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Biological removal of fine-grained lithogenic particles from a large river plume

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ABSTRACT

The pelagic tunicate, *Oikopleura dioica,* feeds by non-selectively filtering particles in the size range of 0.2–20 μm. In the northern Gulf of Mexico, particulate matter in this size range contains large amounts of fine-grained lithogenic material because of the influence of the Mississippi River. During May 1992, *O. dioica* populations filtered between 2 and 44% (mean = 20%) of the upper 5 m each day. The filtered lithogenic particles either remain in the oikopleurid house or are defecated in fecal pellets which have high sinking velocities. Either way, the larvacean populations significantly alter the fates of fine-grained lithogenic particles in these waters and thereby enhance light penetration. The widespread occurrence of oikopleurids in coastal regions of temperate and subtropical oceans suggests they could have a significant influence on the fates of fine-grained lithogenic particles in discharge plumes of many of the world's large, sediment-laden rivers.

1. Introduction

The Mississippi River is one of the 10 large rivers that account for approximately 40% of the suspended lithogenic material introduced annually into the coastal ocean (Milliman, 1991). Typically, much of this material settles to the bottom within short distances from river discharge. Fine-grained (<62 μm) lithogenic materials however, have low settling velocities as individual particles and would be transported large distances if aggregation processes did not lead to an effective increase in particle size. Aggregation results from complex interactions between physical, chemical and biological processes that lead to the incorporation of fine-grained materials into larger particles with higher sinking velocities (e.g., McCave, 1984; Alldredge and Jackson, 1995).

Zooplankton feeding is a potentially significant mechanism for directly affecting the fate of fine-grained lithogenic particles. Copepods commonly consume lithogenic particles in the vicinity of the Mississippi River (Turner, 1984), and populations that

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are sufficiently large to remove between 4–62% of phytoplankton production daily (Dagg, 1995) have an obvious potential for removing a significant portion of the lithogenic materials from surface waters. Copepods however, are inefficient feeders on particles smaller than 2–3 μm (e.g. Nival and Nival, 1976) and are incapable of ingesting submicron sized particles. Thus, the smallest lithogenic particles will be unaffected by copepod feeding processes regardless of the size of the copepod population.

Many protozooplankton can ingest smaller particles than copepods, including bacteria-sized particles < 1 μm. In a recent study on the Louisiana shelf, Strom and Strom (1996) reported microzooplankton grazing on phytoplankton at rates between 0.0–0.7 d^{-1} but it is not known whether fine-grained lithogenic particles would be ingested at similar rates. Such high grazing rates suggest that protozoan feeding processes are potentially a significant source of biological aggregation for fine-grained lithogenic particles; further examination of this is required.

Gelatinous zooplankton, particularly the pelagic tunicates, are also potentially important consumers of fine-grained lithogenic particles and the larvacean, *Oikopleura dioica,* is often abundant in coastal regions of the northern Gulf of Mexico (Dagg, 1995). Because *O. dioica* feeds by non-selectively concentrating suspended particles in the size range between 0.2 and about 20 μm (Bedo *et al.,* 1993), it can contribute significantly to the aggregation of fine-grained lithogenic particles in this size range. In this paper, we quantify the significance of biogenic aggregation from populations of *O. dioica* in the northern Gulf of Mexico.

2. Methods

The abundance of *O. dioica* in the coastal waters near the discharge plume of the Mississippi River was determined by three methods during three springtime cruises.

In May, 1988 *O. dioica* were collected from the immediate surface with a 5-liter Niskin bottle at several sites across the plume-ocean gradient in the vicinity of Southwest Pass of the Mississippi River (Fig. 1). Four liters from each bottle were immediately withdrawn and screened through a 20 μm mesh sieve and back-washed with filtered GF/F seawater into a small jar, then preserved in formalin-seawater. The entire sample was later analyzed in the laboratory.

