

RATES AND EFFECTS OF BIOTURBATION BY INVERTEBRATES AND FISHES AT ENEWETAK AND BIKINI ATOLLS

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ABSTRACT

Over 50 species from seven phyla of invertebrates have been identified as infauna from within lagoon sediments at Enewetak Atoll. These infauna, as well as representatives from at least 15 families of mobile fishes, disrupt the soft benthos and contribute to the process of sediment mixing. Callianassid shrimp and hemichordate worms (enteropneusts) appear to have the greatest impact, both visually as well as quantitatively (i.e., in terms of depths and rates of bioturbation). Three different field techniques were used to measure rates of sediment processing by callianassids and/or enteropneusts at Enewetak and Bikini Atolls. For some individual callianassid mounds, sediment production exceeded 1,300 cc/day; some individual enteropneusts could process over 700 cc/day. Mean estimates per m² yielded rates as high as 800 cc/m²/day for callianassids and ca. 600 cc/m²/day for enteropneusts. Although callianassids are known to alter the grain size distribution of sediments, we have observed that enteropneusts do little, if any, sorting and consequently do not appear to alter sediment grain size in their environment. The potential consequences of massive bioturbation and mixing of lagoon sediments is discussed in light of long-lived transuranic radionuclide elements that are deeply buried in the lagoon. Deep bioturbation provides a mechanism whereby these radionuclides are pumped to the sediment/water interface and this process could facilitate their re-entry into higher level marine food chains.

Bioturbation by a wide variety of organisms is well recognized as a significant factor in disrupting and mixing sediments (Ginsburg and Lowenstam, 1958; Hulsemann and Emery, 1961; Rhoads, 1967; 1970; Shinn, 1968; Rhoads and Young, 1971). However, not until relatively recently have we begun to fully appreciate the implications of this process for marine ecosystems, both on the physical regime (Ott et al., 1976; Myers, 1977a; Jumars et al., 1981; Nowell et al., 1981; Suchanek, 1983) as well as on aspects of community ecology (Rhoads and Young, 1970; Aller and Dodge, 1974; Myers, 1977b; Brenchley, 1981; Suchanek, 1983).

Most bioturbators exist at or near the sediment/water interface. Some organisms, however, such as certain callianassid shrimp and enteropneusts typically burrow into sediments to depths of 2 m or more and not only disrupt sediment layers at these levels, but often excavate this deep material, mixing it with surface sediments (Pemberton et al., 1976; Suchanek, 1983; Suchanek et al., 1986). This process has serious implications when these buried sediments contain potentially hazardous materials such as long-lived transuranic radionuclides (Noshkin, 1980; McMurtry et al., 1985; 1986) or toxic pollutants. In three other papers in this volume we report on 1) the concentrations of radionuclides at depth within the lagoon sediments at Enewetak Atoll (McMurtry et al., 1986), 2) the influence of callianassid shrimp on the redistribution of those sediments (Suchanek et al., 1986) and 3) the resuspension of sediments in the form of fine particulate matter in the water column (Colin et al., 1986).

Here we report on specific rates of bioturbation at Enewetak Atoll by callianassid shrimp and enteropneusts. In addition, we identify a wide variety of other organisms, both invertebrates and fishes in this ecosystem capable of disrupting and

