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Spatiotemporal Size-Class Distribution of *Turbanella mustela* (Gastrotricha: Macrodasyida) on a Northern California Beach and Its Effect on Tidal Suspension[1]

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ABSTRACT: The size-class distribution of the marine interstitial gastrotrich *Turbanella mustela* Wieser was analyzed at a high-energy beach in northern California. Five 100-μm size classes, each corresponding to a particular sexual phase of the species, fluctuated in percentage abundance at both temporal and spatial scales. On average, the most abundant size classes over the 3-day period were the 100–199-μm group (prereproductive juveniles) and the 200–299-μm group (male phase). Significant differences were evident spatially, where aggregations at the vertical and horizontal level contributed to patchy size-class distributions. Members of the largest size class (postreproductive or male phase) were in low abundance, and juveniles and reproductive individuals made up the bulk of the population. The smallest size class (100–199 μm) was most aggregated in the top 5 cm of sand and differed significantly in percentage abundance from all other size classes at that depth. This size class is also the only size class to decrease significantly in percentage abundance on a vertical scale and increase in percentage abundance on a horizontal scale. Three hypotheses accounting for the observed size-class variations are entertained: sexual phase stratification, interspecific interactions, and intraspecific trophic relations. All three hypotheses are important for understanding the importance of these size-class aggregations and may lead to a better understanding of the factors that influence local spatial patterns in gastrotrichs. Size-class stratification may also function in the planktonic dispersal of individuals in both tidal and longshore directions, ultimately affecting the geographic distribution of the species.

THE PHYLUM GASTROTRICHA is a small and enigmatic group of microscopic metazoa common to the benthic interstitial environment. Interstitial habitats contain faunas with conspicuous morphological features not characteristic of the larger macrofauna (Swedmark 1964, McIntyre 1969). The body plan of the Gastrotricha exemplifies many of these unique features such as a dorsoventrally flattened body, a thick and often ornamented cuticle, and prominent adhesive organs. The dimensions of the interstitial environment impose obvious limitations on the size and shape of its fauna, and many animals display evidence of convergent evolution in both morphology and life-history patterns (Giere 1993). Reproductive and developmental adaptations to this unique habitat often include hermaphroditism, unique methods of sperm transfer and copulation (see Ruppert 1978), reduced egg number, and direct development (Giere 1993). The latter adaptation is hypothesized to be a potential impediment to gene flow between widely separated populations because these animals are all exclusively benthic and rarely actively enter the water column. Furthermore, the interstitial metazoa are morphologically and behaviorly adapted to remain benthic through the use of adhesive structures and negative phototaxis. Such adaptations cross both systematic and

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ecological boundaries (marine, freshwater, phytal [Giere 1993]).

Despite their ubiquitous distribution in most freshwater and marine biotopes, gastrotrichs are rarely reported from such habitats on the Pacific coast of North America (Wieser 1957, 1959, Hummon 1966, 1969, 1972, Todaro 1995). The high-energy beaches on the northern California coastline are home to many species of meiofaunal-sized invertebrates including numerous species of Gastrotricha. Preliminary observations suggest that many species on this coast are also found elsewhere in the world. Such cases of cosmopolitanism appear to be common for the microscopic metazoa (Sterrer 1973, Ruppert 1977).

Several studies have implicated passive erosion and active migration from the substratum as leading causes for meiofaunal dispersal (Hagerman and Rieger 1981, Fegley 1987, 1988, Armonies 1988, 1990, Hicks 1988, Palmer 1988*a,b*). Plankton tows often net suspended meiofauna, including the rather poor-swimming gastrotrichs (Gerlach 1977: appendix). Yet, there exist few reports of suspended meiofauna from areas where wave action is relatively high, such as exposed sand beaches, where the likelihood for passive dispersal should also be high (Boaden 1968, Rieger and Ott 1971). The intertidal distribution and abundance of many meiofaunal animals are undoubtedly related to their potential for wave-borne suspension and dispersal (Bell and Sherman 1980, Service and Bell 1987). This has yet to be demonstrated for the Gastrotricha.