In May, 1992 *O. dioica* were collected in the same general vicinity (Fig. 1) with a 1 m net (202 μm mesh) towed obliquely from 25 m to the surface. The volume of water filtered was measured with a General Oceanics model 2030R flowmeter attached in the net mouth. Net tows were made at 3–6 hour intervals over two days while the vessel was following a free-floating array of sediment traps deployed in the plume of the Mississippi River (Fig. 1). Samples were preserved in 10% formalin-seawater solution and later analyzed in the laboratory.

In April, 1993 detailed information on the subsurface distribution and abundance of *O. dioica* was obtained on a cross-shelf transect west of the Mississippi River delta
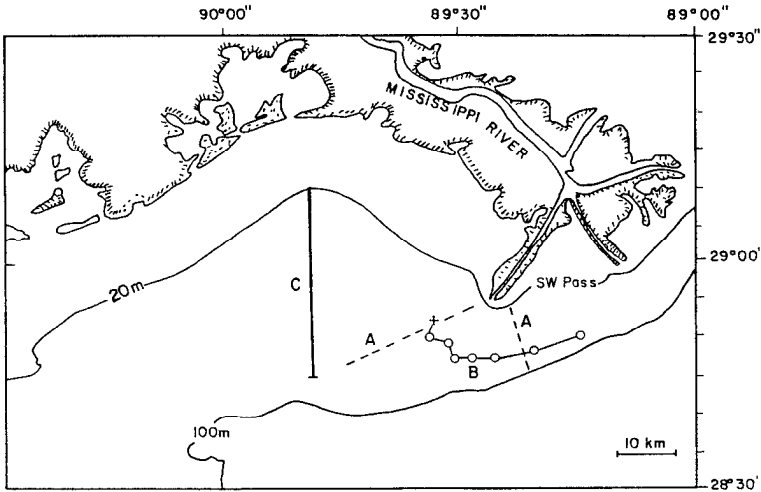
Figure 1. Location of sampling sites: (A) May 1988, two transects radiating from Southwest Pass, surface samples only; (B) May 1992, drift track of sediment trap array deployed at '+' and followed for 52 h, open circles represent CTD stations; (C) April 1993, transect line monitored by the towed sensor array and optical plankton counter (see text).

(Fig. 1) using an optical particle counter-video identification system (Ortner *et al.,* 1995). Water from approx. 1–3 m was continuously pumped through the instrument array on board the ship, which was underway at 5 knots. The pump intake was attached to an Endeco V-fin which contained temperature, salinity, fluorescence and turbidity sensors.

To obtain fecal pellets, some *O. dioica* were removed from the net tow samples collected in May, 1992. Pellets were removed from the guts for microscopic determination of their size and contents. Whole and squashed pellets were examined under transmitted and epifluorescence light. Although most small lithogenic and organic particles were difficult to distinguish, one particular type of lithogenic particle was easily identified by its shape and black color. The longest and widest parts of all representatives of this single type of lithogenic particle were measured in 12 pellets (30–50 particles pellet^{-1}). The size-frequency distribution of these particles is assumed to be representative of all lithogenic particles in the pellets.

