Animal Sediment Relationships Revisited – Cause Versus Effect

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ANIMAL–SEDIMENT RELATIONSHIPS REVISITED: CAUSE VERSUS EFFECT*

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Abstract Over the last few decades, many studies have correlated infaunal invertebrate distributions with sediment grain size, leading to the generalization of distinct associations between animals and specific sediment types. When these data are compiled and reviewed critically, however, animal–sediment relationships are much more variable than traditionally purported. There is, in fact, little evidence that sedimentary grain size alone is the primary determinant of infaunal species distributions. In addition to observed variability in animal–sediment relationships, a clear mechanism by which grain size *per se* limits distributions has not been demonstrated. Furthermore, sediment grain size has usually been determined on completely disaggregated samples which may have little relevance to what an organism actually encounters in nature. Likewise, patterns have been documented using primarily sediment and biological samples that were not integrated over the same vertical scales within the bed, or on samples that were integrated over much larger vertical scales than those relevant to most organisms. Thus, the grain-size distributions described for a given habitat may be very different from those within the ambit of the organism. In addition to grain size, other proposed causative factors include organic content, microbial content, food supply and trophic interactions, but no single mechanism has been able to explain patterns observed across many different environments.

One common generalization is that deposit-feeders are more abundant in muddy habitats and suspension-feeders dominate sandy habitats. A predominant hypothesis to explain this pattern is that suspension-feeders are excluded from muddy habitats by amensalistic interactions with deposit-feeders. In most studies that tested or evaluated trophic-group amensalism, however, the hypothesis generally became qualified to such a degree that it was no longer meaningful. Critical re-examination of data on animal–sediment relationships suggests, in fact, that many species are not always associated with a single sediment type, and that suspension- and deposit-feeders often co-occur in large numbers. Furthermore, a number of species alter their trophic mode in response to flow and food flux conditions; therefore, the simple dichotomy between suspension- and deposit-feeding is no longer valid.

The complexity of soft-sediment communities may defy any simple paradigm relating to any single factor, and we propose a shift in focus towards understanding relationships between organism distributions and the dynamic sedimentary and hydrodynamic environment. Grain size covaries with sedimentary organic matter content, pore-water chemistry, and microbial abundance and composition, all of which are influenced by the near-bed flow regime. These variables could directly or indirectly influence infaunal distributions via several compelling

mechanisms. Moreover, because the sedimentary environment in a given area is, to a large extent, the direct result of near-bed flow conditions, factors such as larval supply and particulate flux that are similarly determined by the boundary-layer flow may be particularly important determinants of species distributions. It is unlikely that any one of these factors alone can explain patterns of distribution across all sedimentary habitats; however, meaningful and predictive relationships are more likely to emerge once the influence of these dynamic variables is examined systematically in controlled experiments.

Much of the early research on animal–sediment relationships was conducted at a time when it was technologically and conceptually infeasible to evaluate and manipulate many relevant aspects of the hydrodynamic and sediment-transport regime, which correlate directly with, and are responsible for, sediment distributions, as well as factors such as food supply and larval supply, which may correspond with sediment distributions. Most studies of animal–sediment associations were conducted when the complex inter-relationships among these variables was poorly understood. Recent major advances in measuring or simulating (i.e. in laboratory flumes) critical aspects of the dynamic sedimentary environment and in understanding relationships among hydrodynamics, sediment transport and benthic biology have created an entirely new framework for studying animal–sediment interactions. Sorely needed are laboratory and field measurements and experiments that utilize this new technology, capitalize on the emerging interdisciplinary focus of research in the oceans, and test specific, innovative hypotheses concerning animal distributions and their environment.

Introduction

The relationship between the distribution of infaunal invertebrate species and the sediments in which they reside has been the subject of numerous correlative studies, some experimental manipulations, and several syntheses and reviews during the three or so decades since Thorson (1957) developed the concept of "parallel level-bottom communities". A universally predictive and cogent explanation for observed "animal–sediment relationships" has not yet, however, stood firmly the test of time. This may reflect fundamental deficiencies in the conceptualization of the issues and relevant scales, limitations in the quality or quantity of the data, including the paucity of experimental studies, or simply the inherent complexity of a system that may defy a simple paradigm. This review addresses these alternatives in the spirit of the opening statements of Hutchinson's (1953) address to the Academy of Natural Sciences of Philadelphia on "The Concept of Pattern in Ecology":

> In any general discussion of structure, relating to an isolated part of the universe, we are faced with an initial difficulty in having no *a priori* criteria as to the amount of structure it is reasonable to expect. We do not, therefore, always know, until we have had a great deal of empirical experience, whether a given example of structure is very extraordinary, or a mere trivial expression of something which we may learn to expect all the time.

Indeed, the significance of animal–sediment associations is difficult to evaluate because the mechanism(s) determining the distributions of organisms are so poorly understood. The growing appreciation of the influence of bottom boundary-layer flow and related dynamic processes on benthic communities (Nowell & Jumars 1984, C. A. Butman 1987, Miller & Sternberg 1988, Palmer 1988a), and the contemporary view of hydrodynamics and sediment-transport processes in general (e.g. Nowell 1983, Grant & Madsen 1986, B. Butman 1987a, b, Cacchione & Drake 1990) warrant a re-examination of the information on animal–sediment relationships.

This review evaluates whether the data exist to support the generalization of distinct animal–sediment relationships and examines critically the experimental evidence for the mechanism(s) that may produce such associations. In contrast to conclusions of previous reviews (Purdy 1964, Gray 1974, 1981, Rhoads 1974, Pérès 1982, Probert 1984), this review finds little evidence that animal distributions are determined by any of the classical parameters of grain size, organic content, micro-organisms and sediment "stability" alone. The major conclusion of this review is that more meaningful and predictive explanations for infaunal distributions may well emerge if, in addition to experimental evaluation of traditional sediment and biological factors, organism distributions are evaluated relative to the hydrodynamic and sediment-transport processes that are responsible for sediment distributions (Jumars & Nowell 1984b).

Some definitions and caveats

In this review "infauna" are defined to include those benthic invertebrates that live largely within the sediment bed, including animals traditionally referred to as "macrofauna" (i.e. those animals retained on 500- or 300-μm sieves) and "meiofauna" (i.e. those animals that are smaller than macrofauna but are retained on a 63-μm sieve), although our own interests in macrofaunal biology are certainly reflected in the studies selected. This review is not exhaustive; it is unconscionable to include in a single review all relevant benthic ecological studies that directly or indirectly address animal–sediment relationships. Thus, only those studies most central to the theme of animal–sediment relationships are included here. Not included, for example, is the vast pollution literature and studies on hard-substratum fauna. Because of logistics, the review is limited largely to literature on animal–sediment relationships that is written in English. We hope the review is not badly biased by our North American perspective.

