bottom, 15–30 min were allowed for any disturbed bottom sediments to settle before the chambers were completely lowered by acoustic command. The lander was equipped with a video camera, light, and power supply to document proper operation of components. Video camera recordings were coordinated with timed or acoustic manipulations to monitor possible sediment disturbance during chamber lowering, depth and/or success of chamber penetration, syringe withdrawals, or disturbances by large animals. A sensitive hydrophone picked up critical sounds such as acoustic signals, motor drive, weight drops, etc. Hydraulic dampers attached to both ends of the chamber assembly slowed chamber descent onto the substrate and minimized bottom disturbance when the lander hit bottom. The chambers were left on the bottom for predetermined periods of 6–14 h to provide reliable time-series measurements.

Each benthic chamber was equipped with a polarographic oxygen sensor with an internal thermistor, a submersible pump, an additional stirring

motor, and three spring-loaded 60-ml syringes configured to collect filtered (0.2- μm pore size) water samples at timed intervals for later nutrient analysis. Water samples were collected at the beginning, middle, and end of each chamber deployment. Microbial activity in syringe samples during deployment was minimized by drawing the water into the syringes through a 0.2- μm filter. An open syringe needle penetrated each chamber to allow outside water to replace that drawn from the chambers into the syringes, without pulling pore water out of the sediments. A Sea Bird Sealogger SBE 20 powered the two oxygen sensors and submersible pumps and continuously recorded the voltage output data from the temperature and oxygen sensors. The polarographic sensors produced an oxygen-dependent electrical current and were equipped with a manifold to permit active pumping of water directly onto the sensor membranes with minimal fluctuations in flow velocity. The pumps drew water from inside the chambers directly over the sensor membranes. Return flow was directed back into the chamber through a baffle to prevent suspension of bottom sediments. Final concentration of dissolved oxygen was computed using calibration values derived in the laboratory using prepackaged Sea Bird software.

Upon recovery aboard ship, videotapes were viewed to confirm success of the bottom sequence and syringe samples were analyzed for dissolved inorganic nutrients (Technicon Autoanalyzer). Net fluxes of ammonium and nitrate were calculated from concentration changes. Denitrification losses were estimated stoichiometrically from oxygen depletion rates, assuming that the difference between net organic nitrogen degradation rate and inorganic nitrogen ion accumulation rates could be accounted for by denitrification. Net organic nitrogen degradation rates were estimated stoichiometrically from O_2 depletion rates and ammonium accumulation rates. The net organic nitrogen flux due to mineralization was assumed to equal the sum of nitrogen oxidation rate and ammonium accumulation rate. Note, ammonium that accumulated in the chambers represented the portion of remineralized nitrogen that was not oxidized. The net organic nitrogen (and/or ammonium) oxidation rate was estimated from oxygen demand by assuming a ratio of 16 mmole organic nitrogen oxidized to 138 mmole O_2 consumed according to "Redfield" stoichiometry for organic matter oxidation as presented by Jahnke et al. (1982):

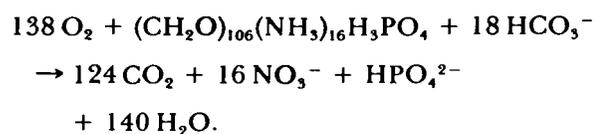


TABLE 1. Mean biomass per individual and biomass-specific ammonium excretion rates for macroinvertebrates sampled from four sites in the Gulf of Mexico. Excretion rate units = [nmole NH₄⁺ (mg DW)⁻¹ h⁻¹].

