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Coastal upwelling in the Rias Bajas, NW Spain: Contrasting the benthic regimes of the Rias de Arosa and de Muros

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ABSTRACT

Nutrient-rich North Atlantic water upwells off the NW coast of Spain and intermittently intrudes into the rias, coastal embayments, by displacement during periods of offshore winds. High primary production associated with the upwelling supports an intensive raft culture of the edible mussel, *Mytilus edulis*. This culture is most intensive (ca. 2000 rafts) in the Ria de Arosa, and results in one of the highest protein yields per unit area on earth. Mussel feces, in turn, serve as food for other species of epifauna which live on, or between the densely-packed mussels. These epifauna, in turn, serve as food for demersal fish and crabs. The epifauna mineralize a great deal of the mussel feces but still there is high deposition of organic-rich deposits to the seafloor, where they are utilized by a low diversity benthic assemblage dominated by the polychaete *Spiochaetopterus costarum* and comesomatid nematodes.

Sedimentary structures, profiles of pore-water constituents, and C/N and ²¹⁰Pb vertical profiles show that sediment deposits under the rafts are mixed to a depth of about 20 cm. Bioturbation is a relatively unimportant advective process in Ria de Arosa sediments, and mixing is apparently accomplished by bottom current erosion. Mixing may take place with a frequency of less than one month, releasing pore water ammonium and phosphate into the water column and replenishing pore water sulphate.

The Ria de Muros, an embayment north of the Ria de Arosa, has few (< 100) mussel rafts. The benthos in muddy sediments of the Muros consists of a high diversity, equilibrium assemblage dominated by a subsurface deposit-feeding polychaete (*Maldane glebifex*), an ophiuroid (*Amphiura chiajei*), a holothurian (*Leptosynapta bergensis*) and desmodorid nematodes. Bioturbation is an important mixing process in Muros sediments. This biogenic process is reflected in high rates of pore-water exchange and mixed vertical profiles of Pb²¹⁰.

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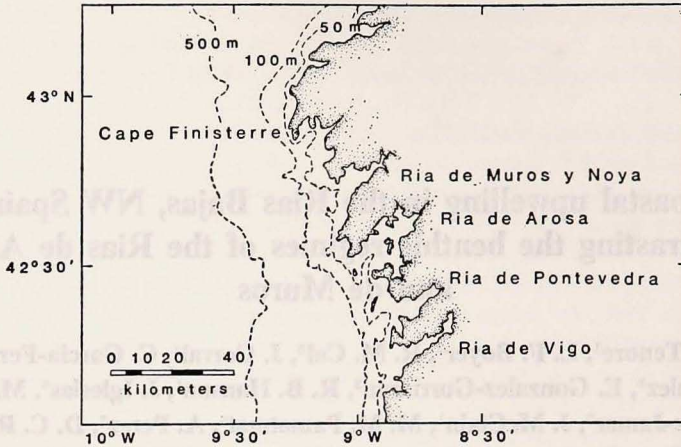


Figure 1. The Rias Bajas of the northwest coast of Spain.

The introduction of mussel aquaculture into the Arosa about 40 years ago dramatically changed the benthos from a diverse equilibrium assemblage (like that described here for the Muros) to a low diversity polychaete-nematode assemblage. Sulphate reduction rates in the bottom are presently higher in the Arosa than the Muros. However, concentrations of sediment ATP and microbial turnover rates are higher in the Muros than the Arosa, possibly because of enhanced activity due to bioturbation.

INTRODUCTION

The Rias Bajas are oceanic bays on Spain's northwest Atlantic coast (Fig. 1). These rias, especially the Ria de Arosa, support high shellfish production by intensive raft culture of the edible mussel *Mytilus edulis*.⁹ The Arosa has a total area of 230 km² and annually produces ca. 100,000 metric tons total wet weight of mussels. This is one of the highest known protein yields per unit area. This high production is made possible by intermittent upwelling of nutrient-rich deep water into the rias. During the past seven years the Spanish-American Rias Study (SARS) has investigated the role of upwelling in producing high primary production and the effect of intensive mussel raft culture practices on food chain patterns in the rias. In this paper we review the hydrography and available information on the pelagic food chains of the Ria de Arosa, which has intensive raft culture, and the Ria de Muros, which has few mussel rafts. We also contrast the benthic regimes of these two rias to illustrate the effect that the mussel culture has on sediment composition, benthos, and nutrient regeneration.

9. Although the Rias Bajas fall within the supposed zoogeographic range of *Mytilus galloprovincialis*, the introduction of *Mytilus edulis* L. seed from France into the Ria de Arosa at the beginning of the aquaculture development (1945) and the hydrographic conditions resulting in a "disjunct" environment for more northern species results in dominance of *Mytilus edulis* L.

Physical description of the rias

The Arosa, the largest (230 km² surface area; 25 km long) of the Rias Bajas, is 65 m deep at its mouth and averages 19 m in depth. Mean tidal range is 2.7 m. Two rivers, the Rios Ulla and Umia, discharge approximately 70 to 120 m³/sec in winter and 5 to 75 m³/sec in summer into the Arosa.

Seasonal ranges in salinity and temperature are not large (Gomez-Gallego, 1971 and 1975). Surface-water temperatures annually range from 10 to 20°C with bottom temperature constant at 11 to 13°C. Surface salinity ranges from 30 to 35‰ with bottom salinity at 35.6‰. The water column is stratified in summer and mixed or weakly stratified at other times.

The Muros is smaller (120 km² surface area; 12 km long) and deeper (avg. 22 m) than the Arosa. The Rio Tambre discharges approximately 60 to 290 m³/sec in winter and 15 to 30 m³/sec in summer into the Muros.

The Rias are greatly affected by changes in the Azores high pressure cells. In summer, the influence of the Azores high usually extends along NW Spain, north-west winds (Portuguese Trades) dominate, and precipitation is at a maximum. During other seasons, the effect of the Azore high pressure cell is less constant and depressions and fronts frequently cause southeasterly winds and precipitation.

Raft culture of mussels

In the late 1940's, raft culture of the edible mussel *Mytilus edulis* was introduced into several Rias (Fig. 2). There are presently about 2200 rafts (about 200 of which are of oysters) in the Arosa. Rafts (average 19 × 16 m) are grouped into polygons, which occupy approximately 10% of the surface area of the Arosa (Fig. 3). These polygons are situated in more protected nearshore bays within the ria. A typical raft contains 500 ropes, each rope averaging 8.5 m in length.

New seed mussels are allowed to settle on ropes, which are "unfolded" several times during the year. That is, as the mussels grow and begin to crowd each other, the ropes are pulled out of the water, the mussels are removed from the ropes, and a larger number, e.g., 3 new ropes from the one rope (with fewer numbers of mussels per meter), are prepared by wrapping the mussels around the rope with a rayon mesh. The mesh disintegrates in a few days, by which time the mussels have reattached to the ropes. The unfolding process may be repeated several times during the growing season.

In 9 to 14 months the mussels can grow to about 7 cm in length and one raft can produce about 50 metric tons (total wet weight) of mussels per year. Estimates of total production in the Arosa range from 90,000 to 120,000 metric tons (total wet weight) per year, more than one half of the total mussel production in Spain (for further information about mussel production see Tenore and Gonzalez, 1975; Koringa, 1976; Perez and Roman, 1979). The next ria to the north, the Muros, has

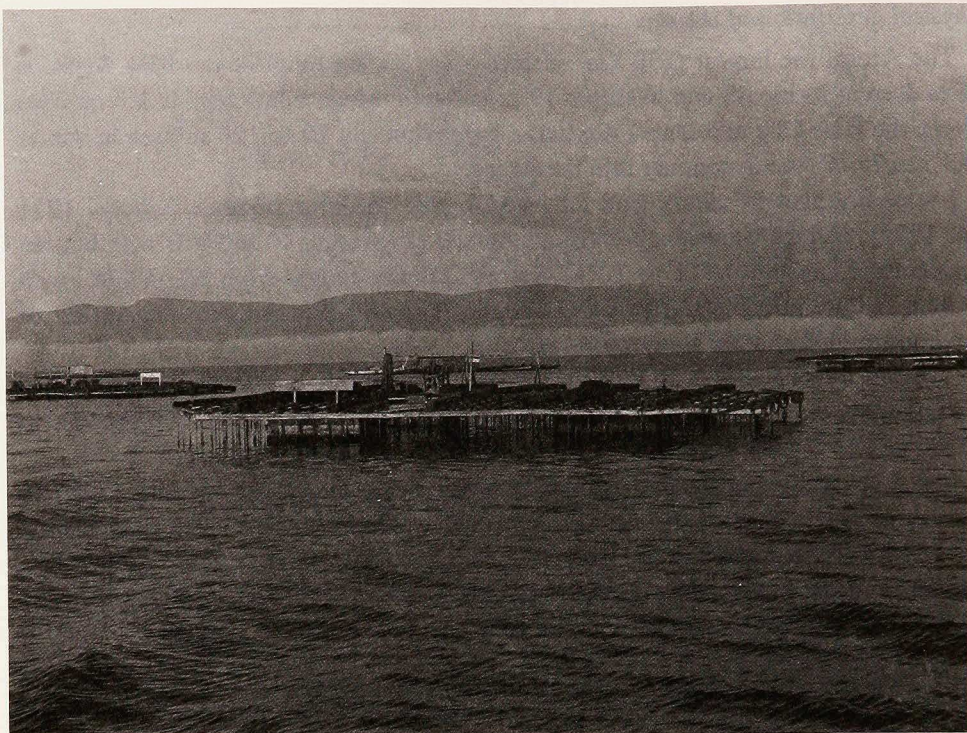


Figure 2. Photograph showing rafts (each ca. 19×16 m) in the Ria de Arosa.

few rafts (< 200) because the mouth of the ria is less protected and rafts are easily damaged by sea swell and storms.

The rafts provide three-dimensional space and detrital food, in the form of mussel feces, to a dense epifaunal community of over 100 invertebrate species living on the ropes of mussels (Tenore and Gonzalez, 1975; Roman and Perez, 1979). Epifaunal biomass, exclusive of the adult mussels, is generally dominated by the small crab *Pisidia longicornis*, the sea cucumber *Cucumaria normani*, young mussels, the snail *Nucella lapillus*, and the lug worm *Arenicola ecaudata*. As the mussels grow, large suspension-feeding epifauna, such as the sea cucumber *C. normani*, sea squirts *Ciona intestinalis* and *Phallusia manillata*, young mussel seed and barnacles, colonize the ropes and become a significant component of the community. Total epifauna biomass on ropes with large mussels can be as high as 450 g ash-free dry wt (AFDW)/meter length of rope, the equivalent of 3 g carbon per m^2 averaged over the entire ria surface. A large seaweed community, dominated by green and red algae in fall and winter succeeding to kelps in the summer, also grows on the mussel ropes (Lapointe *et al.*, 1981). Seaweed production on the rafts ranges from ca. $0.5 \text{ g C} \cdot \text{m}^{-2}\text{raft} \cdot \text{d}^{-1}$ in the winter to $6 \text{ g C} \cdot \text{m}^{-2}\text{raft} \cdot \text{d}^{-1}$ in the summer.

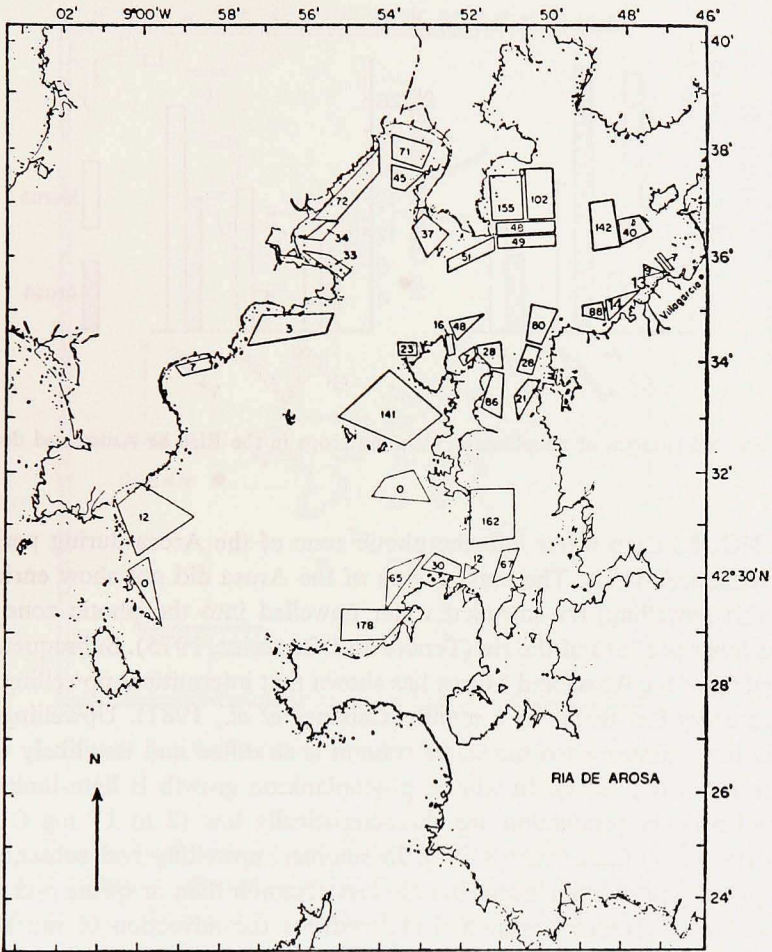


Figure 3. The Ria de Arosa (NW Spain) showing groupings ("polygons") of mussel rafts. The number with the "polygons" represents the number of rafts in that polygon.

Hydrographic and pelagic conditions in the rias

Upwelling persists over the continental shelf off the Rias Bajas (Madelain, 1967; Molina, 1972; Manriquez *et al.*, 1978). Under favorable conditions, such as northerly winds, upwelled waters advect into the rias (Tenore and Gonzalez, 1975). Otto (1975) calculated that during one event, 30% of the water below a depth of 40 m in the Ria de Arosa was unmodified North Atlantic central water and that this water moved toward the surface at the middle to inner part of the ria.

Tenore and Gonzalez (1975) correlated periods of high nutrient concentrations and primary production in the ria with intermittent upwelling of nutrient-rich (10

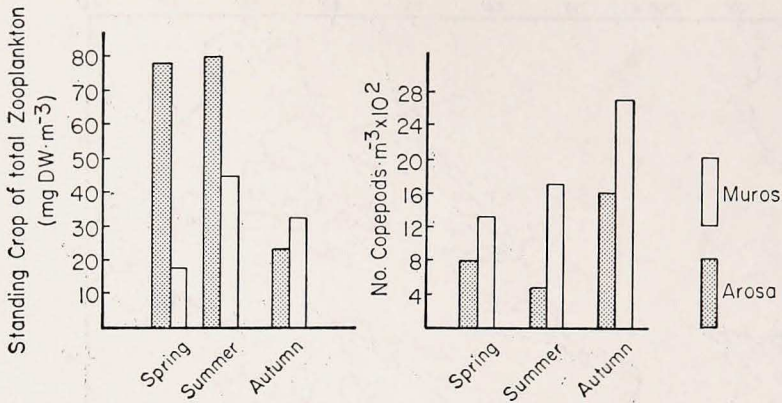


Figure 4. Seasonal changes of zooplankton standing crops in the Rias de Arosa and de Muros.

to 20 μm $\text{NO}_3\text{-N}$) deep water into the photic zone of the Arosa during periods of northeast (offshore) winds. The outer region of the Arosa did not show enrichment effects of this upwelling; the intruded water upwelled into the photic zone in the middle and inner portions of the ria (Tenore and Gonzalez, 1975). Subsequent time-series sampling of the Arosa and Muros has shown that intermittent upwelling occurs in both rias every few weeks to a month (Cabanas *et al.*, 1981). Upwelling is less common in the summer when the water column is stratified and less likely to turnover (Gonzalez *et al.*, 1981). In winter, phytoplankton growth is light-limited, and biomass and primary production are characteristically low (2 to 17 mg Chl-*a*/m² and 30 to 100 mg C fixed \cdot m⁻² \cdot d⁻²). In summer, upwelling and subsequent increases in primary production occur but are less common than in spring and autumn because the water column is stratified and reduces the advection of nutrient-rich deep water into the photic zone. However, strong NE winds can mix the water column in summer. Spring and autumn are characterized by periodic peaks in phytoplankton biomass (> 20 mg Chl-*a*/m²) and primary production (> 1000 mg C fixed \cdot m⁻² \cdot d⁻¹) in the middle and inner ria. The effects of sporadic upwelling on the species composition of the phytoplankton communities in the two rias are superimposed upon typical seasonal changes in plant density and species composition. Short-term (i.e., weeks) peaks of small-celled diatoms (*Chaetoceros* spp.) cluster around typical spring blooms of *Skeletonema costatum* (Campos and Marino, 1982a and b; Campos and Gonzalez, 1975). Related increases in microbial heterotrophy in the middle and inner ria are associated with bursts in phytoplankton production (Santiago *et al.*, in manuscript).

Zooplankton communities in the Arosa are dominated (30 to 90% of total numbers and $> 90\%$ of total biomass) by zoea larvae of the small crab *Pisidia longicornis*, the adult of which lives on mussel ropes (Alvarez, 1977; Corral and Alvarez,

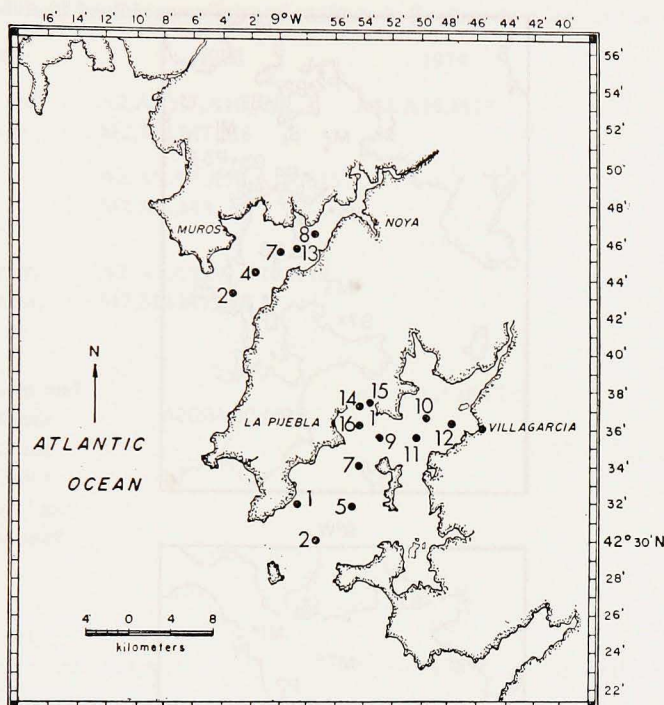


Figure 5. Sampling stations in the Rias de Arosa and de Muros.

1978) (Fig. 4). In the Arosa, zooplankton standing crops are $> 70 \text{ mg DW} \cdot \text{m}^{-3}$ in spring and summer because of great numbers of zoea larvae of *P. longicornis*. Only in the autumn does the zooplankton in the Muros surpass that of the Arosa because of high copepod densities. In the Arosa in autumn small copepods (*Acartia clausi*, *A. discaudata*, *Paracalanus parvus*, *Temora longicornis* and *Pseudocalanus elongatus*) dominate (50 to 95%) total numbers. In winter, zooplankton biomass is $< 70 \text{ mg DW} \cdot \text{m}^{-3}$ in both rias.

GENERAL METHODS

Benthic samples were collected at stations from the mouth to the inner part of the Arosa and Muros, and in the Arosa in the Bay of Barrana at stations inside (A15) and outside (A14 and A16) raft polygons (Fig. 5). Stations in the Bay of Barrana were at similar depth (16 m) and these were used to determine the effects of rafts upon the intermediate bottom area.

Sediment samples were collected by scuba divers and with a Bouma box corer (0.02 m surface area and 20 cm deep boxes). Megabenthic trawl samples were col-

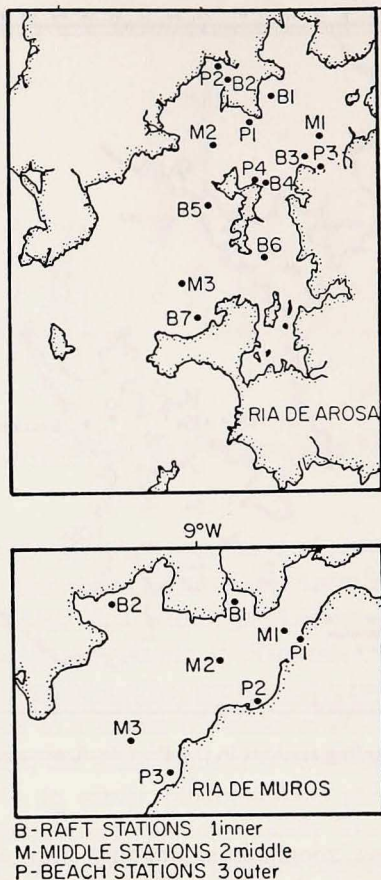


Figure 6. Trawl stations in the Rias de Arosa and de Muros.

lected with a semi-balloon trawl at beach (B), raft (R), and middle (M) habitats in the outer, middle, and inner Arosa and in the outer to middle Muros (Fig. 6). Detailed descriptions of sampling procedures are discussed in later sections.

Various analyses carried out during three fall cruises in 1978, 1979 and 1980 and the schedule of sampling are given in Table 1. Most data were collected during two week cruises in late September. A few determinations were made later in the fall and are indicated in the individual sections. As no significant year-to-year changes were noted, the data have been combined to pursue the main interest of comparing the two rias to ascertain effects due to raft cultures of mussels.

Raft dynamics (Tenore)

Mussel as a "key industry" species

Intense raft culture of mussels causes radical changes in food chain patterns in

Table 1. Schedule of benthic sampling and analyses in the Rias de Arosa and de Muros.

Type of analysis	1978	1979	1980
Macrofauna and sediment analysis	A2,A5,A7,A10,A12 M2,M4,M7,M8	A15,A16,M13	
Meiofauna	A2,A5,A7,A10,A10,A15 M2,M4,M8		
Microbenthos			
—heterotrophy, ATP biomass, and glucose analysis	A2,A5,A8,A9,A10,A15 M2,M4,M7,M8		
—ATP biomass and DNA synthesis		A2,A15,A16,M13	
—epifluorescence counting, DNA synthesis and gas chromatography work			A2,A15,A16,M2,M13,M13
Geochemistry			
—sediment x-ray			
—sulfate pore water analysis and rate of sulfate reduction	A15,A16	A15,A16,M13	A15,A16,M13
—nutrient flux			

the Arosa. Zooplankton are commonly the major herbivore, and pelagic fish the major food chain pathway of secondary production in coastal systems. In the Arosa, filter-feeding mussels are the dominant herbivore.