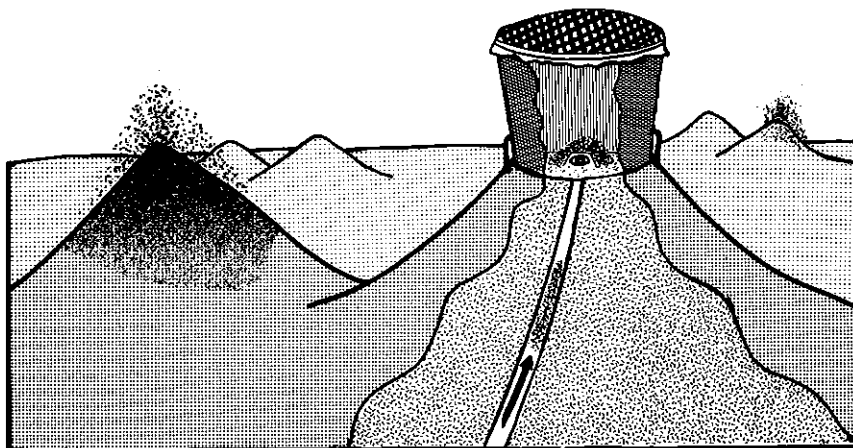


Figure 1. Diagram of sediment collection bucket in place on flattened callianassid mound. Cut-away view through mound and bucket shows route of fine-grained sediments being pumped out of burrow.

mixing sediments in the lagoon. Finally, we discuss the broad implications of such bioturbation activities on the redistribution of long-lived radionuclides buried deep within the sediments and the potential consequences of such processes to community ecology, including the human ecology of the Marshallese people who have recently returned to Enewetak Atoll.

METHODS

Lagoon sediment bioturbation rates at Enewetak and Bikini Atolls were determined using three techniques. First, sediment production for callianassid shrimp only was measured by capturing ejected sediment from mounds in buckets with a 4-cm hole cut into the bottom of each bucket. With the aid of SCUBA each bucket was placed over the flattened top of a callianassid mound and secured with wire stakes (Fig. 1). Gauze mesh was fitted over each bucket to prevent influx or efflux of sediments or disturbance by mobile fauna. After 12–24 h sediment samples were collected, placed in sealed plastic bags, poured into graduated cylinders in the laboratory and after 1 h of settling, the volume of each sample was determined. Normally about 6 replicates were run concurrently for each collection period at water depths of 10–30 m. Only callianassid mounds > 5 cm in height were used for these estimates. See Suchanek et al. (1986) for details of burrow morphologies and densities of large (> 5 cm high) and small (< 5 cm high) mounds within the lagoon.

A second method was used to determine volumes of sediment processed by all bioturbators (including callianassid shrimp) operating at the sediment/water interface. Fixed 1.85 × 1.85-m aluminum quadrats were placed haphazardly over the sediment surface at depths of 20–30 m. For each run, two replicate quadrats were placed about 10 m apart, and all sediment was leveled to the top of each quadrat frame using a long piece of angle iron run back and forth over the frame. For each run, frames were left in place for up to 4 days and at 24-, 48-, 72-, 96-h intervals the amount of sediment processed was determined by measuring the size of positive features (e.g., mounds and/or castings) and negative features (e.g., pits or depressions) on the sediment surface. Because these features very closely resembled either positive or negative cones, the diameter and height of each feature was measured and later converted to volumetric values by use of the formula for the volume of a cone and subsequently totalled for the entire frame. Frames were repositioned over new areas for each run.

A third method was used for enteropneusts only. By direct observation with the aid of SCUBA, divers measured the length and diameter of castings being produced over 30- and 60-sec intervals. These measurements were taken at 15 m water depth off Enewetak Island (refer to Colin et al., 1986 for location map). Grain size analyses for enteropneust castings were performed using the techniques of Folk (1974).

The density of infaunal sediment dwellers was determined by placing replicate 6.25-m² black plastic sheets (0.004-inch thick) on the sediment surface with the aid of SCUBA. These were sealed by weighting the edges with sand and a 1.0-lb packet of rotenone powder was dispersed under each sheet. After 4–

Table 1. Densities of sediment infauna collected by rotenone tarp experiments (values given have been normalized to estimates of per m² abundance).

