

CHAPTER 9

BENTHOS AND ITS INTERACTION WITH BOTTOM BOUNDARY LAYER PROCESSES

P.A. Jumars and K. Banse

School of Oceanography, University of Washington, Seattle, WA 98195

9.1 INTRODUCTION

Work on the continental shelf benthos of the Pacific Northwest prior to the 1970s has been presented and summarized by Lie and Kisker (1970), Pamatmat (1973) and numerous chapters in Pruter and Alverson (1972). Since then, investigations in the area have been fragmentary and episodic. During these years, however, continental shelf benthos elsewhere within the United States has been studied intensively and extensively in preparation for oil exploration and recovery and basic research efforts in several other shelf settings around the globe have been continued or initiated. In addition, the bottom boundary layer environments of continental shelf benthos have become much better known through work on the Washington continental shelf and elsewhere. The study of organism-sediment relations has also matured and expanded to include fluid dynamics. It is our intent to use these various advances to place historical data from the U.S. Northwest continental shelf in a new context, underscoring gaps in existing information and consequent opportunities for future research. This examination can go little below the size range of the macrofauna, however, because the meiofauna and microbiota of the Northwest shelf are so little studied.

9.2 BENTHOS OF THE WASHINGTON SHELF**9.2.1 Spatial and Temporal Structure of Communities**

Most of what is known about the standing crops and species compositions of the infaunal communities comes from a series of papers by Lie and his coworkers (Lie, 1969; Lie and Kelley, 1970; Lie and Kisker, 1970). The basic data set consists of 22 stations off the northwestern coast of Washington and 18 stations off the mid- and southwestern coast of Washington (Fig. 9.1). The fairly broadly distributed stations north of about 47° 50'N were occupied in May to August of 1967 and those further south, in July 1968. In most cases, 3 replicate, 0.2-m² van Veen grab samples were taken per site and sieved through a 1-mm mesh, with the retained animals identified to species, weighed and counted. For polychaetes the identification task was so large that only the species dominating in numbers or biomass were treated at the species level. The grab used was neither screened nor otherwise vented, so that epifauna probably were seriously under-sampled. The stations fall primarily in what is now known (Kachel and Smith, 1989, Chapter 8) as the mid-shelf silt deposit and in the sands inshore of it, although a few are scattered seaward of the mid-shelf silts.

At the most gross level, but one entirely appropriate to the sparsity of samples, community classification yields three major groupings of stations on the basis of taxonomic composition

Jumars, P.A., and K. Banse. 1989.

Benthos and its interaction with bottom boundary layer processes.

Pp. 349-365 in M.R. Landry and B.M. Hickey, Eds.

Coastal Oceanography of Washington and Oregon.

Elsevier, Amsterdam.

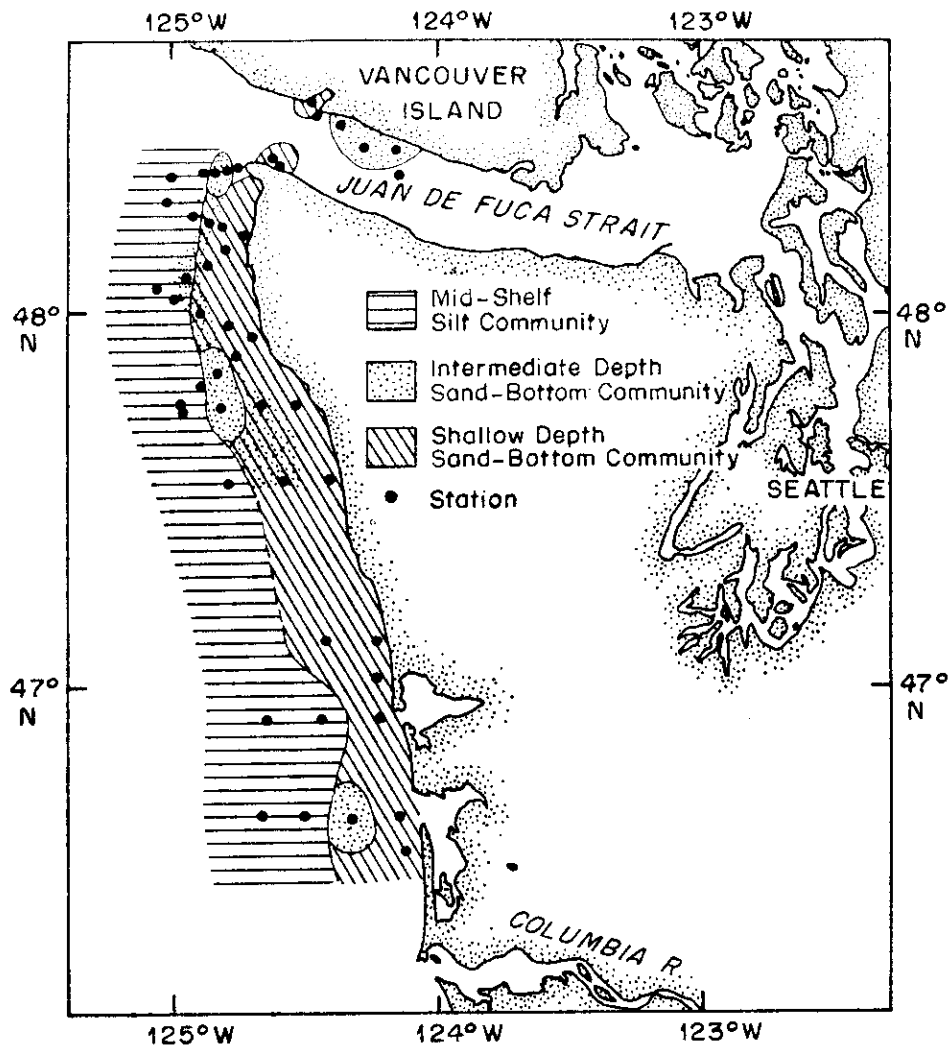


Fig. 9.1 Location of sampling and geographic distribution of the three offshore benthos communities. Modified from Lie and Kisker (1970).

(Lie and Kisker, 1970 and Fig. 9.1 herein). The community identified by them as a deep-water, mud-bottom community can on the basis of recent geological work be more accurately termed a mid-shelf silt community. It apparently extends (on the basis of two of Lie and Kisker's stations) some distance onto the muddy sands of the outer shelf. Immediately shoreward of this mid-shelf silt community and extending until the sediments reach approximately 80% sand is an intermediate-depth, muddy sand community. Still further landward, but offshore of the breakers, is a shallow-water sand community. Median ash-free dry weights (AFDW) of the macrofauna for the three communities at the stations north of 47° 50' (Fig. 9.1) are, respectively, 1.94, 1.98 and 1.17 g m^{-2} (based on Table 2 of Lie, 1969, with stations 7 and 20 omitted because they were classified differently in Lie and Kisker, 1970). Lie's (1969) biomass means for these three groups (2.27, 2.34 and 1.35 g m^{-2} AFDW), respectively, were influenced by a few stations with unusually high values. The same problem holds for the widely quoted means for all stations, of

3.06, 2.53 and 1.40 g m⁻² AFDW in Lie and Kisker (1970). Recognizing the difficulty of comparing and interpreting biomass data from studies employing different gears and sieves, Lie (1969) discussed only briefly that his means appeared to be low relative to other temperate sites (e.g., < 50 % of the infauna in Long Island Sound or off Santa Barbara, California, but comparable to the then-existing data from the Gulf of Alaska). A.G. Carey (Oregon State University, personal communication) using finer sieves and better vented sampling gear on the Oregon shelf has reported substantially higher standing crops. Without intercalibration it is only safe to make internal comparisons. Within Lie's samples, surface deposit feeders are important throughout and the relative abundance of suspension feeders decreases with water depth (Table 9.1). Unfortunately, the depth series does not extend much beyond the mid-shelf depths.