Species	Number	Biomass (mg DW)		Excretion Rate	
		\bar{x}	SE	\bar{x}	SE
Station 100					
Depth 40 m					
7-21-90					
<i>Magelona</i> sp. (Polychaeta)	7	1.67	0.36	27.0	7.1
<i>Paraprionaspio pinnata</i> (Polychaeta)	4	0.36	0.17	5.9	1.5
<i>Chasmocarcinus mississippiensis</i> (Decapoda)	2	29.6	7.7	15.9	13.2
<i>Speocarcinus</i> sp. (Decapoda)	1	12.43		3.8	
Station 111a					
Depth 28 m					
7-23-90					
<i>P. pinnata</i> (Polychaeta)	7	1.61	0.35	12.6	2.4
<i>Ampelisca abdita</i> (Amphipoda)	1	0.29		5.4	
<i>Ampelisca vadorum</i> (Amphipoda)	1	0.36		3.2	
<i>Tetraxanthus rathbunae</i> (Decapoda)	1	5.94		7.7	
Station 113					
Depth 39 m					
7-24-90					
<i>P. pinnata</i> (Polychaeta)	9	0.52	0.15	11.0	4.3
<i>Magelona</i> sp. (Polychaeta)	4	0.64	0.11	53.1	23.4
<i>Callinassa setimanus</i> (Decapoda)	1	1.43		21.3	
<i>Capitellidae</i> sp. (Polychaeta)	1	8.65		0.7	
Station 112					
Depth 100 m					
7-23-90					
<i>Anasimus latus</i> (Decapoda)	2	2,358	196	4.3	2.0
<i>Nereis</i> sp. (Polychaeta)	1	0.16		1.3	
<i>Pagurus longicarpus</i> (Decapoda)	1	12.81		2.3	
<i>Microcardium peramabile</i> (Pelecypoda)	1	8.31		0.6	

This calculation may provide a slightly conservative estimate of total organic nitrogen mineralization rate because it ignores any conversion of organic nitrogen to inorganic nitrogen under conditions of oxygen deprivation (e.g., during denitrification).

Results

MACROINVERTEBRATE COMPOSITION AND EXCRETION RATES

The polychaetes *Magelona* sp. and *Paraprionaspio pinnata* were the most easily-obtained taxonomic groups of macroinvertebrates from three relatively shallow stations (28–40-m depths) in the Mississippi River plume region where we measured excretion rates (Table 1). On average, individuals of these two species accounted for about 80% of the total number of invertebrates that were collected alive for excretion rate measurements. However, later evaluation of preserved specimens indicated that they constituted a smaller proportion (3–45%) of the total macrobenthic biomass at the respective sampling sites. They may have been preferentially selected from the box core surface-sediments for

excretion rate measurements because of their comparatively large size. We emphasize results from these two species in the discussion below because excretion measurements were replicated for them at the respective stations. In addition, excretion rates were measured for some amphipods, decapods, and a few other species collected at the sampling sites.

Magelona sp. accounted for 38% of the total macrobenthic biomass at station 100 (40-m depth) near the river outflow as compared to 0.9% at station 111 (28-m depth) and 2.6% at station 113 (39-m depth) that were located sequentially further from the Mississippi River outflow (Fig. 1). *Magelona* sp. individuals collected from station 100 for excretion measurements were much larger (1.7 mg DW individual⁻¹) than those obtained from station 113 (39-m depth) further offshore from the plume (0.5 mg DW individual⁻¹) (Table 1). *P. pinnata* accounted for 4.1% and 4.5% of the total macrobenthic biomass at stations 100 and 111a, respectively, but only 0.4% of the total at station 113. The mean weights of *P. pinnata* used for excretion rate measurements ranged from 0.36 mg DW individual⁻¹

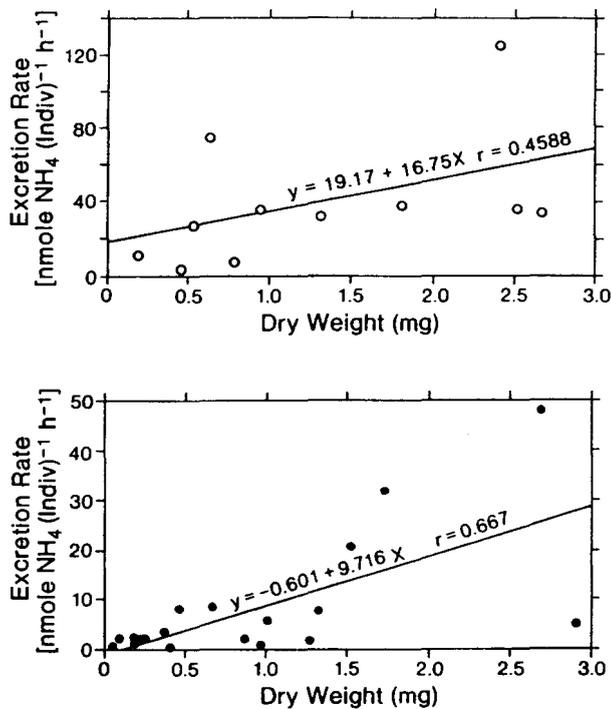


Fig. 2. Ammonium excretion rates for individual Gulf of Mexico polychaetes relative to biomass. (Top) *Magelona* sp. (Bottom) *Paraprionaspio pinnata*.

at station 100 to 1.6 mg DW individual⁻¹ at station 111a (Table 1).