The sinking velocity of fresh, not preserved, pellets from *O. dioica* was measured in the laboratory.These experimental animals and pellets were collected from Terrebonne Bay at approximately 29°02′N and 90°33′W and returned to the laboratory in less than 1 h. Sinking velocity was determined by placing single pellets with premeasured dimensions in an unmodified 1 liter graduated cylinder containing seawater of approximately 25‰ at room temperature (25°C). In an effort to reduce convection, the cylinder was left undisturbed for several h prior to use and back-lit
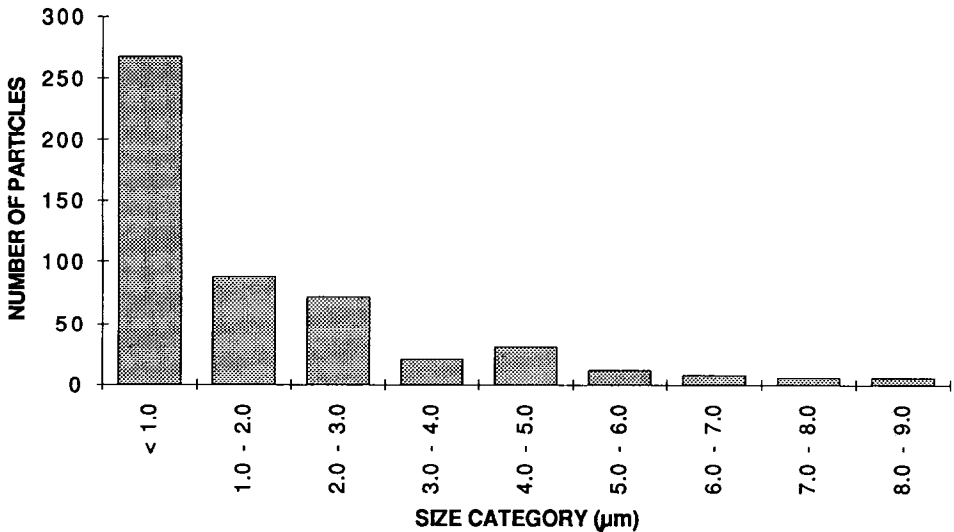
Figure 2. The size frequency distribution of lithogenic particles in fecal pellets of *Oikopleura dioica* collected during May 1992.

with a cool (fiber optic) light-source during experiments. The time required for each pellet to settle the distance between two markers on the cylinder wall was recorded.

The dry particle density of fine-grained lithogenic particles from the Mississippi River was determined from five samples collected in low salinity (5–10‰) plume waters. Particles from each 15 liter sample were concentrated, wet sieved (62 μm) and dried. Approximately 2.0 g samples of dry sediment (range: 1.79–2.12 g) were added to 25 ml of deionized water in volumetric flasks. Flasks were capped and the wetted sediments allowed to settle for seven days. The volumes of water displaced by the sediments were pipetted off and weighed. Dry particle densities were calculated based on a water density of 1 g cm^{-3}.

3. Results

O. dioica fecal pellets collected from the plume region of the Mississippi River during May 1992 had an ellipsoid shape and ranged in size from 90 × 40 μm to 320 × 115 μm. The lithogenic grains that were measured from these pellets had angular surfaces but were approximately spherical. Size is reported as spherical diameter and · most were <2 μm (Fig. 2).

The density of fine-grained (<62 μm) lithogenic particles collected from the Mississippi River plume ranged from 2.64–2.81 g cm^{-3} ($n = 5$). Based on Stokes' Law, the sinking velocity of a 2 μm diameter spherical particle with a density of 2.75 g cm^{-3} is only 0.35 m d^{-1} at 25°C and 25‰. In contrast, the calculated sinking velocity of an intermediate sized, 200 μm long and 80 μm wide, ellipsoid particle
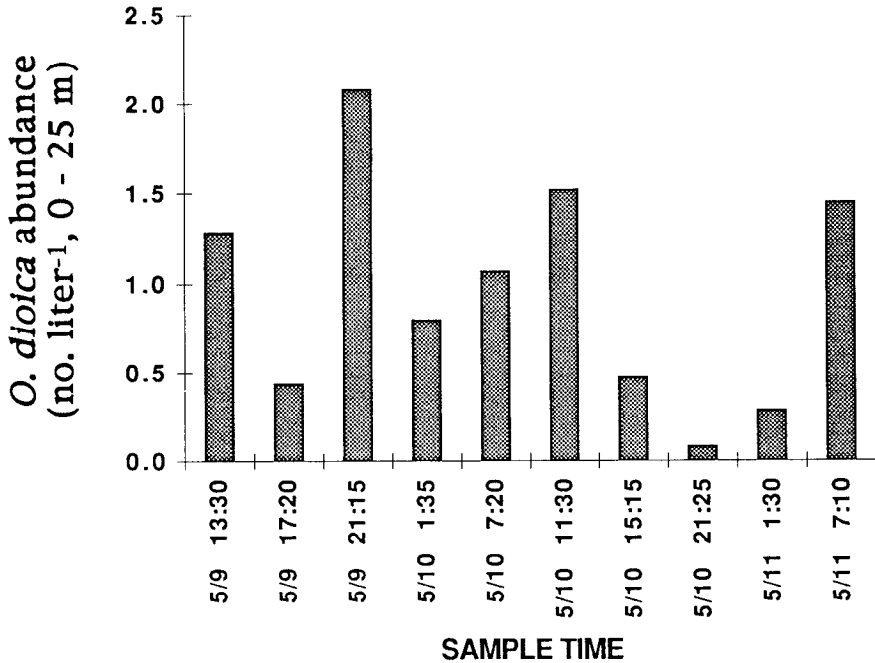
Figure 3. The abundance of *Oikopleura dioica* in the upper 25 m during May 9 to 11, 1992.