No surveys of comparable magnitude have been conducted since 1968 on the Washington shelf. More recent, scattered observations off Washington and off Oregon, however, confirm the general conclusions. In a transect off Newport, Oregon, Carey (1972, using dredges and a sieve of 0.42-mm aperture) also found depth zonation, with increasing importance of burrowing polychaetes and maximal standing crops toward the shelf break. Smethie *et al.* (1981) and Nittrouer and Sternberg (1981), analyzing only the polychaetes (from 0.35-mm-sieved subsamples out of box cores) taken at three sites in the mid-shelf silt deposit from off the Columbia River (about 46° 15' N) northward to off Gray's Harbor (about 46° 55' N), found a much greater prevalence of motile, subsurface deposit feeders (especially capitellid polychaetes) than observed by Lie and coworkers. It is not possible to attribute discrepancies among these studies to differences in sampling gear, station position, or time between the sampling programs.

Epibenthos of the Washington continental shelf has not been studied systematically, though it is probably qualitatively similar to that off Oregon (see Carey, 1972). In the latter region, mobile epifauna and the projecting soft body parts of infauna are very important items in the diets of commercially valuable fishes (e.g., Pearcy and Hancock, 1978; Hogue and Carey, 1982), especially in the youngest age classes.

No time series have been conducted to resolve patterns of benthic community change on the U.S. Pacific Northwest shelf. The evidence that substantial interannual changes may occur is of two kinds: data from a physically different environment in Puget Sound, with some overlap in faunal composition with the open shelf and data from physically similar but geographically remote environments with little faunistic overlap. Nichols (1975, 1985) has maintained a time series for over a two decades at a 203-m station (his Station 2) within the main basin of Puget Sound. This station (Station B of Lie, 1969) is similar in sedimentary and infaunal composition to the mid-shelf silt stations. Nichols (1985) has shown dramatic shifts in infaunal community dominance from one year or group of years to the next. Taking the other possible tack of looking at a time series from the best studied, exposed shelf area (at 55-m depth off Northumberland; Buchanan and Moore, 1986) – albeit one with a different fauna – leads to the same conclusion. Again, dramatic year-to-year shifts in the abundances of some populations were seen. Alone, these independent observations do not provide strong evidence for interannual changes in the

Table 9.1 Numerical (N) and biomass (B) dominants of shelf benthos, by community, numbers at right indicating numerical abundance, converted to m^{-2} . From Lie and Kisker (1970) (\bar{x} = mean; Md = median). Dominants (*sensu* Lie and Kisker, 1970) are those with the highest ranks in mean abundance and biomass.

Genus, species (feeding guild and major taxon)		\bar{x}	Md
Mid-Shelf Silt Community			
(N)	<i>Prionospio malmgreni</i> (surface deposit-feeding, spionid polychaete)	34	13
(N)	<i>Axinopsida serricata</i> (suspension-feeding, thyasirid bivalve)	30	25
(N,B)	<i>Sternaspis fossor</i> (subsurface deposit-feeding, sternaspid polychaete)	28	10
(N)	<i>Adontorhina cyclia</i> (suspension-feeding, thyasirid bivalve)	27	12
(N)	<i>Heterophoxus oculus</i> (omnivorous, subsurface-feeding, phoxocephalid amphipod)	18	18
(N)	<i>Macoma carlottensis</i> (surface deposit-feeding, tellinid bivalve)	17	12
(N)	<i>Ninoe gemmea</i> (omnivorous, burrowing, lumbrinerid polychaete)	17	10
(B)	<i>Brisaster latifrons</i> (subsurface deposit-feeding, irregular urchin)	2	2
(B)	<i>Ophiura luetkeni</i> (omnivorous brittle star)	5	0
(B)	<i>Amphioplus</i> sp. (suspension[?]-feeding brittle star)	5	5
Intermediate-Depth, Muddy Sand Community			
(N,B)	<i>Yoldia ensifera</i> (subsurface deposit-feeding, nuculanid bivalve)	76	3
(N,B)	<i>Paraphoxus variatus</i> (omnivorous, subsurface-feeding, phoxocephalid amphipod)	50	58
(N,B)	<i>Magelona</i> sp. (surface deposit-feeding, magelonid polychaete)	43	8
(N,B)	<i>Sternaspis fossor</i> (subsurface deposit-feeding, sternaspid polychaete)	39	13
(N,B)	<i>Nephtys</i> sp. (burrowing, carnivorous, nephtyid polychaete)	35	30
(N,B)	<i>Haploscoloplos elongatus</i> (subsurface deposit-feeding, orbiniid polychaete)	30	30
(N,B)	<i>Axinopsida serricata</i> (suspension-feeding, thyasirid bivalve)	26	17
(B)	<i>Macoma eliminata</i> (surface deposit-feeding, tellinid bivalve)	15	3
Shallow-Water, Sand Community			
(N,B)	<i>Diastylopsis dawsoni</i> (suspension-feeding cumacean)	900	12
(N,B)	<i>Tellina salmonea</i> (surface deposit-feeding, tellinid bivalve)	613	0
(N,B)	<i>Owenia fusiformis</i> (surface deposit- and suspension-feeding, oweniid polychaete)	126	0
(N,B)	<i>Ampelisca macrocephala</i> (surface deposit- and suspension-feeding, ampeliscid amphipod)	73	47
(N,B)	<i>Paraphoxus obtusidens</i> (omnivorous, subsurface deposit -feeding, phoxocephalid amphipod)	34	8
(N,B)	<i>Macoma expansa</i> (surface deposit-feeding, tellinid bivalve)	33	0
(N,B)	<i>Eohaustorius washingtonensis</i> (burrowing, sand-browsing, haustoriid amphipod)	26	9
(B)	<i>Nephtys</i> sp. (burrowing, carnivorous, nephtyid polychaete)	19	13
(B)	<i>Chaetozone setosa</i> (surface and subsurface deposit-feeding, cirratulid polychaete)	23	10
(B)	<i>Siliqua patula</i> (suspension-feeding, solenid [razor] clam)	20	0

benthos of the Washington continental shelf, but together they are more convincing. There are no obvious reasons why the shelf benthos should be any more stable than the benthos of Puget Sound. The episodic nature of large-magnitude storms on the shelf (Kachel and Smith, 1989, Chapter 8) suggests that even greater population fluctuations might be expected over the continental shelf.