Approximate (but conservative) calculations of reported data on biomass and literature estimates of mussel filtration activity demonstrate the important role played by the mussel in the Arosa. The average biomass of mussels is roughly 2.3×10^9 gC while that of the total zooplankton (including carnivores) is approximately two orders of magnitude less (8.7×10^7 gC). If the mussels on the three-dimensional rafts were spread over the total bottom surface (230 km²), the average standing crop would be roughly $10 \text{ gC} \cdot \text{m}^{-2}$. One raft produces 40 to 60 metric tons (total wet weight) per year, so that annual yield in the total ria is 80 to 120 thousand metric tons (840 to 1260 KgC).

Assuming an average pumping rate of 5 liters \cdot h⁻¹ per mussel (1 to 1.5 g AFDW tissue biomass), the total mussel community in the Arosa, which only occupies 0.1% of the ria surface, could theoretically filter 3.5×10^{12} liters \cdot d⁻¹ or 80% per day of the water volume of the ria. In the fall, when mussel density is highest, these filtering rates would be doubled.

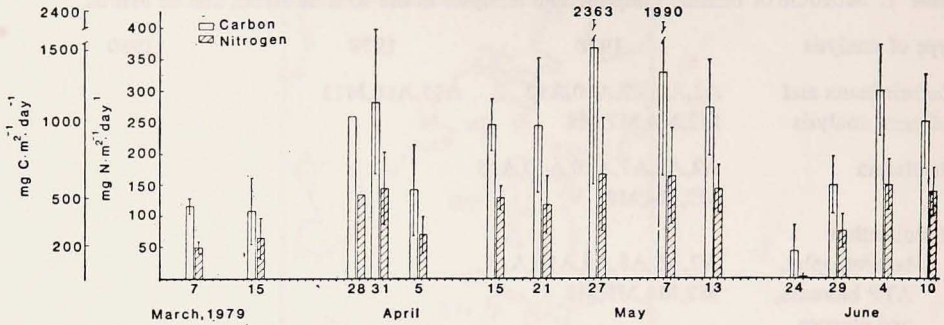


Figure 7. Seasonal changes in sedimentation rates in a raft area in the inner Ria de Arosa.

Sedimentation rates

Methods

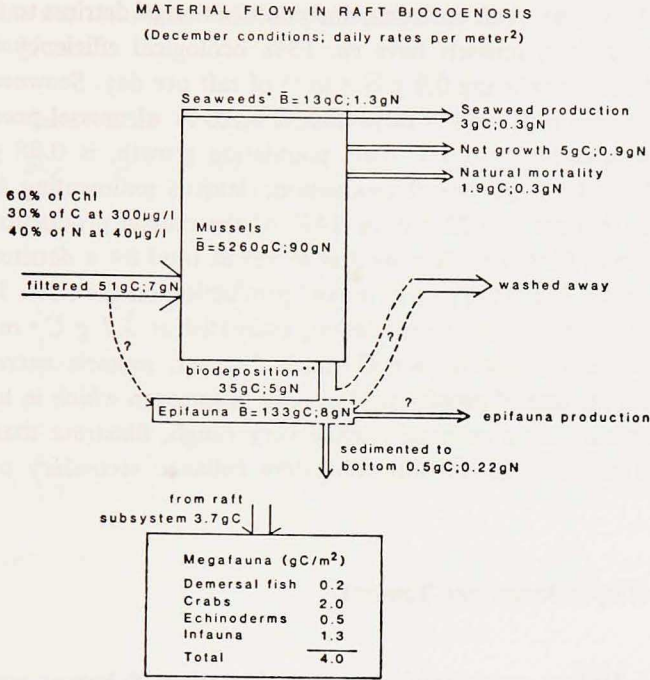
Sediment accumulation rates in a raft polygon area in the inner Arosa between March and June were estimated by attaching 5 sediment traps (0.014 m² diameter; 14.5 cm height) to concrete pads 2 m off the bottom. Visual examination of the sedimented material indicated fresh fecal pellets, with little evidence of entrapment of resuspended material. The traps were placed randomly underneath the polygon. Water depth ranged from 10 to 12 m at mean low tide. Each trap contained two 0.25 g pellets of sodium azide, a bactericide. The traps were positioned by divers and left *in situ* for 24 hours. They were then capped and returned to the laboratory. We recorded wind direction and speed throughout the period.

Each sample was centrifuged, the particulates dried (90°C for 24 h) and combusted (475°C for 12 h) to obtain ash-free dry weights. Subsamples were treated with cold phosphoric acid to remove carbonates and analyzed for organic carbon and nitrogen on a Model 240 Perkin Elmer CHN Analyzer.

Results and discussion

Sediment accumulation rates ranged from *ca.* 200 to over 2400 mgC • m⁻² • d⁻¹ (10 to 150 mgN • m⁻² • d⁻¹) with highest rates in May when mussel biomass was greatest (Fig. 7). Organic matter (% AFDW) in sedimented material ranged from 73 to 81%. The winter of 1978-79 was exceptionally severe. High winds sank over two hundred rafts and high turbidity lasted for several months in late winter-early spring. Thus, low sedimentation values in March might reflect low mussel filtering activity due to turbidity.

Because filtration rate is affected by food concentration, filtration by mussels could fluctuate, with high sedimentation occurring during periods when primary production is high due to upwelling. The periods of 3-15 March and 15-29 May were dominated by southwest winds, which do not favor upwelling; just previous to



*annual averages

**estimated from literature

Figure 8. Box diagram illustrating estimates of carbon and nitrogen standing crops and flow in the raft subsystem in the Ria de Arosa. See text for data sources.

and during periods of high sedimentation (25 March-5 April, 13 April-13 May, and 1-10 May) were characterized by northwest winds which favor upwelling. Data sets are few but suggest variable rates of sedimentation. High sedimentation occurred in early autumn and late spring when mussel standing crop was highest, and during periodic peaks in primary production that would increase mussel filtering and deposition.

Material flow through a raft subsystem

We used literature values on standing crops and production estimates of mussels and epifauna (Tenore and Gonzalez, 1975; Perez and Roman, 1979; Roman and Perez, 1979) and seaweed (Lapointe *et al.*, 1981), sedimentation rates, and literature values for mussel filtration, feeding, and biodeposition capabilities (Tenore and Dunstan, 1973) to construct a budget of daily material flux in a raft subsystem (Fig. 8). Besides mussel production itself, there is significant ancillary production of seaweeds

and associated herbivores, raft epifauna, and contribution of detritus to the sediment. Based on nitrogen data, mussels have *ca.* 13% ecological efficiency (net production/food available), producing $0.9 \text{ g N} \cdot \text{m}^{-2}$ of raft per day. Seaweed production annually averages $0.3 \text{ g N} \cdot \text{m}^{-2} \cdot \text{raft} \cdot \text{day}^{-1}$, or 33% of mussel production; epifaunal production, assuming a 1% daily population growth, is $0.08 \text{ g N} \cdot \text{m}^{-2} \cdot \text{raft} \cdot \text{day}^{-1}$, about 10% of mussel production; detritus sedimenting from the raft subsystem to the bottom is 0.22 g N or 24% of the mussel production. Thus, ancillary production of biota and detritus that serves as food for a detritus-based food chain, is more than half (67%) that of mussel production on the rafts. This ancillary production, plus mortality due to predation, estimated at $3.7 \text{ g C} \cdot \text{m}^{-2}$, supports a megabenthic standing crop of $4 \text{ g C} \cdot \text{m}^{-2}$. Further, mussels excrete ammonia and thus increase the rate of geochemical cycling of nitrogen which in turn enhances primary production. These estimates, while very rough, illustrate that the habitat and biodeposits provided in the raft subsystem enhance secondary production in the ria.

Macroinfauna (Lopez-Jamar and Tenore)

Methods

We collected 10 box cores (0.02 m^2) at each station. Subcores were taken for sediment particle size analysis by pipet technique (Holme and McIntyre, 1971) and for estimates of organic matter by combusting (500°C for 24 h) dried (90°C for 24 h) samples. Subcores were also treated with cold phosphoric acid to remove carbonates, and carbon and nitrogen determined on a Perkin-Elmer Model 240 CHN Analyzer. Cores for macroinfauna enumeration were sieved (0.5 mm) and preserved with 5% buffered formaldehyde. The animals were identified and enumerated. The preserved animals were patted dry and preserved wet weight determined. Subsamples of various taxa were dried (90°C for 24 h) and ashed (475°C for 12 h) to estimate ash-free dry weight (AFDW). All fauna biomass comparisons are based on AFDW.

Dendrograms using percent similarity and matrices using the Morisita index (Morisita, 1959) were used to spatially delimit faunal assemblages.

Results and discussion

a. Sediment characteristics. Organic matter was high ($> 10\%$) in sediments from both rias except at the outer regions of the Muros ($< 8\%$) (Table 2) and increased from the mouth to inner portions (Fig. 9). Outer stations of the Muros were more sandy whereas the Arosa had a higher percentage of silt-clay fraction. The Trask sorting coefficient ($S_o = \sqrt{Q_{25}/Q_{75}}$) indicates poor to moderate sorting (1.5 to 2.9) for sediments in both rias.

Table 2. Particle size and organic content (% O.M.) analysis of sediments from the Rias de Arosa and de Muros.

Station	%Sand	%Silt	%Clay	%Silt-Clay	Median		%O.M.	%C ^{a,b}	%N ^b
					(μ m)	S ₀			
A2	20.3	68.9	10.8	79.7	36	2.4	10.2	4.0	0.29
A5	34.6	47.3	18.2	65.5	78	2.9	12.6	4.5	0.43
A7	11.1	75.6	13.3	88.9	44	2.8	10.7	4.7	0.41
A10	24.0	67.4	8.7	76.1	69	2.5	13.5	4.7	0.41
A12	26.7	53.5	19.7	73.2	72	2.6	14.7	5.7	0.43
A15	3.6	78.9	17.5	96.4	19	1.7		7.0	0.65
A16	4.7	78.1	17.2	95.3	15	1.8		5.5	0.65
M2	49.6	45.8	4.7	50.5	125	1.7	4.0	2.1	0.09
M4	38.3	53.2	8.5	61.7	91	2.3	8.8	6.5	0.29
M7	6.3	81.3	12.4	93.7	40	1.8	13.7	5.8	0.45
M8	5.5	78.5	16.0	94.5	38	2.5	13.5	5.6	0.46
M13	2.9	84.0	13.1	97.1	18	1.5			

^a Carbonate free.

^b Based on predigested sediment dry wt.

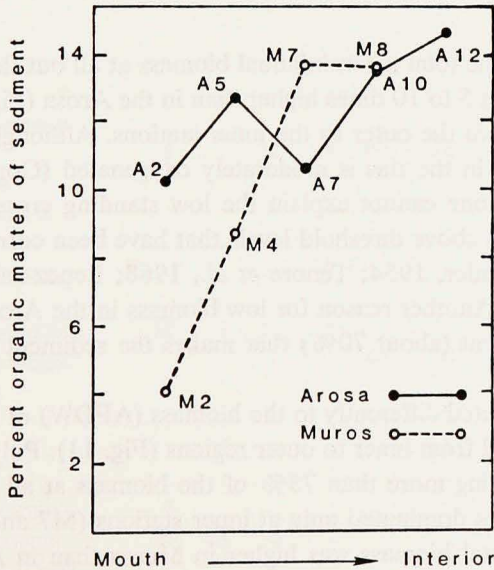


Figure 9. Percent organic matter (by combustion) of sediments in the Rias de Arosa and de Muros in September 1978.

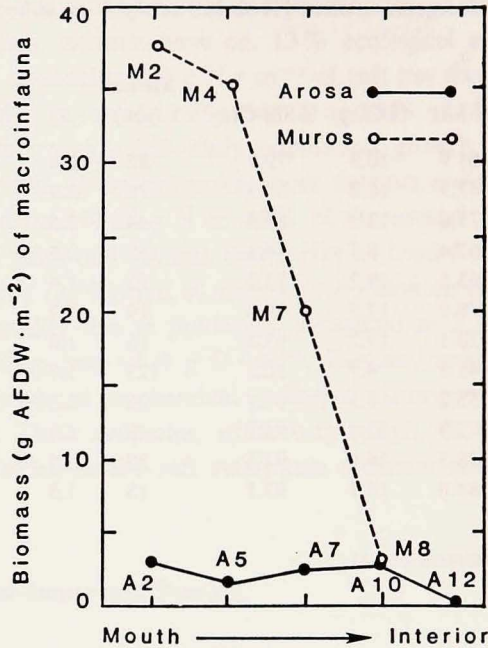


Figure 10. Macrofaunal (≥ 0.5 mm) biomass (AFDW) in the Rias de Arosa and de Muros in September 1978.

b. Faunal biomass. The total macrofaunal biomass at all but the innermost station (M8) in the Muros was 5 to 10 times higher than in the Arosa (Fig. 10). In both rias, biomass decreased from the outer to the inner stations. Although the sediment was anoxic, bottom water in the rias is moderately oxygenated (Gonzalez *et al.*, 1981) so that low oxygen alone cannot explain the low standing crops. Still, the organic carbon values are well above threshold levels that have been correlated with adverse effects on benthos (Bader, 1954; Tenore *et al.*, 1968; Lopez-Jamar, 1978a and b; Theede *et al.*, 1969). Another reason for low biomass in the Arosa may be the high interstitial water content (about 70%) that makes the sediment physically unstable for many infauna.

Major taxa contributed differently to the biomass (AFDW) of the infaunal assemblages of both rias and from inner to outer regions (Fig. 11). Polychaetes dominated in the Arosa, comprising more than 75% of the biomass at all but Station A5. In the Muros, polychaetes dominated only at inner stations (M7 and 8). The contribution of molluscs to total biomass was higher in Muros than in Arosa, especially at the outer Station M4. Echinoderms formed most of the biomass at the outer Station M2 of Muros, but in Arosa they were only important at Station A5.

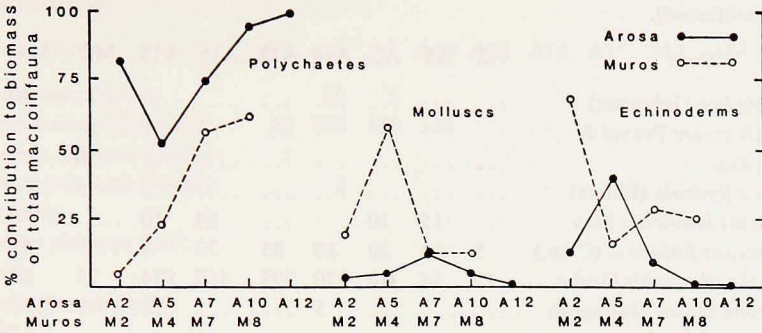


Figure 11. Contribution of major taxa to the total macrofaunal biomass (AFDW) in the Rias de Arosa and de Muros in September 1978.

c. *Infauna species composition.* Over one hundred taxa were found in the two Rias (Table 3). Overall polychaetes accounted for 59% and molluscs 20% of the number of taxa but polychaetes accounted for 65% for the Arosa and 50% for the Muros of total number of individuals. Especially abundant polychaetes were *Tharyx multibranchiis* and *Spiochaetopterus costarum*. Echinoderms were more abundant in the Muros.

Table 3. Species composition of benthic samples from the Rias de Arosa (A) and Muros (M). Values given as mean number of individuals/m².

Taxa	A2	A5	A7	A10	A12	A16	A15	M2	M4	M7	M8
Polychaetes											
<i>Chaetopterus variopedatus</i> (Renier)	5	...
<i>Spiochaetopterus costarum</i> Clap.	5	...	25	95	60	16	12	...	20	20	265
<i>Glycera alba</i> Rathke	15
<i>Glycera rouxii</i> Adouin & M. Edwards	2	2	5
<i>Glycera unicornis</i> Savigny	5	20	75	...
<i>Glycera</i> sp. 1	5
<i>Prionospio malmgreni</i> Clap.	10	5	15	5	25	...	5	...
<i>Prionospio cirrifera</i> Wiren	44	38
<i>Polydora antennata</i> Claparede	10	2
<i>Polydora</i> sp.	...	5	50	60
<i>Spionidae</i> indet.	20	5
<i>Lagisca extenuata</i> (Grube)	5
<i>Leanira yhleni</i> Malmgren	35	25	5
<i>Harmothoe lunulata</i> (Delle Chiaje)	120	45	25	...
<i>Harmothoe</i> sp.	2

Table 3. (continued).

Taxa	A2	A5	A7	A10	A12	A16	A15	M2	M4	M7	M8
<i>Sthenelais boa</i> (Johnston)	10	5	5
<i>Sthenelais minor</i> Pruvot & Racovitza	10
<i>Sthenelais limicola</i> (Ehlers)	5
<i>Notomastus latericeus</i> Sars	...	15	10	84	10	...	10	25	5
<i>Heteromastus filiformis</i> (Clap.)	5	10	20	30	35	72	8	...	55	5	...
<i>Tharyx multibranchis</i> Grube	15	35	10	270	275	460	134	25	35	5	5
<i>Chaetozone setosa</i> Malmgren	5
<i>Heterocirrus bioculatus</i> (Keferstein)	10	5	5
<i>Nephtys incisa</i> Malmgren	10
<i>Nephtys longosetosa</i> Oersted	15
<i>Nephtys hystricis</i> McIntosh	10	2	...	25
<i>Nephtys</i> sp. 1	5
<i>Gyptis propinqua</i> Marion & Bobretzky	10	...	5	10	10	30	20
<i>Ophiodromus flexuosus</i> Delle Chiaje	8
<i>Castalia punctata</i> O. F. Müller	4	4
<i>Melinna palmata</i> Grube	...	40	15	128	6	5	...
<i>Amage adspersa</i> (Grube)	20	5
<i>Ampharete grubei</i> Malmgren	52	12
<i>Pectinaria koreni</i> Malmgren	2
<i>Pectinaria auricoma</i> (Müller)	2
<i>Lumbrineris impatiens</i> Clap.	...	5	5	85	25	40	...
<i>Lumbrineris latreilli</i> Adouin & M. Edw.	5
<i>Lumbrineris fragilis</i> (O. F. Müller)	5	5	10	...
<i>Lumbrineris</i> sp.	2
<i>Euclymene oerstedii</i> Clap.	12	2	25	...	10	...
<i>Euclymene lombricoides</i> Quatrefages	25	25	10	...
<i>Maldane glebifex</i> Grube	30	235	30	5
<i>Terebellides stroemi</i> Sars	15
<i>Polycirrus</i> sp.	...	10	35	2	...	10	5	15	...
<i>Amphitrite edwardsi</i> (Quat.)?	2
<i>Aricia latreilli</i> Adouin & M. Edwards?	5
<i>Eulalia fuscens</i> St. Joseph	5
<i>Phyllodoce kosteriensis</i> (Malmgren)	5
<i>Leptonereis glauca</i> Clap.	5
<i>Nereis</i> sp. 1	4	4
<i>Poecilochaetus serpens</i> Allen	...	10	5	5	10	...

Table 3. (continued).

Taxa	A2	A5	A7	A10	A12	A16	A15	M2	M4	M7	M8
<i>Magelona rosea</i> Moore	...	20	5
<i>Sternaspis scutata</i> (Ranzani)	35	205	135	160
<i>Scalibregma inflatum</i> Rathke	5
<i>Fauvelia martinensis</i> Gravier	...	5
Syllidae indet.	10	...
<i>Stylarioides plumosa</i> (O.F. Müller)	10
<i>Owenia fusiformis</i> Delle Chiaje	5
<i>Eunicidae</i> indet.	5
TOTAL POLYCHAETE DENSITY	205	395	305	632	436	850	186	415	565	390	365
TOTAL NO. POLYCHAETE SPECIES	14	14	16	9	8	18	11	17	19	20	7
Molluscs											
<i>Abra nitida</i> (Müller)	10	8	5	20
<i>Venus casina</i> L.	10	20
<i>Venus striatula</i> (da Costa)	55	5	...
<i>Myrtea spinifera</i> (Montagu)	5	...	10	90	20	...
<i>Mytilus edulis</i> L.	5
<i>Acanthocardia tuberculata</i> (L.)	5
<i>Gari fervensis</i> (Gmelin)	10
<i>Nucula</i> sp.	15
<i>Corbula gibba</i> (Olivi)	5	5
<i>Diplodonta rotundata</i> (Montagu) ?	5
<i>Thyasira flexuosa</i> (Montagu)	44	2
Bivalve indet. no. 1	2	2
TOTAL DENSITY BIVALVES	10	0	20	35	0	46	12	20	170	25	20
<i>Turritella triplicata</i> (Brocchi)	5	...	10	145	10	...
<i>Nassarius semistriatus</i> (Brocchi)	...	5
<i>Nassarius pygmaeus</i> (Lamarck)	...	5
<i>Nassarius incrassatus</i> (Ström)	5
<i>Gibbula cineraria</i> (L.)	5
Gastropod indet.	4
<i>Dentalium novemcostatum</i> Lamarck	15	...
<i>Nudibranch</i> indet. no. 1	5	...	5
TOTAL DENSITY GASTROPODS	10	10	10	0	0	4	0	0	155	25	5
Echinoderms											
<i>Amphiura chiajei</i> Forbes	25	...	30	2	...	65	170	185	...

Table 3. (continued).