Taxa	(# spp.)	Water depth (m)			
		20	17	7	3
Annelida					
Polychaeta	(5-10)	2.2 ± 0.1	2.7 ± 0.7	—	—
Sipunculida	(ca. 6)	2.2 ± 1.0	2.0 ± 0.2	—	—
Mollusca					
Bivalvia	(>3)	1.1 ± 1.1	2.1 ± 0.4	—	—
Gastropoda	(>10)	3.5 ± 0.4	2.3 ± 0.6	—	—
Arthropoda					
Callianassids	(5-10)	50.0 ± 5.8	54.8 ± 2.1	1.1 ± 0.7	0.1 ± 0.1
Stomatopods	(??)	3.3 ± 2.9	2.8 ± 1.3	—	—
Misc. crabs	(ca. 3)	3.7 ± 1.5	1.3 ± 0.2	—	—
Misc. shrimp	(??)	1.1 ± 0.6	3.1 ± 2.1	—	—
Echinodermata					
Echinoidea	(1-3)	>10.0 ± 5.7	>32.5 ± 14.9	—	—
Ophiuroidea	(1)	0.3 ± 0.4	0.1 ± 0.1	—	—
Hemichordata					
Enteropneusta	(3-4)	1.1 ± 1.1	0.9 ± 0.1	—	—
Chordata					
Vertebrata (fish)	(??)	2.3 ± 1.6	1.9 ± 1.5	—	—
Cephalochordata (lancets)	(1)	>"1,000"	—	—	—

24 h the sheets were carefully rolled back and the dead or moribund organisms which evacuated the sediments immediately underneath were collected by hand. Due to the time/depth limitations using SCUBA it was impossible to collect all individuals of some infaunal groups (e.g., lancets, echinoids), so only representative samples were collected for those groups. For major bioturbators we attempted to collect all individuals of those groups. Density estimates of the infauna collected in this manner necessarily underestimated the true numbers because: a) not all fauna evacuated the sediments, and b) some few individuals inevitably were impossible to collect because they escaped and drifted off into the water column as the sheets were rolled back.

RESULTS

At least seven phyla of macrofauna utilize, process or disrupt sediments within the lagoons at Enewetak and Bikini Atolls. Table 1 represents the results of the rotenone sheet collections at different lagoon depths. These values have been normalized to abundance per m² and show that callianassids represent by far some of the most abundant infauna. The species identification of the callianassids as well as many of the other sediment infaunal groups is poorly known. Here we present preliminary results of the identification of some of the more influential invertebrate bioturbators (especially the callianassids and enteropneusts) and some of the more important fish that disrupt these sediments.

From seven callianassid specimens collected at Enewetak in 1981 by P. L. Colin and D. M. Devaney and identified by M. de Saint-Laurent, we have at least four different species, each in a separate genus and all from the family Callianassidae (*Callianassa* sp., *Calliax* aff. *C. novaebritanniae* (Borradaile), *Callichirus vigilax* (de Man) and *Thomassinia* sp.). Since that time we have collected several more species, but identification of these specimens is incomplete at this time. Because

of the diameter and depth of the burrows, we feel it is most likely that we still have not yet captured the callianassid species responsible for the larger mounds (i.e., > 5 cm high) in the lagoon. Attempts at resin casting (Suchanek et al., 1986) and air-lifting have shown burrows extending well beyond 1–2 m below the sediment surface. In addition, the diameter of several resin-casted burrows reaches 37 mm (mean = 29.4 ± 4.4 mm), indicating a resident shrimp size much larger than we have ever collected.

Several small enteropneusts collected at Enewetak lagoon and identified by M. G. Hadfield were all found to be *Ptychodera flava* Eschscholtz (family Ptychoderidae). Several other larger individuals were collected by means of airlifting equipment and by manual digging. Because of the inherent difficulty in collecting whole specimens, identification of these fragmented individuals to the specific level was not possible; however, at least two other species of enteropneusts were identified to the familial level. One species was another member of the Ptychoderidae (but not *P. flava*) and the other was a member of the Spengelidae (most likely *Spengelia*).

At least four species of sipunculids from Enewetak lagoon have been identified by S. J. Edmonds. These are represented by *Sipunculus indicus* Peters, *Sipunculus* sp. (but not *S. indicus*), *Siphonosoma (Damosiphon) cumanense* (Kerfstein) and *Paraspidosiphon johnstoni* Edmonds. Since then it appears that at least two other as yet unidentified species have been collected from these sediments.