It is perhaps worthwhile at this point to mention effects caused by El Niño. It is clear that both currents (see Hickey, 1989, Chapter 2) and water properties such as temperature, salinity and nutrients (see Landry *et al.*, 1989, Chapter 1) over the shelf in the Pacific Northwest have

interannual fluctuations that are often related to El Niño events. Recruitment of shelf benthos certainly is likely to be affected too, both directly and through effects on predators of benthos (cf. the changed food ingested by planktonic larvae of sable fish, Grover and Olla, 1987). It is remarkable, though, how difficult it was to recognize change of abundance during the "century Niño" of 1982-1983 against the background, normal year-to-year variability in the intertidal benthos of the outer coast of Washington (Paine, 1986). Even when a change can be observed, the unresolved issue is to identify the mechanism. An obvious step is to correlate the series of some biotic parameter with any environmental data available over the same period. Temperature data are the most easily obtained. We caution against the temptation to leap from such correlations to assumptions that temperature is a root cause of population change (e.g., Pearson *et al.*, 1986; Buchanan and Moore, 1986). Many environmental variables, e.g., nutrient supply to phytoplankton (themselves food for planktotrophic larvae), correlate with temperature in upwelling regions and correlation is no better evidence of cause in time series of community structure than correlation with sediment type is of cause in spatial analyses of community structure.

Benthic rate information for the Washington shelf comes from measurements of oxygen consumption and calculations of fluxes from concentration gradients of a number of constituents. Pamatmat (1973) determined total oxygen consumption and community respiration in shipboard incubations of retrieved samples. He had tested for artifacts by comparing *in situ*-measured rates with core incubations down to 22-m depth in analog settings in Puget Sound and studying pressure effects up to 19.5 atm without finding any significant technique- or pressure-dependent differences (Pamatmat, 1971). Biological (community) oxygen consumption on the continental shelf, determined at about 8.5° C, ranged only between 1.8 and 6.9 ml m⁻² h⁻¹ in cores from seven stations in 25 to 115 m of water and showed no trend with depth over this limited range (n = 7, Spearman's r = 0.08, p > 0.5).

From conservative assumptions applied to their measurements of sulfate reduction at three stations of 85-m depth during August 1978, Christensen *et al.* (1987a) estimated that this process oxidized 3.1, 1.9 and 1.2 times as much carbon as did oxygen consumption from aerobic respiration and abiotic oxidation of reduced substances as previously measured by Pamatmat (1973) at three nearby sites; the ratio was 0.7 for a shelf-break station of 147-m depth. On the three shallow stations, the uppermost two or so centimeters presumably were metabolically most active (aerobic processes) but sulfate reduction integrated over 30-cm or more of depth in the sediment more than compensated for a low rate per unit volume of sediment. The equivalent release and flux into the overlying water column of ammonium should be high, enough to support several tens of percent of the primary production of the overlying water column where the nutrients are made available to the photic zone. Ammonium flux out of the sediment calculated from nutrient profiles, combined with considerations of radon fluxes at the same stations published by Smethie *et al.* (1981), however, amounted to only 19% of the expected rate. Instead, the seabed consumed bound nitrogen during August, owing to nitrification (oxidation of ammonium) in the sediment coupled with denitrification of nitrate fluxing in from the overlying bottom water. Christensen *et al.* (1987b) suggested that this coupling of nitrification and denitrification, with

the resulting nitrogen balance, is common on continental shelves with aerated bottom water. Also noteworthy for the observations on the Washington shelf is that irrigation by burrowing animals approximately trebled the influx of nitrate (and, presumably, of other solutes) over that due to molecular vertical diffusion (Christensen *et al.*, 1987a). The calculated 'diffuse' (approximately three-dimensional, see Christensen *et al.*, 1984) irrigation coefficient changed materially with season so that one must expect large seasonality of nutrient fluxes; Christensen *et al.* (1984) had assumed a reduction by 60% for the cool season. Christensen *et al.* (1984) also noted for the same stations that animal irrigation affected principally the depths between 2 and 10 cm in the sediments.

9.2.2 Comparison with other shelves

In view of the meager local information, extensive comparison with other shelves would be unwise. In view of the limited information on shelves worldwide, it is impossible. The paucity of information on benthos can be exemplified by the complete lack of any papers dealing with it in a 1,200-page, two-volume collection on the sedimentary record of coastal upwelling (Suess and Thiede, 1983; Thiede and Suess, 1983). Two gross kinds of comparisons can be made, however, i.e., with other shelves in upwelling regions and with shelves from non-upwelling situations.

In the upwelling-region shelves of Peru and northwestern Africa, the abundance of aerobic benthos is linked to the rate of supply of organic material to the bottom vs. the rate of supply of oxygen. The latter in turn depends on bottom water concentrations of oxygen and advective-diffusive exchange. Including the Washington-Oregon shelf, all three regions are characterized by high rates of organic-matter flux to the bottom, but differ in the supply of oxygen by bottom currents (Barber and Smith, 1981), with the Washington continental shelf being intermediate in character. Standing stocks of aerobic benthos are high off Northwest Africa (Nichols and Rowe, 1977; Thiel, 1978 and 1982) because shelf currents prevent oxygen-demanding sedimentary accumulation yet provide high fluxes of particulate material. Consequently, suspension feeders are more prevalent than on the Washington shelf. Off Peru, shelf bottom currents are the weakest of the three regions and macrofauna is absent in this anoxic bottom (Rowe, 1971); much of the sediment-water interface is covered by filamentous bacteria (Gallardo, 1977).

Passive continental margins (or more specifically coasts with too little particulate material supply to yet have filled their estuaries since deglaciation, e.g., the U.S. east coast) show little accumulation of fine material in contrast to the Washington shelf. The shelf-estuary systems of the U.S. east coast are in early stages of geologic evolution and fine materials are mostly trapped in estuaries with the remainder being swept from the shelf in winter storms. There is no appreciable mid-shelf silt after winter storms. The benthos of shelves on the east coast of the U.S. is little studied, but densities are high and variable (Frankenberg and Leiper, 1977). Episodically, high abundance is supported by phenomena such as upwelling along the west wall of the Gulf Stream (Yoder *et al.*, 1983) and much of the variability is correlated with small- and medium-scale variation in topography (e.g., Schaffner and Boesch 1982). Following apparently universal generalizations about benthos, communities are zoned by depth and correlated with

sediment type (Weston, 1988; Boesch and Bowen, in press). These generalizations hold for all shelf types classified by geological history and modern sedimentary regime (Curry, 1965; Swift, 1970): shelves with autochthonous (e.g., the east coast shelf), or allochthonous (e.g., the west coast shelf from northern California northward) and climax-graded (showing progressively finer sediments with increasing depth, e.g., south Texas, cf. Flint, 1981).