Taxa	A2	A5	A7	A10	A12	A16	A15	M2	M4	M7	M8
<i>Amphiura filiformis</i> O. F.											
Müller	1085	65	35	...
<i>Acronida brachiata</i> (Montagu)	10
<i>Echinocucumis hispida</i> (Barrett)	5	5
<i>Cucumaria elongata</i> Düben & Koren	5
<i>Leptosynapta</i> sp.	10	35	5	...
<i>Labidoplax digitata</i> (Montagu)	14	40
<i>Leptosynapta bergensis</i> (Ost.)	50	50	5	140	60	15
<i>Thyone fusus</i> (O. F. Müller)	115	5
<i>Echinocardium cordatum</i> (Pennant)	25	35
TOTAL DENSITY OF ECHINODERMS	80	55	30	0	0	16	0	1320	455	285	50
Crustaceans											
Amphipoda	35	35	90	40	10	82	62	50	45	15	...
Cumacea	...	5	5	10
<i>Parvipalpus</i> sp. ?	...	5	5
<i>Pisidia longicornis</i> (L.)	30	10
<i>Asthenognathus atlanticus</i> Monod	10
<i>Processa</i> sp.	45	...
Paguridae indet.	5
Decapoda larvae	5
TOTAL DENSITY OF CRUSTACEANS	65	45	95	50	10	82	62	60	70	60	0
Others											
Turbellaria indet.	...	15	80	5	...	10	...	25	30	15	20
Echiuroid ?	10
Nemertean	4
TOTAL DENSITY OF OTHERS	0	15	80	5	0	14	0	25	40	15	20
TOTAL DENSITY • M ⁻²	370	520	540	722	446	1012	260	1840	1455	800	460

Cluster analysis (Fig. 12) showed three faunal groupings: (1) the inner stations of the Arosa (A15, A16, A12 and A10); (2) the outer and middle stations of the Arosa (A5, A7 and A2); (3) the middle stations of the Muros (M4 and M7). The outer (M2) and inner (M8) of the Muros had very low similarity with any other group.

The polychaete *Sternaspis scutata* dominated both in number and biomass in the outer and middle area of the Arosa (group 2). At outermost stations, with coarser

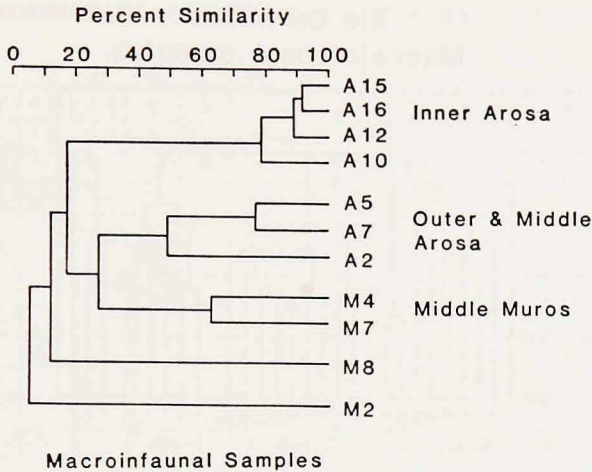


Figure 12. Cluster analysis of macroinfaunal stations from the Rias de Arosa and de Muros in September 1978.

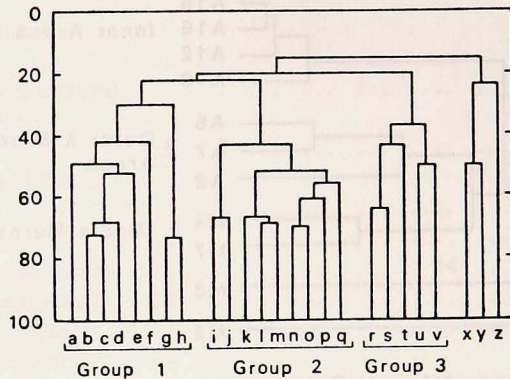
sediment and lower organic content, the holothurian *Leptosynapta bergensis* dominated. This group 2 community is similar to the *Amphiura filiformis-Virgularia tuberculata-Sternaspis scutata* community off Brittany where characteristic water depths are 10-40 m and sediments have a high percentage of silt-clay (Glémarec, 1965).

The polychaetes *Tharyx multibranchiis* and *S. costarum* dominated numerically and *S. costarum* in biomass in the inner part of the Arosa (group 1). *Sternaspis scutata* dominated the biomass at Station A10 and the community overlapped with group 2. This community is similar to the *Maldane glebifex-Spiochaetopterus costarum* community characteristic of soft bottoms off Brittany (Glémarec, 1965), except that *S. costarum* was much more abundant in the inner Arosa assemblage.

Amphiura chiajei, *Leptosynapta bergensis* and *Maldane glebifex* dominated numerically and *M. glebifex*, *Venus striatula* and *A. chiajei* dominated the AFDW biomass in the middle part of the Muros. This assemblage seems to be a transition between the *Amphiura filiformis-Amphiura chiajei* community in the North Sea (Thorson, 1957) and the *Maldane glebifex-Spiochaetopterus costarum* community of Glémarec (1965).

In the outer part of the Muros (Station M2), *Amphiura filiformis* was overwhelmingly dominant in number and biomass with densities reaching more than 1000 ind/m². The holothurian *Thyone fusus* was also important in biomass. This community appears to be a transition between the *Amphiura filiformis-Amphiura chiajei* community of Thorson (1957) and the *Echinocardium cordatum-Amphiura filiformis* community in Danish waters (Petersen, 1915).

Ria De Muros
Macroinfaunal Samples



- | | |
|----------------------------------|-------------------------------------|
| a: <i>Euclymene lombricoides</i> | n: <i>Maldane glebifex</i> |
| b: <i>Harmothoe lunulata</i> | o: <i>Venus striatula</i> |
| c: <i>Amphiura filiformis</i> | p: <i>Labidoplax digitata</i> |
| d: <i>Lumbrineris impatiens</i> | q: <i>Heteromastus filiformis</i> |
| e: <i>Thyone fusus</i> | r: <i>Spiochaetopterus costarum</i> |
| f: <i>Leptosynapta</i> sp. | s: <i>Polydora</i> sp. |
| g: <i>Euclymene oerstedii</i> | t: <i>Gyptis propinqua</i> |
| h: <i>Tharyx multibranchiis</i> | u: <i>Abra</i> sp. |
| i: <i>Nephtys hystericis</i> | v: <i>Echinocardium cordatum</i> |
| j: <i>Turritella triplicata</i> | x: <i>Notomastus latericeus</i> |
| k: <i>Leptosynapta bergensis</i> | y: <i>Glycera unicornis</i> |
| l: <i>Amphiura chiajei</i> | z: <i>Processa</i> sp. |
| m: <i>Myrtea spinifera</i> | |

Figure 13. Cluster analysis showing association of macroinfaunal species in the Ria de Muros.

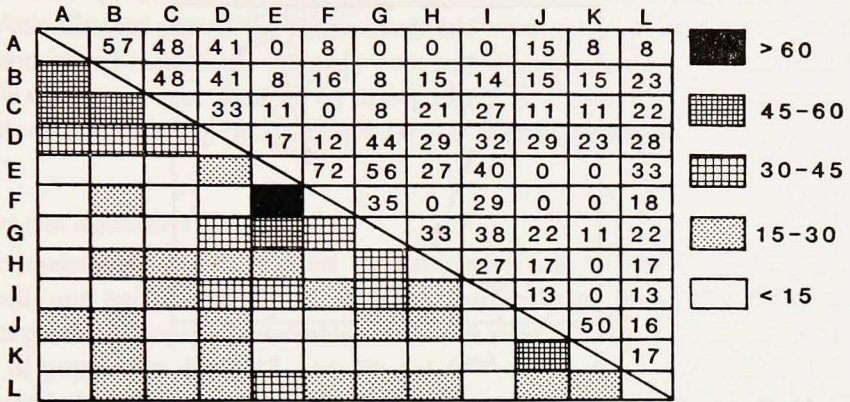
In the Muros, the number of species having a relatively high abundance was greater than in Arosa, permitting a cluster diagram for species associations (Fig. 13). Distinct faunal assemblages inhabited: (1) the outer area of the Muros in sandy sediments with moderate organic levels; (2) middle part of the Muros; and (3) the inner Muros.

Fager's Index of species association (Fager, 1957) was used to estimate the degree of association between the dominant species in the Arosa. The Trellis diagram (Fig. 14) showed three species having high levels of association: *Tharyx multibranchiis*, *Spiochaetopterus costarum*, and *Heteromastus filiformis*. These species occurred more frequently at eutrophic inner stations. *S. costarum* is strongly associated with organically polluted areas in the nearby Ria de Pontevedra (Lopez-Jamar, 1978b).

d. *Species diversity*. Diversity was calculated using numbers of species (Shannon and Weaver, 1963) and biomass (Wilhm, 1968) (Table 4). Because the actual total densities that provide the raw data for the diversity measurements are low (< 500),

MACROINFAUNAL SAMPLES

RIA DE AROSA



A: *Tharyx multibranchiis*
B: *Spiochaetopterus costarum*
C: *Heteromastus filiformis*
D: *Sternaspis scutata*
E: *Maldane glebifex*
F: *Pisidia longicornis*

G: *Leptosynapta bergensis*
H: *Melinna palmata*
I: *Leanira yhleni*
J: *Prionospio malmgreni*
K: *Polycirrus* sp.
L: *Amphiura chiajei*

Figure 14. Trellis diagram showing association of macroinfaunal species in the Ria de Arosa.

the calculated diversities may be overestimates (Sanders, pers. comm.). Thus, the values should be treated with caution.

In the Arosa, diversity was lowest at the inner stations (A10 and A12), but

Table 4. Species diversity (H'), maximum diversity (H'_m) and evenness (J) of macroinfauna based on abundance and biomass in the Rias de Arosa and de Muros.

	Abundance diversity			Biomass diversity		
	H'	H'_m	J	H'	H'_m	J
A2	4.17	4.58	0.91	2.85	4.52	0.63
A5	3.46	4.64	0.74	3.16	4.52	0.70
A7	3.80	4.64	0.82	3.00	4.58	0.65
A10	2.55	3.81	0.67	1.71	3.70	0.46
A12	1.21	2.00	0.61	1.00	2.00	0.50
A16	3.05	4.75	0.64	2.48	4.70	0.53
A15	2.75	4.17	0.66	2.93	4.17	0.70
M2	2.71	5.17	0.52	2.51	5.13	0.49
M4	4.46	5.55	0.80	2.78	5.39	0.52
M7	4.30	5.13	0.84	2.79	4.95	0.56
M8	2.97	4.17	0.71	2.24	3.70	0.60

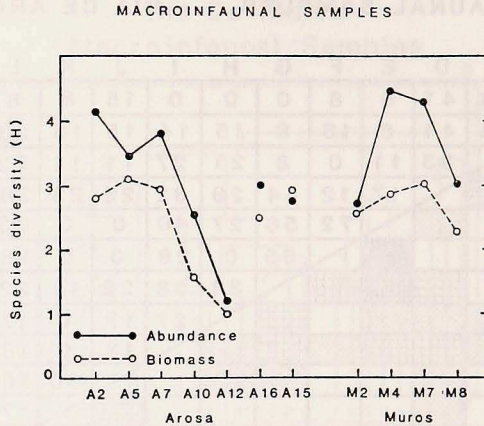


Figure 15. Species diversity of macroinfauna from the Rias de Arosa and de Muros based on number and biomass. Stations A16 and A15 are in raft areas.

slightly higher at raft stations (Fig. 15). Diversity in the Muros was generally higher than in the Arosa. In the Muros, highest diversity values were found at the middle stations (M4 and M7). The relatively low diversity of Station M2 in the Muros was due to the great dominance of *Amphiura filiformis*. Low diversity values in the inner stations of both rias resulted from two factors: (a) a decrease in number of species at these stations, possibly caused by sediment instability (see Organism-sediment relations and sediment geochemistry section); and (b) the high dominance of only one or two species at inner station (*S. costarum* and *T. multibranchiis* in the Arosa and *S. costarum* in the Muros).

e. Comparison of inside and outside raft areas. Although the species composition was quite similar inside (A15) and outside (A16) raft areas, there was a larger number of species and individuals at the outside station (A16). Diversity was slightly higher and biomass was four times greater at the outside station. The abundance of some species was similar in both areas (*Spiochaetopterus costarum*, *Prionospio cirrifera*, etc.) but many were much more abundant in the outside station (*Tharyx multibranchiis*, *Melinna palmata*, *Ampharete grubei*, *Thyasira flexuosa*, etc.).

Meiofauna (Tietjen)

Methods

Two box cores per station were subsampled by inserting four 2.5 cm (inside diameter) plastic core tubes to a depth of five cm, yielding a minimum of eight samples per station. The samples were preserved in 5% formalin seawater containing Rose Bengal (0.5 g/l).

In the laboratory the samples were washed through a set of two sieves, the larger with a mesh opening of 0.500 mm and the smaller with a mesh opening of 0.044 mm. Animals that passed the larger sieve and were retained by the smaller sieve were considered meiofauna. Animals were sorted and major taxa enumerated. Dry weights of all taxa were obtained by drying (90°C to constant weight) representative individuals and weighing ($\pm 1 \mu\text{g}$) on a Mettler HS Microbalance.

Results and discussion

The meiofauna was dominated by nematodes but also included harpacticoid copepods and polychaetes (Table 5). The overall relative dominance of nematodes and harpacticoid copepods was similar in both rias. Nematodes comprised 71 and 77% of population densities, and 49 and 68% of biomass of meiofauna in the Arosa and the Muros, respectively. Harpacticoid copepods were second in importance, constituting 18 and 14% of individuals, and 41 and 20% of biomass, respectively in the Arosa and Muros. Occasional ostracods, kinorhynchs or pelecypods were found, but none exceeded 5% of the total number of individuals present. Foraminifera were also found in several samples but their densities were very low ($28 \pm 24 \times 10^3 \cdot \text{m}^{-2}$).

A total of 44 species of nematodes representing 20 families were identified and their areal distribution examined (Fig. 16). Nematode densities at Muros Station M7 and Arosa Station A9 were too low to permit adequate taxonomic study and these stations are not discussed further. In the Arosa, the Comesomatidae was the most abundant nematode family, particularly at Stations A12 and A15 where *Sabatieria pulchra* and *Metacomesoma punctatum* were highly dominant. *S. pulchra* constituted 46% at A12 and 28% at A15 of the nematode fauna. *M. punctatum*, which occurred only at these two stations, comprised 12% at A12 and 55% at A15. Also significant was the absence of the Richtersiidae and the low abundance of the Chromadoridae in the Arosa. In the Muros the family Comesomatidae comprised only 1% of the nematoda fauna, and both the Richtersiidae and Chromadoridae were present (the latter averaging 14% of the fauna). The dominant family was the Desmodoridae, which comprised 43% of the total number of individuals in the Muros samples (as compared to 13% for the Arosa). The dominant species in the Muros were *Aponema torosus*, *Neochromadora poecilosoma*, and *Synonchiella riemanni*. Muros Station M2 was unique in that it was dominated by *Spirinia parasitifera*, a species that occurred nowhere else and *Dichromadora geophila*, which occurred only at Muros Stations M2 and M4.

Cluster analysis of the abundances of nematode families showed little faunal similarity among stations (Fig. 17). Only Stations A12 and A15 had > 50% similarity. These two stations were quite dissimilar (ca. 10% similarity) from all other stations.

Table 5. Abundance (number $\times 10^3 \cdot m^{-2}$) and biomass (mgDW $\cdot m^{-2}$) of meiofauna in the Rias de Arosa (A) and de Muros (M), September 1978. Data given are means of five samples \pm one standard deviation.

Stations	M2	M4	M7	M8	A3	A5	A7	A9	A10	A12	A15
Abundance											
Nematode	20 \pm 18	100 \pm 91	6 \pm 3	55 \pm 49	24 \pm 24	74 \pm 51	65 \pm 42	7 \pm 4	75 \pm 40	529 \pm 32	1524 \pm 766
Harpacticoida	2 \pm 1	48 \pm 35	2 \pm 1	9 \pm 2	6 \pm 4	14 \pm 16	12 \pm 7	5 \pm 4	10 \pm 7	2 \pm 1	29 \pm 21
Polychaeta	0.3 \pm 0.4	2.3 \pm 2.0	0	0.7 \pm 0.9	2 \pm 1	3 \pm 2	0.5 \pm 0.5	0	0	0.4 \pm 0.3	10 \pm 6
Total Meiofauna	23 \pm 21	163 \pm 132	10 \pm 8	71 \pm 65	49 \pm 45	106 \pm 87	84 \pm 75	12 \pm 8	88 \pm 80	531 \pm 33	1664 \pm 783
Biomass											
Nematoda	6 \pm 5.4	30 \pm 27.3	1.8 \pm 0.9	38.5 \pm 34.3	16.8 \pm 16.8	51.8 \pm 35.7	45.5 \pm 29.4	4.9 \pm 2.8	52.5 \pm 28.0	396.6 \pm 22.4	1137 \pm 536
Harpacticoida	2.6 \pm 1.3	62.4 \pm 45.5	2.6 \pm 1.3	11.7 \pm 2.6	7.8 \pm 5.2	18.2 \pm 20.8	15.6 \pm 9.1	6.5 \pm 5.2	13.0 \pm 9.1	2.6 \pm 1.3	37.7 \pm 27.3
Polychaeta	1.5 \pm 2.0	11.5 \pm 10	0	3.5 \pm 4.5	10 \pm 5	15 \pm 10	2.5 \pm 2.5	0	0	2.0 \pm 1.5	50 \pm 30
Total Meiofauna	10.2 \pm 9.8	105.2 \pm 82.8	4.5 \pm 2.7	56.7 \pm 43.4	39.3 \pm 30.3	92.3 \pm 71.2	73.6 \pm 51.0	11.4 \pm 8.0	66.2 \pm 39.2	372.3 \pm 25.2	1224.7 \pm 593.3

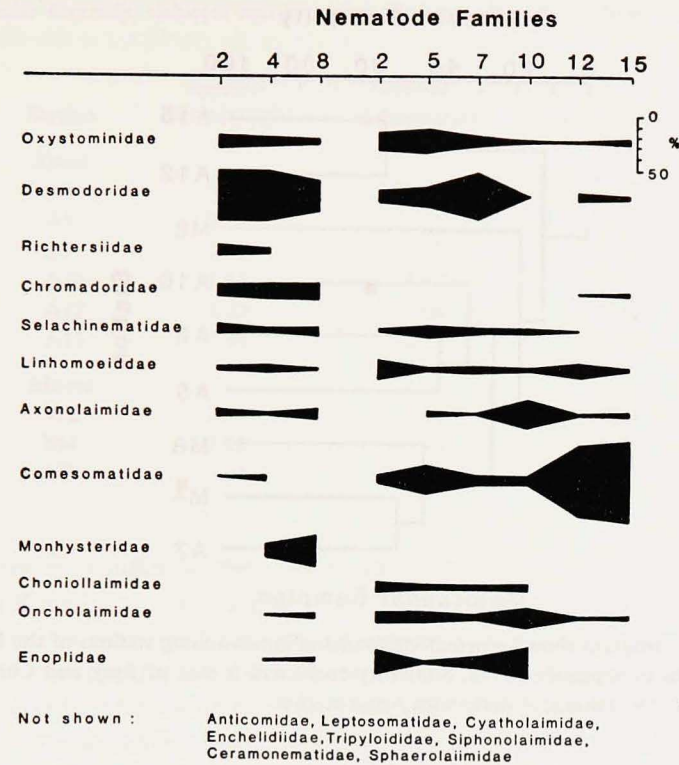


Figure 16. Distribution and relative abundances of nematode families in the Rias de Arosa and de Muros in September 1978.

Nematode species diversity (H') (Pielou, 1966) was highest at Muros Station M2 and lowest at the inner stations of the Arosa (Table 6). Of interest is the low species richness component (SR measured according to Margalef, 1958) at all stations in both rias, especially at the inner stations of the Arosa, and the low equitability component (Pielou, 1966) at Stations A12 and A15 in the Arosa. However, as discussed in the Macroinfaunal section, the actual total densities of meiofauna that provide the raw data for the diversity calculations are low. This causes overestimation of equitability and diversity. In both rias, species diversity was not correlated with increasing median grain size (Kendall's $Y = +0.47$, $p > .05$), but was negatively correlated with increasing organic content ($Y = -0.87$, $p < 0.01$). The latter relation was especially evident in the Muros, where a gradient in increasing organic content from the outer to the inner ria was accompanied by a decrease in species diversity.

With the exception of significantly higher densities at Stations A12 and A15 in the Arosa (one-way ANOVA, $p < .05$), no differences in density and biomass of meiofauna between the two rias existed; nor were there significant differences in density and biomass between the inner and outer stations in either ria.

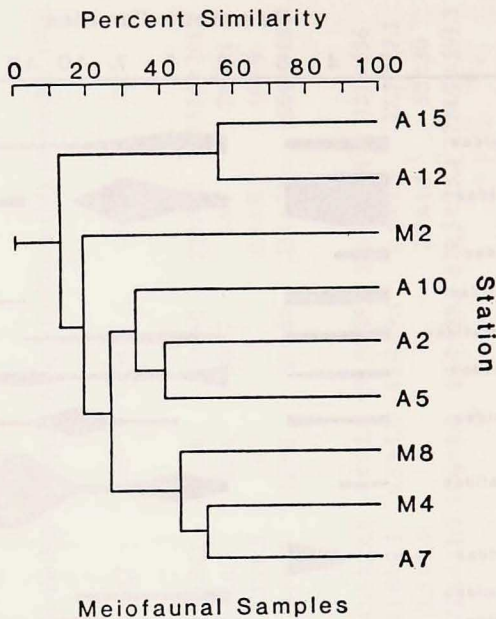


Figure 17. Dendrogram showing nematode faunal affinities among stations of the Rias de Arosa and de Muros in September 1978. Similarity coefficient is that of Bray and Curtis (1957). *M* designates Muros stations; *A* designates Arosa station.

Only Arosa Stations A12 and A15 supported meiofauna densities comparable to those that have been reported from similar environments (Buzzards Bay, Wieser, 1960; North Sea, Warwick and Buchanan, 1970; Bay of Piran, Marcotte and Coull, 1974; Banyuls-sur Mer, de Bovee and Soyer, 1974; Long Island Sound, Tietjen, 1977; New York Bight, Tietjen, 1980). Densities and biomass at the other stations were one to two orders of magnitude below those expected and were more like meiofauna densities found at greater depths (Thiel, 1975). Low meiofauna densities in both rias appear to be functions of either high sediment organic load (and reducing conditions), sediment instability, and/or interactions with the meiofauna.

The Arosa is characterized by the physical composition and high organic load of the sediment and low macrobenthic abundance. While the effects of high (> 5%) sedimentation or organic matter on the meiofaunal densities may vary as a result of differences in other environmental variables that accompany organic enrichment (Marcotte and Coull, 1974; Tietjen, 1977, 1980), decreases in meiofauna densities associated with elevated organic loads and low oxygen tensions have been observed (Tietjen, 1980). Interstitial water of the Arosa sediments below the few millimeters of the surface is anoxic (see Microbenthos section). Meiofauna are sensitive to depressed oxygen levels that usually accompany organic enrichment; crustaceans are especially sensitive (Lassere and Renaud-Mornant, 1973). Further, within a given

Table 6. Species diversity, richness and evenness of nematodes of the Rias de Arosa and de Muros.