One other invertebrate group that very likely has a substantial impact on bioturbation of near-surface sediments at Enewetak is the Echinoidea. Herds of the spatangoid urchin, *Maretia planulata* (Lamarck), process massive amounts of sediment and can become locally very abundant (100–200/m²) usually in the summer and fall (V. S. Frey, pers. comm.). *Maretia* was quite abundant in the rotenone sheet collections, but not all individuals were collected in each run so Table 1 reflects only minimum values for *Maretia*.

Several species of fishes at Enewetak and Bikini are especially influential in disrupting sediments during their normal course of feeding, seeking shelter or avoiding predators. Table 2 lists these fishes by families and the nature of their contribution to bioturbation of lagoon sediments. Although it is clear that fishes have a significant effect on mixing sediments, especially near the sediment/water interface, we have as yet no conclusive bioturbation rates for these groups.

Field estimates of bioturbation rates were collected for callianassid shrimp and enteropneusts. Table 3 gives individual sediment processing rates for callianassid mounds and/or enteropneust castings using three methods of estimation. For callianassids producing large mounds (> 5 cm high) the sediment collection buckets (Fig. 1) yielded individual sediment pumping rates as high as 780 cc/mound/day. However, estimates using the leveled frames produced values nearly twice that (1,390 cc/mound/day), although this is more likely due to random positioning of the frames over an especially active region rather than any real differences in the techniques themselves. The mean values for the two methods are not significantly different at $P = 0.05$ (t -test, Sokal and Rohlf, 1969) and both appear to increase from the May to the August collections, although that increase is only statistically significant for the leveled frame experiment (at $P < 0.01$).

Large enteropneusts have sediment processing rates comparable to large callianassids at Enewetak when compared on an individual basis (Table 3). However, the absolute bioturbation impact by each group is obviously dependent on their respective population densities. The leveled frame experiment was designed specifically to obtain population effects on measured areas in order to determine relative contribution of various bioturbators. In Figure 2 total daily sediment

Table 2. Fishes that disrupt sediments at Enewetak Atoll. Key to mode of disturbances: A, live in permanent burrows or permanently under the sediment surface; B, live in semi-permanent burrows; C, withdraw or bury into sediment at night to sleep; D, withdraw or dive into sediment with the approach of danger; E, dig large pits in sediment to excavate prey items; F, dive into sediment after prey items; G, process or filter sediment for food

Common name	Family	Species	Mode disturbance	Approximate bioturbation depth (cm)
Gobies	Gobiidae	<i>Amblygobius phalaena</i> (Cuvier and Valenciennes)	A	1-3
	Gobiidae	<i>Valenciennea</i> spp. (6 spp. known from Enewetak)	A	1-3
Sand tilefishes	Malacanthidae	<i>Malacanthus</i> spp.	A	?
Snake eels	Opichthidae	<i>Brachysomophis</i>	A	ca. 30-40
		<i>Myrichthys</i>		
		<i>Callechelys</i>		
		<i>Cirricaecula</i>		
		<i>Leiruanus</i>		
		<i>Phyllophichthus</i>		
		<i>Schimorhynchus</i>		
		<i>Schultzidia</i>		
Worm eels	Moringuidae	<i>Moringua</i> spp.	A	ca. 30-40
Garden eels	Congridae	<i>Heteroconger hassi</i> (Klausewitz and Eible-Eibesfeldt)	B, C, D	?
	Congridae	<i>Gorgasia</i> sp.	B, C, D	
Wrasses	Labridae	<i>Cheilinus undulatus</i> Rüppell	C, F	7-10
	Labridae	<i>Cheilinus unifasciatus</i> (=rhodochrous)	C, F	1-3
	Labridae	<i>Coris</i> spp.	C, F	1-3
	Labridae	<i>Hemigymnus</i> spp. (2 spp. known from Enewetak)	G	3-5
	Labridae	<i>Stethojulis</i> spp.	G	3-5
(razorfishes)	Labridae	+ others	G	3-5
	Labridae	<i>Xyrichtys</i> spp.	D	10-15
	Labridae	<i>Cymolutes</i> spp.	D	10-15
Eagle rays	Mylobatidae	<i>Aetobatus narinari</i> (Euphrasen)	E	15
Stingrays	Dasyatidae	<i>Dasyatis</i> sp.	E	15
	Dasyatidae	<i>Taeniura melanospilos</i> Blecker	E	15
Bonefish	Albulidae	<i>Albula glossodonta</i> (Forsskål)	F	?
Sand divers	Trichonotidae	<i>Trichonotus</i> sp.	F	10-15
Emperors	Lethrinidae	<i>Lethrinus</i> spp.	F	3-5
	Lethrinidae	<i>Gymnocranius</i> sp.	F	3-5
	Lethrinidae	<i>Monotaxis grandoculis</i> (Forsskål)	F	3-5
Mojarras	Gerreidae	<i>Gerres</i> spp.	G	3-5
Mulletts	Mugilidae	<i>Chaenomugil</i> sp.	G	3-5
	Mugilidae	<i>Chelon</i> sp.		
	Mugilidae	<i>Crenimugil</i> sp.		
	Mugilidae	<i>Liza</i> sp.		
	Mugilidae	<i>Valamugil</i> sp.		
Surgeonfish	Acanthuridae	<i>Acanthurus</i> spp.	G	3-5
	Acanthuridae	<i>Ctenochaetus</i> spp.	G	3-5
Goatfishes	Mullidae	<i>Parupeneus</i> spp.	G	8-10
	Mullidae	<i>Mulloidis</i> spp.	G	8-10