9.2.3 Organism-Sediment Relations on U.S. Pacific Northwest Shelves

Whether one is interested because of intellectual curiosity, because of importance to demersal shelf fisheries, or because of the potential for pollution impact on shelves, the interaction between shelf benthos and shelf sediments merits attention. Unravelling cause and effect in any system with tight feedbacks is a challenge. For example, productivity of the animals that demersal fishes eat may be tied to the frequency of sediment disturbance of the sediments (Rhoads *et al.*, 1978), which is difficult to quantify. Also, particulate or particle-adsorbed pollutants are most likely to enter the food web through deposit feeding.

Correlation of sediment type with community structure has in the past been interpreted as biological structure determined by geological structure. That interpretation is no longer tenable as the only possibility or even as the most likely one. As an example of the tight feedbacks in the organism-sediment system (see also papers in McCall and Tevesz, 1982), organisms can alter sedimentary structure by altering sediment erodibility (Jumars and Nowell, 1984). Therefore, part of the correlation between sedimentary structure and benthic community structure may involve a biological cause of a geological effect (see also Eckman *et al.*, 1981). DeFlaun and Mayer (1983) go so far as to suggest that bacteria cause clays to accumulate--rather than the other way around. On Pacific Northwest shelves prior to storms, organisms and their structures are likely to dominate surface roughness and therefore affect the fluid drag on the bottom within the mid-shelf silts (Cacchione *et al.*, 1983). Bioturbation and armoring of the bed by a lag layer of large grains (the so-called lag layer left behind from a heterogeneous mixture of grains when the finer ones are eroded) are now known to be strongly interactive (Butman, in preparation); during periods of high animal density and individual activity, disturbance can quickly eliminate lag layers. The sensitivity of dispersal of larvae of bottom animals to the physical characteristics of the larvae and to the local flow regime also has been recently documented (Eckman, 1983; Hannan, 1984; Butman, 1987). Thus, community structure and sediment type may correlate well in part because larvae of given species and sediments of given grain sizes have similar settling velocities rather than the grain size of the bed determining the larval choice. Finally, frequency and intensity of sediment transport determine food supply to deposit feeders (Miller *et al.*, 1984; Jumars and Self, 1986; Miller and Jumars, 1986; Miller and Sternberg, in press). Bottom boundary-layer fluid dynamics thus are likely to be strong determinants of both geological and biological structure.

Other water column-benthic interactions are also significant, in particular, the benthic regeneration of nutrients used by phytoplankton (e.g., Pilson, 1985) and the hatching of benthic resting stages of both phytoplankton (e.g., Anderson *et al.*, 1982) and zooplankton (e.g., Marcus, 1984). Benthic nutrient recycling as well as recruitment from benthic resting stages are favored

by an upwelling circulation (Hermann *et al.*, 1989, Chapter 6), so that both processes are more likely to be important on the Washington shelf than in a non-upwelling setting. Sediment transport is likely to enhance both release of benthic nutrients (Fanning *et al.*, 1982) and hatching of benthic resting stages (Anderson and Wall, 1978). Evidence of benthic nutrient regeneration is present in nutrient profiles from the Washington shelf (Dortch and Postel, 1989, Chapter 4), but so few local measurements are available on either nutrient regeneration (Pamatmat, 1973) or recruitment of plankton from resting stages that one can do little more than assert their likely importance.

9.2.4 Feeding

Although local work on feeding, physical disturbance and recruitment of benthos is hardly better developed than studies of animal-sediment relations, enough pieces of the puzzle can be visualized from work in other locations and in the laboratory to discuss the outlines of a coherent picture. The benthos of the mid and outer-shelf off Washington is dominated by motile deposit feeders (Nittrouer and Sternberg, 1981, Figs. 6 and 7). On the inner shelf, suspension feeders also comprise an appreciable fraction of total fauna. If these fauna depend very directly on the flux of particulate organic matter to the bottom, either in the form of phytoplankton cells or fecal pellets (Landry *et al.*, 1989, Chapter 1), then one would expect feeding rates, pools of storage products, somatic growth and fitness to reflect and lag only slightly (by days or weeks) the pattern of primary production (Perry *et al.*, 1989, Chapter 3) on this shelf. Major responses would occur during the summer upwelling season. In the extreme view, there should be little organic material of any food value left by the time the late fall and winter storm season arrives. We know this view to be wrong in its most extreme, however, because of the prevalence of subsurface deposit feeders in the mid-shelf silts (Nittrouer and Sternberg, 1981, Figs. 6 and 7).

A complicating factor in the rate of supply of food to sedentary benthos is the redistribution of sediments by physical transport processes. Transport can enhance the size of the pool of organic matter available to any sedentary animal (Miller *et al.*, 1984) and stimulate bacterial production in sediments (Findlay *et al.*, 1985). If animals depend for their food supply on this redistribution or stimulation, then one would expect to see positive faunal responses (accrued storage products, somatic growth and increased fitness) to transport events. As opposed to the intertidal zone (Miller, 1985; Jumars and Self, 1986; Miller and Sternberg, in press) redistribution of sediment via wave action is not a daily occurrence on the mid-shelf. Kachel and Smith (1989, Chapter 8) estimate that waves capable of moving sediments at 100-m depth off Washington occur 14% of the time and are strongly concentrated in the winter storm season. Also, feeding-rate depression in both surface (Miller and Jumars, 1986) and subsurface (Fuller *et al.*, in press) deposit feeders from shallow water has been observed when fecal material is allowed to accrue for a few hours. If this phenomenon extends to shelf faunas, then feeding rate enhancement may take place during and shortly after storms. Again, whether such rapid feeding bouts occur and whether they are important in the energetics of the individuals involved remain to be seen. A related issue is whether microbes and non-living organic coatings will be significantly abraded from sediments during transport events. Evidence from the intertidal zone, where trans-

port is a daily occurrence, suggests that effects of storms on attached microbes are minimal (Miller, 1985 and in review). The infrequency of sediment transport at shelf depths may, however, make a larger fraction of the attached microbial flora susceptible to abrasive removal.

A particularly interesting occurrence that may help to evaluate the importance of sediment redistribution is the occasional arrival of Antarctic swells capable of moving bottom sediments during the (local) non-storm season. Because of the weak low frequency currents in this season (Kachel and Smith, 1989, Chapter 8), such events are ineffectual in moving bottom sediments over large scales. They certainly can redistribute sediments over the scale of tens or hundreds of individual feeding ambits (Miller *et al.*, 1984), however, and generate sufficient disturbance to affect microbial populations.

Animals experiencing daily- or tidally-repeating cycles of sediment transport often show switching from deposit to suspension feeding and back again in response to suspended loads (e.g., Taghon *et al.*, 1980; Dauer *et al.*, 1981; Muschenheim, 1987). The selective pressure to engage in such switching should be reduced in an environment where physical resuspension is much less frequent and predictable, such as during the spring and summer seasons in the Pacific Northwest. An added complication to feeding dynamics is that organisms would be expected to respond to the annual cycle of change in sediment grain size. At one site just landward of the Washington mid-shelf silt, for example, sediment composition varies from 20% silt and clay in summer to < 1% in winter, with median grain diameter shifting from 90 μm to 290 μm (Nittrouer, 1978).