In this paper the potential rôle of biological interactions (e.g. competition and predation) in determining infaunal distributions is not reviewed specifically, but there is no doubt that distributions of many soft-sediment invertebrates are influenced (sometimes greatly) by other species (see review by Wilson 1991). The emphasis here is placed largely on abiotic factors because species interactions do not necessarily explain how animal–sediment associations are initiated. For example, a species may occur only in sandy sediments because another species out-competes it elsewhere, leaving unexplained why the dominant competitor does not occur in sands. Thus, at some level, animal–sediment relationships are likely to be important. Furthermore, abiotic factors such as fluid flow and sediment transport can also determine how and if an organism colonizes a given habitat, and initial colonization obviously precedes subsequent interactions among recruits. Nonetheless, biological interactions in infaunal community structure are important, but because this topic was recently reviewed by Wilson (1991) it would be redundant to do so again here.

Evidence for distinct associations between infauna and sediments

An historical perspective

The formal study of animal–sediment associations began with the classification of bottom communities based on dominant species by Petersen (1913), who noted that communities

differed among bottom types. Greater importance was placed on bottom sediments by Ford (1923), who suggested that substratum was a key factor contributing to community differences, and Davis (1925), who suggested that grain-size groupings could be used to predict dominant taxa. Synthesizing existing data on communities from the North Sea, Jones (1950) placed "communities" and "zones" into specific sediment types, noting that differences in the supply of detritus and organism mobility might contribute to observed patterns. Still, when Thorson (1957) synthesized the data available on infaunal distributions, developing the concept of "parallel level-bottom communities", very few studies included quantitative information on the sediments (e.g. grain-size distributions) in which the organisms were collected (some exceptions include Ford 1923, Spärck 1933, Stephen 1933, Thorson & Ussing 1934, Holme 1949). In fact, it was the dual effect of Thorson's (1957) generalizations and Sanders's (1958) observation that different infaunal feeding types tended to dominate sandy versus muddy sediments that prompted the plethora of subsequent studies of the relationship between distributions of infauna and sediments (Table 1). Although a variety of collecting and processing techniques were used, the premise and goals of these studies were similar – to describe patterns of distribution and, in most instances, to suggest an underlying mechanism to account for such distributions.

The mechanism proposed by Sanders (1958) to account for observed associations between infauna and sediments was that differences in food supply resulted in the domination of sandy habitats by suspension-feeders and muddy habitats by deposit-feeders. Data forming the basis for Sanders's (1958) and most subsequent hypotheses concerning animal–sediment relationships consist of comparisons between bulk sediment characteristics (usually the grain-size distribution integrated over the top few centimetres) and densities of dominant species, both documented over spatial scales of metres to kilometres (Table 1). Of the most commonly cited studies on animal–sediment relationships (see Table 1), most show at least some sort of relationship between faunal distribution and sediment type.

These descriptive studies have represented an important advance in understanding soft-sediment communities, particularly in providing an atlas of animal distributions from shallow-water habitats in many different areas of the world (Table 1). As a first step towards understanding why organisms live where they do, information on the distribution of organisms is vital; descriptive and correlative data cannot explain, however, why these distributions exist. They should, instead, form the foundation for guiding research directions on mechanistic relationships responsible for animal–sediment associations. What is perhaps most striking about the studies summarized in Table 1 is that so few provide strong evidence of causality; most studies are correlative, and sediment type is a covariate of other causative variables, for example Jansson's (1967b) concept of grain size as a "super parameter". Results and conclusions of these studies must be re-evaluated within the context of current understanding of life histories and habits of benthic invertebrates under realistic field conditions, particularly with reference to larval settlement and infaunal feeding ecology, and how these factors are related to the transport of bottom sediments and the boundary-layer flow regime.

A contemporary view

A major difficulty in interpreting most of the previously collected information on animal–sediment associations is that grain size alone is not an adequate descriptor of the sedimentary environment, due to the complex nature of bottom sediments (Johnson 1974, 1977,

Table 1 Benthic studies on animal–sediment associations in marine habitats. Studies that did not specifically compare animal distributions to bottom type in some way are not included. "Not given" does not suggest analysis was not performed; it indicates that methodology was not described. Studies were chosen to be representative and the table is not exhaustive in coverage. Question marks in the table denote instances where information was vague and some inference was necessary. [1] Correlation denotes direct correlational analyses as well as ordination and classification techniques where sediment and biological samples were independently grouped based on composition and then compared. In many studies no statistical comparison was made and the term "correlation" describes an implied association based on "correlative" sampling of organisms and sediment. [2] Although not stated as such in the original studies, we believe these studies used roughly comparable methodologies for grain-size analysis.

Area	Sediment types	Species	Association/ Analysis[1]	Comments	Sampling gear	Vertical integration	Grain size[2]/ Carbon	Reference
Danish coast	Sand to mud	Community	Yes/ Correlative	Strong groupings described as statistical, not biological units	Petersen grab, trawls	3 cm or greater	Visual/ Kjeldahl 1891	Petersen 1913
Plymouth, UK	Sand to mud	Community	Yes/ Correlative	Petersen type groupings though some species not sediment specific	Petersen grab?	3cm or greater?	Not given/ Not done	Ford 1923
East Greenland	Sand to mud	Community	Yes/ Correlative	Extended Petersen's communities but no discussion of mechanism	Petersen grab	Entire grab	Visual/ Not done	Spärck 1933
North Sea, UK	Sand to mud	Molluscs	Yes/ Correlative	Extreme sediment groupings gave good separation of communities	Petersen grab and shovel	15cm	Visual/ Not done	Stephen 1933
East Greenland	Sand to mud	Community	Yes/ Correlative	Groupings similar to 1913 study though some discrepancies	Petersen grab	3cm or greater	Visual/ Not done	Thorson & Ussing 1934
Exe Estuary, UK	Sand to mud	Community	Yes/ Correlative	Distributions related to silt content, organic carbon mentioned	Shovel?	6 inches	Piper 1942/ Not done	Holme 1949
Danish Wadden Sea	Sand to mud	Community	Yes/ Correlative	General association of most species with one bottom type	Tube core	3cm	Visual/ Not done	Smidt 1951
Narragansett Bay, USA	Sand to mud	*Mercenaria*	Yes/ Transplants	Most common in shell/rock, Faster growth in sand	Dredge	Not given	Visual/ Not done	Pratt 1953
Long Island Sound, NY, USA	Sand to mud	Community	Yes/ Correlative	No replication within site and date	Forster anchor dredge	7.6cm	Bouyoucos 1951/ Not done	Sanders 1956