Station	Species diversity(H')	Species richness(SR)	Equitability(J')
Arosa			
A2	2.09	2.58	0.95
A5	2.47	3.32	0.87
A7	2.16	3.29	0.77
A10	1.85	2.62	0.77
A12	1.59	2.06	0.66
A15	1.39	2.58	0.53
Muros			
M2	2.53	4.40	0.86
M4	2.26	3.85	0.68
M8	2.04	2.83	0.77

taxon, species may differ in their tolerance of anoxic or near-anoxic conditions (Wieser and Kanwisher, 1961; Wieser *et al.*, 1974; Vernberg and Coull, 1975). The nematode family Comesomatidae contains several species that commonly occur in muddy, poorly oxygenated sediments; among them is *Sabatieria pulchra*, which exploits stressed sediments within the New York Bight (Tietjen, 1980). *S. pulchra* and *Metacomesoma punctatum*, both comesomatids, were found in high densities at Arosa Stations A12 and A15, perhaps because they were the only species capable of existing in these sediments.

Besides oxygen stress, sediment instability (see Organism-sediment relations and sediment geochemistry section) would cause low meiofaunal densities.

Another factor that may contribute to increased densities of nematodes at Arosa Stations A12 and A15 was low macrofauna biomass (see Macroinfauna section). While macrofauna biomass in the entire Arosa was low (0.5-3.0 g AFDW \cdot m⁻²), it was the lowest at Stations A12 and A15.

In the Muros, low densities of meiofauna could be more a function of elevated macrofaunal biomass, or even changes in macrofaunal species composition rather than organic enrichment. The presence of high densities of *Amphiura* species at Stations M2, M4 and M7, of *Maldane glebifex* at Station M4, of *Spiochaetopterus costarum* at Station M8, and of *Thyone fusus* and *Leptosynapta bergensis* at Stations M2 and M4, respectively, were probably the primary contributors to the low densities of meiofauna. The correlation between macrofaunal and meiofaunal biomass for both rias was -0.68 (Kendall's Υ , $p < 0.05$); for the Muros it was -0.46 ($p < 0.1$). A similar inverse relationship in biomass has been observed on the Georgia shelf of the USA (Tenore *et al.*, 1978; Hanson *et al.*, 1981) and in the Baltic Sea (Elmgren, 1978). The brittlestar *Amphiura* and holothurians may ingest

meiofauna, depressing the latter's population levels at Stations M2, M4, and M7. Meiobenthic animals have been found in guts and food boluses of another ophiuroid (*Ophiothrix fragilis*; Warner and Woodley, 1975), and Tietjen (1971) suggested they are an important consumer of deep-sea meiobenthos.

Meiofauna, especially nematodes, feed extensively on bacteria (Gerlach, 1977; Tietjen and Lee, 1977; Alongi and Tietjen, 1980). In the Arosa, there was a significant positive correlation between microbenthic and meiobenthic biomass ($Y = +0.64$, $p < .05$). This positive relationship might be facilitated by the absence of significant competition for food from the low densities of macrofauna in the estuary; in other words, in the benthic regime of the Arosa there might exist a simple microbenthos-meiobenthos food chain that is subject to little impact from the macrofauna.

However, in the Muros, there was no clear relation between microbenthos and meiobenthos ($Y = +0.15$, $p > .05$). High densities of macrofauna probably impact the relation between microbenthos-meiobenthos within Muros by: (a) competing with the meiobenthos for living space and microbial food, and (b) preying on the meiobenthos itself. Because of the interactions between the macrobenthos and meiobenthos in the Muros, the trophic relationships between the latter and the microbenthos are less well defined than in the Arosa.

Areal differences, species composition, and diversity of nematodes in the two rias closely paralleled that of the macroinfauna. A decrease in nematode species diversity from outer toward inner stations in both rias may reflect the response of these animals to accompanying increases in organic enrichment and sediment instability. The decrease in diversity was due mainly to a decline in species richness along the enrichment gradient; at the inner stations of the Arosa, lowered species equitability also contributed to the low diversity of nematode species. Highest diversity occurred at the outermost station in the Muros where organic enrichment was lowest and where the predation effects of the dense populations of *Amphiura filiformis* may have relaxed competition among the nematodes. Sediment at Station 2 was also the coarsest of any station; coarser sediments tend to support a more diverse nematode fauna than do silts and sandy silts (Warwick and Buchanan, 1970; Heip and Decraemer, 1974; Tietjen, 1977, 1980). Further, a decrease in nematode diversity as a function of increased organic enrichment has been observed several times (Heip and Decraemer, 1974; Tietjen, 1980), although other factors such as sediment granulometry often complicates the relation between (the structure of the) nematode species assemblages and organic load (Tietjen, 1977, 1980).

Benthic megafauna (Iglesias, Gonzalez-Gurriaran and McClain)

Methods

Three habitat types in the rias were selected for study: (1) beach areas (3 to 8 m depth) with sandy bottoms, (2) mussel raft areas (8 to 20 m depth) with mud bot-

toms containing significant shell debris, and (3) middle areas (14 to 40 m depth) outside of raft clusters with mud to sandy-mud bottoms. Stations representative of each of these habitat types were selected in the inner, middle and outer portions of the Arosa and the middle to outer Muros (Fig. 6).

Replicate samples were collected using a 4.8 m width semiballoon trawl with a stretched mesh of 1 cm and a bait seine liner in the cod end. The effective opening of the trawl is 4 m wide by 1 m high (Haedrich and Haedrich, 1974), and ten minute trawls at a given trawling speed covered approximately 800 m². Samples were collected in both rias in October 1978 but fish data from sampling in October 1977 and 1979 are also used. Samples were also collected at three-month intervals in the Arosa. Species numbers and biomass estimates were obtained for demersal fish, starfish, and crabs.

Spatial and seasonal changes in species composition and community delimitation of the megabenthos are reported elsewhere (Chesney and Iglesias, 1979; Olaso, 1979 and 1981; Iglesias, 1982; Gonzalez-Gurriaran, 1981). In this paper we present a summary of areal and seasonal changes of these data to contrast the two rias.

Results and discussion

Species of megabenthos in the Arosa and Muros are quite similar. For example, demersal fish communities are dominated by gobies *Lesueurigobius friesii*, *Gobius niger*, *Callionymus reticulatus*, *Symphodus cinereus*, *Pomatoschistus minutus* (Iglesias, 1981). These species comprised 70% of the total number of demersal fish in both rias (Iglesias, 1981). Echinoderms and crabs are also similar (Olaso, 1979 and 1981; Gonzalez-Gurriaran, 1981). The starfish, *Asterias rubens*, and the sea cucumber, *Cucumaria normani*, dominate, especially in raft areas. *Macropipus depurator* consistently made up > 70% of the biomass of crabs in both rias.

However, the biomass of all groups of the megabenthos was generally higher at all three habitat types in the Arosa than in the Muros (Fig. 18). In both rias, the biomass in raft areas, compared to middle and beach areas, was strikingly higher for crabs and echinoderms but not for demersal fish. The "rain" of mussels and epifauna falling from the rafts provides a large food resource to megabenthos under the rafts. Demersal fish are more motile than invertebrates so that their habitat includes much of the ria while still feeding in raft areas. Seasonal data from the Arosa show an increase in megafauna, especially in raft stations, in spring when the biomass of mussels and associated epifauna on the rafts is highest (Fig. 19).

Spatial and temporal changes in the megabenthic communities of the total rias result primarily from the raft culture of mussels in the ria. First, the raft fauna change the physical and chemical characteristics of sediments by depositing large quantities of shell and biodeposits (feces) on the bottom, thus creating a muddy sediment high in organic matter. This may be detrimental to infauna and most megabenthos but seems to favor the goby *Lesueurigobius friesii*. This fish is most

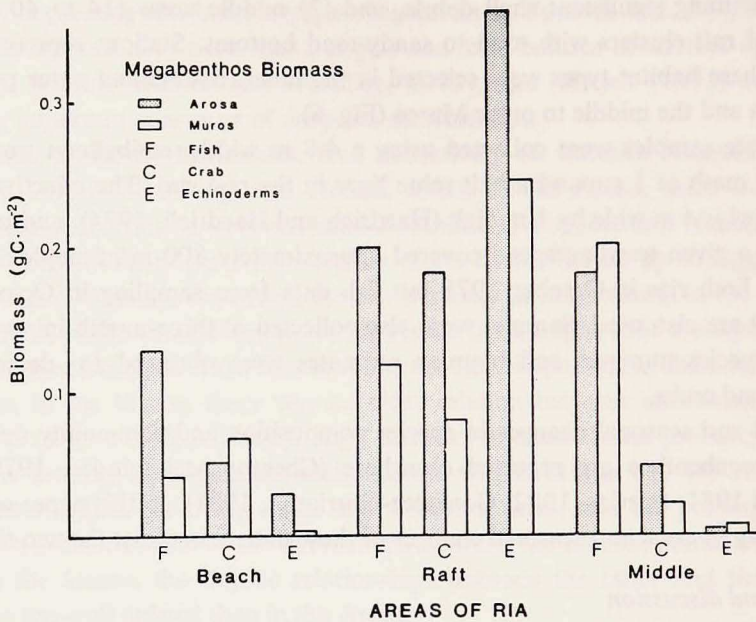


Figure 18. Comparison of biomass of megabenthos at beach, raft, and middle habitats of the Rias Arosa and de Muros in October 1978.

abundant in middle areas of the Arosa (0.099 ind/m^2), less abundant in middle areas of the Muros (0.011 ind/m^2) and sometimes lives in the burrows of *Nephtys norvegicus* (Wheeler, 1969). It thus may prefer the soft sedimentary habitat created by mussel detritus.

Although the effect of mussel culture on sediment composition is important, its primary influence is upon the food chain pathways in the Arosa. The relative enhancement of megabenthic biomass in raft areas clearly results from the high standing crop of the mussels and epifauna (see Raft dynamics section). Raft epifauna includes mainly holothurians, ascidians, and seed mussels which, along with the adult mussels, provide abundant food for the crabs and starfish. In contrast, food preferred by demersal fish, such as polychaetes, amphipods and small crabs, comprise only about 30% of the epifaunal biomass (Tenore and Gonzalez, 1975). This partitioning of the food results in a greater enrichment of the crabs and starfish than demersal fish in raft areas (Chesney and Iglesias, 1979).

Finally, there is an important effect of human activity on the megabenthos. If we compare the annual cycle of megabenthic biomass within the two rias with mussel biomass we observe synchrony between maximal biomass of the raft fauna and megabenthos. Although this synchronous cycle could be explained in terms of seasonal changes in growth and production, we believe the pattern man has imposed

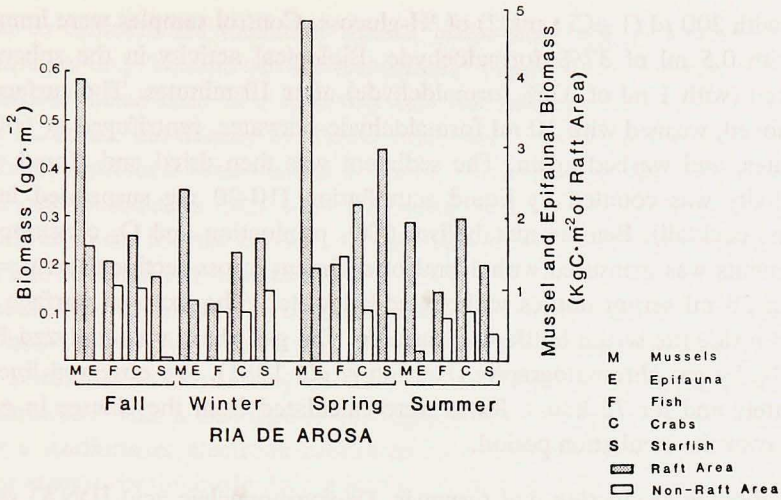


Figure 19. Seasonal changes in biomass of the megabenthos related to changes in mussel and epifauna biomass of the rafts in the Ria de Arosa.

by mussel culture influences the dynamics of megabenthos. The pattern results from two factors: (1) the loss of material from the mussel ropes is in direct proportion to the abundance of fauna and thus as the mussels and epifauna increase during the growing season, the material sloughed from the ropes also increases; and (2) in the process of harvesting, epifauna are scraped from the mussels and returned to the sea by the harvesters. Thus at harvest time the greatest amount of food is available for the megabenthos and a peak in biomass is expected.

Microbenthos (Hanson, Pamatmat, Perez, Rodriguez, Santiago and Westrich)

Methods

a. Microbenthic biomass. Adenosine triphosphate (ATP), used to estimate microbenthic biomass of the sediment, reflects bacteria, fungi, protozoans, and some meiofauna. The surface 2 mm of plastic subcores (4.9 cm² in 1978 and 1.65 cm² in 1979) was extracted in 15 ml of boiling bicarbonate buffer (Bancroft *et al.*, 1976) and ATP was measured with a Dupont Bioluminescent Photometer. Quench due to various ions and fulvic acid reactions was reduced by dilution. Measurements of bacterial cell numbers were determined by epifluorescent microscopy (Hobbie *et al.*, 1977).

b. Benthic heterotrophic activity. Heterotrophic activity was estimated by measuring C-14 labelled glucose uptake. Three 4.9 cm² subcores were taken from each of three box cores taken at each station. The sediment surface of the subcores was

flooded with 200 μl ($1 \mu\text{Ci} \cdot \text{ml}^{-1}$) of ^3H -glucose. Control samples were immediately killed with 0.5 ml of 37% formaldehyde. Biological activity in the subcores was terminated (with 1 ml of 37% formaldehyde) after 10 minutes. The surface 2 mm was removed, washed with 10 ml formaldehyde-seawater, centrifuged at 6000 g for 10 minutes, and washed again. The sediment was then dried and stored at 60°C until activity was counted by liquid scintillation (10-20 mg suspended in Triton X-toluene cocktail). Benthic metabolism (CO_2 production and O_2 consumption) of the sediments was measured with 1 cm^3 of sediment (cross-sectional area = 1 cm^2) placed in 38 ml serum bottles without added water. The exposed surface area of sediment inside the serum bottle was variable. The gas phase was analyzed for CO_2 , O_2 and N_2 by gas chromatography (Hanson *et al.*, 1981). We observed linear rates immediately and for 72 hours. Rates were calculated from the change in gas composition over the incubation period.

c. Microbenthic production and turnover. Deoxyribonucleic acid (DNA) synthesis, estimated by thymidine incorporation into DNA (Tobin and Anthony, 1978), provides a relative measure of cell growth for microbenthos. ^3H -thymidine (300 μl of $10 \mu\text{Ci} \cdot \text{ml}^{-1}$) was added to the surface of three subcores (4.9 cm^2) taken from a box core. A fourth subcore was killed with 500 μl of m-cresol. The reactions were terminated after 3 h with 1 ml of 37% formaldehyde and washed twice with 10 ml of 5% formaldehyde in distilled water. The cells were hydrolyzed overnight with 0.3 M NaOH at 37°C and centrifuged at $6000 \times g$ for 45 minutes. After neutralizing the supernatant, the TCA precipitable materials were centrifuged, and washed with 5% TCA before the precipitated DNA was hydrolyzed at 85°C for 15 minutes. The DNA was counted in a Triton X-100 in a toluene scintillation fluor and corrected to $\text{dpm} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$. In September 1980, these measurements were repeated.

d. Sulfate reduction. The *in situ* rate of sulfate reduction was measured by a variation of the direct-injection radiotracer technique of Jørgensen (1978). A relatively undisturbed sediment sample was taken with a 210 cm^2 surface box core by a SCUBA diver and immediately returned to the laboratory. ^{35}S -labelled SO_4^{-2} was injected directly into the sediment and the core was incubated in the dark at field temperature for 6 to 10 hours. The core was then sectioned under nitrogen atmosphere in a glove bag, and the sediment from each 2 cm interval was poisoned with sodium azide and the sulfide fixed with zinc chloride.

Triplicate analyses for each sediment depth were run to determine the distribution of the label between sulfide and sulfate phases. Free hydrogen sulfide and acid volatile sulfide were separated from the sediment by acid digestion. The activity of the sulfate and sulfide fractions was determined by scintillation counting and the rate of sulfate reduction was calculated (Jørgensen, 1978).

e. Rates of metabolic activity. The metabolic activity of the benthic community was

measured to estimate the oxidation rate of sedimented organic matter. Rates of oxygen uptake, i.e., "benthic surface respiration," represent the net effect of aerobic and anaerobic metabolism in a relatively thin but indeterminate surface layer (the finer the sediment, the thinner the layer) while heat production by the whole sediment column represents total benthic community energy flow. In 1979 oxygen uptake and heat production rates were measured in the Arosa; only oxygen uptake was measured in the Muros. In 1980, oxygen uptake was measured at more stations in Arosa and repeated at two stations in the Muros.

Sediment cores were taken by SCUBA divers and brought back to the laboratory within 2 hrs. The overlying water was gently bubbled with air through a fritted glass tube for 5 minutes before sealing the core. Initial and final oxygen concentrations were determined with a Scholander microgasometric analyzer (Scholander *et al.*, 1955) or a Radiometer electrode calibrated by gasometric analysis. The overlying water was stirred continuously during incubation with a 1.25 cm ceramic disc magnet. For comparison, some replicate cores were not stirred. Water samples from *in situ* Plexiglas boxes were taken with syringes at various time intervals for oxygen analysis (see Organism-sediment relation and sediment geochemistry section).

To measure anaerobic metabolism by calorimetry, sediment cores were sectioned into three layers, (0 to 9.5, 9.5 to 19, and 19 to 28.4 cm) in a nitrogen-filled glove bag. Each layer completely filled two glass Petri dishes. The two dishes were placed over each other, enclosing a total volume of 235 cm³ of sediment, and were sealed with 1.5 cm Neoprene rubber band. The samples were then placed in a metal canister filled with Silicone oil as heat-conducting medium. The heat flux from each sample was measured with a twin calorimeter, equilibrated in a water bath at 13.9°C (Pamatmat, 1978). The top layer was run first because heat production of surface layers rapidly decreases. In contrast, anaerobic subsurface sediments have steady low rates of heat production from the beginning. One microvolt of steady state or slowly changing thermopile signal is equivalent to 1.35×10^{-5} Joule \cdot sec⁻¹ of heat flow.

Results and discussion

a. Microbenthic biomass. Microbenthic biomass (ATP) was lower in the Arosa (0.1 to 0.4) than the Muros (0.4 to 1.6 μ g ATP \cdot cm⁻³) (Fig. 20). In the raft area (Station A15) ATP concentrations were higher (0.6 μ g \cdot cm⁻³) than at other stations in the Arosa. In general, ATP concentrations increased from the mouth to the inner region in both rias. However, in the Arosa microbenthic biomass decreased substantially between the inner ria and the river Ulla.

Estimates of microbenthic biomass by ATP concentration may be influenced by the presence of meiofauna in sampled sediments (Sikora *et al.*, 1977; Yingst, 1978). In the Muros, meiofaunal biomass was less than 2% of the total microbenthic biomass (assuming a conversion factor for ATP to carbon of 100); in the Arosa, the

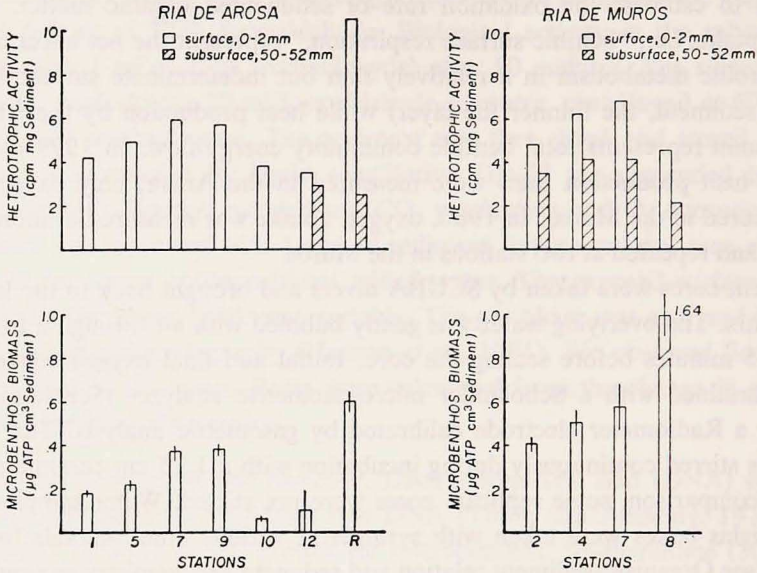


Figure 20. Heterotrophic uptake of labeled glucose and ATP concentration in the sediments of the Ria de Arosa and Ria de Muros in September 1978.

meiofauna biomass was less than 4% of the microbenthic biomass in the outer Arosa, but in the upper ria (Stations A10 and A12) meiofauna could have contributed 10 to 40% to microbenthic biomass estimates. The microbenthic biomass in the Muros was slightly higher than that in the Arosa. Physical resuspension in the Arosa and the bioturbation (and related nutrient regeneration) in the Muros may account for these differences.

Bacterial cell numbers in the Arosa and Muros ranged from 1.1 to 2.0×10^9 cells \cdot cm $^{-3}$ of surface sediment. There was no significant difference in the numbers found between the rias. However, in the Arosa, the numbers ($1.65 \pm .15 \times 10^9$ cells \cdot cm $^{-3}$) under the mussel rafts (Station A15) were significantly ($p < 0.05$) higher than those ($1.10 \pm .05 \times 10^9$ cells \cdot cm $^{-3}$) in the nonraft area (Station A16). In the Muros, bacterial number at Station M8 near the Rio Tambre was $1.95 \pm .50 \times 10^9$ cells \cdot cm $^{-3}$ while at M13 the bacterial number was $1.10 \pm 0.8 \times 10^9$ cells \cdot cm $^{-3}$.