Before attempting to address this issue, we have to remind ourselves of the biology and ecology of *Turbanella mustela*. This macrodasyid species is a small (100–550 μm) yet highly vermiform worm equipped with four groups of adhesive tubules: dorsal, ventral, lateral, and caudal. Locomotion in all gastrotrichs is usually by mean of ventral cilia; body musculature and adhesive tubules are used during escape responses (backing up) and for adhering to the substratum. *Turbanella mustela* is an alternating, sequential, protandric hermaphrodite whose sexual phase coincides with five 100-μm ontogenetic size classes. The stimulus to change sexual phase is unknown, but may be linked to the length of the body or some other factor. Feeding behavior is unknown, but I have witnessed feeding on diatoms in laboratory conditions. This species has been reported from the upper intertidal at a beach in Puget Sound, Washington (Wieser 1957, 1959), and from a single beach in Humboldt County, California (Hochberg 1998); *T. mustela* may be common on the high-energy beaches of northern California. This study adds further evidence implicating passive erosion as an important contributor to changing spatial distributions of meiofauna and further implicates size-class zonation as an important part of the process for marine Gastrotricha.

MATERIALS AND METHODS

Study Site

Gastrotrichs were collected from the intertidal zone of Freshwater Beach (124° 06′ W, 41° 16′ N), a high-energy marine beach in Humboldt County in northern California. The beach faces west and is highly exposed to swell action from the north and west. Meter-high and larger waves break offshore on sandbars and then reconverge directly on the shoreline. These waves create a negative slope to the beach, especially around the low tide line (first few meters of the beach). Approximately 30 m landward from the low tide line is a longshore bar. Landward of the bar is a shallow trough that functions to collect water and associated debris during times of extreme high tide.

Gastrotrich Location and Extraction

A transect 75 m long was established perpendicular to lower low water (LLW, 15 cm) on 15 July 1996 and sampled at each 10-m interval to the high tide line (+256 cm). Three cores (79.6 cm^3 per core) were taken at each 10-m station (0, 10, 20, 30, 40, 50, 60, 70 m) to a depth of 15 cm. Each core was sectioned into three vertical subcores (0–5, 5–10, 10–15 cm) upon removal from the substratum. A total of eight stations was sampled, each station consisting of three cores; each core consisted of three subcores, for a total of 72 subcores. This procedure was repeated for two more consecutive days, giving a total of 216 subcores. The samples were analyzed at the Telonicher Marine Laboratory in Trinidad, California.

Gastrotrichs were extracted from the subcores using an anesthetization-decantation technique with 7.5% $MgCl_2$ solution isotonic to seawater (Ruppert 1988). A 63-µm sieve was used to collect gastrotrichs from the suspension, and they were subsequently washed into a bowl with seawater. Subcores from the same station and depth were combined to increase the number of gastrotrichs per sample and ease the extraction process.

Gastrotrichs were kept in bowls of ambient seawater for 3 hr before further extraction and enumeration to allow for the formation of large multisize class aggregations (cf. Boaden 1985). A glass pipette was then used to extract a set number of individuals from the center of an aggregation. Size-class distribution was estimated by counting the following numbers of gastrotrichs from each of three depths: 200 individuals at meter stations 0, 10, and 20; 100 individuals at station 30; the total individuals from three replicate subcores at stations 40, 50, 60, and 70. The number of gastrotrichs used was dependent on the number available, with the lower elevations often having several thousand individuals and the middle to high elevations having very few. All extracted individuals were placed immediately into a separate bowl of 7.5% $MgCl_2$. Gastrotrichs were measured on a compound microscope (Olympus CH-2) equipped with an ocular micrometer. Five 100-µm size classes were defined beginning with the smallest individuals: 100–199, 200–299, 300–399, 400–499, 500–599 µm. Each size class corresponds to a particular sexual phase of the species as discussed later.

Planktonic Gastrotricha and Sediment Erosion/Accretion

A plankton net (63-µm mesh) was used to collect gastrotrichs from the water column of a tidal surge. Plankton samples from 10 ebbing and 10 flooding tidal surges were collected. Collections came from the 5-m elevation, approximately midway between LLW and the highest flooding surge at the time of collection. The net remained in the water until the flow stopped for the increasing or receding surge. Care was taken to avoid pushing the net into the sand, thereby causing animals to become dislodged from the sediment and washed into the net. The contents from all ebbing and flooding tides were pooled into two containers and observed within 2 hr.