production on an area basis is given for data from the leveled frame experiment for 10 separate runs, 6 at Enewetak and 4 at Bikini (open bars in June). Data from each individual run are connected by a solid line at the base of the histogram bars. Note that total sediment production was measured at Bikini, but information on the relative contribution of different bioturbators was not. The ordinate on

Table 3. Sediment production rates for individual callianassid mounds and enteropneust castings

	Collection buckets cc/day (N) (maximum)	Leveled frames cc/day (N) (maximum)	Direct observation cc/minute (N) (maximum)
Large Callianassids (mounds ≥ 5 cm high)			
Enewetak—May 1981	344 \pm 200 (13) (725)	387 \pm 101 (12) (567)	—
Enewetak—Aug 1981	417 \pm 263 (9) (780)	690 \pm 340 (10) (1,390)	—
Bikini—June 1982	332 \pm 154 (15) (612)	—	—
Small Callianassids (Mounds < 5 cm high)			
	—	4 \pm 12 (535) (151)	—
Large Enteropneusts (Mounds ≥ 5 cm high)			
	—	432 \pm 167 (6) (733)	55 \pm 28 (29) (106)
Small Enteropneusts (Mounds > 5 cm high)			
	—	11 \pm 10 (30) (52)	—

the right is a calculated conversion to demonstrate equivalent depths to which the sediment would be bioturbated if all sediment processed were spread evenly across the surface. While bioturbation obviously occurs much deeper than is indicated by this value, the turnover rate does represent a useful heuristic measure for comparison purposes.

Relative contributions to bioturbation by callianassids and enteropneusts vary widely. This high variability may be dependent upon placement of the experimental frame in an environment highly variable in densities of callianassids and/or enteropneusts. In addition, very little is known about the natural history of the enteropneusts and it is very possible that they could be continually burrowing laterally through a region, causing large differences between days in any one run. Or their activity level may vary greatly from day to day. The relative contribution of large callianassids to total sediment production ranged from 0–98% for any given day; for small callianassids this value was 0–100%; for large enteropneusts it was 0–78% and small enteropneusts contributed 0–69%.

Although on the average they have the capacity to process equally as much sediment as callianassids, enteropneusts generally contribute much less to total bioturbation in Enewetak lagoon because their densities are considerably lower than those of callianassids. In addition, the larger, more influential enteropneusts were found almost exclusively in water depths shallower than about 30 m and data from the leveled frame experiment revealed their densities to be about $0.31 \pm 0.31/\text{m}^2$ during the May runs. None of the large enteropneusts was observed in the August or October runs, although they were seen in the lagoon during these periods. Also, during MAKALII dives #81-28 and #81-36 we never identified any structures in the deep lagoon (30–55 m) as enteropneust castings. Therefore, relative to callianassids, enteropneusts appear to make a minor contribution to total bioturbation within the lagoon. However, where they become locally abundant, they can even overshadow the influence of callianassids (Fig. 2).