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Table 1 *Continued*

Area	Sediment types	Species	Association/Analysis[1]	Comments	Sampling gear	Vertical integration	Grain size[2]/Carbon	Reference
Buzzards Bay, MA, USA	Sand to mud	Community	Yes/Correlative	No within site replication	Forster anchor dredge	7.6cm	Wet sieve and pipette[2]/Not done	Sanders 1958
West Africa	Sand to mud	Community	No/Correlative	Only a few species sediment specific	Dredges, grabs	Not given	Dry dispersed sieve[2]/Not done	Longhurst 1958
Laos Lagoon, Nigeria	Sand to mud	*Branchiostoma nigeriense*	Yes/Correlative and experimental	Trial and error sediment selection in lab. supported field pattern of sand preference	Not given	Not given	Wet sieve[2]/calcined salt	Webb & Hill 1958
Puget Sound, WA, USA	Coarse to fine sand	Community	Yes/Correlative	Suggest $200\,\mu m$ grain size a critical distribution barrier	Small beaker	Not given	Dry sieve[2]/Not done	Wieser 1959
Biscayne Bay, FL, USA	Sand to mud	Community	Yes/Correlative	Filter-feeders found in different grain sizes than Sanders'	Van Veen grabs	Entire grab?	Wet sieve and pipette[2]/Not done	McNulty et al. 1962a, b
Barnstable, MA, USA	Sand to mud	Community	No?/Correlative	Median grain size poor predictor of community composition	Various size cores	3, 8 or 30cm	Wet sieve and pipette[2]/Combustion	Sanders et al. 1962
Northumberland Sea, UK	Gravel to fine sand	Community	No/Correlative	Only a few species showed association	Van Veen grab	Entire grab?	Wet sieve and pipette[2]/Not done	Buchanan 1963
Martha's Vineyard, MA, USA	Sand to mud	Macrofauna and meiofauna	Yes and No/Correlative	Total densities of macro- and meiofauna related to substratum	Smith & McIntyre grab	4cm or entire grab	Not given/Not done	Wigley & McIntyre 1964
Auckland, New Zealand	Sand to mud?	Community	Yes/Correlative	Some species not sediment specific but little data shown in paper	Not given	5–10cm	Wet sieve[2]/Morgans 1956	Cassie & Michael 1968

Location	Sediment	Organism/Community	Relationship/Approach	Finding	Sampling gear	Sample	Sediment method/Organic method	Reference
San Juan Island. WA. USA	Grades of sand	*Leptastacus constrictus*	No/ Correlative and experimental	Field populations unrelated to organic content or bacteria but selection related to bacteria	Not given	Not given	Not done/ 2h incineration	Gray 1968
Puget Sound, WA, USA	Gravelly sand to mud	Community	Yes/ Correlative	Suggests contiguous communities as a function of sediment gradient	Van Veen grab	Entire grab	Krumbein & Pettijohn 1938[2]/ Not done	Lie 1968
Plymouth, UK	Sand to mud	Polychaetes	Yes/ Correlative	General association with grain size though several species vary widely	Perspex corer	12 cm	Morgans 1956/ Not done	Gibbs 1969
Strait of Juan de Fuca. USA	Gravel to mud	Community	Yes/ Correlative	Very extreme sediment groupings gave good separation	Van Veen grab	Entire grab	Krumbein & Pettijohn 1938[2]/ Not done	Lie & Kisker 1970
Kent coast, UK	Sand to fine mud	*Arenicola marina*	Yes/ Correlative	Association with grain size and organic content	"surface sediment samples"	Not given	Disagg. dry sieve[2]/ Morgans 1956	Longbottom 1970
Puget Sound, WA, USA	Fine to silty sand	Polychaetes	Yes/ Correlative	Clay content key variable and thus organic content	Van Veen grab	Entire grab	Dry sieve and pipette[2]/ Not done	Nichols 1970
Scotland sea-lochs, UK	Mud to gravel	Community	Yes and No/ Correlative	Suggests fjord enclosure results in saturation of bottom with larvae, blurring association	Van Veen grab	Entire grab	Dry sieve and pipette[2]/ Wet combustion	Pearson 1970, 1971
Buzzards Bay, MA, USA	Mud to sand	*Mercenaria Nucula*	Yes/ Transplant	Trophic group amensalism related to sediment type	Smith & McIntyre grab	Entire grab?	Dry sieve analyser/ Carbon analyser	Rhoads & Young 1970
Moreton Bay, Australia	Mud to sand	Community	Yes and No/ Correlative	Weakly defined site groups conform to topography	Prawn trawls	Not given	Visual/ Not done	Stephenson et al. 1970
Beaufort, NC, USA	Sand to silty sand	Community	No/ Correlative	No relation of distribution to mean particle size	Van Veen and dredge	Entire grab	Standard elutriation[2]/ Kjeldahl 1891	Day et al. 1971

Table 1 *Continued*

Area	Sediment types	Species	Association/Analysis[1]	Comments	Sampling gear	Vertical integration	Grain size[2]/Carbon	Reference
False Bay, South Africa	Grades of mud	Community	Yes/Correlative	Good association with grain size and organic content	Van Veen	Entire grab	Dry sieve[2]/Morgans 1956	Field 1971
Bideford River, P.E.I., Canada	Mud to sand	Community	No/Correlative	Only a couple of dominants sediment specific	Suction dredge	30–50cm	Wet sieve and pipette[2]/Morgans 1956	Hughes & Thomas 1971
Tomales Bay, CA, USA	Sand to mud	Community	Yes/Correlative	Good association but many species "strayed"	Van Veen grab	Entire grab	Visual/Not done	Johnson 1971
Cape Cod Bay, MA, USA	Sand to mud	Community	No/Correlative	Co-occurrence of deposit- and suspension-feeders attributed to sediment stabilization	Smith & McIntyre grab	Entire grab	Dry sieve and pipette/Leco carbon analyser	Young & Rhoads 1971
Old Tampa Bay, FL, USA	Sand to muddy sand	Community	Yes and No/Correlative	Weak correlations as support for trophic group amensalism	$0.1\,m^2$ grab	20–40cm	Wet sieve[2]/Combustion	Bloom et al. 1972
Scottish sea-lochs, UK	Sand to muddy sand	Community	Yes/Correlative	Acknowledges grain size a key correlate of hydrodynamics	Van Veen grab	Entire grab	Wet sieve and pipette[2]/Not done	Gage 1972
Sapelo Island, GA, USA	Sand and muddy sand	Community	No/Correlative	Several species dominant in both sediment types	$0.2\,m^2$ bulk sample	50cm	Sediment analyser/Not done	Howard & Dörjes 1972
St Margarets Bay, Nova Scotia	Gravel to mud	Community	No/Correlative	Acknowledge importance of currents, organics and other species	Van Veen	Entire grab	Krumbein & Pettijohn 1938[2]/Not done	Hughes et al. 1972
Hampton Roads, VA, USA	Sand to mud	Community	Yes/Correlative	Good association though different from others' results	Van Veen grab	Entire grab	Folk 1961[2]/Not done	Boesch 1973