Measurements of sand erosion and accretion were also taken at the 5-m elevation. A meter stick was placed into the sand and the depth of the meter stick was recorded before and after each tidal surge. The difference between the original depth and the final depth showed either a subtraction of sand from that elevation or an addition of sand to it. Three sediment cores were also taken from the zero and 10-m elevations to account for the fauna that may be eroded from these elevations by the surges.

Data Analysis

SigmaStat (Jandel, copyright 1992) was used for all statistical purposes. Population size structure was estimated using percentage data, so the data were arcsine transformed as suggested by Sokal and Rohlf (1981) before testing. However, this failed to normalize much of the data set, so nonparametric tests were used (Mann-Whitney rank sum test and Spearman rank-order correlation analysis). The Student-Newman-Keuls multiple comparison procedure was used to test for differences between data sets.

RESULTS

Horizontal and Vertical Size-Class Distribution

The 3-day abundance of each size class was recorded for all depths and stations (Table 1) and correlated with distance from

TABLE 1

Horizontal and Vertical Size-Class Abundance Data for the 3-Day Sampling Period

	0 m			10 m			20 m			30 m			40 m			50 m			60 m			70 m		
	DEPTH (cm)			DEPTH (cm)			DEPTH (cm)			DEPTH (cm)			DEPTH (cm)			DEPTH (cm)			DEPTH (cm)			DEPTH (cm)		
	0–5	5–10	10–15	0–5	5–10	10–15	0–5	5–10	10–15	0–5	5–10	10–15	0–5	5–10	10–15	0–5	5–10	10–15	0–5	5–10	10–15	0–5	5–10	10–15
	100–199 μm*			100–199 μm			100–199 μm*			100–199 μm*			100–199 μm			100–199 μm			100–199 μm*			100–199 μm		
Mean	49	27	22.3	35.3	12.3	7.8	46.5	29.4	16.1	47.3	23.7	19.8	84.3	38.6	16.3	58.7	47.3	43.9	81.4	61.1	12.1	80	53.2	52.8
SD	5.1	4.0	5.4	17.3	9.8	4.9	11.9	6.7	6.7	8.8	4.3	3.9	27.1	10.5	4.6	21.6	25.4	37.7	20.2	5.2	4.3	34.6	45.3	41.1
	200–299 μm			200–299 μm			200–299 μm			200–299 μm			200–299 μm			200–299 μm			200–299 μm			200–299 μm		
Mean	32.2	32.7	26.5	34.3	27	29.3	28.5	57.7	52.9	29.5	44.4	38.3	37	34.5	24.2	43.5	36.7	44.1	48.9	34.4	55.5	55.7	41	38.9
SD	7.52	8.4	6.6	4.0	4.4	13.3	14.9	6.8	24.6	3.9	6.2	16.6	4.4	15.9	14.1	3.0	11.5	33.3	1.9	5.8	16.9	5.1	36.6	34.7
	300–399 μm			300–399 μm			300–399 μm			300–399 μm*			300–399 μm			300–399 μm			300–399 μm*			300–399 μm		
Mean	10	23.8	23.8	21.2	30.5	41.3	19.6	9.3	27.3	4.2	25.6	30.6	0	26.9	40.1	5.6	17.1	12	0	4.5	15	0	4.4	5.3
SD	4.0	10.8	14	9.4	13.8	6.0	2.1	5.2	12.5	7.2	1.5	13.5	0	23.8	3.0	9.7	29.7	20.7	0	4.4	10	0	4.0	3.8
	400–499 μm			400–499 μm			400–499 μm			400–499 μm			400–499 μm			400–499 μm			400–499 μm			400–499 μm		
Mean	7.8	9.17	20.7	9.2	28	18	5.7	0	3.7	0	6.3	5.0	0	0	19.4	0	0	0	0	0	0	0	0	0
SD	5.2	3.8	8.3	5.0	11.5	11	4.7	0	6.4	0	10.9	8.6	0	0	16.9	0	0	0	0	0	0	0	0	0
	500–599 μm			500–599 μm			500–599 μm			500–599 μm			500–599 μm			500–599 μm			500–599 μm			500–599 μm		
Mean	1.2	4	6.7	0	0.8	3.8	0	0.4	0	0	0	6.3	0	0	0	0	0	0	0	0	0	0	0	0
SD	1.3	1.7	8.3	0	1.4	5.0	0	0.6	0	0	0	10.9	0	0	0	0	0	0	0	0	0	0	0	0

*Indicates significant differences in size-class abundances among depths (Mann-Whitney, $P \leq 0.015$).