Biomass-specific ammonium excretion rates of the benthic invertebrates varied from <1 to >50 nmole NH₄⁺ (mg DW)⁻¹ h⁻¹ (Table 1). The individual crustaceans (amphipods and decapods) that were examined had rates ranging from 2 to 21 (mean = 8.5, median = 5.4) nmole NH₄⁺ (mg DW)⁻¹ h⁻¹ (Table 1). These rates were not dependent on sampling depth ($r = 0.262$) or animal size ($r = -0.017$). The mean excretion rates for the two major groups of polychaetes were 36.5 nmole NH₄⁺ (mg DW)⁻¹ h⁻¹ [SE = 9.7 (11)] for *Magelona* sp. and 11.8 nmole NH₄⁺ (mg DW)⁻¹ h⁻¹ [SE = 2.8 (15)] for *P. pinnata* when results from the different sites were combined. Although the data were scattered, excretion rates per individual animal were significantly related to biomass for both *P. pinnata* ($r = 0.667$, $p < 0.01$) and *Magelona* sp. ($r = 0.459$, $p < 0.1$) (Fig. 2). However, biomass-specific excretion rates within a species were not significantly correlated with polychaete size (Fig. 3).

SEDIMENT-WATER NITROGEN FLUXES

To examine the potential importance of macroinvertebrate excretion to areal benthic nitrogen regeneration in the region of the Mississippi River plume, we multiplied the mean weight-specific am-

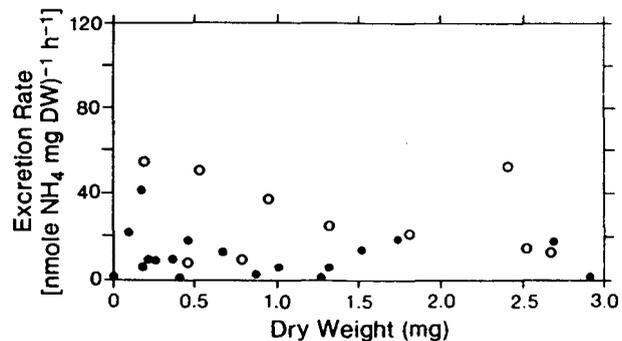


Fig. 3. Relationship of biomass-specific ammonium excretion rates to dry weight for *Magelona* sp. (open circles) and *Paraprionaspio pinnata* (dots).

monium excretion rate for our measured animals times the total areal macrofaunal biomasses for all species at stations 100, 111a, and 113, respectively. Mean excretion rates for all the animals that were measured ranged from 10 to 21 nmole NH₄⁺ (mg DW)⁻¹ h⁻¹ at the three stations (Table 2). The calculated areal excretion rates, based on extrapolating these results to total macrobenthic biomass, ranged from 7 to 18 $\mu\text{mole NH}_4^+$ m⁻² h⁻¹ (Table 2).

Areal oxygen demand and net sediment-water fluxes of organic nitrogen (estimated), ammonium, nitrate, nitrite, and nitrogen gas (estimated by difference), determined with the bottom lander at four Gulf of Mexico stations, are presented in Table 3. Inorganic ion fluxes ranged from about -25 $\mu\text{g atom N m}^{-2}$ h⁻¹ for nitrate at station 112 to 54 $\mu\text{g atom N m}^{-2}$ h⁻¹ for ammonium at site BL1 (20 km east of station 113, Fig. 1). Net organic nitrogen fluxes, as calculated from oxygen demand, ranged from -37.8 to -86.3 $\mu\text{g atom N m}^{-2}$ h⁻¹. However, the "total" organic nitrogen oxidation rates at stations 112 and BL1 were likely underestimated because of photosynthetic oxygen production in the benthic lander chambers. [In contrast to other sites where rates were comparable,

TABLE 2. Mean measured biomass-specific excretion rates ($\mu\text{mole NH}_4^+$ (g DW)⁻¹ h⁻¹), total macrofaunal biomass (g organic carbon m⁻²), and calculated areal excretion rates ($\mu\text{mole NH}_4^+$ m⁻² h⁻¹) for benthic macrofauna at three stations in the Mississippi River plume-Gulf shelf region. n = number sampled.