Close association between enteropneusts and callianassid populations have been noted for Enewetak (Suchanek et al., 1986) as well as for the U.S. Virgin Islands (Suchanek, 1983). At times, enteropneusts will obtain and process sediment from callianassid burrows as evidenced by colored sediments which had been experi-

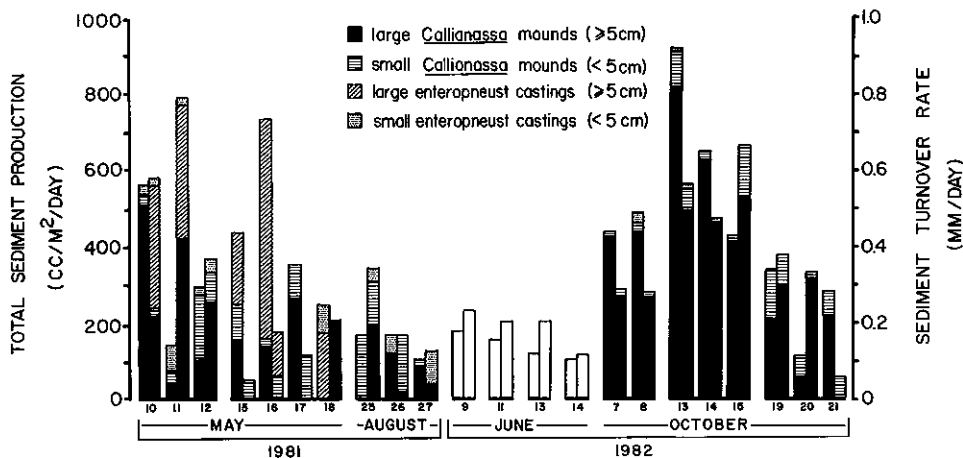


Figure 2. Rates of sediment production for callianassids and enteropneusts derived from the leveled square experiments. Each run of 2-4 days is connected by a solid line at the base of each set of bars. Shaded bars are runs from Enewetak. The four runs with open bars in June 1982 represent estimates from Bikini.

mentally seeded into callianassid burrows turning up in nearby enteropneust castings (Suchanek et al., 1986 for details). Whether there is any cooperation between these two groups remains unknown.

In contrast to callianassid bioturbation, enteropneusts do not appear to modify the nature of sediment grain sizes. Where callianassids will pump fine-grained sediments and tend to store coarse-grained material, enteropneusts from the same region at Enewetak appear to have virtually no effect on grain size. Figure 3 shows the grain size distribution of typical sediments found on the surface (i.e., those available to enteropneusts) and that of enteropneust castings, showing virtually the same size distribution for each. The mechanism of sediment movement and processing is also very different in the two groups. Callianassids may be unable to move larger particles either because of a size restriction through mound openings, or because particles may be too heavy to pump with pleopod currents. Enteropneusts, on the other hand, extract organics from large volumes of ingested sediment and appear able to pass virtually all size fractions encountered through their digestive tract.

DISCUSSION

Virtually nothing is known about the dynamic processes of the soft benthos of any Micronesian atoll, Enewetak included. We feel that we have barely scratched the surface in determining the magnitude of influence of bioturbation on this system, both in terms of its physical and its biological impact. Our preliminary findings indicate that bioturbation at Enewetak and Bikini by both invertebrates and fishes is a significant and ongoing process. Similar bioturbation in the Caribbean has been shown to 1) contribute significantly to sediment transport in shallow lagoons (Roberts et al., 1982) and 2) control the distribution of seagrass beds and thereby have second and third-order effects on other nearby ecosystems that are energetically tied to these plant communities (Suchanek, 1983). Although there are no seagrasses at Enewetak, large regions of the lagoon floor are covered by the calcareous green algae *Halimeda* spp. or *Tydemania expeditionis* Weber van