with the same density is 858 m d^{-1} (Eq. 4 from Komar *et al.,* 1981). The sinking velocity of a fecal pellet of these dimensions would of course be less because pellet contents consist partly of other, less dense, materials. The measured sinking velocity of *O. dioica* pellets collected from Terrebonne Bay averaged 219 m d^{-1} (*n* = 23, sd = 63). These pellets probably contained less lithogenic material than pellets collected closer to the Mississippi River where water contains higher concentrations of suspended particulate materials, so pellets produced at our study site (Fig. 1) would probably have higher sinking velocities.

During May 1992, it was determined from net tows that *O. dioica* concentrations in the 0–25 m depth stratum were, with one exception, between 0.4 and 2.1 liter^{-1} (Fig. 3). These *O. dioica* were probably not homogeneously distributed throughout the 25 m depth zone integrated by each net tow but instead were concentrated in the upper, particle-rich, plume. Phytoplankton stock at this time was concentrated within the upper 5–10 m (Fig. 4) and it is reasonable to assume that most of the *O. dioica* collected in the net tows would be in this upper, food-rich, layer. Support for this assumption comes from the collections made in May 1988 and April 1993. Larvacean concentrations in surface samples, collected by Niskin bottle in May 1988, were typically between 10 and 40 liter^{-1}, and sometimes approached 100 liter^{-1} at intermediate salinities (Fig. 5). If all the *O. dioica* collected in our net tows during May 1992 were in the upper 5 m, concentrations would typically be 2–10 liter^{-1} in this
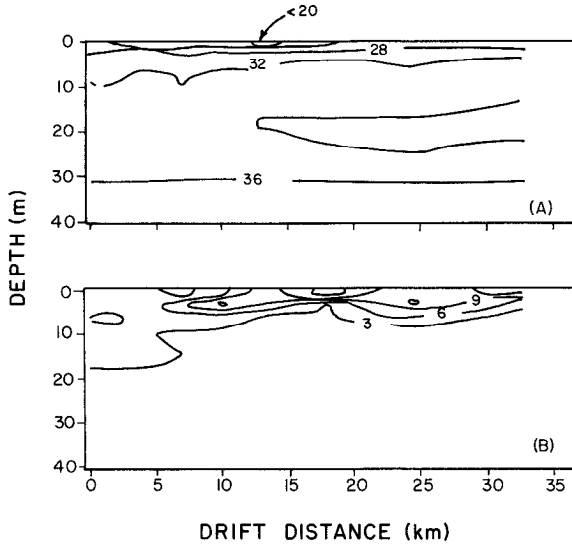
Figure 4. (A) salinity (‰) and (B) chlorophyll concentration (μg liter^{-1}) along the drift track of the sediment trap array, May 1992.