Station	Depth (m)	Mean Biomass-specific Excretion Rate \pm SD	Total Macrofaunal Biomass	Calculated Areal Excretion Rate
100	40	17.8 \pm 4.6 (14)	0.364	6.7
111a	28	10.3 \pm 1.8 (11)	1.77	18.4
113*	39	22.3 \pm 8.0 (15)	0.381	8.0
Mean		16.5	0.83	11.0

* Sampled for macrofaunal biomass in 1989.

TABLE 3. Sediment-water fluxes of oxygen and nitrogen components in bottom lander chambers. Denitrification (N_2 production) rate was estimated as the net rate of decrease in organic nitrogen (ON) concentration minus the rate of increase in ammonium, nitrate, and nitrite concentrations. The net ON flux was assumed to equal the sum of net ON oxidation rate and ammonium accumulation rate. The ON oxidation rate was calculated from O_2 demand by assuming a ratio of 16 mg atom ON oxidized to 138 mmoles O_2 consumed (Jahnke et al. 1982). Values in parentheses are second estimates for N_2 fluxes that were calculated from net oxygen consumption using an empirical relationship between community respiration and denitrification observed over several aquatic systems (Seitzinger 1990). See text for formula. Calculated net organic nitrogen fluxes are lower than the "total" organic nitrogen fluxes at stations BL1 and 112 because net oxygen depletion rates in the lander chambers were affected by oxygen production due to primary production in these chambers (see text).

Benthic Lander Station (Fig. 1 Station location)	Depth (m)	Oxygen Demand (mmoles O_2 $m^{-2} h^{-1}$)	Nitrogen Flux (μg atom N $m^{-2} h^{-1}$)				
			ON	NH_4^+	NO_3^-	NO_2^-	N_2
BL1 (20 km east of 113)	25	0.28*	-86.3	53.8	21.5	-10.0	21.0 (49.8)
81	53	0.42	-64.4	15.4	8.5	-0.2	40.7 (69.6)
92	29	0.39	-50.3	33.1	-25.4	-1.4	44.0 (65.4)
112	106	0.22*	-37.8	12.3	-10.8	2.1	34.2 (41.2)

* Net O_2 removal rates.

the oxygen uptake rates at these sites were higher in dark, incubated cores (0.63 and 1.98 mmoles O_2 $m^{-2} h^{-1}$) than in the bottom lander chambers (0.22 and 0.28 mmoles O_2 $m^{-2} h^{-1}$ (Rowe et al. unpublished data).] Estimated denitrification rates, reported as N_2 flux, ranged from 21 to 44 μg atom N $m^{-2} h^{-1}$ (Table 3). These denitrification rates, calculated as the difference between estimated net organic nitrogen decreases and inorganic nitrogen ion increases, were on average 62% (SE = 7) of values predicted directly from oxygen uptake rates using an empirical relationship between community respiration and N_2 flux measurements obtained from a variety of aquatic systems [i.e., N_2 flux (μg atom N $m^{-2} h^{-1}$) = $0.071 \times O_2$ flux (μg atom O $m^{-2} h^{-1}$) + 10; based on data from Fig. 3 of Seitzinger 1990] (Table 3).

Discussion

COMPARISON OF GULF OF MEXICO POLYCHAETE AND CRUSTACEA EXCRETION RATE DATA TO PREVIOUSLY REPORTED INVERTEBRATE EXCRETION DATA