Kachel and Smith (1989, Chapter 8) convincingly argue that redistribution routes and rates of transport of particles should vary with their settling velocities, more precisely with their Rouse numbers. Since organic content and sediment grain size are inversely correlated and since even fairly large organic particles or aggregates will have low settling velocities (Rouse numbers), then one might expect transport of food materials to follow isobaths and resuspended food particles to move on the order of 10-100 km per year northward (cf. Kachel and Smith, 1989, Chapter 8). Further, at the crudest level, organic matter tends to fall into one of two types, labile and refractory, characterized by different first-order rate constants for decomposition (Westrich and Berner, 1984). The effects of increased labile organic matter inputs from the Columbia River (due both to import and nutrient-caused enhancement of local phytoplankton production) in its immediate vicinity are readily observed as increased abundances and activities of organisms (Smethie *et al.*, 1981; Nittrouer and Sternberg, 1981). Sampling intensity northward along the mid-shelf silt has not been sufficient to resolve whether the northward-moving 'conveyor belt' of ever more refractory material also is responsible for a larger-scale gradient in organism abundance. However, there is some evidence for decreasing bioturbation rates on this broader alongshelf scale with distance northward from the Columbia river (Carpenter and Peterson, 1989, Chapter 10). Thus, the along-isobath transport of organic matter in the mid-shelf silts may display in the horizontal on very large scales, what would, in the absence of horizontal transport be limited to very small-scale vertical gradients.

9.2.5 Disturbance, Dispersal and Recruitment

Disturbances more frequent than the generation time must be accommodated via functional responses, while less frequent disturbances cause population fluctuations (Southwood, 1981). What makes the continental shelf benthos an interesting test case for such hypotheses is the lack of obvious abiotic disturbance other than sediment transport (here counting settling of organic matter from upwelling events as a biotic disturbance). In contrast to intertidal settings, the frequency, intensity and spatial scale of disturbance are quite readily predictable from time series measurements and transport models (Kachel and Smith, 1989, Chapter 8). What is virtually unknown, however, is organism response. The best time series of population abundance and size composition for shelf species come from deep sites in the comparatively protected environment of Puget Sound (Nichols, 1975, 1985), where sediment transport from wave-current interaction is lacking. Such a time series could be used as an experimental control for studies of re-suspension effects on biota dwelling on the shelf.

Field data from the literature allow a spectrum of opinion regarding the importance of transport events as disturbance agents. Clearly from lifestyle and life history studies, faunas are adapted evolutionarily to the local transport regime (Purdy, 1964; Jumars and Fauchald, 1977; Maurer and Leathem, 1981). That extreme transport events do produce mortality of macrofauna nonetheless is undeniable (Lammens, 1967; Eagle, 1975; Rees *et al.*, 1976). The issue is further complicated by the fact that sediment transport also has an immigration or emigration role because animals as well as sediments are transported (Grant, 1981; Dobbs and Vozarik, 1983; Veer *et al.*, 1985). Consequently, apparent mortality (disappearance) due to sediment transport may be no more than lateral displacement, lateral displacement may or may not cause reduction in fitness or induce mortality and sediment transport may be an important term in the recovery (immigration) equation.

There are virtually no observations of organisms under realistically simulated conditions of sediment erosion, deposition and transport and the few that do exist (Nowell *et al.*, in press) place past experiments on burial effects in serious doubt. Most experiments have buried animals impulsively under a given depth of sediments in aquaria with comparatively still water, while natural burial by bedload is a grain-by-grain process, as is burial by sedimentation from suspension in a gradually waning transport event. Oxygen stress is less likely a problem under grain-by-grain deposition and natural fluid dynamics and animal digging rates are less likely to be exceeded. Also, sediment transport is dominated by horizontal velocities. Therefore, it is difficult to interpret results of mesocosm simulations of sediment transport produced by an up-and-down oscillating plunger (Oviatt *et al.*, 1981). The results of Oviatt *et al.* (1981), suggesting benthos insensitivity to burial, are in marked contrast, for example, to those of Brenchley (1981). Both the taxa and the simulations are different, however, making the reason for the differences obscure.

There is no doubt that animals which experience daily bedload transport show striking behavioral adaptations (Nowell *et al.*, in press). What is unclear is whether the low frequency (less than daily) of sediment transport at mid-shelf depths will result in strong functional re-

sponses. The effects of erosion and deposition might be expected to be most severe in the in-shore silt-to-sand transition zone. Because zone shifts occur on a seasonal basis, any sessile organism will experience an annual cycle of changing grain size (Nittrouer, 1978). Again because of the frequency issue, it is unclear whether the animal responses will be behavioral or at a population level.

Large, deep-burrowing infauna are not expected to be seriously affected (in terms of transport or mortality) by large storm events. Numerous large *Brisaster* that have weathered major storms (judging from the age-size relation in this species observed in Puget Sound, cf. Nichols, 1975) are seen on the continental shelf off northern California (Cacchione *et al.*, 1983; Nichols, submitted) in an even more severe wave climate (Cacchione *et al.*, 1987) than that prevailing off Washington. It is not clear what fraction of the benthic fauna and microbes on the Washington shelf will be disturbed by either the major (about 3 cm of sediment eroded and redeposited at 100-m water depth, mean recurrence time about 9.4 y) or minor (about 3 mm reworked at 100-m depth, mean recurrence time about 1.8 y) transport events (estimates from Kachel and Smith, 1989, Chapter 8).

Recent work (Palmer, 1986 and references therein) suggests that meiofauna may often be transported passively along with sediments of similar settling velocity. A large wave-current event removes a net volume of 6.2×10^6 m³ of sediments from the shelf between the Columbia River and Quinault Canyon (Kachel and Smith, 1989, Chapter 8). If only 10% of the meiofauna were carried along (conservatively assuming 20 cm^{-3} meiofaunal specimens in the surficial sediments from which meiofauna were eroded), such an event would expatriate about 10^{13} meiofaunal individuals. Local (Oregon shelf) evidence that meiofauna is redistributed by winter storms comes from observed homogenization of the small-scale horizontal distributions (Hogue and Miller, 1981; Hogue, 1982). Hogue (1982) further found a marked faunal boundary in nematode species composition at 25-m water depth, which appears from bottom photographic evidence to be a depth below which wave disturbance becomes much less frequent. His conclusion regarding the cause for this faunal change also is supported by morphological adaptations in the shallower-zone species, apparently for gaining or retaining purchase on the grains surrounding interstices.