TABLE 2

SPEARMAN RANK-ORDER CORRELATIONS BETWEEN MEAN SIZE-CLASS ABUNDANCE (3-DAY MEAN) AT THREE TIDAL HEIGHTS FOR ALL THREE DEPTHS

		SIZE CLASS				
	Depth	100–199 μm	200–299 μm	300–399 μm	400–499 μm	500–599 μm
Tidal height	0–5 cm	0.413	−0.174	−0.776	−0.820	−0.460
Tidal height	5–10 cm	0.526	0.097	−0.465	−0.700	−0.659
Tidal height	10–15 cm	0.330	0.268	−0.274	−0.642	−0.540

NOTE: Significance for all at $P < 0.05$.

LLW (Table 2). Significant differences were evident between vertical abundances at individual stations. The smallest size classes of *Turbanella mustela* were the most abundant over the 3-day period. The percentage abundance of these classes was highly variable along the length of the transect. The 100–199-μm size class was nearly always present at each of the eight stations and was either the dominant or the subdominant group when all horizontal stations were taken into account.

100–199-μm SIZE CLASS. Whole-transect abundance of this size class was significantly higher than that of the 300–399-, 400–499-, and 500–599-μm size classes ($P < 0.05$). Median abundance at the 0–5-cm depth (50.5%) differed from that at the 5–10-cm depth (29.7%) and the 10–15-cm depth (19.3%) (Mann-Whitney rank sum test, $P < 0.002$). At all depths, abundance of this size class was positively correlated with distance from LLW ($r \geq 0.330$, $P < 0.005$). Significant differences also existed among 3-day mean abundances at four separate stations along the transect (Table 1). This size class was always significantly more abundant at the 0–5-cm depth than any other size class ($P < 0.001$).

200–299-μm SIZE CLASS. Whole-transect abundance was significantly higher than that of the 300–399-, 400–499-, and 500–599-μm size classes ($P < 0.05$). No significant differences ($P \geq 0.123$) in median abundance existed among depths for the length of the transect: 0–5 cm (39.5%), 5–10 cm (36.5%), and 10–15 cm (38.9%). Also, no significant difference existed among depths at any of the individual stations along the transect ($P = \geq 0.160$ for all stations). The abundance at all three depths was positively correlated with distance from LLW, but only abundance at the 0–5-cm depth was strongly so ($r = 0.763$, $P < 0.005$).

300–399-μm SIZE CLASS. Whole-transect abundance differed significantly from that of the 500–599-μm group ($P < 0.05$). Median abundances were significantly lower at the 0–5-cm depth (0.0%) compared with the 5–10-cm depth (15.0%) and the 10–15-cm depth (31.8%) ($P \leq 0.031$). Two stations displayed significant differences between depths. At all depths, this size class was negatively correlated with distance from LLW ($r \geq -0.458$, $P < 0.005$).

400–499-μm SIZE CLASS. This size class was rarer than the previous size classes at most stations and depths. No significant differences in median abundance existed among depths for the length of the transect ($P \geq 0.241$): 0–5 cm (0%), 5–10 cm (0%), and 10–15 cm (0%). No significant differences existed among depths at any of the individual stations along the transect ($P = \geq 0.133$ for all stations). Abundance at all depths was negatively correlated with distance from LLW ($r \geq -0.642$).