The microbenthic biomass in the raft area (Station A15) was approximately one-third of that in nonraft Station A16 (Fig. 21). This difference cannot be explained by differences in the amount of detritus deposited because sedimentation rates within and without raft areas do not differ greatly (see Raft dynamics section). At the mouth of the Arosa (Station A2), microbenthic biomass was slightly lower than biomass under the polygon. In the Muros, microbenthic biomass at Station M13 was similar to that in the Arosa. The high biomass at Station M13 was attributed to

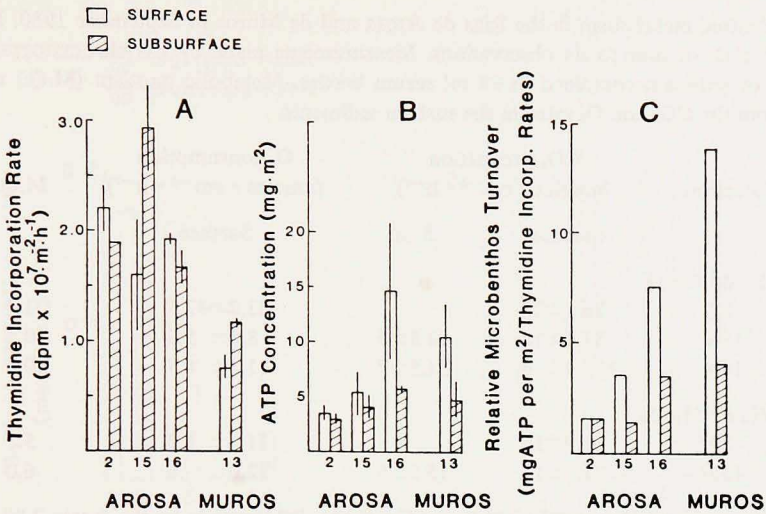


Figure 21. Thymidine incorporation rates (A) into DNA of microbenthos, ATP concentrations (B), and relative microbenthos turnover (C) in the sediments of the Ria de Arosa and Ria de Muros.

plant detritus received from wetlands around the Rio Tambre. In addition, subsurface ATP concentrations were highly correlated ($r = 0.99$, $p < .01$) with surface ATP. This suggests that the microbenthos at 5 cm depends on detritus and nutrients deposited to the sediment from the overlying water and bioturbation.

b. Benthic heterotrophic activity. Heterotrophic activity (glucose uptake) in the sediments of the Arosa and the Muros was similar, increasing from the mouths to inner regions of both rias and then decreasing toward the rivers Ulla and Tambre, respectively (Fig. 20). Rates at 5 cm sediment depth were always less than at the surface. In the inner Arosa, glucose uptake by surface sediment was two to three times higher at the raft area (Station A15) than in other parts of the ria. At 5 cm, there was no difference between these areas. Microbenthic biomass (ATP) was positively correlated ($r = 0.93$, $p < 0.05$) with heterotrophic activity (glucose uptake) and correlated with the distribution of organic matter. However, at Stations A10 and A12, in the Arosa, microbenthos biomass and heterotrophic activity were greatly reduced.

Benthic surface respiration (oxygen consumption) was similar in the inner zones of both rias (Table 7). Oxygen consumption rates range from 1.9 ml O₂ · m⁻² · h⁻¹ at Station A15 to 11.9 at Station A2 in the Arosa, the other three stations (Table 7) having intermediate rates of ca. 2.7 ml · m⁻² · h⁻¹. These rates are one tenth to one half as high as the oxygen flux measured in sediment cores and *in situ* boxes (section e, Metabolic activity). One possible reason for getting lower rates by the

Table 7. Benthic metabolism in the Rias de Arosa and de Muros in September 1980. Rates are means \pm S.D. of four to six observations. Measurements made by gas chromatography with one cm³ of sediment contained in 38 ml serum bottles. Metabolic quotient (M.Q.) was computed from the CO₂ and O₂ rates in the surface sediments.

Location	CO ₂ production (nmoles \cdot cm ⁻³ \cdot h ⁻¹)		O ₂ consumption (nmoles \cdot cm ⁻³ \cdot h ⁻¹)	M.Q.
	Surface	5 cm	Surface	
Ria de Arosa				
2A	76.4 \pm 25		53.2 \pm 47.5	1.4
15A	87.8 \pm 12	24.8 \pm 5	8.6 \pm 5.6	10.2
16A	125.9 \pm 6	31.5 \pm 7	11.8 \pm 4.5	10.7
Ria de Muros				
2M	66.9 \pm 16		11.7 \pm 1.7	5.7
13M	71.4 \pm 17	15.5 \pm 5	12.0 \pm .6	6.0

To convert nmoles CO₂ \cdot cm⁻³ \cdot h⁻¹ to mg C \cdot m⁻² \cdot d⁻¹ multiply by the factor 2.88.

To convert nmoles O₂ \cdot cm⁻³ \cdot h⁻¹ to ml O₂ \cdot m⁻² \cdot h⁻¹ multiply by the factor 0.224.

gas chromatography technique is exclusion of macrofauna whose effect on sediment oxygen uptake could be greater than its metabolic activity alone.

The mineralization (CO₂ production) rates were significantly lower under the rafts than those outside the rafts in the Arosa (Table 7). In addition, the amount of carbon loss was higher in the Arosa (76 to 125 nmoles \cdot cm⁻³ \cdot h⁻¹) than in the Ria de Muros (66 to 71 nmoles \cdot cm⁻³ \cdot h⁻¹). The amount of carbon loss from the top layer (1 cm) of sediments due to CO₂ production ranged from 220 to 360 mg C \cdot m⁻² \cdot d⁻¹ or about 44 to 72% of the organic carbon flux into the sediment of the Arosa (Fig. 7). In addition, this amount is equivalent to the amount of carbon utilization by sulfate reducers in the top 14 cm (Fig. 22). The metabolic quotient (MQ) provides a relative measure of carbon loss by aerobic and anaerobic metabolism relative to benthic surface respiration. The MQ inside the Arosa (\sim 10:1) and in the Muros (\sim 6:1) indicates that anaerobic mineralization of detritus was important in both rias (Table 7). Similar values have been reported for other marine environments (Hanson and Tenore, 1981; Hanson *et al.*, 1981).

c. Microbenthic production and turnover. Estimates of cell growth by thymidine incorporation indicated that the Arosa is more productive than the Muros (Fig. 21). In the Arosa, thymidine incorporation in surface sediments was similar in raft (Station A15) and nonraft (Station A16) areas and at the mouth of the ria (Station A2). A major difference was observed at 5 cm sediment depth at Station A15 where incorporation was twice that of the surface. In addition incorporation rates in the Arosa (especially in raft areas) were approximately twice the rates in the Muros. Similar rates and relationship were observed in September 1980. Measurement of

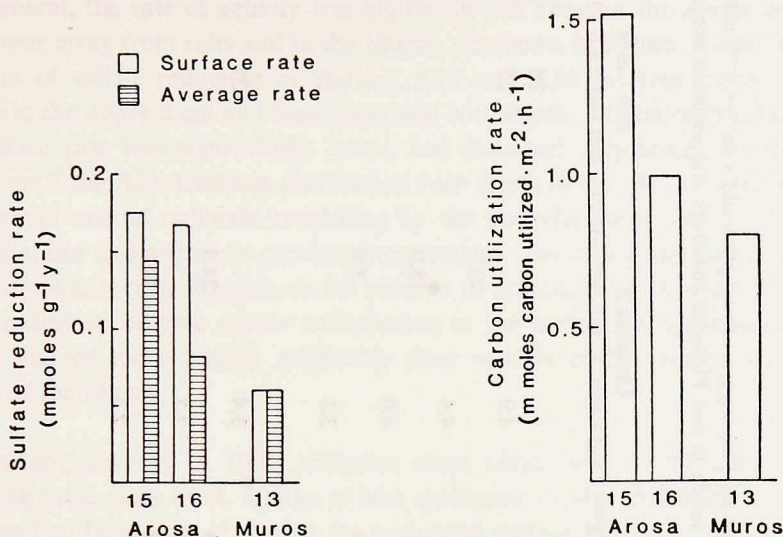


Figure 22. Sulfate reduction rates measured in the sediments of the Ria de Arosa and Ria de Muros in September 1979. Sulfate reduction rates, measured using ³⁵S-labelled sulfate, and rates of carbon utilization, calculated using the commonly used ratio of 2 moles carbon oxidized per mole of sulfate reduced.

DNA synthesis was not possible because intracellular thymidine triphosphate concentration and specific activity were not determined.

Because thymidine incorporation is proportional to production, and ATP concentration is a measure of cell biomass, a relative measure of the microbenthos turnover in the sediment can be obtained (Fig. 21). The values, though relative, suggest that the microbenthos turn over rapidly in the inner Arosa, but more rapidly in the bioturbated sediments of the Muros.

d. Sulfate reduction. *In situ* rates of bacterial sulfate reduction (with an estimated precision of $\pm 10\%$) are given in Table 12 in units of mmoles sulfate \cdot l⁻¹ pore water \cdot y⁻¹ (mM/yr). To compare these data with other microbial information, we calculated the average rate of sulfate reduction (mmoles \cdot g⁻¹ \cdot y⁻¹) for the top 14 cm at each station (Fig. 22). Assuming that 2 moles of CO₂ are produced in reducing 1 mole of sulfate, we also calculated the amount of carbon utilization in the sediment due to bacterial sulfate reduction (in units of mmoles carbon \cdot m⁻² \cdot h⁻¹ (Fig. 22)). From literature values of the depth distribution of the activity of bacterial sulfate reduction in other nearshore marine sediments we can assume the activity in the top 14 cm to be 75 to 90% of the total activity in anaerobic marine sediments. Thus we calculated organic carbon utilization rates to be equivalent to 444 mg C m⁻² d⁻¹ at Station 15 in the Arosa, 288 in Station 16, and 248 in Station 13 of the Muros. In comparison, the measured carbon dioxide production rates

Table 8. Dissolved oxygen concentrations of bottom water ($\text{ml} \cdot \text{l}^{-1}$) and rates of oxygen consumption ($\text{ml} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) calculated from the decrease in dissolved oxygen concentrations of water inside *in situ* Plexiglas chambers and sediment cores incubated in the laboratory.

Station	Sampling time	Bottom water ($\text{ml} \cdot \text{l}^{-1}$)	Chamber 1		Chamber 2		Lab Cores ($\text{ml} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$)
			($\text{ml} \cdot \text{l}^{-1}$)	($\text{ml} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$)	($\text{ml} \cdot \text{l}^{-1}$)	($\text{ml} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$)	
Ria de Arosa							
Station 15		4.3					25
Station 16	Initial	4.6	4.4 (turbid)		4.9		25
	3 h later	4.3	4.3	4.8		23.0	
	6 h later	3.7	3.9	19.0	4.4	18.0	
	24 h later	4.2	3.4	4.0	4.0	3.8	
Station 2		4.7			3.5		
Ria de Muros							
Station 13	Initial	3.4	2.8		3.4		29
	3 h later	3.3	—	20.0	2.7	24.0	
	6 h later		1.9	2.8		14.0	
	24 h later		1.6		2.3		

from the top 1 cm layer (previous section) was equivalent to $253 \text{ mg C m}^{-2} \text{ d}^{-1}$, 363 and 205 in the three respective stations. This shows that anaerobic decomposition is an important part of the total benthic metabolism in both rias.

In general, the rate of activity was highest in raft areas in the Arosa and somewhat lower away from rafts and in the Muros. As shown in Figure 22 and Table 12, the rates of sulfate reduction at Stations A15 and A16 in Arosa showed similar activity in the upper 2 cm and then decreased with depth. At Station M13 in Muros, the surface rate was significantly lower, but remained surprisingly constant with depth (see Table 12). Uniform distribution with depth in the Muros is probably due to the rapid rate of sediment reworking by the macrobenthos (see Organism-sediment relations and sediment geochemistry section). Assuming that the rate of bacterial sulfate reduction depends on the amount of utilizable organic matter deposited to the sediment, organic matter sedimenting to the bottom of the Arosa must be greater and/or more readily oxidizable than organic matter sedimenting to the bottom of the Muros.

e. Metabolic activity. In 1979, sediment cores taken back to the laboratory had about the same rates of O_2 uptake as box enclosures *in situ* (Table 8). Low *in situ* rates resulted from lack of stirring for prolonged periods (6 to 24 h intervals). The few measurements indicate no large difference, if at all, between Muros and Arosa and within and without a polygon of rafts. Our best estimate in 1979 of oxygen consumption rate by the sediments of the two rias was 21.3 ± 3.9 (S.D.) $ml O_2 \cdot m^{-2} \cdot h^{-1}$.

There was a noticeable trend of a negative correlation between dissolved oxygen and ammonia concentrations both inside and outside the box enclosures. Such a trend is expected as a consequence of ammonia production during metabolism. The variability in ammonia values, however, together with unusually high values occurring at the time of suspected sediment disturbance (Station 16, Box 1) raises the possibility that some ammonia was liberated by advection of pore water.

The oxygen uptake rates in 1980 (Table 9) were practically the same as the values obtained in 1979 from the same stations. There was no significant difference between overall means of oxygen uptake in 1980 in Muros (= $30 ml O_2 m^{-2} h^{-1}$ vs. 29 in 1979) and Arosa (= $26 ml O_2 m^{-2} h^{-1}$ vs. 25 for 2 stations in 1979). Average rates of total uptake at particular stations were significantly different and ranged from 15 to $43 ml m^{-2} h^{-1}$ in Arosa and 27 to 34 in Muros.

Aerobic respiration rate at the different stations averaged 50% and from 42 to 57% of total uptake. There appears to be no difference between the Arosa and Muros in the ratio of aerobic respiration to total oxygen uptake. In the Arosa the coarse sand bottoms in both the intertidal and the deep water at the entrance to the bay show much higher relative rates of aerobic respiration (85 to 65%, respectively, of total uptake rates), undoubtedly because of suppressed anaerobic metabolism in coarse sediments. No sandy bottoms were sampled in Muros, but the same conditions can be presumed.

Table 9. Mean rates of benthic oxygen uptake ($\text{ml O}_2 \text{ m}^{-2} \cdot \text{h}^{-1}$) in the Rias de Arosa and de Muros at 15°C in September 1980.

Location	Water depth (m)	Total uptake \pm S.D.		Residual uptake ^a \pm S.D.		Respiration ^b / total uptake
Ria de Arosa						
14a*	17	17	2.8	10	4.3	.42
14b	17	38	2.8	19	1.3	.50
14c	17	43	3.2	—		
15	13	22	5.4	10	0.8	.55
16	19	21	3.0	9	0.7	.57
10	31	24	1.8	12	0.2	.50
12	12	21	0.2	12	2.0	.44
2	34	27	5.5	9	2.7	.65
Harbor entrance	5	29	6.2	—		
Intertidal		41	51.3	6	3.1	.85
Ria de Muros						
8	17	34	11.0	16	4.4	.53
13	22	27	1.9	15	0.2	.46

^a After poisoning with formaldehyde.

^b Equals Total minus Residual Uptake.

* Edge of polygon of rafts near Station 14.

Heat production in sediment was found above but not below the 19 cm depth (Table 10). The rate of heat production per cm^3 of sediment was about 3.5 times higher in the top 9.5 cm layer than between 9.5 to 19 cm, and 4 times higher in terms of rate per g of sediment. The entire core (surface area = 25.3 cm^2) had a heat flux of $178 \times 10^{-5} \text{ W}$ or a metabolic rate of 0.7 W m^{-2} ($= 2.5 \times 10^3 \text{ J} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$). To compare this rate with the measured rates of oxygen uptake, the O_2 consumption data were converted so that 1 ml O_2 consumed by aerobic organisms equals the production of 4.8 cal of heat (Pamatmat, 1978, 1981) and 860 cal h^{-1} equals 1 W . An average rate of benthic oxygen uptake of $21.3 \text{ ml O}_2 \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ in the rias is equivalent to $0.12 \text{ W} \cdot \text{m}^{-2}$, or 0.17 of directly measured heat production. Anaerobic metabolism was therefore six times the rate of aerobic activity at the surface. Only a few measurements of sediment heat production are available for regional comparison. Rates in the Arosa are about 10 times higher than those of sandy beach and subtidal sediment from the southwestern Baltic Sea at 15°C (Pamatmat *et al.*, 1981). This difference is attributed to higher primary productivity in the water column, higher sedimentation rates of organic matter, and higher biological activity in the sediment of the rias than in the Baltic. The relative contribution of different metabolic groups to total sediment heat production is not known. To calculate equivalent heat production by sulfate reducers, we assume that 1 mole

Table 10. Heat production rates at 13.9°C of sediment from Station 15 beneath a polygon in Ria de Arosa, NW Spain, September 1979.

Layer (cm)	Sediment volume (cm ³)	Sediment dry weight (g)	Heat production rate*		
			(Joules • sec ⁻¹)	(Watt • cm ³)	(Watt • g ⁻¹)
0-9.5	235	61.1	138×10^{-5}	5.87×10^{-6}	2.26×10^{-6}
9.5-19	235	70.3	40×10^{-5}	1.70×10^{-6}	5.69×10^{-6}
19-28.5	235		0	0	0

* 1 watt = 1 Joule • sec⁻¹.

of sulfate reduced equals 2 moles of organic carbon oxidized, with an accompanying free energy change of 192 kJ (Howarth and Teal, 1979). Because enthalpy generally dominates free energy change in biological processes (Morowitz, 1968), and the magnitude of entropy change is within the range of experimental error, we can assume that each mole of sulfate reduced is equivalent to 192 kJ of heat production. The integrated sulfate reduction rate in the top 14 cm sediment column (calculated from the data in Table 12) equals 8.2×10^{-4} mole • m⁻² • h⁻¹, which is equivalent to 157 J • m⁻² • h⁻¹. This is only 6% of total anaerobic heat production rate. The rest would be due to facultative anaerobes, fermentors, other anaerobic types, and heat from unknown extracellular chemical reactions. On this basis sulfate reduction seems of lesser importance than in other aquatic ecosystems (Jørgensen, 1978; Howarth and Teal, 1979). However, when the rates of sulfate reduction at Station A15 and A16 in the Arosa and 13 in the Muros (equivalent to an average of 327 mg C • m⁻² • d⁻¹) are compared with respiratory oxygen uptake averaging 12 ml • m⁻² • h⁻¹ (Table 9), which is equivalent to 154 mg C • m⁻² • d⁻¹ (assuming $RQ = 1$), then sulfate reducers seem more important than aerobes. Unfortunately, this inconsistency cannot be explained at this time.

Besides the discrepancy between integrated heat production and total oxygen uptake, other evidences point to the underestimation of subsurface activity by measured fluxes at the surface. For example, the sulfate reduction rate of 8.2×10^{-4} mole • m⁻² • h⁻¹ would theoretically produce 8.2×10^{-4} mole of sulfide • m⁻² • h⁻¹. If this metabolic product were oxidized to sulfate as fast as it is produced, the rate of oxygen uptake by chemical oxidation should be equal to 1.64 mmole • m⁻² • h⁻¹ (= 36.7 ml O₂ • m⁻² • h⁻¹). The estimated chemical oxidation rate at Station A15 is 50% of total oxygen uptake (25 ml • m⁻² • h⁻¹), or 12.5 ml • m⁻² • h⁻¹, which is only one-third the rate of sulfide formation. It follows that sulfide must accumulate and intermittently get oxidized, for example, during periods of sediment resuspension. Other indications that subsurface processes are not instantaneously coupled to surface fluxes are discussed in the next section (Organism-sediment relations and sediment geochemistry).

**Organism-sediment relations, sediment geochemistry, and bottom resuspension
(Rhoads, Boyer, Garcia-Fernandez, Gonzalez, Krom, Westrich, Windom)**

Methods

Sediment radiographs were made of samples collected by SCUBA divers using hand-held Plexiglas box cores (30 cm long and 2.5 cm thick and 15 cm wide). Divers carefully pushed these cores into the bottom, withdrew them and placed a plate under each core before returning them to the sea surface. The cores were x-rayed with a medical field x-ray unit in the laboratory a few hours after collection.

The ^{210}Pb of ria sediments was determined on diver-obtained cores by the technique of Flynn (1968) where ^{210}Po is measured and secular equilibrium with ^{210}Pb is assumed.

Sediment collected for pore water and sediment chemistry was also taken from Plexiglas box cores collected by SCUBA divers (Aller, 1977, 1980a). The cores were transported to the laboratory and sampled within 3 hours in a glove bag under a N_2 atmosphere.

Sediment subcores were taken and samples at various sediment depths were used to determine vertical profiles of sediment water content (80°C for 12 hrs). The dried sediment was analyzed for organic carbon and total nitrogen on a Perkin Elmer CHN Analyzer after acid volatile compounds were removed with cold dilute phosphoric acid. Total organic matter was determined by measuring weight loss after combustion at 450°C for 12 hr.

Subcores for pore-water analysis were divided into discrete depth intervals and placed into centrifuge tubes. The tubes were sealed with air-tight plastic caps, centrifuged, and returned to the glove bag. Supernatant pore water from each tube was drawn off with a syringe and filtered ($0.45\ \mu\text{m}$ Millipore) into acid-cleaned plastic containers.

Sulfate content of the pore water was determined gravimetrically by the methods of Strickland and Parsons (1969) and Arevalo and Garcia-Fernandez (1975). Ammonium was determined using the method of Krom (1980) and phosphate was determined with the method of Murphy and Riley (1962). Chloride was determined by silver nitrate titration (Strickland and Parsons, 1969).

The method used to measure *in situ* rates of sulfate reduction using ^{35}S labelled sulphate is described in the Microbenthos section.

Ammonium fluxes from sediments were measured by two different techniques. In 1978, the flux of ammonium into the overlying water was estimated using a procedure developed by Aller (1977, 1980b). A diver-obtained box core was brought into the lab. The water overlying the sediment was sampled and analyzed for ammonia immediately and 3 times over a 24 hour period. Flux from the sediment to the overlying water was obtained from temporal changes in ammonium concentra-

tion. In 1979, *in situ* ammonium flux was measured using clear Plexiglas boxes placed on the bottom. The open-bottomed boxes were 38 cm deep, 30 by 30 wide. The top of the flux box had rubber stoppered holes. The stoppers were removed while the box was gently pushed into the bottom by SCUBA divers. Once deployed, the stoppers were reinserted making the box water-tight. The depth of the overlying water in the box was noted. The volume of water inside individual boxes varied between 9.5 to 16 liters depending on the location of the sediment-water interface inside the box. Before sampling, manually operated stirrers were rotated 30 times by the diver to mix the water in the box. The stirrers were constructed so that mixing did not resuspend the bottom sediment. Water samples were taken by inserting a syringe needle through a rubber sampling port located on top of each box. The 50 cc syringe sample withdrawn from the box was replaced by ambient outside water by opening a valve. This small dilution factor has been considered in calculating the concentration of ammonia in the supernatant water. At each sampling time, a 50 ml sample of the ambient water outside of the box was also collected and analyzed. Two replicate boxes were sampled at each station after 0, 3, 6 and 21 to 23 hours.