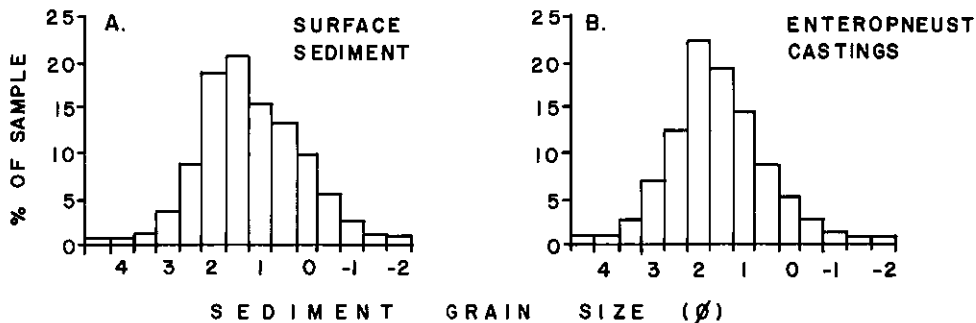


Figure 3. A) Typical grain size distribution of naturally occurring surface sediments off Enewetak Island. B) Grain size distribution of fecal castings from large enteropneusts in same region as A showing virtually no selective sorting or change in grain sizes after processing by the worms.

Bosse (Gilmartin, 1960; 1966; Hillis-Colinvaux, 1977; 1980). As yet we do not know what relationship (if any) exists between *Halimeda* and/or *Tydemania* distributions and callianassid shrimp or other bioturbators.

Our results do clearly indicate that the most dramatic impact, both visually and quantitatively (in terms of bioturbation depth and processing rates) derives mostly from the activities of callianassid shrimp, with significant contributions from hemichordate worms and some fishes. Given the high concentrations of transuranic radionuclides at various depths within sediments at Enewetak that we have reported elsewhere (McMurtry et al., 1985; 1986), and the high densities of organisms capable of substantial rates of bioturbation that we present here, we speculate that mixing and redistribution of these long-lived radionuclides must be continually occurring not only within the lagoon at Enewetak, but in other lagoons where radioactive fallout has also occurred such as Bikini and Rongelap Atolls (Welander, 1969; Robison et al., 1982).

In McMurtry et al. (1985; 1986) we have shown that some of the highest radionuclide levels are found associated with extremely fine-grained sediments. We have also shown that at least some species of callianassids tend to pump the finer grained sediments to the surface while storing coarse-grained particles at depth (Suchanek, 1983; Suchanek et al., 1986). Bringing these deeply buried radionuclides to the sediment/water interface could facilitate their re-entry into marine food chains and potentially pose special dangers for native Marshallese people who consume abundant marine resources such as fish, turtles, crabs and lobsters (USDOE, 1979; 1982; Robison et al., 1982). However, at this time we do not know if, or to what extent, such facilitation occurs. Noshkin (1972) has shown that algae, and specifically the calcareous green algae such as *Halimeda*, tend to selectively uptake and concentrate radionuclides such as $^{239+240}\text{Plutonium}$ from the surrounding medium at concentration factors of up to 32×10^4 . One major herbivore on algae at Enewetak is the green turtle *Chelonia mydas* (Linnaeus). We suggest that top carnivores and large herbivores such as *Chelonia* that are potential human food resources should be examined more carefully to determine if the facilitation described above is a significant process within the contaminated atolls.

There remains much to be learned about the dynamic processes involved with bioturbation of the soft benthos in the Marshall Islands. Our preliminary findings leave many important questions unanswered such as 1) Are populations of enteropneusts linked energetically or in some other ways to those of callianassids?

And if so, is this relationship an important factor in the redistribution of radio-nuclides? 2) What quantitative contribution do mobile fishes make to overall bioturbation within these atoll lagoons? 3) How are permanent subsurface infauna (e.g., those species captured in the rotenone sheet experiments) contributing to sediment mixing? and 4) Of greater consequence, are any of these bioturbators facilitating re-entry of deeply buried radionuclides back into marine food chains? And, if so, what is the ultimate fate of these elements once they are remobilized?

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