500–599-μm SIZE CLASS. This size class had the lowest overall abundance at any of the depths and stations for the length of the transect. These individuals were rarely seen and when found were usually in the deepest sand layers. No significant differences ($P \geq 0.408$) in median abundance existed among any of the three depths for the length of the transect: 0–5 cm (0%), 5–10 cm (0%), and 10–15 cm (0%). No stations displayed significant differences among depths ($P \geq 0.368$ for all stations). Abundance at all depths was negatively correlated with distance from LLW ($r \geq -0.460$, $P < 0.005$).

Sediment Erosion/Accretion and Planktonic Metazoa

Eighty percent of the 15 sediment measurements showed a loss of sediment from the immediate area. The loss ranged from 0.5 to 2.5 cm per tidal surge, with an average loss of 0.90 cm per tidal surge. Seventy percent of the surges resulting in a loss of sediment took away less than 1 cm of sand, with 30% of the surges removing one or more centimeters of sand. Three flooding surges deposited sand, with a mean gain of 0.67 cm of sand per surge. For the 15 total measurements, an average of 0.58 cm of sand was eroded away.

Fauna was recorded from both the plankton and the 0-m and 10-m elevations (Table 3). *Turbanella mustela* made up 59% (16) of the total planktonic animals (27) caught in the flooding tides. Measurements of the 16 individuals revealed that 13 were within the 100–199-μm size class and three were within the 200–299-μm size class. *Turbanella mustela* made up 38% of the plankton in the ebbing tides. All individuals were within the 100–199-μm size class.

DISCUSSION

As noted by Kern and Bell (1984), there is a paucity of data on spatial and temporal size-class heterogeneity of meiofauna. As for the planktonic occurrence of gastrotrichs, studies have noted it either in passing (Boaden 1968) or as part of a well-designed experiment (Hagerman and Rieger 1981). In this study, both spatial and temporal variation in size-class structure of a gastrotrich population was readily apparent on a high-energy sand beach and could be indirectly linked to the sexual condition of the species, biotic factors in its environment, and its potential for passive dispersal.

All size classes of *Turbanella mustela* fluctuate in percentage abundance between depths, horizontal elevations, and days. The smallest individuals (100–199 μm) are nearly always the numerically dominant size group at the surface depths and increase in relative abundance toward the high-tide line. The 200–299-μm size class is also readily abundant and even exceeds the smallest size class in mean percentage abundance at the deeper

TABLE 3

METAZOA FOUND IN THE SEDIMENT AT TWO STATIONS AND THOSE FOUND SUSPENDED IN THE WATER COLUMN

METAZOA	METER 0	METER 10	EBBING TIDE	FLOODING TIDE
Annelida				
Syllidae	16	16	1	0
"Archiannelida"	8	3	0	0
Crustacea				
Harpacticoida	3	1	7	4
Nauplii	228	331	1	0
Gastrotricha				
Turbanella mustela	644	2,980	6	16
Chaetonotida	2	0	0	0
Mollusca: Gastropoda				
Veliger larvae	0	1	1	0
Nematoda	136	155	1	5
Platyhelminthes				
Turbellaria	41	34	0	2

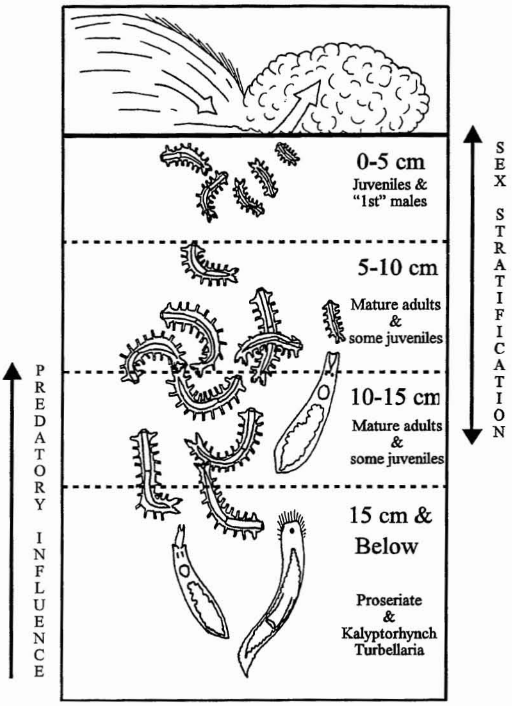

FIGURE 1. General size-class stratification of *Turbanella mustela* at Freshwater Beach and two hypotheses that may account for this vertical zonation: sex stratification and predatory influence of turbellarian flatworms.