Location	Sediment	Taxon	Correlation	Findings	Sampling gear	Fraction	Method	Reference
Liverpool Bay, UK	Sand and muddy sand	Community	Yes and No/ Correlative	Ratios differ but many species common in both habitats	Smith & McIntyre grab, beam trawls	Entire grab	Wet sieve and pipette[2]/ Strickland & Parsons 1968	Eagle 1973
Discovery Bay, Jamaica	Grades of sand	Community	No/ Correlative	Found absence of deposit-feeders in sandy habitats	31 cm core	20–25 cm	Wet sieve[2]/ Not done	Aller & Dodge 1974
Bristol Channel, UK	Sand to mud	Community	Yes/ Correlative	Admit sediment affiliation not very specific	Smith & McIntyre grab, dredge	Entire grab	Sonar and visual/ Not done	Warwick & Davies 1977
Chesapeake Bay, MD, USA	Shell & sand to mud	Community	Yes/ Correlative	No obvious relation between trophic mode and sediment type	Forster anchor dredge	Entire grab	Buchanan & Kain 1971[2]/ Not done	Mountford et al. 1977
Bristol Channel, UK	Gravelly to muddy sand	Ophiuroids	No/ Correlative	Poor correlation between adult density and sediment parameters	Shipek grab	Entire grab	Folk 1961[2]/ Oxidation	Tyler & Banner 1977
Barnstable, MA, USA	Sandy gravel to mud	Community	Yes/ Correlative	Grain size better predictor than in Sanders et al. 1962 study	12.5 cm core	Entire core	Wet sieve[2]/ Morgans 1956	Whitlatch 1977
Northumberland coast, UK	Sand to silty sand	Community	Yes/ Correlative	Association with silt but long-term changes in dominants	Van Veen grab	Entire grab	Wet sieve?[2]/ Not done	Buchanan et al. 1978
Sheepscot Estuary, ME, USA	Silty sand to mud?	Community	No/ Correlative	No strong association but little range in sediment type	Ponar grab	Entire grab	Standard method[2]/ Not given	Larsen 1979
Delaware coast, USA	Gravelly sand to sandy mud	Community	Yes/ Correlative	Noted silty-sand troughs in sand environments had silty-sand fauna	Petersen grab	Entire grab	Folk 1968[2]/ % volatiles	Maurer et al. 1979
Gulf of Mexico, TX, USA	Sandy mud to mud	Community	Yes and No/ Correlative	Bottom water variability more important than sediment type	Smith & McIntyre grab	Entire grab	Particle analyser/ Not done	Flint & Holland 1980
Bristol Channel, UK	Sand to mud	Community	Yes/ Correlative	Relate tidal stress to distributions of organisms and sediment type	Smith & McIntyre grab	Entire grab	Sonar/ Not done	Warwick & Uncles 1980

Table 1 *Continued*

Area	Sediment types	Species	Association/Analysis[1]	Comments	Sampling gear	Vertical integration	Grain size[2]/Carbon	Reference
Hong Kong Harbour	Grades of mud	Community	Yes and No/ Correlative	Silt-clay good predictor but salinity better	Smith & McIntyre grab	Entire grab	Bouyoucos 1951/ Combustion	Shin & Thompson 1982
Chesapeake Bay, USA	Sand to mud	Community	Yes and No/ Correlative	Only clean sand fauna was restricted in distribution, other fauna widespread	Ponar grab	Entire grab	Dry sieve?/ Combustion	Tourtellette & Dauer 1983
Swansea Bay, UK	Sand to mud	Community	Yes/ Correlative	Suggests faunal associations predict gross changes in sediment	Day & Shipek grabs	Entire grab	Wet sieve[2]/ Not done	Shackley & Collins 1984
South Carolina, USA	Sand and mud	Meiofauna	Yes/ Correlative	Timing and magnitude of abundances varied greatly between sites	Cores	1 to 2 cm	Folk 1968[2]/ Wet oxidation	Coull 1985
Chesapeake Bay, USA	Sand to mud	Community	Yes/ Correlative	Many species widely distributed but different dominants	Several types of grabs	Entire grab	Not given/ Not given	Holland 1985
East China Sea	Sand to mud	Community	Yes/ Correlative	Good associations with sediment, sedimentation also important	Spade-boxcorers & Petersen grabs	Entire grab	X-radiographs/ Not done	Rhoads et al. 1985
Gulf of St Lawrence, Canada	Gravel sand to mud	Community	Yes/ Correlative	Good correlation with feeding type	Van Veen grab	Entire grab	Particle analyser/ Not done	Long & Lewis 1987
Georges Bank, USA	Sand to mud	Community	Yes/ Correlative	Verbally describe different faunas in mud and sand but no statistics	Smith & McIntyre grab	Entire grab	Particle analyser/ Not done	Theroux & Grosslein 1987