An issue that must be considered, when measuring excretion rates by benthic animals, is the possibility that experimental handling, such as removing the animals from their sediment substrate, may affect their excretion rates. For example, respiration rates were increased by about 50% by removing benthic invertebrates from sediment substrates, possibly due to organism stress (Vernberg et al. 1977). In contrast, Lake Michigan benthic invertebrate phosphorus excretion rates were not significantly affected by removal from sediment substrates (Nalepa et al. 1983). Kinetic studies of ammonium release by Lake Michigan chironomids and tubificids indicated that excretion rates usually did not change significantly with time after removal of the animals from their sediment sub-

strates (Gardner et al. 1983). Ammonium excretion rates by *Daphnia* were not affected by stress from the presence of contaminants (Gardner and Miller 1981). Likewise, changing the densities of *Artemia salina* from 200 to 2,000 individuals l^{-1} did not affect biomass-specific ammonium excretion rates (Moffett and Fisher 1978). However, organism activity may affect excretion rates as "excited" white shrimp had higher ammonium excretion rates than resting ones (Foreman 1983). For the purposes of our calculations, we arbitrarily assumed that the absence of a sediment substrate during incubations did not significantly affect the excretion rates of the macroinvertebrates. However, this assumption needs further verification for marine benthic invertebrates.

To place our excretion rate results in a broader context, it is helpful to compare them to previous results for aquatic invertebrates of comparable size. Previous ammonium excretion rate data for marine polychaetes were collected in the Middle Atlantic Bight (Buzzards Bay, Florek and Rowe 1983) and in Danish coastal waters (Blackburn and Henriksen 1983; Henriksen et al. 1983). Rates for four individual polychaetes (Orbiniid) and two amphipods (Haustoriid) from Buzzards Bay, which were incubated at temperatures of 20–25°C, ranged from 4 to 9 nmole NH_4^+ (mg DW) $^{-1} h^{-1}$ (Florek and Rowe 1983). Release rates for the polychaetes *Nereis virens* in "rich sediment" and *Arenicola marina* in "poor sediment" from relatively cold Danish coastal waters were 6.9 ± 1.6 nmole NH_4^+ (mg DW) $^{-1} h^{-1}$ and 2.0 ± 0.03 nmole NH_4^+ (mg DW) $^{-1} h^{-1}$ at 13–15°C if dry weight is assumed to be 10% of wet weight (Henriksen et al. 1983). Polychaetes incubated at temperatures ranging from 5°C to 14°C had mean excretion rates of ca 2–3 nmole NH_4^+ (mg DW) $^{-1} h^{-1}$, whereas other species from the same sediments had rates of 0.3 to 1.5 nmole NH_4^+ (mg DW) $^{-1} h^{-1}$ (as estimated from Fig. 9 of

Blackburn and Henriksen 1983). *Corophium volutator*, and the bivalve *Macoma balthica* had mean excretion rates of 10.4 ± 1.2 nmole NH_4^+ (mg DW) $^{-1}$ h $^{-1}$ and 1.0 ± 0.1 nmole NH_4^+ (mg DW) $^{-1}$ h $^{-1}$, respectively (Henriksen et al. 1983). These excretion rates were similar or lower than our values for *P. pinnata* and *Magelona* sp. but fell within the range of excretion rates that we observed for crustacea (Table 1). Our results for *P. pinnata* were comparable to mean rates obtained for *C. volutator* at 22°C [\bar{x} = 5.66, range = 0.66–24.4 nmole NH_4^+ (mg DW) $^{-1}$ h $^{-1}$ for individuals ranging in weight from 0.1 mg to 1.87 mg (Hawkins and Keizer 1982)]. Our *Magelona* sp. excretion results resemble those obtained for laboratory-cultured *Artemia salina* of similar size (0.77 mg DW individual $^{-1}$) and incubated at 20°C and 25°C [15–42 nmole NH_4^+ (mg AFDW) $^{-1}$ h $^{-1}$ (Moffett and Fisher 1978)]. Mean excretion rates for similar size (i.e., ca 0.5 mg AFDW individual $^{-1}$) freshwater oligochaetes (tubificids) and Chironomid larvae sampled from Lake Michigan and measured at 22°C [5–11 nmole NH_4^+ (mg AFDW) $^{-1}$ h $^{-1}$; Gardner et al. 1983] overlapped with our rates for *P. pinnata* but were lower than our rates for *Magelona* sp. (Table 1).