stratum; if in the upper 1 m, concentrations would be 10–50 liter^{-1}, similar to concentrations observed in May 1988. Larvacean concentrations at subsurface depths between 1–3 m, measured during the underway survey in April 1993, were in the range of 1–8 liter^{-1} (Fig. 6). Higher concentrations in May 1988 compared to April 1993 may indicate either larvacean populations are especially high at the immediate surface or that populations are higher nearer the river plume. Lastly, in both May 1988 (Fig. 5) and April 1993 (Fig. 6), highest concentrations of *O. dioica*
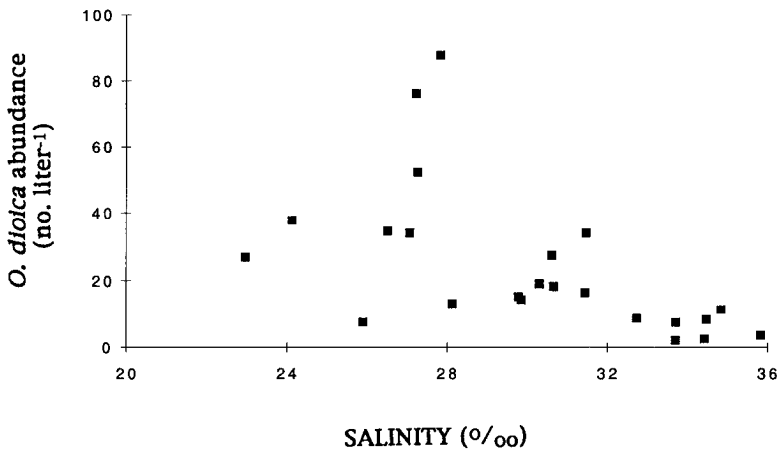

Figure 5. Concentrations of *Oikopleura dioica* in the surface layer near the Mississippi River delta, May 1988.
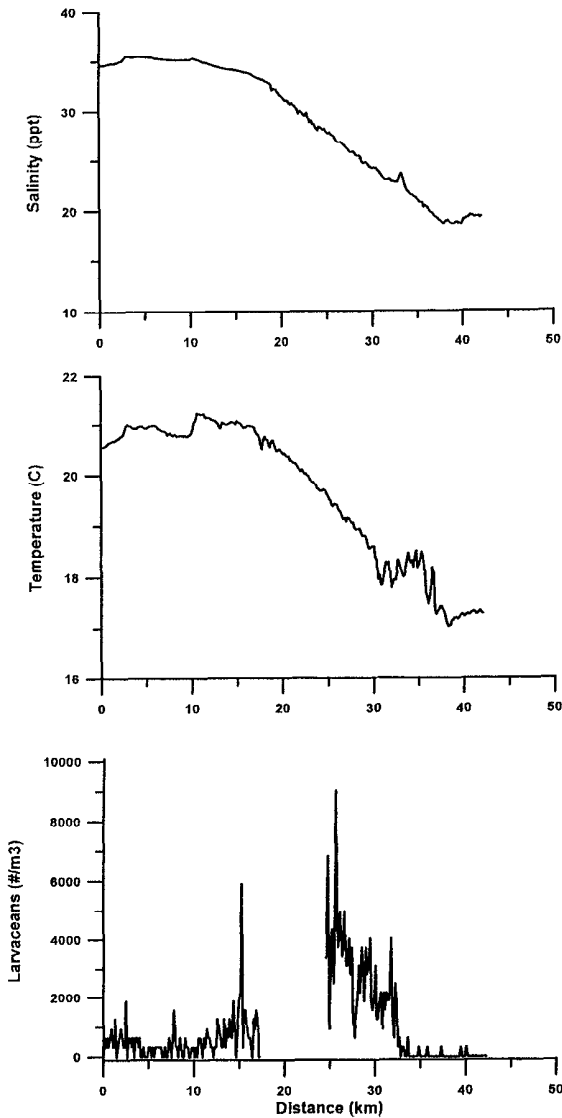
Figure 6. Hydrography and larvacean abundance during the cross shelf, underway transect of April 1993. The gap in the larvacean abundance data is due to partial instrument malfunction.

were observed at intermediate salinities where maximum phytoplankton stocks and rates of production are typically observed (Lohrenz *et al.*, 1990; Redalje *et al.*, 1994). It is not unreasonable to assume that larvacean concentrations measured by our net tows through the upper 25 m represent populations that are predominantly in the upper few m.