Location	Sediment			Findings	Sampler	Depth	Grain size / organic method	Reference
North Carolina, USA	Grades of sand	Community	Yes/ Correlative	Various sediment parameters related to distributions, food supply cited	Smith & McIntyre grab	Entire grab	Dry sieve[2]/ Not done	Weston 1988
Northern North Sea	Sand to silt	Community	Yes/ Correlative	Depth, grain size and carbon said to determine distributions	Smith & McIntyre grab	Entire grab	Dry sieve[2]/ Wet oxidation	Eleftheriou & Basford 1989
Oppa Bay, Japan	Sand to mud	Community	Yes/ Correlative	Good correlation with sediment grain size, organic content	Smith & McIntyre grab	Entire grab	Particle analyser/ CHN analyser	Ishikawa 1989
Northwest Spain	Sand to mud	Community	Yes and No/ Correlative	Some mixing of station clusters for different sediment types	Shovel?	30 cm	Not given/ Not given	Junoy & Viéitez 1990
North Sea	Sand to muddy-sand	Community	Yes/ Correlative	Suggest different fauna in sediments related to local production, deposition, stress	Grabs and boxcorers	Entire grab	Not given/ Not done	Duineveld et al. 1991
California, USA	Sandy-mud to mud	Community	Yes/ Correlative	Oxygen and depth more important but percentage of sand also useful	Hessler-Sandia box corer	10 cm	Not given/ Not given	Hyland et al. 1991
Western Mediterranean	Sand to mud	Community	Yes/ Correlative	Granulometry strongly related with many species' distributions	Corers	8–20 cm	Not given/ Not given	Palacín et al. 1991
Great Barrier Reef	Sand to silt	Community	Yes/ Correlative	Detrital loading well correlated with distributions	0.027 m[2] Boxcorers	10 cm	Folk 1974[2]/ CHN analyser	Alongi & Christoffersen 1992
South Carolina, USA	Sand and mud	Community	Yes/ Correlative	Sand and mud faunas differed, with more burrowers in mud	Hand-held corers	5–10 cm	Visual?/ Not done	Service & Feller 1992
Arcachon Bay, France	Coarse to fine sand	Community	Yes and No/ Correlative	Tide and salinity important but many station faunas hard to group	0.25 m[2] Boxcorers	30 cm	Wet sieve[2]/ Combustion	Bachelet & Dauvin 1993
Perdido Key, FL, USA	Medium to fine sand	Community	Yes/ Correlative	Depth, grain size and turbulence delimit species distributions	0.016 m[2] Boxcorers	20–25 cm	Folk 1974[2]/ Not done	Rakocinski et al. 1993

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Whitlatch & Johnson 1974, Jumars & Nowell 1984a, Watling 1988) and associated boundary-layer flow and sediment-transport regimes (Komar 1976a, b, Nowell 1983, Nowell & Jumars 1984, Grant & Madsen 1986). In fact, sediment grain size correlates with a number of potential causative factors (discussed later, p. 150), which may explain why, in some cases, grain size is a poor correlate of benthic community composition (Table 1). *Nephthys/Nucula* communities in Buzzards Bay, Massachusetts, for example, occur in sediments with a substantially higher silt+clay (hereafter called "mud") content than similar communities in Long Island Sound, New York (Buchanan 1963). Even within Sanders's (1958) Buzzards Bay study area, mixed trophic assemblages were observed in some sediments containing similar proportions of mud as those sediments where deposit-feeders dominated. These examples suggest that grain size is correlated with poorly identified causative variable(s) such that the relationship between grain size and species distribution is at least partially indirect.

Likewise, because of an increasing appreciation for the rôle of boundary-layer flow and sediment transport in benthic ecology, an understanding of the ways in which infaunal organisms interact with sediments and the near-bed flow regime is undergoing a transformation. For example, most natural history information has been derived from observations of organisms in still water; such observations are now known to present an incomplete picture of the flow-dependent feeding behaviour of many infauna that have been tested under hydrodynamic and sediment-transport conditions that occur in the field (Taghon et al. 1980, Muschenheim 1987a, Grizzle & Morin 1989, Nowell et al. 1989, Brandon 1991, Turner & Miller 1991a, b, Miller et al. 1992, Taghon & Greene 1992). Thus, many species may switch from suspension- to deposit-feeding as flow conditions change (discussed at length later, p. 151).

In this paper, first we critically review studies of the relationship between infaunal distributions and the grain size, organic content, bacteria and algae, and "stability" (including amensalistic interactions) of sediments, subject areas that were treated in past reviews and overviews on this subject (Gray 1974, 1981, Rhoads 1974, Pérès 1982, Probert 1984). These aspects of sediments are not mutually exclusive; we use these groupings for historical reasons and emphasize the relationships among these sediment "characteristics" wherever possible. We then review existing data on two infaunal species (the bivalve *Mercenaria mercenaria* and the polychaete *Owenia fusiformis*) which we have chosen to illustrate how even relatively well-studied species have distributions that are not well understood. Next, processes responsible for surficial sediment distributions are discussed to provide background concerning the dynamic nature of benthic ecosystems and to evaluate the ways in which flow, sediment transport and related processes may affect benthic organisms. Infaunal distributions are then evaluated relative to the dynamic variables that may covary with sediment type, including flow regime, larval supply and food supply. We conclude with a brief discussion of the kinds of experiments and sampling which may be useful in clarifying issues that previous correlative studies simply could not address.

Aspects of sediments to which animals may respond

Grain size

Although numerous studies are cited in support of the notion that infaunal distributions are correlated with sediment grain size (Table 1), most studies provide little insight regarding

the mechanism(s) responsible for such associations. Furthermore, associations between animals and grain-size distributions generally have been evaluated using somewhat subjective criteria, such as comparisons of species lists among sediment habitats (Petersen 1913, Spärck 1933, McNulty et al. 1962a, b, Young & Rhoads 1971), community trellis diagrams (Sanders 1958, Sanders et al. 1962, Bloom et al. 1972) and classification analysis (Pearson 1970, Stephenson et al. 1970, Eagle 1973, Ishikawa 1989). The subjectivity of many earlier studies may have contributed to the varying strength of animal–sediment associations that different investigators reported; however, even analyses that provide some form of statistical evaluation of the strength of association, such as ordination (Cassie & Michael 1968, Hughes & Thomas 1971, Flint & Holland 1980) or correlation (Bloom et al. 1972), have found strong relationships in some instances (e.g. Nichols 1970, Ishikawa 1989, Palacín et al. 1991) but not others (Hughes & Thomas 1971, Bloom et al. 1972, Flint & Holland 1980). In general, these studies have shown that there are many species that are characteristically associated with a given sedimentary habitat, although their distributions are rarely confined to that environment. Some species show little affinity with any one particular sediment type, and the faunas within different sediment environments invariably show some degree of overlap. One explanation for these inconsistencies is that grain size may be a correlate of the actual causative factor(s).

Sediment sampling has often failed to reflect the vertical position of fauna of different trophic groups within the sediment bed. For example, grain-size distributions were invariably determined on sediments integrated over at least the top several centimetres (Table 1). These homogenized samples may be deceptive in sediments that have different grain-size distributions at different depths (Rhoads & Stanley 1965, Grant & Butman 1987). Thus, grain sizes encountered by organisms within a given stratum may be poorly represented by vertically integrated sediment samples (Hughes & Thomas 1971, Grehen 1990). Vertical partitioning of organisms in sediments is known to occur (Mangum 1964, Rhoads 1967, Boaden & Platt 1971, Whitlatch 1980, Joint et al. 1982, Palmer & Molloy 1986) and surficial sediments available to surface deposit-feeders, for example, may differ considerably in grain-size distribution and carbon content from sediments scavenged at depth in the bed by subsurface, "conveyor-belt" species (Mangum 1964, Rhoads 1967, Fauchald & Jumars 1979). Furthermore, standard grain-size analysis has always involved disintegration of natural aggregates. Samples collected for grain-size distributions have usually been processed using a dispersant to disintegrate natural aggregates, such as faecal pellets, into primary sediment particles (Folk 1968). Resulting grain-size distributions may not be meaningful if the animals respond to natural, intact aggregates, rather than to primary (i.e. disaggregated) sediment particles (Jumars & Nowell 1984a, b, Fuller & Butman 1988).