Our measured mean ammonium excretion rates for *P. pinnata* and *Magelona* sp. [6–53 nmole NH_4^+ (mg DW) $^{-1}$ h $^{-1}$; Table 1], as well as the rate for the decapod *Callinassa setimanus*, were higher than the mean rates that would be predicted from their dry weights [ca 3–6 nmole NH_4^+ (mg DW) $^{-1}$ h $^{-1}$] based on a relationship between excretion rate and animal size, at 22°C, established from more than 200 measurements of marine zooplankton from inshore waters of the Great Barrier Reef (Ikeda et al. 1982). This result was contrary to our presumption that benthic animals would have lower excretion rates than comparably-sized pelagic invertebrates at similar temperatures, particularly if their growth were limited by organic nitrogen supply as has been observed for the marine polychaete *Capitella capitata* (Tenore 1981; Tenore et al. 1982).

Although we cannot exclude the possibility that the high rates observed for *P. pinnata* and particularly *Magelona* sp. may have been caused in part by animal handling, our results suggest that these invertebrates may obtain nutrition from "fresh" food with a relatively low C:N ratio (e.g., algae, bacteria, or microzooplankton) rather than from detritus that is low in nitrogen content. In addition to temperature, salinity, and animal size effects, ammonium excretion rates are affected by food quality (Le Borgne 1986; Regnault 1987). Animals that assimilate food with high available nitrogen content (e.g., animal or plant biomass) have higher biomass-specific excretion rates than those that in-

gest foods with low nitrogen content (e.g., detritus) (Le Borgne 1986). The Gulf of Mexico polychaetes that were sampled near the river outflow may have had a nitrogen-rich food supply from high algal production in the river plume (Lohrenz et al. 1990). In agreement with this hypothesis, the atomic C:N ratio of settling particulate organic matter in the plume was 5.6 in summer and 7.2 in winter (Redalje et al. 1992). Also, *Magelona* sp. and *P. pinnata* are selective feeders (Hunt 1925; Gettleson 1976), whereas *C. capitata* is a nonselective feeder (Fau-chald and Jumars 1979). As a nonselective feeder, *C. capitata* often ingests organic material with a relatively high C:N ratio (Tenore 1981). In agreement with results expected from this difference in feeding strategies, the one relatively large *Capitellidae* sp. individual that was examined in our study had a low excretion rate [0.7 nmole NH_4^+ (mg DW) $^{-1}$ h $^{-1}$] compared to either *P. pinnata* or *Magelona* sp. (Table 1).

The high biomass-specific excretion rate observed for *Magelona* sp. relative to that for *P. pinnata* at station 100 differs from the expected inverse relationship between biomass-specific excretion rate and organism size (Bigadare 1983). However, as a selective feeder (Hunt 1925) that eats small animals as well as detritus and diatoms (Mare 1942; Jones 1968), *Magelona* sp. may select food with a C:N ratio that is low relative to the food ingested by *P. pinnata*. As mentioned above, *Magelona* sp. was much more abundant at station 100, near the river outflow, than was *P. pinnata*.

SEDIMENT-WATER NITROGEN FLUXES AND POTENTIAL CONTRIBUTION OF INVERTEBRATE EXCRETION

Our measurements for inorganic nitrogen ion fluxes (Table 3) were comparable to previous results for coastal marine systems (Blackburn and Henriksen 1983; Henriksen et al. 1983; Jensen et al. 1990; Pomeroy et al. 1991). As expected, ammonium fluxes in these Gulf of Mexico shelf sediments were generally lower than values reported for eutrophic estuarine sediments (Nixon et al. 1980; Callender and Hammond 1982; Fisher et al. 1982; Nowicki and Nixon 1985) but higher values reported for deep-sea sediments (e.g., Smith et al. 1978).

Denitrification rates were not measured directly in this study, but the relatively close agreement between the two methods of estimating N_2 fluxes from O_2 uptake measurements (Table 3) suggests that our estimates of organic nitrogen flux, based on oxygen uptake and ammonium accumulation rates, are reasonable. The tendency of our calculated estimates for denitrification to be lower than the values obtained by the empirical comparison

(Seitzinger 1990) could be due in part to the fact that inorganic nitrogen produced by breakdown of organic nitrogen during denitrification was not included in our estimates of organic nitrogen oxidation obtained from measured oxygen uptake rates. Also, some N_2 could possibly have been produced from the oxidation of reduced sulfur compounds with nitrate as the terminal electron acceptor (Fenchel and Blackburn 1979). Alternatively, it may reflect site differences in labile C:N ratios or indicate that the oxidation rates of organic carbon and nitrogen were not exactly proportional to the relative contents of these elements in the organic matter.