During 1979, we measured the diffusive flux of sulfate across the tube wall of the polychaete *Spiochaetopterus costarum* using $^{35}\text{S-SO}_4^-$. From this measurement and the geometry of the tubes, the sulfate diffusion coefficient across the tube wall was calculated. One end of four tube segments was carefully tied shut with fine sewing thread, the tubes were filled with a solution containing $^{35}\text{S-SO}_4^-$ and the other ends of the tubes were tied shut. The outside of the tubes was then gently washed with seawater to remove contaminating isotope and the tubes were placed in beakers of clean seawater. This seawater was sampled over a 47 hour period and ^{35}S activity analyzed by scintillation counting.

Water column turbidity was measured with a custom-built 10 cm light-path optical transmissometer. This instrument also measured water temperature and depth of the instrument below the sea surface. Vertical turbidity profiles were measured by lowering the instrument from an anchored vessel. Measurements were made at from 1 to 3 m intervals from 1 m below the sea surface to 1 m above the bottom. The recorded values represent percent light transmission. The instrument was adjusted so that 100% transmission was recorded in air. The relative light transmission values in water were converted to suspended loads ($\text{mg} \cdot \text{l}^{-1}$) in the laboratory. Aliquots of a surface sediment sample of the bottom were introduced into a well-stirred test tank containing filtered 30‰ seawater. The transmissometer was then placed into the tank and light transmission values were recorded. The concentration of suspended sediment for each transmissometer reading was determined by removing a liter of water and determining the particulate load by filtering the sample through a $2 \mu\text{m}$ millipore filter at 20 psi.

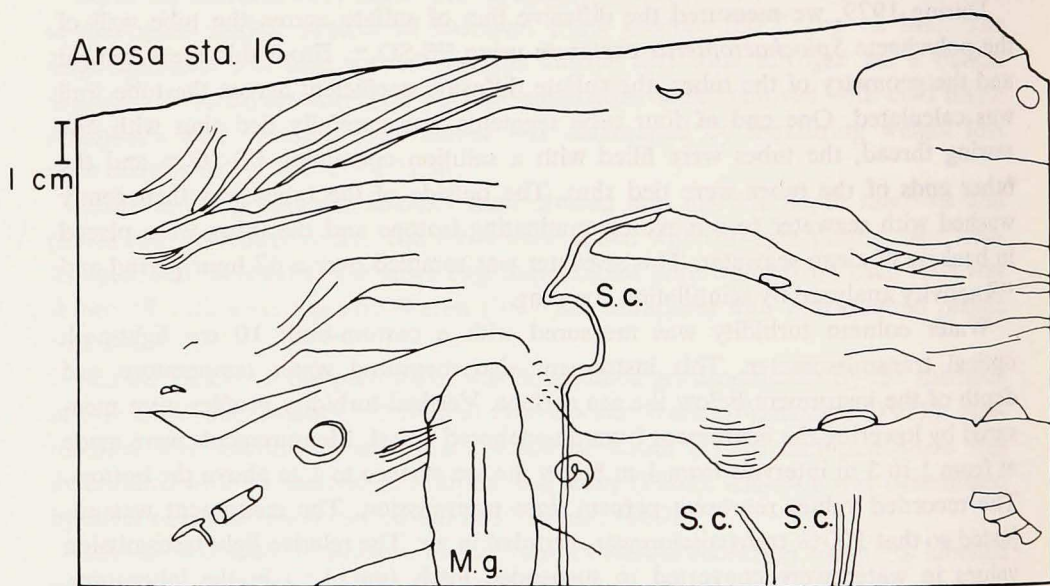


Figure 23. Sedimentary structures at Station A16, Ria de Arosa. Top—positive print of an x-radiograph of a diver-obtained box core. Light areas on the radiograph are fractures and are an artifact caused by sample dessication during preparation. Bottom—interpretive drawing of major sedimentary features as seen in the above radiograph. Erosional interfaces and crossbedded units are delineated by the subhorizontal lines. A relict tube of *Maldane glebifex* (M.g.) is present as well as a few tubes of *Spiochaetopterus costarum* (S.c.). Structures in this core are similar to those observed in sediments from the raft polygon station A15 (not illustrated).

Results and discussion

a. *Sedimentary structures.* The radiograph of sediment from Station A16 (inner Arosa but outside of a raft area) exhibits a low-angle cross-bedding, buried erosional surfaces, shell fragments, and in-place and exhumed tubes of *S. costarum* (Fig. 23). A relict tube of *Maldane glebifex* can be seen at a depth of 6 to 8 cm below the sediment surface. This maldanid polychaete, common in the Muros, is rarely encountered alive in the inner part of the Arosa. The presence of relict *M. glebifex* tubes at depth in the sediment of the inner regions of the Arosa suggests that a change in the benthic community has taken place after the raft culture was introduced to the Arosa about 40 years ago. Based on the observed depth of the relict *M. glebifex* tube shown in Figure 23 (6 to 8 cm), we estimate an average minimum sedimentation rate of 0.15 to 2.0 cm yr⁻¹ at Station A16.

At Station A15 (not shown), small mounds and depressions exist on the sediment surface (2-10 cm in relief). Some of the mounds appear to be occupied by colonial coelenterates or burrowing anemones. These elevations may result from local sediment stabilization by the accumulation of mucus shed by the coelenterates.

The radiograph of sediments from Station A14 (inner Arosa in a raft area) differs from that of Station A16 in having a higher density of *S. costarum* tubes and fewer shell fragments (Fig. 24). The lower end of many tubes of *S. costarum* is oriented vertically with bent or twisted upper ends. This orientation suggests that sediment formerly supporting the upper parts of the tubes has been eroded and re-deposited, causing the flexible tubes to change their original vertical orientation. All inner benthic stations in the Arosa were dominated by the polychaete *S. costarum* and showed sedimentological evidence of resuspension or erosion. The tubes of *S. costarum* are apparently long enough to extend below the mean depth of sediment resuspension providing an anchoring mechanism to resist washout. Tubes frequently protruded 2 to 6 cm above the sediment-water interface reflecting scouring of previously buried tubes. Other tubes appeared to be buried by sedimentation. Following erosion, some tubes may be reconstructed by the worms to communicate with the newly established sediment-water interface.

The influence of *S. costarum* on sediment bioturbation appears to be minimum because of its surficial feeding behavior. Many pioneering polychaetes are tubicolous and feed at the upper end of their tubes by extending tentacles into the water column or onto the sediment surface (Pearson and Rosenberg, 1976; Rhoads *et al.*, 1978a and b). The lower end of the tube is laterally compressed (collapsed) by the confining pressure of the sediment surrounding the tube.

Polychaetes can also play an important role in oxidizing sediment by pumping water through their tubes. Such irrigation may promote high rates of exchange of sediment pore water solutes (Aller, 1980a and b). The effect of polychaetes on sediment pore-water chemistry depends on the diffusion properties of the tube wall, tube

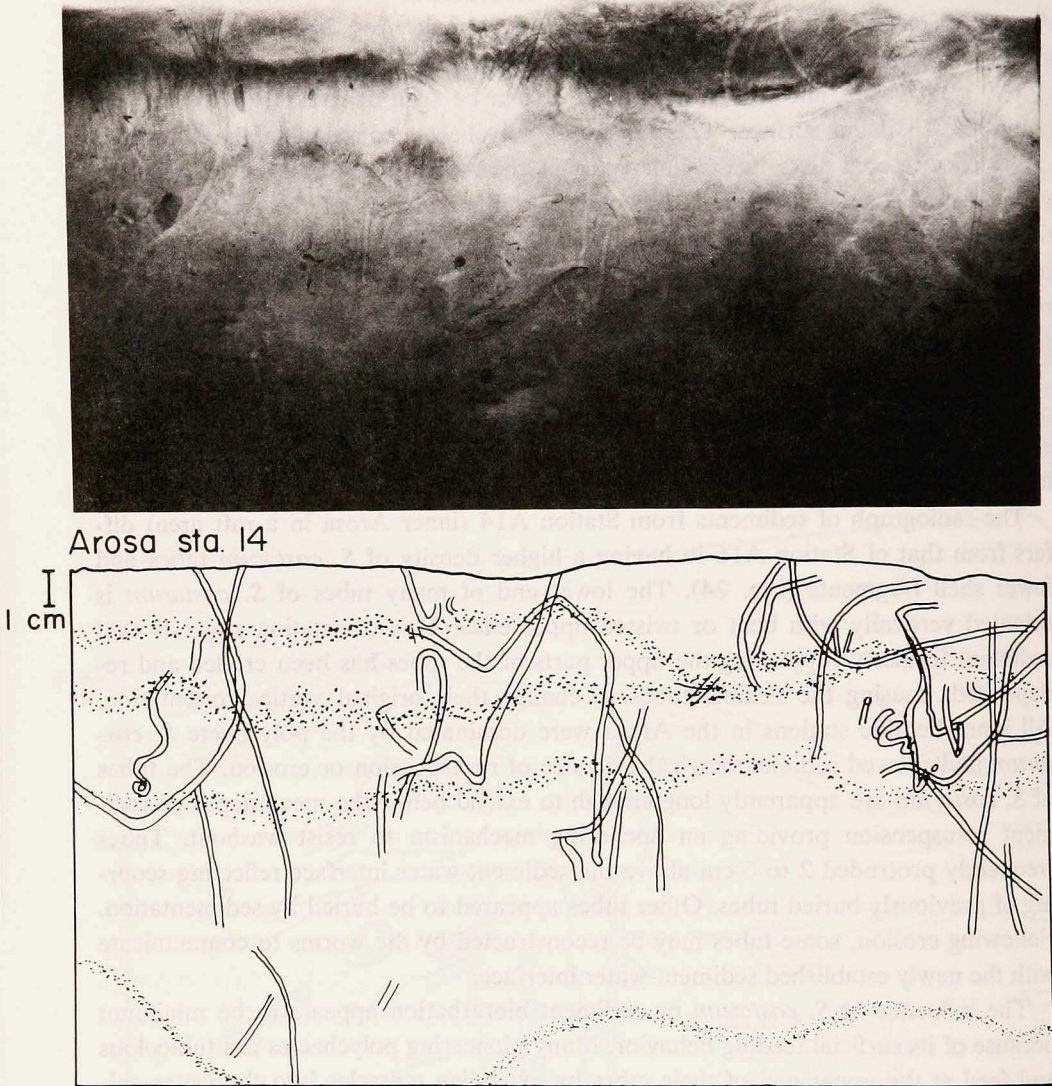


Figure 24. Sedimentary structures at Station A14, Ria de Arosa. Top—positive print of an x-radiograph of a diver-obtained box core. Bottom—interpretive drawing of major sedimentary features as seen in the above radiograph. This bottom contains abundant tubes of *Spiochaetopterus costarum*. At least four buried (erosional?) interfaces are shown as stippled horizons.

abundance, and tube diameter (Aller, 1980b). For a particular organism to be effective in exchanging sediment pore water, the tube walls must not severely limit diffusion of dissolved substances.

Studies of the diffusional properties of the tube wall of *S. costarum* using ^{35}S labelled $\text{SO}_4^{=}$ indicate that this polychaete has little effect on pore-water chemistry. Within six hours, 4 to 12% of the labelled sulphate diffused through segments of the tube. From the measured dimensions of the tube segments and the diffusion rate data, we calculated the diffusion coefficient for $\text{SO}_4^{=}$ across the tube wall by mathematical solution (Crank, 1956, p. 62). Tube segments were 3.3 ± 0.9 cm long, 0.2 cm wide, and the wall thickness was 0.01 cm. Each tube segment contained an initial ^{35}S activity of 1.46×10^6 cpm. The calculated diffusion coefficient for $\text{SO}_4^{=}$ across the tube material is 1.6 to 4.6×10^{-9} $\text{cm}^{-2} \cdot \text{sec}^{-1}$ ($N=3$). This range in values is three orders of magnitude lower than the 3 to 5×10^{-6} $\text{cm}^{-2} \cdot \text{sec}^{-1}$ molecular diffusion coefficient for $\text{SO}_4^{=}$ in marine sediments (Krom and Berner, 1980). The diffusion of other dissolved substances should similarly be inhibited by the tube wall of *S. costarum*. *Spiochaetopterus costarum* is apparently not effective in exchanging pore-water solutes with overlying water.

The radiograph from Station M8 in the Muros (located nearshore in the inner ria) shows light areas that represent organic-rich (x-ray transparent) concentrations of decomposing macrophytes (Fig. 25). Low-angle cross-bedding is also present. There is little radiographic evidence of bioturbation. *S. costarum* tubes exist mainly as relicts (i.e., buried). Sediments in the inner Muros, like most of the inner Arosa, are dominated by the tubicolous polychaete *S. costarum*. Cross-bedding in the sediment suggests that the sediment is periodically disturbed by turbulence. The distribution of *S. costarum* in both the Muros and the Arosa suggests that this polychaete is commonly encountered in areas of bottom scour. *S. costarum* is the dominant member of a low diversity disturbance faunal assemblage that is typical of much of the Arosa and raft areas in the Muros (see Macroinfaunal section).

In contrast, Stations M4, M7 and M13, located in deeper and less turbulent water, are dominated by deep infaunal deposit feeders. Three species numerically dominate these stations: the polychaete *Maldane glebifex*, the ophiuroid *Amphiura chiaje* and the holothurian *Leptosynapta bergensis* (See Macroinfaunal section). These species are vertically oriented and feed headdown in the sediment (conveyor-belt species *in sensu* Rhoads, 1974). This feeding orientation is important in transporting particles from below the RDP (Redox potential discontinuity, i.e., where $Eh = 0$) to the sediment surface. Such a deep-feeding infaunal assemblage probably represents an 'equilibrium' mud community (*in sensu* Rhoads et al., 1978a). Vertical particle advection by this method of bioturbation may stimulate microbial turnover rates (Yingst and Rhoads, 1980).

Sediment from Station M7, located in the middle of the Muros in 32 m of water,

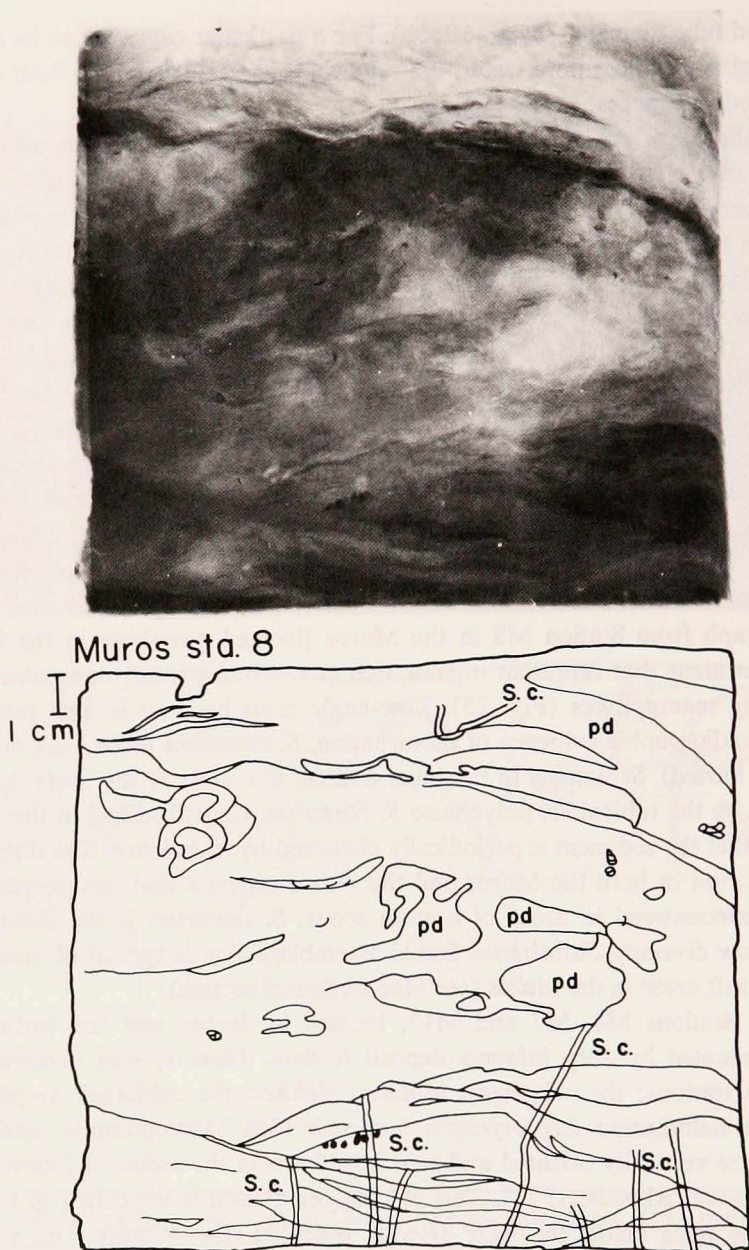


Figure 25. Sedimentary structures at Station M8, Ria de Muros. Top—positive print of an x-radiograph of a diver-obtained box core. Bottom—interpretive drawing of major sedimentary features seen in the above radiograph. Cross-bedding can be seen at the bottom of the radiograph as well as tubes of *Spiochaetopterus costarum* (S.c.). X-ray transparent areas (light) probably represent concentrations of plant detritus (pd).

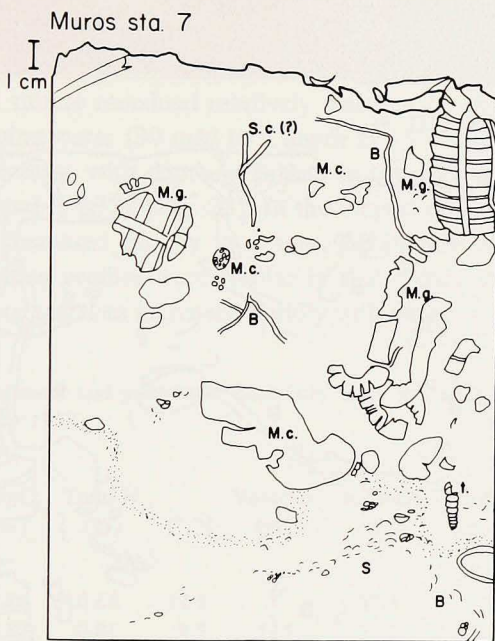
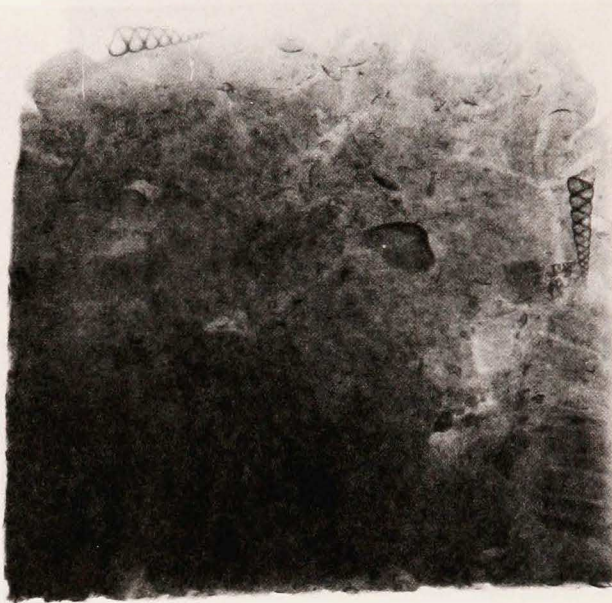


Figure 26. Sedimentary structures at Station M7, Ria de Muros. Top—positive print of an x-radiograph of a diver-obtained box core. Bottom—interpretive drawing of major sedimentary features seen in the above radiograph. The mottled appearance of the radiograph is related to the presence of dense mud clasts (mc). Transversely laminated mud tubes of the maldanid polychaete *Maldane glebifex* (M.g.) are also present. The bottom of the intensely bioturbated zone is stippled. Tubes of *S. costarum* (S.c.) may be present in this core. Several burrows (B) of other polychaetes (?) can also be seen. A large diameter relict burrow (B) is present in the lower right-hand corner. This burrow, and its entrance appears to be surrounded by a concentration of shell debris (S) including a turrillid (T) gastropod. The orientation of the gastropod is apex down, an orientation caused by the shell sinking through the quasi-fluid mud.



Muros sta. 4

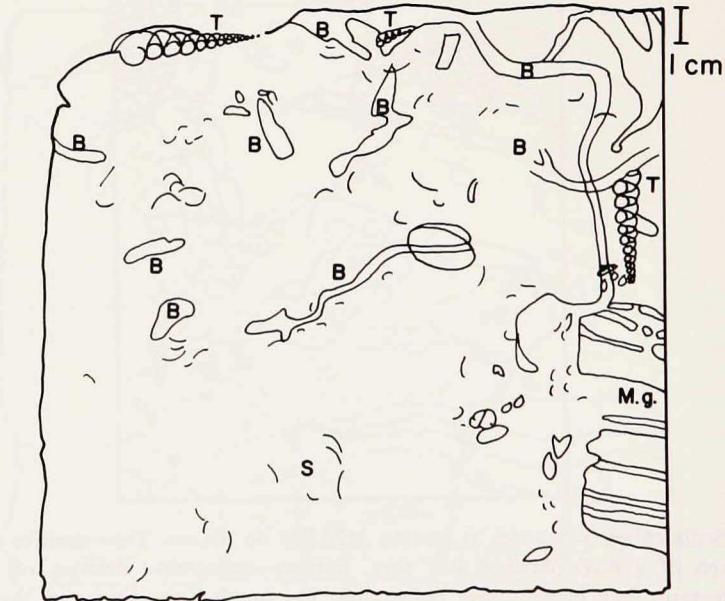


Figure 27. Sedimentary structures at Station M4, Ria de Muros. Top—positive print of an x-radiograph of a diver-obtained box core. Bottom—interpretive drawing of major sedimentary features seen in the above radiograph. A buried tube of *Maldane glebifex* (M.g.) is in its former life-position. A turrillid shell (T) above the *M. glebifex* is oriented apex downward, a sinking orientation of other mollusc shells (S). Many burrows (B) are present.

has a mottled fabric (Fig. 26). Many of the small irregular dark areas represent fragments of mud tubes or pieces of consolidated sediment that have been incompletely mixed or disaggregated by bioturbation. The biogenetically reworked zone extends to a depth of 14 to 20 cm. Below this zone the density of the sediment increases. The transversely laminated cylinder in the upper right-hand corner of Figure 26 is the tube of a maldanid polychaete *M. glebifex*. The worm occupies the small diameter (3 to 4 mm) tube that extends down the center of the mud cylinder. A tube apparently persists after the death of the polychaete as disoriented and disintegrating fragments of old tubes can be seen at depth in the sediment.