If, in any of the above contexts, sediment transport events make resources available (Thistle, 1981) either by inducing mortality (reducing demand) or stimulating microbial production and redistributing it (increasing effective supply), then the large spatial extent of the shelf affected during storm events would argue for the efficacy of planktonic larvae in exploiting those resources. An interesting but as yet undocumented strategy would be to have larval dispersal coincide with the late fall/winter transport season. Besides affording the usual benefits of dispersal (Strathmann, 1974), such a strategy could serve as insurance against adult mortality due to erosion and deposition. Conversely, adults that release larvae after the winter storm season must have effective protection from these sediment transport events.

Kachel and Smith's results (1989, Chapter 8) have other implications for larval transport. The recent hypothesis of passively spread larvae, has already passed several successful tests

(Eckman, 1983; Hannan, 1984; Jackson and Strathmann, 1981; Banse, 1986). While the Kachel and Smith model has little sediment transport interest outside the storm season (because sediments do not move extensively then), it may have considerable application to larval dispersal in other seasons. If larval dispersal occurs during winter, one would expect to see the same sorting and divergence of paths among larvae of varying settling velocities as is seen among sediments of differing grain sizes.

9.3 CONCLUSION AND PROSPECTUS

There has never been a shelf study with sufficiently closely coupled measurements of sediment transport and benthic biological response to explore their relationship in any detail. For many reasons, a shelf with allochthonous sediments, particularly with mid-shelf silt deposits of the U.S. Pacific Northwest from Point Reyes north, is a logical choice for initiating such investigations. It is well studied from the sediment transport perspective (Kachel and Smith, 1989, Chapter 8). Topography is simple, without large bedforms on the mid-shelf, minimizing field measurement problems. Sources (rivers) and sinks (slopes and canyons) of sediments are known. Pulses of organic-matter input from upwelling processes (spring to early fall) are well separated in time from major sediment transport events (late fall to early spring), making responses to them easy to identify without confusion. From the applied perspective, the mid-shelf silts are the site of major demersal fisheries. The three-dimensional, helical circulation of upwelling (Barber and Smith, 1981, Fig. 14) centered over the mid-shelf silts provides a large-scale chromatography column, with sinking fecal pellets and the bottom as the (more or less) stationary phase; hydrophobic pollutants will be concentrated in the mid-shelf silts, where deposit feeders abound. A need to know (Carpenter and Peterson, 1989, Chapter 10) and experimental tractability rarely coincide so well.

ACKNOWLEDGEMENTS

Much of the field work and the subsequent evaluation reviewed here was made possible by extended support from the U.S. Department of Energy and its predecessor, contract DE-AT06-76-EV-75026. Further, we gratefully record partial support for the manuscript preparation by grant No. 86-08157 from the National Science Foundation to P.A. Jumars and A.R.M. Nowell and grant No. NAGW-1007 from the National Aeronautics and Space Administration to K. Banse. The patient help of S. Fagerberg is also acknowledged. This is a component of contribution No. 1784 from the School of Oceanography, University of Washington.

REFERENCES

- Anderson, D.M. and D. Wall. 1978. The potential importance of benthic cysts of *Gonyaulax tamarensis* and *Gonyaulax excavata* in initiating toxic dinoflagellate blooms. *J. Phycol.*, 14: 224-234.
- Anderson, D.M., D.G. Aubrey, M.A. Tyler and D.W. Coats. 1982. Vertical and horizontal distributions of dinoflagellate cysts in sediments. *Limnol. Oceanogr.*, 27: 757-765.
- Banse, K. 1986. Vertical distribution and horizontal transport of planktonic larvae of echinoderms and benthic polychaetes in an open coastal sea. *Bull. Mar. Sci.*, 39: 162-175.

- Barber, R.T. and R.L. Smith. 1981. Coastal upwelling systems. Pages 31-58 in: A. Longhurst (ed.), *Analysis of Marine Ecosystems*. Academic Press, New York, N.Y.
- Boesch, D.F. and M.A. Bowen. In press. Bathymetric distribution of assemblages of macrobenthos in the Middle Atlantic Bight, U.S.A. *Mar. Biol.*
- Brenchley, G.A. 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-sediment environments. *J. Mar. Res.*, 39: 767-790.
- Buchanan, J.B. and J.J. Moore. 1986. Long-term studies at a benthic station off the coast of Northumberland. *Hydrobiologia*, 142: 12-127.
- Butman, C.A. 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol. Ann. Rev.*, 25: 113-165.
- Cacchione, D.A., D.E. Drake, W.D. Grant, A.J. Williams, III and G.B. Tate. 1983. Variability of sea-floor roughness within the Coastal Ocean Dynamics Experiment (CODE) region. Woods Hole Oceanogr. Inst., Woods Hole, Mass., Tech. Rep. WHOI-83-25, 44 pp.
- Cacchione, D.A., W.D. Grant, D.E. Drake and S.M. Glenn. 1987. Storm-dominated bottom boundary layer dynamics on the northern California continental shelf: measurements and predictions. *J. Geophys. Res.*, 92: 1817-1827.
- Carey, A.G., Jr. 1972. Ecological observations on the benthic invertebrates from the central Oregon continental shelf. Pages 422-443 in: A.T. Pruter and D.L. Alverson (eds.), *The Columbia River Estuary and Adjacent Ocean Waters: Bioenvironmental Studies*. Univ. of Washington Press, Seattle, Wa.
- Carpenter, R. and M.L. Peterson. 1989. Chemical cycling in Washington's coastal zone. Pages 366-510 in: M.L. Landry and B.M. Hickey (eds.), *Coastal Oceanography of Washington and Oregon*. Elsevier, Amsterdam, Neth.
- Christensen, J.P., A.H. Devol and W.M. Smethie, Jr. 1984. Biological enhancement of solute exchange between sediments and bottom water on the Washington continental shelf. *Cont. Shelf Res.*, 3: 9-23.
- Christensen, J.P., W.M. Smethie, Jr. and A.H. Devol. 1987a. Benthic nutrient regeneration and denitrification on the Washington continental shelf. *Deep-Sea Res.*, 34: 1027-1047.
- Christensen, J.P., J.W. Murray, A.H. Devol and L.A. Codispoti. 1987b. Denitrification in continental shelf sediments has a major impact on the oceanic nitrogen budget. *Global Biogeochem. Cycles*, 1: 97-116.
- Curray, J.R. 1965. Late Quaternary history, continental shelves of the United States. Pages 723-735 in: H.E. Wright, Jr. and D.G. Frey (eds.), *The Quaternary of the United States*. Princeton Univ. Press, Princeton, N.J.
- Dauer, D.M., C.A. Maybury and R.M. Ewing. 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.*, 54: 21-38.
- DeFlaun, M.F. and L.M. Mayer. 1983. Relationships between bacteria and grain surfaces in intertidal sediments. *Limnol. Oceanogr.*, 28: 873-881.
- Dobbs, F.C. and J.M. Vozarik. 1983. Immediate effects of a storm on coastal infauna. *Mar. Ecol. Progr. Ser.*, 11: 273-279.
- Dortch, Q. and J.R. Postel. 1989. Phytoplankton-nitrogen interactions. Pages 139-174 in: M.L. Landry and B.M. Hickey (eds.), *Coastal Oceanography of Washington and Oregon*. Elsevier, Amsterdam, Neth.