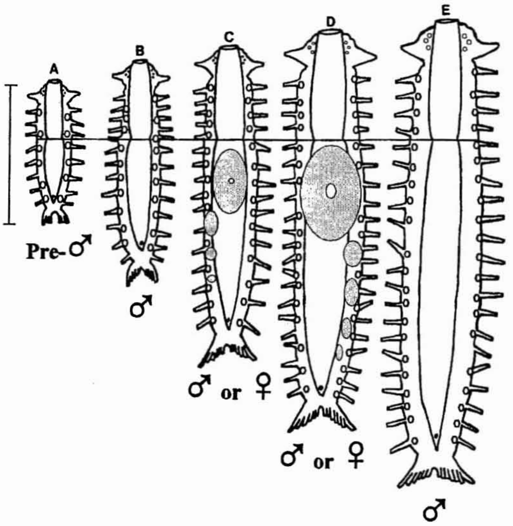

FIGURE 2. Ontogenetic changes in the morphology of *Turbanella mustela* and the sexual condition of the following 100-μm size classes: *A*, 100–199 μm; *B*, 200–299 μm; *C*, 300–399 μm, with developing eggs; *D*, 400–499 μm, with developing eggs; *E*, 500–599 μm.

depths. The 300–399-μm size class becomes more abundant with depth, as do the 400–499-μm and 500–599-μm size classes. These observed variations in vertical distribution patterns may be explained by three hypotheses that concern ontogenetic change (Figure 1):

(1) The distribution pattern may reflect a form of sexual-phase stratification. *Turbanella mustela* is a protandric, alternating, sequential hermaphrodite that consistently displays a relationship between sexual phase and body length (Figure 2). Individuals in the smallest 100–199-μm size class are always prereproductive (no observed ova, testes, or male copulatory organ), whereas most members of the 200–299-μm size class are in the male phase. The next two larger size classes are occupied by both male- and female-phase individuals, and members of the 500–599-μm size class are either postreproductive (no observed sperm or ova) or in male phase. The overwhelming abundance of juveniles in the top 5 cm of sand with larger size classes dispersed deeper in the sediment clearly reflects a type of sexual gregariousness.

Gregarious behavior in gastrotrichs is commonly observed in nature (Nixon 1976) and laboratory settings (Boaden 1985) and can be assumed to enhance chance encounters with a mate by reducing intermate distances (Boaden 1985). This may explain the observed patchiness at Freshwater Beach at 15-cm vertical scales, but it does not adequately explain the patchiness of reproductively immature individuals (juveniles) at smaller spatial scales (5-cm depth). A likely explanation for the latter form of gregarious behavior could be the maintenance of reproductive "pools" that stratify themselves following some chemical mating cue. Juveniles remain out of such "pools" until maturity, upon which they migrate deeper to engage in copulation. Such behavior is unheard of in gastrotrichs and may be important in reducing unsuccessful mating encounters with immature individuals.

(2) The exposure of *Turbanella mustela* to predation or competition can change with ontogenetic stage. Proseriate and kalyptorhynch turbellarians are common predators in the deep meiobenthos (10–20-cm depth) at Freshwater Beach and may selectively seek out small prey such as juvenile gastrotrichs. The preponderance of predatory flatworms at deeper depths likely forces juvenile gastrotrichs to the surface layers. Such turbellarians are highly mobile predators, and I have witnessed numerous instances of predation on juvenile *T. mustela*, harpacticoid copepods, and pieces of syllid and hessionid polychaetes in laboratory studies. However, I have never witnessed any turbellarians prey on large gastrotrichs (>250 µm) and they never enter large aggregations of gastrotrichs (>50), which could indicate that gregarious behavior serves a protective function in this species. This behavior may account for the presence of juveniles in deeper sediment layers.