Table 1. *Oikopleura dioica* population size structure and clearance rate at 13:30 h May 9, 1992. The total number of *O. dioica* in this sample, collected from 25–0 m, was 32,070 m^{-2}. The total clearance rate of the population was 1392 liters m^{-2} d^{-1}. (TL = trunk length)

Body size (TL, mm)	% of popul	Clear rt indiv^{-1} (ml h^{-1})	Indiv m^{-2} (0–25 m)	Popul clear rt (ml m^{-2} h^{-1})
0.20–0.24	13	0.82	4169	3419
0.26–0.30	19	1.21	6093	7372
0.32–0.36	27	1.50	8659	12988
0.38–0.42	21	1.98	6734	13335
0.44–0.48	10	2.70	3207	8659
0.50–0.54	8	3.29	2566	8441
>0.56	3	3.93	962	3781

The volume of water cleared of particles hourly (clearance rate) by each *O. dioica* is related to the individual's body size and the water temperature (Paffenhöfer, 1976; Alldredge, 1981). The size distribution of the population in May 1992 was determined by measuring 200 individuals and applying this distribution to the measured population abundance (example in Table 1). The clearance rate for an individual in each size category was calculated from Alldredge's (1981) relationship between clearance rate and body size in *O. dioica* derived for temperatures between 23.2°C and 23.8°C. Temperatures in our study area ranged between 21°C and 22°C in May 1992. Calculated clearance rates per individual *O. dioica* are shown in Table 1. We have no direct measurements of *O. dioica* clearance rates in our study area.

The clearance rate calculated for individuals in each size category is applied to the number of individuals in each size category and summation of all categories provides a measure of the volume of water filtered daily by the larvacean population (example in Table 1). If the larvacean population was homogeneously distributed throughout the upper 25 m, it would filter between <1 and 9% of this stratum daily (Table 2). Alternatively, if the larvacean population was concentrated in the surface plume, the

Table 2. Daily clearance rate of the *O. dioica* population during each sampling interval in May 1992.

Date	Sample time	Population size (no. m^{-2})	Popul clear rt (liters m^{-2} d^{-1})	% top 25 m (d^{-1})	% top 5 m (d^{-1})
May 9	13:30	32,070	1392	6	28
	17:20	10,870	465	2	9
	21:15	51,995	2224	9	44
May 10	1:35	19,874	850	3	17
	7:20	26,629	1139	5	23
	11:30	37,914	1605	6	32
	15:15	11,730	502	2	10
	21:25	1,937	83	<1	2
May 11	1:30	7,019	304	1	6
	7:10	36,129	1545	6	31

% of this shallower layer that is filtered daily would be greater. For example, if the May 1992 population was concentrated in the upper 5 m, then between 2–44% (mean = 20%) of the small particles in this surface layer would be cleared daily (Table 2). These estimates (Table 2) indicate that *O. dioica* populations remove a significant fraction of the small lithogenic particles from the plume each day. Over several days, this process would be proportionally more significant.

4. Discussion

It has long been known that fecal pellets from mesozooplankton have settling velocities of 10s to 100s m d^{-1} when measured under ideal conditions (Komar *et al.,* 1981; Small *et al.,* 1979) but that these velocities are not always achieved in the ocean where there are several processes that can modify the pellets and thereby affect their settling velocity (reviewed in Noji, 1991). In waters containing high concentrations of lithogenic materials, settling velocities are likely to be higher than predicted on the basis of pellet size alone because of the high density materials contained in these pellets. We demonstrate that pellets produced in the plume of the Mississippi River contain large amounts of lithogenic materials and could sink to the bottom on the shelf in periods as short as several hours. Nevertheless, these high settling velocities do not necessarily indicate these pellets settle to the bottom. Some may be reingested or broken by other organisms in the water column. Some may be retained in the discarded larvacean houses and become part of a larger aggregates with different settling dynamics.