At Station M4, located in the outer Muros in 35 m of water, the sediment was completely bioturbated to a depth of 10 to 16 cm (Fig. 27). A buried tube of *M. glebifex* was present. This station was similar to Station M7 in these features, but differed from Station M7 by having fewer mud clasts perhaps reflecting more active bioturbation at Station M4 than at Station M7. The random orientation of bivalve shell fragments also indicates intensive particle mixing by bioturbation.

b. Sediment geochemistry. At Station A15, within a raft area in the inner Arosa, the depth profile of sulfate remained relatively constant at, or close to, the concentration of the overlying water (30 mM to a depth of 18 cm) (Table 11). There was a slightly greater decrease with depth in sulfate in the core collected in 1978 than in three cores collected in 1979 (Fig. 28). In the longest core, the sulfate concentration below 18 cm decreased rapidly to a value of 16 mM at 30 to 34 cm. Ammonium and phosphate profiles were similar in that they remained relatively constant in the top 18 cm and then increased rapidly with depth.

Table 11. Table of sediment and pore-water chemistry from Ria de Arosa (Station A15). Data collected in September 1978.

Depth (cm)	Water content	OrgC (%)	Total N (%)	C/N	Volatiles (%)	Acid soluble (%)	Sulphate (mM)	Ammonium (μ M)	Phosphate (μ M)
Overlying water							30.4	3	
0-1	0.79	7.24	0.65	11.1		35.4		51	19
1-2	0.80	5.87	0.81	7.3	15.9	25.3		67	10
2-3	0.76	5.37	0.74	7.3	15.5	23.4	28.7	137	
3-5		5.50	0.84	6.6	16.2	39.0		122	65
5-6	0.72	5.26	0.60	8.8	13.8	20.9	29.9	223	123
6-8	0.67	5.18	0.55	9.4		17.2	28.8	125	77
8-11		5.56	0.74	7.5	15.6	22.7		89	56
11-15	0.63	4.07	0.50	8.1	12.0	16.5		26	37
15-18	0.59	4.09	0.52	7.9	11.6	12.9	29.7	70	20
18-22	0.56	4.13	0.50	8.3	12.1	11.4	22.5	427	160
26-30							18.2	1350	133
30-34	0.55	4.24	0.27	15.4	16.1	18.4	16.2	1440	140

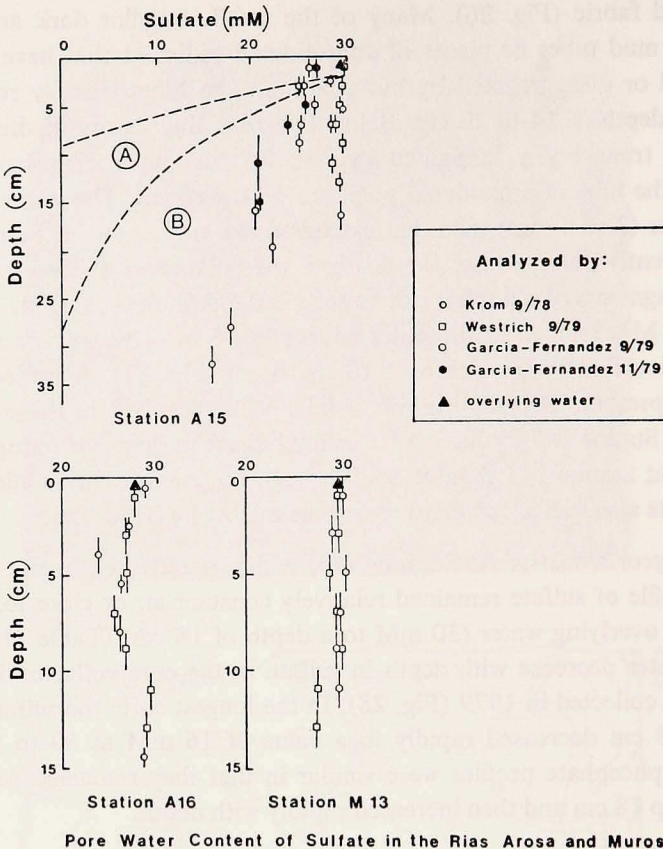


Figure 28. Sulfate profiles of Stations A15 and A16, Ria de Arosa and Station M13, Ria de Muros. Curve A plotted on the Station A15 profile is the predicted SO_4^{2-} pore water profile assuming a molecular diffusion coefficient of $158 \text{ cm}^2 \cdot \text{yr}^{-1}$. Curve B is the predicted profile for a diffusion coefficient of twice this value. All of the measured profiles have much higher concentrations than the model predicted curves. We therefore assume that advective processes are mainly responsible for the vertical nature of the observed data.

Ammonium continued to increase with depth below 18 cm while phosphate increased to $130\text{-}160 \mu\text{M}$ and then remained constant. The latter trend may reflect precipitation of insoluble phosphate. The chloride content of the pore waters decreased slightly with depth, but the range of the values is within experimental error. Thus there is no good evidence that the sediment is flushed by subsurface fresh water. The rate of sulfate reduction (Table 12) increased from $54 \text{ mM} \cdot \text{y}^{-1}$ at 0 to 2 cm to $91 \text{ mM} \cdot \text{y}^{-1}$ at 2 to 4 cm, and then decreased approximately exponentially to $31 \text{ mM} \cdot \text{y}^{-1}$ at 12 to 14 cm.

The flux of ammonium from the sediment into the overlying water, calculated from laboratory and *in situ* measurements, is 11 to $33 \mu\text{M} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ (Table 14).

Table 12. *In situ* rates of sulfate reduction and sediment water content. Data collected in September, 1979. Temperature $15 \pm 1^\circ\text{C}$. In units of mmoles sulfate per liter of pore water per year.

Depth (cm)	Ria Arosa—Station 15 within the raft polygon		Ria Arosa—Station 16 outside of raft polygons		Ria Muros Station 13	
	%H ₂ O	SO ₄ ²⁻ reduction rate mM/yr	%H ₂ O	SO ₄ ²⁻ reduction rate mM/yr	%H ₂ O	SO ₄ ²⁻ reduction rate mM/yr
0-2	80.6	54	76.7	57	69.3	24
2-4	73.3	91	70.2	54	64.6	32
4-6	71.2	65	65.4	33	63.5	36
6-8	70.5	49	63.9	28	63.0	35
8-10	67.9	59	62.9	31	61.7	32
10-12	64.3	41	62.2	27	61.2	25
12-14	63.0	31	—	20	—	26

These estimates include the combined effects of molecular diffusion and pore-water irrigation by organisms. Ammonium diffusion at Stations A14 and A16 estimated by Fick's first law is similar in magnitude to observed fluxes of 24 to $48 \mu\text{m} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$. All of the measured ammonium flux can be accounted for by Fickian diffusion and there appears to be little or no effective pore water flushing by the polychaete *S. costarum*.

The concentration of ²¹⁰Pb is constant in the top 15 to 18 cm of sediment (Fig. 29). Below this depth there is a rapid and steady decrease, corresponding to an average sedimentation rate of $1.6 \text{ cm} \cdot \text{y}^{-1}$. The water content is greater than 60% in the top 15 cm and greater than 70% in the top 6 cm. Organic carbon and total nitrogen in September 1978 and September 1979 (Fig. 30) varied irregularly down to 18 cm ranging from 4 to 7% for organic carbon and from 0.4 to 0.8 for total nitrogen.

At Station A14, outside the raft area, sulfate is relatively constant throughout the core. Ammonium increased somewhat with depth while the phosphate decreased from 380 mM at a depth of 2 to 3 cm to 60 mM at 17 to 18 cm (Table 14).

The ²¹⁰Pb profile at Station A14 is similar to that at Station A15 in a raft area (Fig. 26) with a major discontinuity at about 5 cm. The total inventory of ²¹⁰Pb at Station A16 is considerably lower than that at Station A15, even though sedimentation rates are similar below the 5 cm deep discontinuity.

During September 1978 the water content of sediment at A14 was greater than 70% over the 0 to 18 cm depth interval (Table 12). However, in September 1979 the water content was greater than 70% only in the top 4 cm. Temporal differences can also be seen in organic carbon and total nitrogen. In September 1978, organic carbon varied from 5 to 7% over the top 17 cm, with most values between 5 and 6% (Table 13). At 17 to 18 cm organic carbon dropped to 4.3%. In September 1979, the organic carbon content varied from 4 to 5% down to 10 cm, with most

210 Pb Excess (log)

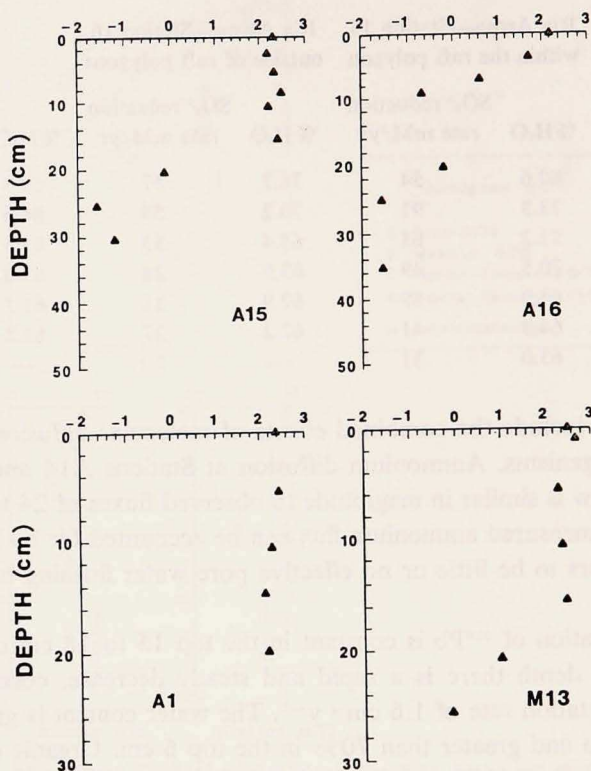


Figure 29. Profiles of excess ^{210}Pb at Stations A1, A15, and A16, Ria de Arosa and Station M13, Ria de Muros. Values at the bottom of each curve are assumed to represent the quantity of ^{226}Ra supported ^{210}Pb .

values clustering around 4% (Fig. 27). Total nitrogen was also higher in 1978 ranging from 0.50 to 0.68% in September 1978 and from 0.38 to 0.43% in September 1979.

We did not measure pore-water chemistry at Station A1. However, ^{210}Pb concentrations were constant to at least 20 cm. This is markedly different from profiles at Stations A15 and A16 in the inner ria.

At Station M13 in the inner Muros, the concentration of sulfate in pore waters was relatively constant to a depth of 14 cm and was close to values for overlying water (Fig. 28). Within this same depth interval, the rate of sulfate reduction also remained relatively constant (25 to 26 $\text{mM} \cdot \text{y}^{-1}$).

The ^{210}Pb activity at Station M13 decreased very slowly from 18 $\text{dpm} \cdot \text{g}^{-1}$ at the surface, which yields an apparent sedimentation rate of approximately 2.5

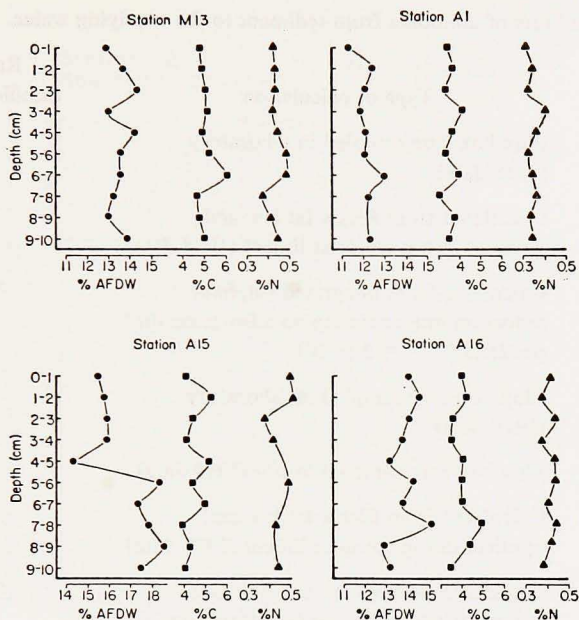


Figure 30. Profiles of percent ash-free dry wt. (AFDW) carbon and percent total nitrogen of sediment at Ria de Arosa Stations A1, A15 and A16 and Station M13, Ria de Muros. Data taken in September 1979.

Table 13. Sediment and pore-water chemistry from Ria de Arosa (Station A14). Data collected in September, 1978.

Depth (cm)	Water content	OrgC (%)	Total N (%)	C/N	Volatiles (%)	Acid soluble (%)	Sulphate (μM)	Ammonium (μM)	Phosphate (μM)
Overlying water							30.4		
F.S.L.*		5.71	0.68	8.4	16.1	19.8			
0-1	0.80	5.46	0.63	8.7	16.1	22.5	28.7	104	
1-2								245	
2-3	0.77	5.30	0.56	9.5	16.1	18.2	26.7	196	383
3-5		5.05	0.62	8.2	16.3	18.8	23.7	270	320
5-6	0.75	4.91	0.65	7.6	16.3	18.4	26.2	347	313
7-9	0.74	5.19	0.62	8.4	16.1	10.8	26.0	401	268
12-13								402	206
14-15	0.85	7.73	0.50	15.5	16.3	25.2	28.5	343	82
17-18	0.71	4.28	0.44	9.8	16.3	20.3		375	60

* F.S.L. is the flocculant surface layer, approximately the top 1 mm of the sediment.

Table 14. Calculated flux of ammonia from sediment to the overlying water.

Sample location	Type of calculation	Range of flux ($\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$)
Ria de Arosa Station 15	Flux box core sampled in laboratory (1978 data)	29
	Calculated from Fick's 1st law and gradient in top cm of sediment (1978 data)	24
	Calculated from integrated sulphate reduction rate assuming no adsorption on particles (C/N = 2 to 10)	918 to 178
Ria de Arosa Stations 14 and 16	Flux box core sampled in laboratory (1978 data)	20 to 38
	Flux box core sampled <i>in situ</i> (1979 data)	11 to 33
	Calculated from Fick's 1st law and gradient in top cm of sediment (1978 data)	48
	Calculated from integrated sulphate reduction rate assuming no adsorption on particles (C/N = 2 to 10)	625 to 125
Ria de Muros Station 13	Flux box core sampled <i>in situ</i> (1979 data)	8 to 66
	Calculated from integrated sulphate reduction rate assuming adsorption (K = 1.5) on particles (C/N = 2 to 10)	208 to 42

cm \cdot y⁻¹ (Fig. 29). Below 14 cm, ²¹⁰Pb activity decreased rapidly down to 25 cm, the deepest point sampled. There was no major discontinuity in the ²¹⁰Pb depth profile, only a sharp change in the gradient. Water content decreased slowly with depth, but was greater than 60% throughout the total depth intervals sampled. Organic carbon and total nitrogen were relatively constant at 5.0% and 0.4 to 0.5%, respectively, over the top 10 cm (Fig. 30).

c. Bottom resuspension. Because the physical and geochemical data from the Arosa strongly suggest the presence of bottom scour activity, we attempted to measure this phenomenon with optical transmissometry over the period September 23-30, 1980 during a period of +3 m amplitude spring tides. Water column turbidity was measured on both flooding and ebbing tides at Stations A10, A11, and A14 (Figs. 31, 32 and 33).

The transmissometer does not measure qualitative differences in type or size of suspended particulates. Inferences about the composition or sources of the particulates can be made from the shapes of the turbidity profiles. The separation of sur-

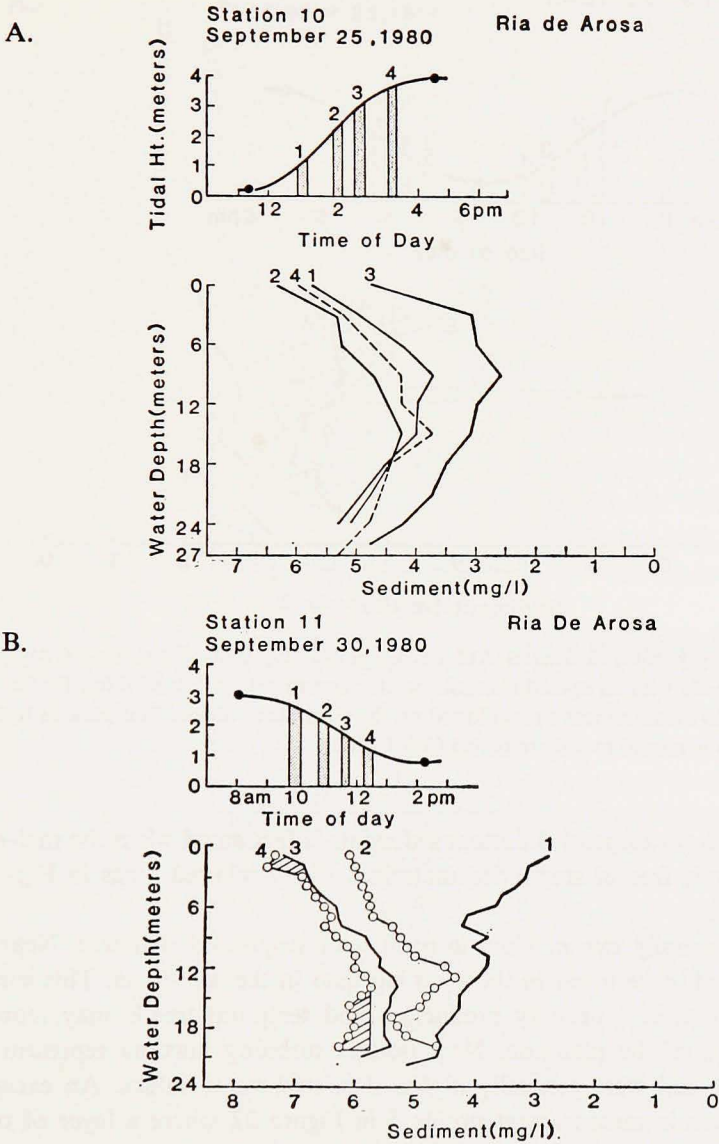


Figure 31. Turbidity profiles at Stations A10 and A11. (a) Estimates of vertical profiles of particulate concentrations as measured with optical transmissometry at Station A10 during flood tide on September 25, 1980. Profile numbers are related to measurement times plotted on the tidal curve above. (b) Estimates of vertical profiles of particulate concentrations as measured with optical transmissometry at Station A11 during ebb tide on September 30, 1980. Profile numbers are related to measurement times plotted on the tidal curve above.

Station 11

Ria de Arosa

September 29, 1980

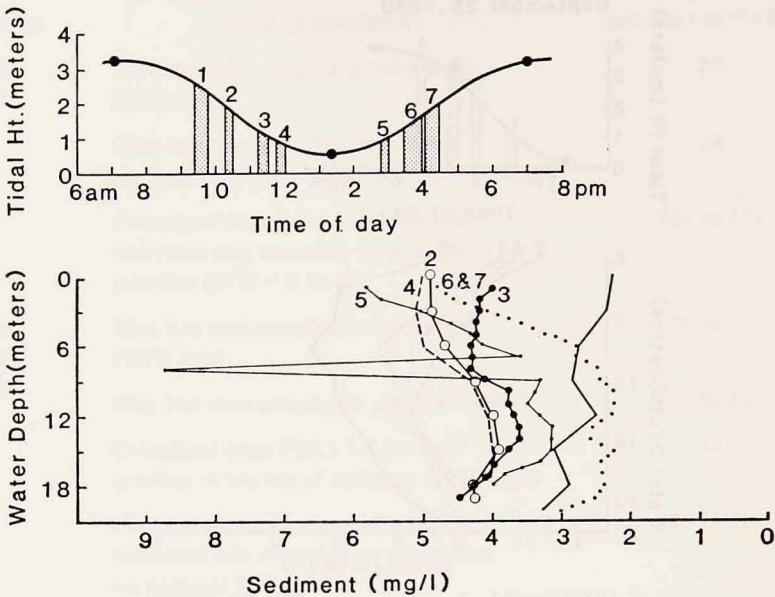


Figure 32. Turbidity profiles at Station A11 on September 29, 1980. Estimates of particulate concentrations made with an optical transmissometer during ebb and flood tides. Profile numbers are related to measurement times plotted on the tidal curve above. The peak in turbidity at 8 m (profile 5) is related to a thermocline (Δt of 1°C).

face particulates from suspended bottom sediments is facilitated when the mid-water column is relatively free of suspended materials. (See hachured areas in Figs. 31b and 33b profiles.)

There were generally two maxima in profiles of suspended sediment. Near surface values tended to be lower in the morning than in the afternoon. This surficial maximum may represent primary production and temporal trends may represent vertical migration of the plankton. Near bottom turbidity maxima represent suspended sediment and were generally higher than mid-water values. An exception to this can be seen in measurement profile 5 in Figure 32 where a layer of turbid water is associated with a thermocline ($\Delta t = 1^{\circ}\text{C}$ over a vertical distance of 1 m). Most of the near bottom turbidity values ranged from 3 to $6 \text{ mg} \cdot \text{l}^{-1}$.