(3) Intraspecific trophic relations may also alter the distribution pattern of the species. Food size, an unexplored factor in this study, may be important if juvenile gastrotrichs have size-selective prey (small pennate diatoms [pers. obs.]) that also display aggregated distributions in the sediment. Ontogenetic differences in the diameter of the mouth of *T. mustela* (Hochberg 1998) could presumably enhance these spatial differences and might effect a partitioning of the environment if food resources are also distributed by size (cf. Hummon 1974).

The horizontal distribution of the species also reflects some size-class differences. The relative abundance of the 100–199-µm and 200–299-µm size classes increases with increasing tidal height, but the larger size classes are negatively correlated with tidal height. A concurrent study on the numerical abundance of this species indicates that its abundance is not correlated with grain size nor pore volume, but instead with water saturation and water temperature (pers. obs.). Gradients in these latter two factors may be responsible for the observed variations in horizontal size-class distribution and reflect ontogenetic changes in the physiological tolerances of the species.

Despite the fact that juvenile abundance is strongly correlated with increasing tidal height, individuals in the higher reaches of the beach are always in low abundance compared with those at the low-tide line. This correlation obviously reflects more upon the absence of any larger size classes in the upper tidal regions than on the increasing abundance of juveniles. Based on this evidence, it seems unlikely that juveniles are being born at high tidal elevations. Very few reproductive individuals are ever found in these areas; reproductively mature gastrotrichs present in the higher reaches are generally in their first male phase or first female phase. The best explanation for this unusual size-class zonation is therefore supported by a passive erosion scenario.

Wave action and sediment erosion are thought to cause gastrotrich suspension and dispersal (Boaden 1968, Hagerman and Rieger 1981). At Freshwater Beach, meter-high waves break directly onshore, stirring up sediment and any contained surface-dwelling, microscopic metazoa. Erosion of surface sediment due to wave action at low tidal levels could presumably suspend and transport juvenile gastrotrichs. In fact, only juveniles were found suspended in the flooding and ebbing tides. Whether or not this suspension is the result of juvenile aggregation at low tidal levels (most likely) or the result of ontogenetic changes in growth is uncertain (Figure 2). Meristic changes in adhesive tubule development are well documented for this species (Hochberg 1998), and I hypothesize that such variations during ontogeny could contribute to high juvenile suspension (because they have fewer adhesive tubules than adults). This latter possibility is intriguing but appears unlikely because gastrotrichs of all sizes are adept at adhering to sand grains, and meristic development probably means little to an animal floating on a miniature raft (sand grain) at the whim of the sea (Figure 3). In this case, the length of the animal in the water column and its potential for dispersal would be determined by the settling velocity of the sand grain. Numerous possibilities also exist with regard to where the juveniles (and their respective sand grains)