- Eagle, R.A. 1975. Natural fluctuations in a soft bottom benthic community. *J. Mar. Biol. Assoc. U.K.*, 55: 865-878.
- Eckman, J.E. 1983. Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.*, 28: 241-257.
- Eckman, J.E., A.R.M. Nowell and P.A. Jumars. 1981. Sediment destabilization by animal tubes. *J. Mar. Res.*, 39: 361-374.
- Fanning, K.A., C.L. Carder and P.R. Betzer. 1982. Sediment resuspension by coastal waters: a potential mechanism for nutrient re-cycling on the ocean's margins. *Deep-Sea Res.*, 29: 953-965.
- Findlay, R.H., P.C. Pollard, D.J.W. Moriarty and D.C. White. 1985. Quantitative determination of microbial activity and community nutritional status in estuarine sediment: evidence for a disturbance artifact. *Can. J. Microbiol.*, 31: 493-498.
- Flint, R.W. 1981. Gulf of Mexico outer-continental shelf benthos: macroinfaunal-environmental relationships. *Biol. Oceanogr.*, 1: 135-155.
- Frankenberg, D. and A.S. Leiper. 1977. Seasonal cycles in benthic communities of the Georgia continental shelf. Pages 383-397 in: B.C. Coull (ed.), *Ecology of marine benthos*. Univ. of South Carolina Press, Columbia, S.C.
- Fuller, C.M., C.A. Butman and N.M. Conway. In press. Periodicity in fecal pellet production by the capitellid polychaete, *Mediomastus ambiseta*, throughout the day. Proc. 2nd Int. Polychaete Conf., Copenhagen, Aug. 1986.
- Gallardo, V.F. 1977. Large benthic microbial communities in sulphide biota under Peru-Chile subsurface countercurrent. *Nature*, 268: 331-332.
- Grant, J. 1981. Sediment transport and disturbance on an intertidal sandflat: epifaunal distribution and recolonization. *Mar. Ecol. Progr. Ser.*, 6: 249-255.
- Grover, J.J. and B.L. Olla. 1987. Effects of an El Niño event on the food habits of larval sablefish, *Anoplopoma fimbria*, off Oregon and Washington. *Fishery Bull., U.S.*, 85: 71-79.
- Hannan, C.A. 1984. Planktonic larvae may act like passive particles in turbulent near-bottom flows. *Limnol. Oceanogr.*, 29: 1108-1116.
- Hogue, E.W. 1982. Sediment disturbance and the spatial distributions of shallow water meiobenthic nematodes on the open Oregon coast. *J. Mar. Res.*, 40: 551-573.
- Hogue, E.W. and A.G. Carey, Jr. 1982. Feeding ecology of 0-age flatfishes at a nursery ground on the Oregon coast. *Fishery Bull.*, 80: 555-565.
- Hogue, E.W. and C.B. Miller. 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. *J. Exp. Mar. Biol. Ecol.*, 53: 181-191.
- Jackson, G.A. and R.R. Strathmann. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. *Am. Nat.*, 118: 16-26.
- Jumars, P.A. and K. Fauchald. 1977. Between-community contrasts in successful polychaete feeding strategies. Pages 1-20 in: B.C. Coull (ed.), *Ecology of Marine Benthos*. Univ. of South Carolina Press, Columbia, S.C.
- Jumars, P.A. and A.R.M. Nowell. 1984. Effects of benthos on sediment transport: difficulties with functional grouping. *Cont. Shelf Res.* 3: 115-130.
-

- Jumars, P.A. and R.F.L. Self. 1986. Gut-marker and gut-fullness methods for estimating field and laboratory effects of sediment transport on deposit feeders. *J. Exp. Mar. Biol. Ecol.*, 98: 293-310.
- Kachel, N.B. and J.D. Smith. 1989. Sediment transport and Deposition. Pages 287-348 in: M.L. Landry and B.M. Hickey (eds.), *Coastal Oceanography of Washington and Oregon*. Elsevier, Amsterdam, Neth.
- Lammens, J.J. 1967. Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). *Neth. J. Sea Res.*, 3: 315-382.
- Landry, M.R., J. R. Postel, W.K. Peterson and J. Newman. 1989. Broad scale patterns in the distribution of hydrographic variables. Pages 1-40 in: M.L. Landry and B.M. Hickey (eds.), *Coastal Oceanography of Washington and Oregon*. Elsevier, Amsterdam, Neth.
- Lie, U. 1969. Standing crop of benthic infauna in and off the coast of Washington. *J. Fish. Res. Bd. Canada*, 26: 55-62.
- Lie, U. and J.C. Kelley. 1970. Benthic infauna communities off the coast of Washington and in Puget Sound: identification and distribution of the communities. *J. Fish. Res. Bd. Canada*, 27: 621-651.
- Lie, U. and D.S. Kisker. 1970. Species composition and structure of benthic infauna communities off the coast of Washington. *J. Fish. Res. Bd. Canada*, 27: 2273-2285.
- Marcus, N.H. 1984. Recruitment of copepod nauplii into the plankton: importance of diapause eggs and benthic processes. *Mar. Ecol. Progr. Ser.*, 15: 47-54.
- Maurer, D. and W. Leathem. 1981. Polychaete feeding guilds from Georges Bank, U.S.A. *Mar. Biol.* 62: 161-171.
- McCall, P.L. and M.J.S. Tevesz (eds.). 1982. *Animal-Sediment Relations*. Plenum Press, New York, N.Y., 336 pp.
- Miller, D.C. 1985. Interactions of marine sediment transport with deposit feeding and microbial growth. Ph.D. Diss., School of Oceanogr., Univ. of Washington, Seattle, Wa., 156 pp.
- Miller, D.C. and P.A. Jumars. 1986. Pellet accumulation, sediment supply and crowding as determinants of surface deposit-feeding rate in *Pseudopolydora kempii japonica* Imajima and Hartman (Polychaeta: Spionidae). *J. Exp. Mar. Biol. Ecol.*, 99: 1-17.
- Miller, D.C., P.A. Jumars and A.R.M. Nowell. 1984. Effects of sediment transport on deposit feeding: scaling arguments. *Limnol. Oceanogr.*, 29: 1202-1217.
- Miller, D.C. and R.W. Sternberg. In press. The fluid and sediment dynamic environment of an intertidal deposit feeder. *J. Mar. Res.*
- Muschenheim, D. 1987. The dynamics of near-bed seston flux and suspension-feeding benthos. *J. Mar. Res.*, 45: 57-82.
- Nichols, F.H. 1975. Dynamics and energetics of three deposit-feeding benthic invertebrate populations in Puget Sound, Washington. *Ecol. Monogr.*, 45: 57-82.
- Nichols, F.H. 1985. Abundance fluctuations among benthic invertebrates in two Pacific estuaries. *Estuaries*, 8: 136-144.
- Nichols, J. and G.T. Rowe. 1977. Infaunal macrobenthos off Cape Blanc, Spanish Sahara. *J. Mar. Res.*, 35: 525-536.