The most compelling evidence that grain size may directly influence species distributions comes from small-scale (millimetres to centimetres), still-water, laboratory experiments on larval settlement. Some echinoid larvae did not settle (Mortensen 1921, 1938) and some polychaete larvae delayed metamorphosis (Wilson 1932, 1936, 1951, Day & Wilson 1934) until exposed to sand or, for one species, muddy sand (Wilson, 1937). In other laboratory experiments (Table 2; see also Table V in C. A. Butman 1987) larvae or adults were given a choice of sediment treatments in small dishes and, for the most part, the organisms selected sediment that most closely resembled the natural adult habitat (see reviews by Gray 1974, Scheltema 1974). When the choices were restricted to different grain-size classes, larvae of several species of infaunal invertebrates (Wilson 1948, 1952, Gray 1967a) and several species of mobile adults (Wieser 1956, Webb & Hill 1958, Williams 1958, Meadows 1964a) showed selectivity for a particular size class (Table 2). These experiments strongly suggest

Table 2 Summary table of soft sediment, substratum selection experiments. Experiments on gregarious settlement are not included.

Still water or flow?	Substratum choice	Larvae or adults?	Species	Selection? Expected choice?	Conclusions	Reference
Still water	Sand present or absent	Larvae	*Mellita sexies perforata*	Yes Yes	Sand presence needed to metamorphose	Mortensen 1921
Still water	Sand to mud	Larvae	*Owenia fusiformis*	Yes Yes	No data, but metamorphose only in fine sand, not mud	Wilson 1932
Still water	Sand to mud	Larvae	*Scolecolepis fuliginosa*	Yes Yes	Faster settling in high organic muddy sand	Day & Wilson 1934
Still water	Sand present or absent	Larvae	*Prionocidaris baculosa* *Fromia ghardaquana*	Yes Yes Yes Yes	Settlement in sand but mechanism unknown As above	Mortensen 1938
Still water	"Detritus film" present or absent	Larvae	*Melinna cristata*	Yes Yes	Require non-sterile substratum to metamorphose	Nyholm 1950
Still water	Mud, sand, pebbles	Larvae	*Pygospio elegans*	No	Settlement on all substrata but not sterile sand	Smidt 1951
Still water			*Polydora (ligni?)*	No	As above but some settlement on sterile sand	
Still water	Silty sand present or absent	Larvae	*Phoronis mulleri*	Yes Yes	Needs "adult" habitat sand to metamorphose	Silén 1954
Still water	Treated sands	Larvae	*Ophelia bicornis*	Yes Yes	Microbes must be present on sand for selection	Wilson 1955
Still water	Grades of sand	Adults	*Cumella vulgaris*	Yes Yes	Attracted to aged medium sediment. Food cue implied	Wieser 1956
Still water	Sand to mud	Larvae	*Uca pugilator*	Yes Yes	Selected sand above water line	Teal 1958
Still water		Larvae	*Uca minax*	Yes Yes	Selected mud above and below water line	

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Medium	Sediment	Stage	Species			Observations	Reference
Still water	Coarse sand to silty sand	Larvae	*Uca pugnex*	Yes	Yes	Selected mud above and below water line	
Still water	Coarse sand to silty sand	Adults	*Branchiostoma nigeriense*	Yes	Yes	Attracted to sand of intermediate grain size	Webb & Hill 1958
Still water	Sand to sandy mud	Adults	*Penaeus duorarum*	Yes	Yes	Attracted to shell sand	Williams 1958
		Adults	*Penaeus aztecus*	Yes	Yes	Attracted to muddy sand, sandy mud, and loose peat	
		Adults	*Penaeus setiferus*	Yes	Yes	Attracted to muddy sand, sandy mud, and loose peat	
Still water	Coarse and fine sand	Larvae	*Nassarius obsoletus*	Yes	Yes	Higher metamorphosis in coarse sand. No contact needed	Scheltema 1961
Still water	Treated sands and muds	Adults	*Corophium volutator*	Yes	Yes	Preferred mud but only if untreated. Unable to restore attractivity	Meadows 1964a
		Adults	*Corophium arenarium*	Yes	Yes	Preferred sand, only if untreated, otherwise as above	
Still water	Depths of mud	Adults	*Corophium volutator*	Yes	Yes	Chose muds where it could burrow fairly deeply	Meadows 1964b
Still water	Grades of sand	Adults	*Protodrilus symbioticus*	Yes	Yes	Attractant was specific bacteria, related to grain size	Gray 1966
Still water	Clean or silty sand	Adults	*Haustorius* sp.	Yes	Yes	Preferred clean sand as in nature	Croker 1967
		Adults	*Neohaustorius schmitzi*	Yes	Yes	As above	
		Adults	*Parahaustorius longimerus*	No		No preference. Widely distributed in nature	
		Adults	*Lepidodactylus dytiscus*	No		As above	
		Adults	*Acanthohaustorius* sp.	No		As above	
Still water	Grades of sand	Adults and larvae	*Protodrilus rubriopharyngeus*	Yes	Yes	Attracted to coarse sand, specific bacteria was cue	Gray 1967a

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Table 2 *Continued*

Still water or flow?	Substratum choice	Larvae or adults?	Species	Selection? Expected choice?	Conclusions	Reference
Still water	Grades of sand	Adults and larvae	*Protodrilus hypoleucus*	Yes Yes	Attracted to coarse sand, specific bacteria was cue	Gray 1967b
Still water	Grades of sand	Adults	*Coelogynophora schulzii monospermaticus*	No	Did not select particular grain size	Jansson 1967a
Still water	Grades of sand	Adults	*Leptastacus constrictus*	Yes Yes	Attractant was bacteria in larger grain sediments	Gray 1968
		Adults	*Aktedrilus*	No	As above	
Still water	Mud to sand	Adults	*Fabricia sabella*	No	No preference but wide natural distribution	Lewis 1968
Still water	Grades of sand	Adults	*Haustorius canadensis*	Yes Yes	Preferred coarser grains but attraction lost on combustion	Sameoto 1969
		Adults	*Neohaustorius biarticulatus*	Yes Yes	As above	
		Adults	*Acanthohaustorius millsi*	Yes Yes	Preferred medium grain sediments	
		Adults	*Parahaustorius longimerus*	Yes Yes	As above	
		Adults	*Protohaustorius deichmannae*	Yes Yes	As above	
Still water	Sands with bacteria	Adults	*Turbanella hyalina*	Yes Yes	Attracted to specific bacterial cell wall compound	Gray & Johnson 1970
Still water	Grades of sand	Adults	*Microhedyle milaschewitchii*	Yes Yes	Selected medium grain particles, bacterial settlement cue isolated	Hadl et al. 1970
Still water	Grades of sand	Adults	*Pectenogammarus planicrurus*	Yes Yes	Prefer larger grains. Cannot negotiate small interstices	Morgen 1970