The concentration of sediment loads near the bottom was highest at the end of ebb and flood tides. From the profiles in Figures 31, 32, and 33 we can estimate the depth of bottom erosion that would be required to explain the observed near bottom turbidity maxima. For example, profile 4 (Fig. 31b) shows a concentration of between 5.75 and $6.25 \text{ mg} \cdot \text{l}^{-1}$ in the bottom 6 m of the water column. The

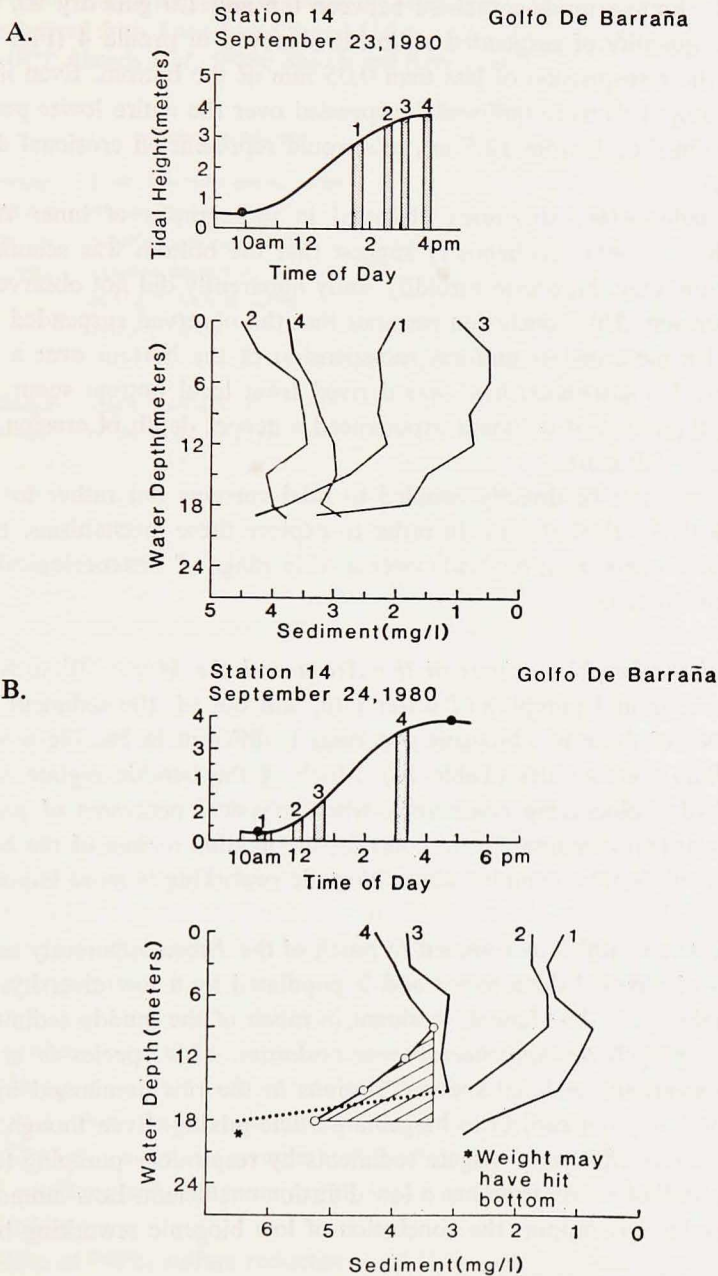


Figure 33. Turbidity profiles at Station A14. (a) Estimates of vertical profiles of particulate concentrations as measured with optical transmissometry on September 23, 1980 during late flood tide. Profile numbers are related to measurement times plotted on the tidal curve above. (b) Turbidity profiles as measured in (a) on September 24, 1980 during slack low water and flood tide.

upper 1 cm of the bottom muds contained between 0.6 and 1.0 gms dry wt. cc⁻¹ of sediment. The quantity of suspended sediment observed in profile 4 (Fig. 31b) would represent the resuspension of less than 0.05 mm of the bottom. Even if this concentration (6 mg · l⁻¹) were uniformly suspended over the entire lower portion of the water column (i.e., bottom 12.5 m), this would represent an erosional depth of only ~ 0.1 mm.

The physical sedimentary structures observed in radiographs of inner Arosa sediments and the sediment geochemistry suggest that the bottom was scoured to depths of 4 to 5 cm. Our short-term turbidity study apparently did not observe this degree of resuspension. This conclusion assumes that the observed suspended sediment represented a more-or-less uniform resuspension of the bottom over a wide area. If, however, this suspended load was derived from local bottom scour, it is possible that small patches of sediment experienced a deeper depth of erosion than we have assumed (> 1.0 mm).

Bottom scour may not be directly coupled to tidal currents but rather to wind waves working with the tidal stream. In order to explore these mechanisms, transmissometry measurements must be made over a wide range of meteorological and hydrographical conditions.

d. Contrasting of the benthic regimes of the Arosa and the Muros. Bioturbation causes particle mixing and pumping of water into, and out of, the sediment. The relative importance of these two biogenic processes is different in benthic pioneering and equilibrium communities (Table 15). Much of the benthic regime of the Arosa is typical of a pioneering community where physical processes of particle mixing enhance nutrient regeneration; in contrast, the benthic regime of the Muros is typically an equilibrium community where biogenic reworking is more important.

Ria de Arosa. The benthic environment in much of the Arosa apparently experiences high levels of physical disturbance and is populated by a low diversity, low-order successional stage.¹⁰ The faunal dominant in much of the muddy sediment is the tube-dwelling polychaete *Spiochaetopterus costarum*. This species is a good example of a pioneer, successional species. Stations in the rias dominated by this polychaete are probably not subject to biogenic particle mixing. Even though some pioneering polychaetes effectively irrigate sediments by respiratory pumping (Aller, 1980b), the tube wall of *S. costarum* has a low diffusion coefficient. Low ammonium flux rates from sediments support the conclusion of low biogenic reworking by the macrobenthos.

10. The term succession has many connotations in the literature. We define primary succession as the predictable appearance of macrobenthic invertebrates belonging to specific functional types following a benthic disturbance. These invertebrates interact with sediment in specific ways. Because functional types are the biological units of interest for this study, our definition does not demand a sequential appearance of particular invertebrate species or genera.

Table 15. Organism-sediment relations in pioneering and equilibrium benthic assemblages. Summarized from Long Island Sound U.S.A. (Aller, 1977, 1980a; McCall, 1977; Rhoads et al., 1977; Rhoads et al., 1978a; Rhoads and Boyer, 1982).

Successional sere	Species attributes	Organism-sediment relations	Examples from this study
Pioneering (high dis- turbance regimes)	Low diversity associations of semi-infaunal tube-dwelling species. Polychaetes common. Feeding at the sediment surface or water column.	Bioturbation by tube irrigation. Particle advection negligible. Molecular diffusion is an important geochemical rate-limiting process. Sediments are compact <50% water.	<i>Spiochaetopterus socialis</i> Assemblage in Ria de Arosa (Stations 15-16) and Station 8 in Ria de Muros.
Equilibrium (low dis- turbance regimes)	High diversity associations of deep infaunal species. Polychaetes, echinoderms, or protobranch bivalves common. Feeding concentrated near the RPD.*	Both particle mixing and pore water exchange are quantitatively important. Molecular diffusion rates \ll biologic advection rates. High sediment water content (> 70%).	<i>Maldane glebifex</i> <i>Amphiura chiajei</i> Assemblage in Ria de Muros (Stations 4, 7 and 13).

* RPD = Redox Potential Discontinuity.

When the importance of biogenic processes in chemical exchange processes is dismissed, data from radiographs, ^{210}Pb , pore-water chemistry (sulfate, phosphate and ammonium), and *in situ* rates of sulfate reduction demand an advective process to explain structures and concentrations and distributions of the nuclide and pore-water constituents within the sediment. Sediment x-rays contain abundant evidence of physical resuspension or erosion in the form of disoriented *S. costarum* tubes, scour surfaces and cross-bedding. The ^{210}Pb profiles from the inner Arosa have no vertical gradient in the upper 5 to 18 cm. Assuming a long-term sedimentation rate of 1 to 2 cm \cdot y $^{-1}$ or lower, other processes must mix ^{210}Pb downward. Moreover ^{210}Pb profiles show a discontinuity below an upper zone of constant concentration. The only way such a profile can be produced is to resuspend the sediment to a given depth and allow the suspended load to settle onto the seafloor in a homogenized state. Though we did not sample ^{210}Pb at Station M8 in the inner Muros one would expect profiles similar to those in the Arosa based on the comparable physical structures and fauna.

Profiles of ^{210}Pb , sulfate reduction, and C/N and water content from Station A16 also suggest recent surface erosion. Assuming that the quantity of ^{226}Ra supported ^{210}Pb is equal to the ^{210}Pb value at depth, the total ^{210}Pb inventory can be calculated for each station. At Station A16 the inventory is a factor of four lower than at Stations A14 and A15. This difference could be explained if the sediment at Station

A16 had recently lost the top 3 to 6 cm due to erosion. Further, no subsurface maximum was observed in sulfate reduction rates at A16. Most nearshore marine sediments with oxygenated overlying water, such as the outer ria Stations A15 and M7, typically show a subsurface maximum (Jørgensen, 1978). This rate maximum is related to the partially aerobic nature of the redox located in the upper 1 to 5 cm. The high sulfate reduction rate at the sediment-water interface at Station A16 can be explained if the top 4 to 5 cm had been recently eroded. Comparisons of water content, organic carbon, and total nitrogen profiles at Stations A14 (sampled September 1978) and A16 (sampled September 1979) also suggest surface erosion.

Although both stations were located in the same general area, the profiles of the above parameters were distinctly different. In the top 18 cm at Station A14, water content varied from 71 to 85%, organic carbon varied from 5 to 7%, and total nitrogen from 0.50 to 0.68%. In contrast, these parameters in the top 10 cm at Station A16 were distinctly lower, being 62 to 76%, 4 to 5%, and 0.38 to 0.43%, respectively. Values recorded for the top few centimeters at Station A16 were similar to those found at a depth of 17 to 18 cm in sediment from Station A14. Sediment water contents were generally below 50%. The sediments at Stations A15 and A16 had high water contents (60 to 70%) with a porosity of $> 0.85\%$ suggesting that resuspension rates exceeded compaction rates. Once fluidized, the Arosa sediments may have had very low critical erosion velocities. Critical erosion velocities for fluid muds are approximately 16 to $19 \text{ cm} \cdot \text{sec}^{-1}$ ($z=100 \text{ cm}$) (Rhoads *et al.*, 1978b). Thus, frequent resuspension keeps the sediment water content high and this, in turn, lowers the critical erosion velocity.

Physical resuspension might also explain the apparent absence of a visual redox boundary (Redox boundary = oxidation-reduction boundary where $Eh = 0$) within the sediment. We did not measure pore-water Eh gradients and so cannot document the depth where $Eh = 0$. At least to the depth sampled the sediment was a uniform olive color and lacked the grey H_2S or black FeS banding commonly observed below the aerobic surface mud so commonly observed in other estuaries or embayments. Frequent bottom resuspension (accompanied by oxygenation) may prevent a visual redox boundary from developing.

In addition to affecting particle resuspension, nutrient regeneration and sulfate reduction physical resuspension leads to flushing and exchange of sediment pore water with overlying water. From the measured rates of sulfate reduction in the sediment (assuming these rates are accurate) it is possible to calculate the sulfate pore-water profile that would develop if transport of sulfate from the overlying water into the sediment was confined to molecular diffusion. The differential, diagenetic equation of Berner (1971, 1980), ignoring compaction, is

$$D \partial^2 c / \partial x^2 - w \partial c / \partial x - R(x) = 0 \quad (1)$$

where

c = concentration of sulfate in mM

x = depth measured positively downward into the sediment

w = sedimentation rate

D = whole sediment molecular diffusion coefficient modified for tortuosity

R = rate of sulfate reduction in $\text{mM} \cdot \text{y}^{-1}$

The assumption of steady-state conditions is appropriate in that the steady-state profile for sulfate is calculated. An exponential function is fit to the sulfate reduction rate profile at Station A15. When the model is developed with the origin at a depth of 2 cm in the sediment the best-fit exponential function to the rate data in Table 12 is:

$$R_o = 98[\exp(-.0934)x] \quad (2)$$

where

$$R_o \equiv \text{rate of sulfate reduction at } (x=0) = 98 \text{ mM} \cdot \text{y}^{-1}$$

$$\beta \equiv \text{curve-fit exponential} = .0934.$$

The solution to equation (1) from Berner (1971, 1980) is:

$$c = (c_o - c_\infty)\exp(-\beta x) + c_\infty \quad (3)$$

where

$$c_o - c_\infty = R_o / (D\beta^2 + w\beta)$$

$$c_o = \text{concentration of } \text{SO}_4^{2-} \text{ at } x=0$$

$$c_\infty = \text{constant of integration, } c \rightarrow c_\infty \text{ as } x \rightarrow \infty.$$

By substituting the curve-fit-parameters R_o and β , a value of c_o equal to the sulfate concentration in the overlying water, a value of the molecular diffusion coefficient corrected for the porosity of the sediment according to Krom and Berner, 1980, and a value of w equal to 2 cm/yr (from the ^{210}Pb data below 18 cm) into equation 4, c_∞ is calculated and a steady-state pore-water SO_4^{2-} profile can be produced. The model curves are relatively insensitive to the exact value of w . Curve A in Figure 9 is the predicted SO_4^{2-} pore-water profile with a molecular diffusion coefficient of $158 \text{ cm}^2 \cdot \text{y}^{-1}$. Doubling the diffusion coefficient results in Curve B. In both cases the measured pore-water sulfate values are much higher than values predicted from measured rates of sulfate reduction. Clearly some process transports sulfate into the sediment at a rate much faster than allowed by molecular diffusion. It should be noted that the measured rates of sulfate reduction are considered fairly accurate (Jørgensen, 1978; Westrich, unpublished data). Therefore the discrepancy between the model-predicted sulfate profile and the actual data cannot be due to an error in the rate measurements.

Further evidence of unusual exchange is obtained from nutrient flux studies. The

fluxes of ammonium from the sediment into the overlying water, calculated in the laboratory and *in situ*, are similar (11 to 33 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$). The estimate obtained by Fick's First Law for these two stations is similar in magnitude (24 to 48 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$). By assuming a C/N ratio of 2 to 10 for organic matter undergoing sulfate reduction, rates of measured sulfate reduction can be used to calculate ammonium production. As shown in Table 14, the amount of ammonium produced during sulfate reduction that should be exchanged with the overlying water is 3 to 35 times greater than that measured.

Ria de Muros. In the Muros, inner stations represent a low-order successional stage and also show sedimentary evidence of physical disturbance by resuspension. In contrast, outer regions of the Muros (M4 and M7 and M13) and the outermost station (A2) of the Arosa, are populated by a deep bioturbating equilibrium community. These stations also show sedimentary evidence of particle bioturbation and little physical disturbance. Bottom sediments at Stations M4, M7 and M13 in the Muros may also experience physical resuspension but the sedimentary record is not preserved because bioturbation rates are extremely high.

The tube-dwelling maldanid polychaete *Maldane glebifex* and ophiuroid *Amphiura chiajei* are faunal dominants. These species are functionally similar to those which dominate bottom communities in central Long Island Sound (Aller, 1977, 1980a) and the central mud basin of Cape Cod Bay (Rhoads and Young, 1971; Rhoads and Young, 1971). Both of these communities have high rates of bioturbation for both particles and pore water. "Conveyor-belt" species (*in sensu* Rhoads, 1974) are an important component causing extensive particle bioturbation (Benninger *et al.*, 1979). The shape of the ^{210}Pb profile at Station M13 may reflect intensive particle advection by such conveyor-belt species. Faunal similarities between Arosa Station A1 and Stations M4, M7 and M13 in the Muros may help explain the similarity between the ^{210}Pb profiles at Arosa Station A1 and M13.

Sulfate concentrations in the pore waters at Station M13 were constant with depth even though rates of sulfate reduction were very high. In contrast to most of the Arosa, the infaunal assemblage in most of the Muros is apparently responsible for flushing or irrigation of the sediment pore water. In addition, constant values for the rate of sulfate reduction in the top 10 cm at Station M13 (Fig. 11) reflect a very high rate of particle bioturbation. In muddy sediments of Long Island Sound (USA) the rate of sulfate reduction in the top 10 cm depends on the supply of fresh particulate organic matter that is mixed downward from the sediment-water interface by bioturbation. The rate of bioturbation is not high enough, however, to maintain equally high rates of sulfate reduction throughout the bioturbated zone. Therefore, in Long Island Sound the rate decreases by a factor of 3 over the top 10 cm. In sediment regimes of the Muros, the rate of particle bioturbation is high enough, at least during the period of our observations, to insure an equal distribution of fresh

organic substrates throughout the zone of bioturbation. This results in a constant high rate of sulfate reduction within the top 10 cm.

SUMMARY AND CONCLUSIONS

Intensive raft culture of the blue mussel, *Mytilus edulis*, profoundly affects food chain patterns and secondary production in the Ria de Arosa (NW Spain). Ropes hanging from rafts provide a large surface area for mussel growth. Because of high standing biomass and high filtration capabilities, the mussel is the "key industry species" (*in sensu* Elton, 1927). Mussels are the major herbivore harvesting bursts of pelagic primary production associated with the intermittent upwelling. Further, mussels produce copious amounts of fecal ribbons which form biodeposits within the interstices of a rope. These deposits support a detritus-based epifaunal biocoenosis. These epifauna in turn are preyed upon by megabenthos, especially dense populations of crabs. Demersal fish assemblages are dominated by small-mouthed gobies that cannot physically ingest much of the epifauna so standing stocks are not higher than that reported for other coastal areas. Temporal changes in standing crops of mussels, their associated epibiota, and concomitant fluctuations in starfish and crab densities result not only from seasonal changes in migrations and recruitment, but can, in part, be related to the culture and harvesting practices of man. For example, highest densities of crabs and starfish occur in areas of rafts during major harvesting periods (November-December and March-April) when portions of mussels and epifauna end up on the bottom. The community dynamics of the epibiota associated with the mussel ropes are profoundly affected (as well as made possible!) by man's aquaculture practices. To date we have documented that succession of the seaweed community associated with the mussel ropes is controlled by the season of initiation and time period of culture of the ropes. We are presently investigating population dynamics of the major epifauna, the cucumbers and the small crab *P. longicornis*. More such work is needed to characterize the "aquaculture ecosystem" developed by man in his mussel culture endeavors. Needless to say: man proposes; nature disposes. The fundamental rules of bioenergetics (conversion efficiencies and production), trophic dynamics (energy transfer among different trophic groups of the epibiota) and population dynamics (reproduction, recruitment, survivorship) that result in the biocoenosis associated with the mussel ropes are those applying in all ecosystems. However, it is of interest how man's activities, in this case—aquaculture, alter "normal" food chain patterns.

We have contrasted in Figure 34 the carbon flux of benthic regimes of raft and nonraft areas. High accumulation rates of biodeposits from the large number of rafts in the Arosa markedly affect sediment composition and benthic infauna. Much of the total organic load produced by the mussels is utilized by the raft epifauna before it reaches the bottom. Still, organic sedimentation rates are high resulting in

high organic content of bottom sediments in all but the outermost region of the Arosa. Sedimenting material is flocculent, resulting in silty bottom muds with high (> 70%) water content. Bottom sediments in the Muros, except in the innermost region, contain less organic matter and are more typically muddy sands.

Most of the Muros and the outermost region of the Arosa contain an equilibrium infaunal community characterized by high biomass and species diversity. Dominant species are typically sediment reworkers and their bioturbation causes extensive vertical mixing and irrigation of sediments, and high benthic activity (benthic surface respiration, microbial turnover and nutrient regeneration).

In contrast, the middle and inner Arosa (where rafts are most abundant) and the innermost region of the Muros contain pioneer infaunal communities, associated with low biomass and diversity. Dominant species were typically tube-building organisms that cause little biogenic reworking. There was low benthic activity except for a high rate of anaerobic metabolism. Rates of oxygen uptake by the sediment under experimental conditions did not reflect the metabolic activity deep below the surface. Material fluxes across the sediment surface do not seem to reflect instantaneously the rates of subsurface processes.

Low concentrations of phosphate and ammonium in the pore waters of the inner Arosa suggest that nutrient exchange, at rates higher than we measured, must occur in the Arosa. Furthermore, the high sulfate concentrations are also inconsistent with the high rates of sulfate reduction, indicating that sulfate is being replenished in the sediment pore waters at a rate faster than 1-D molecular diffusion. Also sediment x-radiographs and lead-210 profiles indicate substantial vertical mixing of sediments that cannot be accounted for by macrobenthic bioturbation. Turbidity profiles measured under spring tide conditions at three stations in the Arosa measured a low degree of bottom resuspension. This measured resuspension is probably not responsible for the deep physical resuspension of the bottom in the Arosa that is required to explain the above sedimentological and geochemical data. If resuspension is responsible, a more extensive turbidity survey is required to document its existence.

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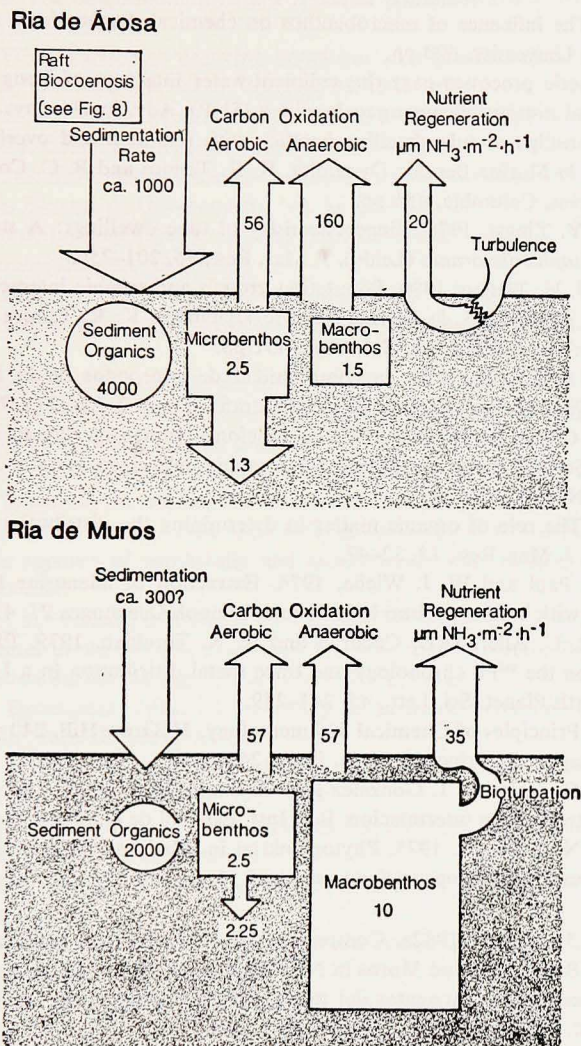


Figure 34. Schematic contrast of benthos and processes of raft and nonraft sediment regimes. All values are presented as $\text{g C} \cdot \text{m}^{-2}$ or $\text{g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$.

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