- Nittrouer, C.A. 1978. The process of detrital sediment accumulation in a continental shelf environment: an examination of the Washington shelf. Ph.D. Diss., Dept. of Oceanogr., Univ. of Washington, Seattle, Wa., 243 pp.
- Nittrouer, C.A. and R.W. Sternberg. 1981. The formation of sedimentary strata in an allochthonous shelf environment: the Washington continental shelf. *Mar. Geol.*, 42: 201-232.
- Nowell, A.R.M., P.A. Jumars, R.F.L. Self and J.D. Southard. In press. Bedload transport effects on infauna. In: G.R. Lopez and G.L. Taghon (eds.), *Marine Deposit Feeding*. Springer-Verlag, New York, N.Y.
- Oviatt, C.A., C.D. Hunt, G.A. Vargo and K.W. Kopchynski. 1981. Simulation of a storm event in marine mesocosms. *J. Mar. Res.*, 39: 605-626.
- Paine, R.T. 1986. Benthic community-water column coupling during the 1982-1983 El Niño. Are community changes at high latitudes attributable to cause or coincidence? *Limnol. Oceanogr.*, 31: 351-360.
- Palmer, M.A. 1986. Hydrodynamics and structure: interactive effects on meiofaunal dispersal. *J. Exp. Mar. Biol. Ecol.*, 104: 53-68.
- Pamatmat, M.M. 1971. Oxygen consumption by the sea bed. VI. Seasonal cycle of chemical oxidation and respiration in Puget Sound. *Int. Rev. ges. Hydrobiol.*, 56: 769-793.
- Pamatmat, M.M. 1973. Benthic community metabolism on the continental terrace and in the deep sea in the North Pacific. *Int. Rev. ges. Hydrobiol.*, 58: 345-368.
- Pearcy, W.G. and D. Hancock. 1978. Feeding habits of Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; slender sole, *Lyopsetta exilis*; and Pacific sanddab, *Citharichthys sordidus*, in a region of diverse sediments and bathymetry off Oregon. *Fishery Bull., U.S.*, 76: 641-651.
- Pearson, T.H., G. Duncan and J. Nuttall. 1986. Long term changes in benthic communities of Loch Linnhe and Loch Eil (Scotland). *Hydrobiologia*, 142: 113-119.
- Perry, M.J., J.P. Bolger and D. English. 1989. Primary Production. Pages 117-138 in: M.L. Landry and B.M. Hickey (eds.), *Coastal Oceanography of Washington and Oregon*. Elsevier, Amsterdam, Neth.
- Pilson, M.E.Q. 1985. Annual cycles of nutrients and chlorophyll in Narragansett Bay, Rhode Island. *J. Mar. Res.*, 43: 849-873.
- Pruter, A.T. and D.L. Alverson (eds.). 1972. *The Columbia River Estuary and Adjacent Ocean Waters*. Univ. of Washington Press, Seattle, Wa., 868 pp.
- Purdy, E.G. 1964. Sediments as substrates. Pages 238-271 in: J. Imbrie and N.D. Newell (eds.), *Approaches to Paleoecology*. Wiley, New York, N.Y.
- Rees, E.I.S., A. Nicholaidou and P. Laskaridou. 1976. The effects of storms on the dynamics of shallow water benthic associations. Pages 465-474 in: B.F. Keegan, P.O. Ceidigh and P.J.S. Boaden (eds.), *Biology of Benthic Organisms*. Pergamon Press, Oxford.
- Rhoads, D.C., P.L. McCall and J.Y. Yingst. 1978. Disturbance and production on the estuarine sea floor. *Am. Sci.*, 66: 577-586.
- Rowe, G.T. 1971. Benthic biomass in the Pisco, Peru upwelling. *Invest. Pesq.*, 35: 127-135.
- Schaffner, L.C. and D.F. Boesch. 1982. Spatial and temporal resource use by dominant benthic Amphipoda (*Ampeliscidae* and *Corophiidae*) on the Middle Atlantic Bight outer-continental shelf. *Mar. Ecol. Progr. Ser.*, 9: 231-243.
-

- Smethie, W.M., Jr., C.A. Nittrouer and R.F.L. Self. 1981. The use of radon-222 as a tracer of sediment irrigation and mixing on the Washington continental shelf. *Mar. Geol.*, 42: 173-200.
- Southwood, T.R.E. 1981. Bionomic strategies and population parameters. Pages 30-52 in: R.M. May (ed.), *Theoretical Ecology*. 2nd ed, Sinauer, Sunderland, Mass.
- Strathmann, R.R. 1974. The spread of sibling larvae of sedentary marine invertebrates. *Am. Nat.*, 108: 29-44.
- Suess, E. and J. Thiede (eds.). 1983. *Coastal Upwelling: Its Sedimentary Record. Part A: Responses of the Sedimentary Regime to Present Coastal Upwelling*. Plenum Press, New York, N.Y., 604 pp.
- Swift, D.J.P. 1970. Quaternary shelves and the return to grade. *Mar. Geol.*, 8: 5-30.
- Taghon, G.L., A.R.M. Nowell and P.A. Jumars. 1980. Induction of suspension feeding in spionid polychaetes by high particulate fluxes. *Science*, 210: 562-564.
- Thiede, J. and E. Suess (eds.). 1983. *Coastal upwelling: Its Sedimentary Record. Part B: Sedimentary Records of Ancient Coastal Upwelling*. Plenum Press, New York, N.Y., 610 pp.
- Thiel, H.J. 1978. Benthos in upwelling regions. Pages 124-138 in: R. Boje and M. Tomczak (eds.), *Upwelling Ecosystems*. Springer-Verlag, Berlin.
- Thiel, H.J. 1982. Zoobenthos of the CINECA area and other upwelling regions. *Rapp. P.-v. Cons. int. Explor. Mer.*, 180: 323-334.
- Thistle, D. 1981. Natural physical disturbance and communities of marine soft bottoms. *Mar. Ecol. Progr. Ser.*, 6: 223-228.
- Veer, H.W. van der, M.J.N. Bergman and J.J. Beukema. 1985. Dredging activities in the Dutch Wadden Sea: Effects on macrobenthic fauna. *Neth. J. Sea Res.*, 19: 183-190.
- Weston, D.P. 1988. Macrobenthos-sediment relationships on the continental shelf off Cape Hatteras, North Carolina. *Cont. Shelf Res.*, 8: 267-286.
- Westrich, J.T. and R.A. Berner. 1984. The role of sedimentary organic matter in bacterial sulfate reduction: the G model tested. *Limnol. Oceanogr.*, 29: 236-249.
- Yoder, J.A., L.P. Atkinson, S.S. Bishop, E.E. Hofmann and T.N. Lee. 1983. Effect of upwelling on phytoplankton productivity of the outer-southeastern United States continental shelf. *Cont. Shelf Res.*, 1: 385-404.