Flow	Substrate	Stage	Species	Pref.	Notes	Reference
Still water	Dried sand and beads	Adults	*Eurydice pulchra*	Yes Yes	Avoids fine grain sediment. Prefers fairly coarse grain.	Jones 1970
		Adults	*Eurydice affinis*	Yes Yes	Avoids fine grain sediments. No mechanism given	
Still water	Sand/no sand	Larvae	*Mediaster aequalis*	Yes Yes	Sand required for settlement but polychaete species presence important	Birkeland et al. 1971
Still water	Grades of sand	Adults	*Scolelepis fuliginosa*	Yes Yes	Specific bacteria restored attractiveness of sand	Gray 1971
Still water	Sand to mud	Adults	*Callianassa islagrande*	Yes? Yes	No data, claim selection preference for sand — mud clogs	Phillips 1971
		Adults	*Callianassa islagrande louisianensis*	Yes? Yes	No data given but preferred mud — sand too hard to burrow	
Still water	Grades of sand	Larvae	*Ptilosarcus guerneyi*	No	Did not select on grain size but did need microbes	Chia & Crawford 1973
Still water	Mud to sand	Larvae	*Mercenaria mercenaria*	Yes Yes	Higher settlement in sand clam "liquor" treated sand	Keck et al. 1974
Still water	Mud, rock and sand	Larvae	*Homarus americanus*	No	Favoured rocky bottom, also settled well on mud	Botero & Atema 1982
Flow (crude)	Mud with sulphide varied	Larvae	*Capitella* sp. I	Yes? Yes	"Settled" where sulphides highest, but see Dubilier (1988)	Cuomo 1985
Still water	Sand and silty-sand	Larvae	*Golfingia misakiana*	No	No substratum selection but combustion reduces attraction	Rice 1986
Both	Mud and beads	Larvae	*Capitella* sp. I	Yes Yes	Select high organic mud over sand	Butman et al. 1988b
Still water	Sandy mud to sand	Adults	*Microphiopholis gracillima*	Yes Yes	Adults selected sediment they normally occur in	Zimmerman et al. 1988
Still water	Mud and beads	Larvae	*Mercenaria mercenaria*	No	No preference observed	Bachelet et al. 1992

Table 2 *Continued*

Still water or flow?	Substratum choice	Larvae or adults?	Species	Selection? Expected choice?	Conclusions	Reference
Both	Mud and beads	Larvae	*Capitella* sp. II	Yes Yes	Choice appears to be related to organic content	Grassle & Butman 1989
Both	Several choices of sediment	Larvae	*Capitella* sp. I	Yes	Selection but evidence for hydrodynamic modification	Butman & Grassle (1992)
Both	Muds, sand and beads	Larvae	*Capitella* sp. I	Yes Yes	Selection of muds over beads and sometimes sand	Grassle et al. 1992a
Both	Mud and beads	Larvae	*Mulinia lateralis*	Yes Yes	Select high organic mud more consistently in flow	Grassle et al. 1992b
Both	Mud and beads	Larvae	*Capitella* sp. I *Mulinia lateralis*	Yes Yes Yes Yes	Evidence for some hydrodynamic influence of settlement Evidence for strong hydrodynamic influence on settlement	Snelgrove et al. 1993

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that selection of habitat may operate on at least some spatial scale, and that some relatively static components of sediments may be important. There was little evidence, however, that the response was to grain size alone; the response may have been to factors associated with the grains (e.g. organic films or microbial populations; Gray 1974, Scheltema 1974) or correlated with grain-size distributions (e.g. sediment "stability"; Rhoads 1974, or the near-bed flow regime; Nowell & Jumars 1984). Indeed, in single-species, sediment-selection experiments in laboratory flume flows, larvae of the polychaetes *Capitella* sp. I (Butman et al. 1988b, Butman & Grassle 1992, Grassle et al. 1992a, Snelgrove et al. 1993) and *Capitella* sp. II (Grassle & Butman 1989) and the bivalve *Mulinia lateralis* (Grassle et al. 1992b, Snelgrove et al. 1993) settled differentially on two sediment treatments with similar grain-size distributions but with different organic contents. The sediment treatments also differed, however, in angularity and composition of the grains and in microbial populations. In field experiments using defaunated sediments in a highly dynamic estuarine environment, Zajac & Whitlatch (1982) found similar settlement in different types of sediment.

Another explanation for the association between particular species and a given sediment type is that larvae may be deposited onto the seabed as passive particles (C. A. Butman 1987). Thus, if characteristics of passive larvae and transported sediment grains (e.g. size, specific gravity, and gravitational fall velocity) are similar, then larvae and sediments could be hydrodynamically sorted in a similar manner (Hannan 1984, Butman 1989), resulting in distinct animal–sediment associations. This mechanism, which is discussed in greater detail later, explicitly accounts for correlations between infaunal and grain-size distributions, but grain size *per se* is irrelevant in producing the pattern.

Another mechanism that could result in sediment-specific species distributions is preferential ingestion or retention of specific grain sizes during feeding. Adults of a variety of deposit-feeders have been shown to ingest specific grain sizes of sediments (Hylleberg & Gallucci 1975, Whitlatch 1977, 1980, Self & Jumars 1978, 1988, Lopez & Kofoed 1980, Taghon 1982, Whitlatch & Weinberg 1982). Selective ingestion of smaller particles (e.g. Taghon 1982) is not exclusive, however, and may become less specialized in larger animals (Self & Jumars 1988). Furthermore, larger particles may be preferred by larger animals within a given species (Whitlatch & Weinberg 1982) and, likewise, newly settled larvae may be restricted to feeding on the finest material within the bed or on particularly rich food items (Jumars et al. 1990); thus, optimal grain size may be different for settling larvae and adults. The preferential ingestion of protein-coated beads over non-coated beads observed for several deposit-feeders (Taghon 1982), and the higher organic content often, although not always (Cammen 1982), associated with smaller (Longbottom 1970, Hargrave 1972, DeFlaun & Mayer 1983) and more angular (Johnson 1974, Whitlatch 1974) grains, suggests that food requirements may be the motivating factor in selective ingestion of particular grain sizes. Habitat selection based on the availability of a preferred grain size in feeding is, however, difficult to conceptualize in view of the ontogenetic and hydrodynamic changes in feeding behaviour and particle selectivity described above. A more detailed treatment of deposit-feeding as a function of sediment quality is given by Lopez & Levinton (1987) and Lopez et al. (1989).