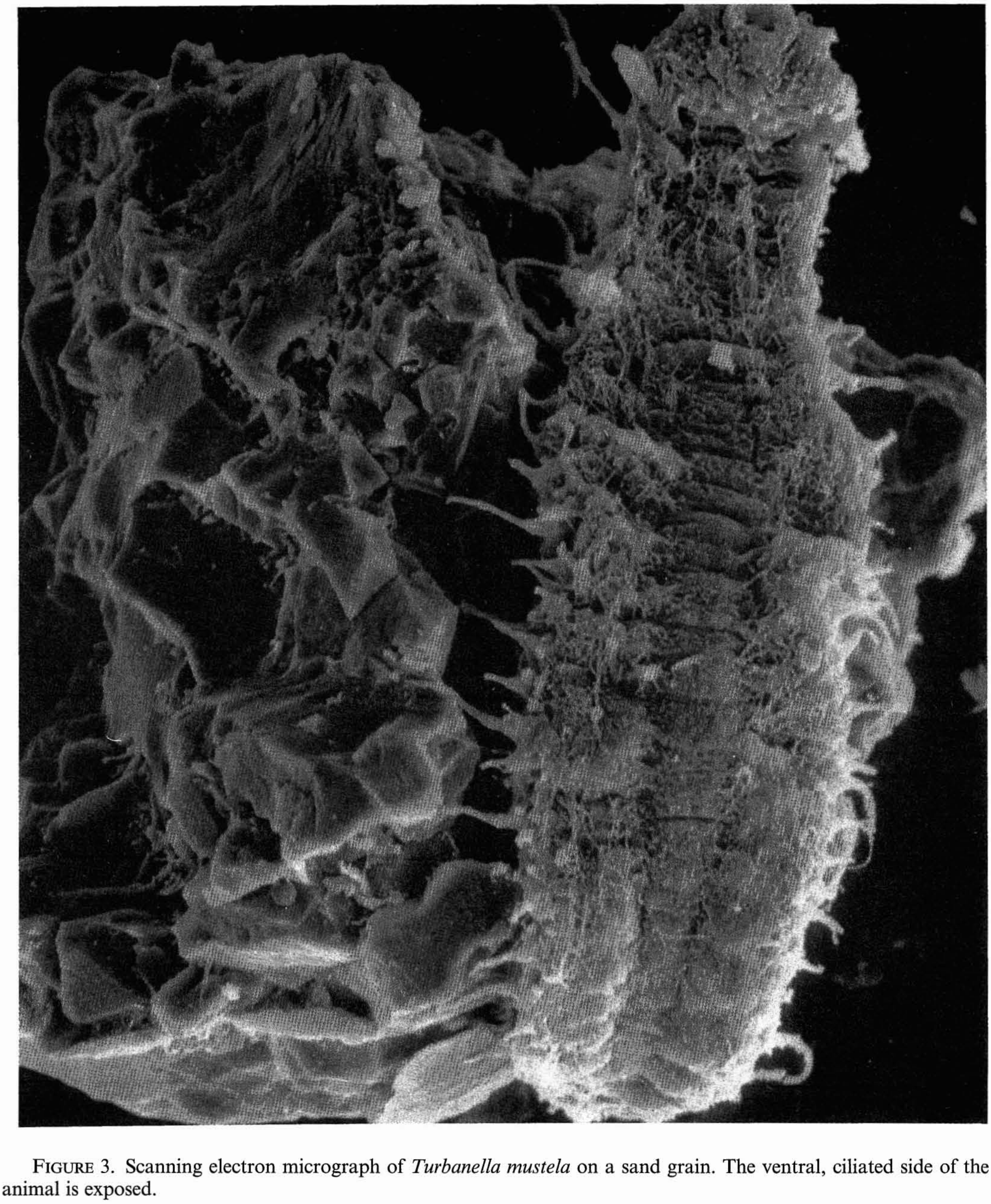

FIGURE 3. Scanning electron micrograph of *Turbanella mustela* on a sand grain. The ventral, ciliated side of the animal is exposed.

became suspended: individuals in flood tides could come from eroded sediments at sublittoral sites or littoral sites (LLW); or gastrotrichs in ebbing tides could be the result of erosion at higher elevations (10-m station in this study).

Redistribution of the species, at the scale of centimeters to kilometers, could effectively occur if advection of juveniles places them in favorable environments. Provided multiple individuals are advected simultaneously and deposited in the same environment, then new patches are likely to develop, effectively creating "stepping-stones" along the length of a single beach or an entire coastline. In fact, I hypothesize that this is how *Turbanella mustela* could colonize both the highest elevations of Freshwater Beach and other local northern California beaches. This may even explain the presence of the species in Puget Sound, Washington. Further sampling, at both intertidal and subtidal sites between California and Washington, would be an important step toward addressing this hypothesis. As it stands now, the geographic distribution of the species is assumed to be artificially isolated because of the lack of sampling.

Distribution by size may also have important implications for both the local population of *T. mustela* at Freshwater Beach and its known, but admittedly artificial, distribution along the Pacific coast of the United States. If juveniles and males are the only stages suspended because of vertical size-class stratification, then the ultimate effect of wave impact might be to decrease their abundance at low tidal elevations. This might effectively deplete the "young" male population and, eventually, the female population (because of the alternate, sequential hermaphroditism of the species). The later deposition of males in new environments (provided they survive suspension) would only contribute to the species overall distribution if certain individuals changed sexual phase while in the plankton. It is not known whether a change in the sexual condition of the individual can be initiated by the lack of the opposite sex or an overwhelming presence of same-sex individuals. Surely, a better understanding of the factors (age, intraspecific chemical cues, environment) that contribute to sex change in this species would be beneficial.

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