Another consideration is that some of the very smallest particles taken into the larvacean house during feeding are not ingested. *O. dioica* uses its gelatinous house to non-selectively concentrate particles in the size range from approx 0.2 to 20 μm (Bedo *et al.,* 1993). Some of the smallest particles however, are not ingested, possibly because they are not retained by the pharyngeal filter. These particles remain trapped in the filter house when the house is abandoned but when, if ever, they are released from the house is not known.

The secondary fates of the larvacean pellets and the uningested particles that remain in the abandoned houses are not of immediate concern. What is clear is that larvacean feeding processes package particles in the micron-submicron size range into fewer, much larger particles and these are unlikely to be returned to the surface layer in their original form, whether or not the pellets or abandoned houses actually sink to the bottom. Larvacean populations are large and, by their feeding processes, they alter the fates of significant amounts of fine-grained lithogenic particles.

Although larvacean feeding processes result in aggregation of small lithogenic particles in our study region, it is important to note that these particles would not remain in the water column as independent particles in the absence of larvaceans but would become aggregated by one of several other processes. For example, flocculation of colloids and dissolved materials carried by river waters occurs at low salinities

(Sholkovitz, 1976). This is probably not significant in our immediate study region because it is essentially complete within <24 h. At intermediate and higher salinities, physical coagulation processes for fine-scale lithogenic particles are slow (McCave, 1984) and interactions between biological and physical-chemical processes are probably required to aggregate fine-grained materials on short time scales. These processes are complex and, in spite of considerable progress in recent years, the rates at which they occur in nature and parameters most influential in altering these rates are not well understood (Alldredge and Jackson, 1995). The relative significance of aggregation from these processes compared to aggregation from larvacean feeding described in this study cannot be stated with certainty but the large volume of water filtered daily by larvaceans indicates their contribution to biological aggregation is important.

After nutrient-rich waters of the Mississippi River discharge onto the continental shelf of the northern Gulf of Mexico, light is limiting to algal photosynthesis until the large suspended load of lithogenic materials has settled from the surface waters (Lohrenz *et al.*, 1990). Turbidity in plumes of other major rivers such as the Amazon (DeMaster *et al.*, 1986) and the Huanghe (Turner *et al.*, 1990) also limits algal photosynthesis for some time and distance after discharge. Generally, processes that affect turbidity in the vicinity of discharge plumes of large turbid rivers will affect the timing and scaling of the phytoplankton response. In the northern Gulf of Mexico, larvacean populations clear significant amounts of fine-grained lithogenic particles from the water in the region around the Mississippi River discharge, which may enhance the light environment sufficiently to stimulate phytoplankton growth. Highest larvacean populations are observed at intermediate salinities and it is in these zones where phytoplankton production and stocks are highest.

These findings are potentially significant for much larger regions of the coastal ocean than the northern Gulf of Mexico. *O. dioica* is widely distributed in temperate and subtropical latitudes and has been reported from a diversity of environments, including many coastal regions of the eastern North Atlantic Ocean (Last, 1978; Martens and Brockmann, 1993; Bedo *et al.*, 1992; Acuna, 1994), the Mediterranean Sea (Gorsky *et al.*, 1988), the southeast Atlantic Ocean off South Africa (Lazarus and Dowler, 1979), the southwestern Atlantic Ocean off Argentina, Brazil and Uruguay (Esnal and Castro, 1977; Esnal *et al.*, 1985); the northwestern Atlantic Ocean and Gulf of Mexico (Costello and Stancyk, 1983; Hopkins, 1977; Dagg, 1995) the eastern Pacific Ocean (King *et al.*, 1980; Buck and Newton, 1995; Alldredge, 1981), the western Pacific Ocean (Ohtsuka *et al.*, 1993), and the central Pacific near Hawaii (Kitalong, 1986). Other oikopleurid species are also widely distributed coastally. It is possible that these organisms significantly affect the fates of fine-grained lithogenic particles discharged into many or all of these coastal zones.

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