Quantifying excretion rates of benthos and relating them to areal biomass provides insights into the importance of macrobenthos excretion to inorganic nitrogen regeneration in shelf sediments (Blackburn and Henriksen 1983). Although the physical effects of animal bioturbation on the release of nutrients out of the sediments have been studied (Aller 1982; McCall and Tevesz 1982), the direct role of macrobenthos excretion in the total remineralization process has often been overlooked. This process should be considered because, in some situations, excretion by infaunal invertebrates is sufficient to account for much of the ammonium flux from the sediments (Henriksen et al. 1983).

Areal excretion rates, based on extrapolating mean biomass-specific excretion rates to total areal biomass at our Gulf of Mexico sites (Table 2), were similar to areal excretion rates reported for benthic animals at several stations in Danish coastal waters ($9\text{--}27 \mu\text{mole NH}_4^+ \text{m}^{-2} \text{h}^{-1}$; Blackburn and Henriksen 1983). Animals from our deeper (39-m and 40-m depth) stations had higher weight-specific excretion rates than animals from station 111a (28-m depth), but the total macrofaunal biomass was much higher at station 111a ($1.77 \text{ g organic carbon m}^{-2}$) than at the other two stations ($0.36\text{--}0.38 \text{ g organic carbon m}^{-2}$; Table 2). Thus, despite relatively low biomass-specific excretion rates, the high areal macroinvertebrate biomass resulted in high areal ammonium excretion rates at station 111a.

Comparing the ranges of calculated areal excretion rates (Table 2) to those of the net fluxes of ammonium and nitrate in the bottom lander chambers (Table 3) indicates that macroinvertebrate excretion could account for a significant, although generally not dominant, fraction of benthic nitrogen regeneration at some sites in the Mississippi River-Gulf shelf region. For example, areal macroinvertebrate excretion rates at station 111a (Table 2) could account for more than one half of the measured flux of ammonium and up to approxi-

mately one third of the calculated organic nitrogen removal rate including estimated denitrification (Table 3) observed at a nearby site (station 92, Fig. 1). Similarly, benthic invertebrate excretion accounted for about 9% to 40% of total sediment water nitrogen flux at two sites (45 m and 100 m deep) in southeastern Lake Michigan (Gardner et al. 1987). Comparison of the mean areal ammonium excretion rates (Table 2) to organic nitrogen flux measurements for comparable stations that did not exhibit measurable photosynthesis (i.e., stations 81 and 92, Table 3) suggests that macroinvertebrate excretion could potentially account for about 45% of the measured ammonium flux or up to about 20% of the calculated organic nitrogen removal rates. Valid estimates could not be made for the chambers with measurable photosynthesis because observed net oxygen demand and nutrient fluxes would underestimate the actual turnover rate of organic nitrogen.

Conclusions

Although excretion rate data for benthic animals must be interpreted with caution because of possible animal handling effects, our results indicate that excretion rates for Gulf of Mexico polychaetes and crustacea collected at stations "downstream" from the Mississippi River plume were comparable or higher than those previously reported for other benthic or pelagic invertebrates of comparable size and at similar temperatures. They were also higher than rates observed for a few epifaunal individuals collected at station 112 that was deeper and more removed from direct plume effects (Table 1). In agreement with previous results from Danish coastal waters, comparison of calculated areal excretion rates with bottom lander results suggests that ammonium excretion by macrofauna can sometimes account for a significant fraction of sediment nitrogen regeneration. If our measured values accurately reflect excretion rates in nature, the relatively high rates of ammonium excretion observed for some Gulf of Mexico polychaetes, particularly *Magelona* sp., as compared to other aquatic invertebrates of similar size and at the same temperature, could indicate that these animals are ingesting nitrogen-rich food materials. Primary production rates (Lohrenz et al. 1990) and concentrations of chlorophyll and particulate organic nitrogen (López-Veneroni and Cifuentes 1992) are highest at intermediate salinities in the plume. Rapid settling of "high-quality" organic matter (Redalje et al. 1992) to the sediments, combined with primary production at the sediment-water interface (Rowe et al. unpublished data), may provide nitrogen-rich food that can be effectively

used and partially recycled by macrobenthic animals.

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