In summary, although grain size is commonly purported to be correlated with faunal distributions, there is little evidence for a mechanism explicitly involving grain size *per se* in producing the pattern. The fact that the relationship is sometimes weak or variable from one habitat to the next (see Table 1, p. 115) suggests that other correlates may be more important. Passive deposition of settling larvae (and survival to adulthood in initial

depositional locales) is one of the most parsimonious explanations whereby sediment grain size could be a predictor of patterns of adult distribution. In this case, it is not grain size that determines the pattern, it is the boundary-layer flow and sediment-transport regime, as well as physical and behavioural characteristics of the larvae, that ultimately determine adult distributions.

Organic content

The organic content of bottom sediments may be a more likely causal factor than sediment grain size in determining infaunal distributions because organic matter in sediments is a dominant source of food for deposit-feeders and, indirectly (e.g. through resuspension), for suspension-feeders. As Sanders et al. (1962) succinctly stated, "The sediment must be considered as an indicator of the availability of food, and not as a first order factor directly determining the distribution of feeding types." Indeed, Sanders's (1958) original hypothesis was that deposit-feeders are more abundant in muddy environments because fine sediments tend to be organic-rich. It was suggested that because clays tend to bind organic matter, clay content (and thus organic carbon content) was one of the better predictors of faunal composition along the Northumberland coast of the UK (Buchanan 1963). Still, of the 67 papers on animal–sediment relationships cited in Table 1, 57 of which were published after Sanders's (1958) benchmark study, the organic carbon content of sediments was measured in fewer than half of them. This may reflect a realization by investigators that bulk carbon measurements may not accurately reflect the amount of carbon that may actually be utilized by an organism (Tenore et al. 1982, Cammen 1989, Mayer 1989, Mayer & Rice 1992). The specific components of organic matter that are of highest food value to deposit-feeders are at present an area of active research (Lopez & Levinton 1987, papers in Lopez et al. 1989, Mayer 1989, Plante et al. 1989, Carey & Mayer 1990, Mayer & Rice 1992) that is likely to add significantly to understanding and predicting animal distributions. Thus, bulk measurements of carbon in correlative studies (Table 1) may suggest avenues for future research but are unlikely to clarify how patterns of distribution are established and maintained. Nonetheless, a number of studies on animal–sediment associations (Longbottom 1970, Nichols 1970, Field 1971, Pearson 1971, Ishikawa 1989) have suggested that there is a strong relationship not only between animal and grain-size distributions but between animal and organic-carbon distributions as well.

Organic matter may limit distributions of organisms through differential settlement of larvae (or post-larvae) or differential post-larval survival. Controlled laboratory experiments on larval settlement suggest that preference for a given grain size may be related to organic content and that the pattern may be determined, at least for some species, by differential settlement rather than by post-settlement survival. A detrital coating was apparently necessary to induce settlement of ampharetid polychaetes (Nyholm 1950), and variation in sediment organic content influenced sea pen settlement (Chia & Crawford 1973). Related studies on bacteria and microalgae are summarized separately (see pp. 132–133). As discussed earlier, differences in organic carbon rather than grain size resulted in selective settlement of larvae in three species that live in organic-rich sediments as adults (Butman et al. 1988b, Butman & Grassle 1992, Grassle et al. 1992a, b); however, settlement was non-selective for a species with low habitat affinity as adults (Bachelet et al. 1992). In field studies, several deposit-feeding, opportunistic species have been shown to colonize preferentially organic-rich sediments over non-enriched sediments with a comparable grain

size in shallow-water (Grassle et al. 1985) and deep-sea (Snelgrove et al. 1992) environments.

Perhaps the most compelling evidence that the supply of organic matter influences infaunal distributions comes from community-level, pollution studies (reviewed by Pearson & Rosenberg 1978, Gray et al. 1990, and others), which have documented dramatic faunal changes resulting from coastal eutrophication. These studies have identified a suite of species that often show dramatic responses to organic loading (either by decreasing or increasing in abundance), and clearly show that supply of organic matter is important. In some instances, increases in the organic content of sediments do not always result in similar faunal changes, and this may be a result, in part, of confounding factors such as toxic compounds, sedimentation, and changes in oxygen availability. In one study where eutrophication occurred as a result of fish farming, and was therefore not confounded by the presence of toxins, faunal changes were observed in the immediate vicinity of the farm where sediments had increased organic matter (Weston 1990). Pollution studies are not reviewed here, but given the complexity and present level of understanding of animal–sediment associations, we suggest caution in interpreting pollution studies that generate predictive equations based on assumed relationships between trophic composition, grain-size distribution, and pollution effects (e.g. Satsmadjis 1982, 1985, Maurer et al. 1991).

The way in which organisms are able to utilize different types of organic matter is a complex issue (Lopez & Levinton 1987) and organic matter may take many different forms (Johnson 1974, Whitlatch & Johnson 1974, Mayer 1989). Indeed, as Johnson (1974) stated two decades ago, "The standard methods of describing sediment are inadequate for under-standing animal–sediment relations and geological processes", and this is still largely true today. Furthermore, different forms of organic matter may be utilized in very different ways (Tenore et al. 1982). For example, harpacticoid copepods may partition "fresh" and "aged" detritus within the sediment, leading to differences in vertical distribution of certain taxa within the sediment (Rudnick 1989). Thus, age of carbon, as well as its source, may determine how it is utilized.

A good example of well-controlled experiments on the rôle of organic matter as a food source is the recent study of Taghon & Greene (1992). They tested the hypothesis that switching from deposit-feeding to suspension-feeding for two infaunal polychaete species was energetically profitable because suspended particles have greater food value in terms of mass-specific concentrations of total organic matter, organic carbon, labile protein, nitrogen, and chlorophyll *a*. In these laboratory flume experiments, both species fed at significantly lower volumetric rates when suspension-feeding (evidently because of the increased food gain per unit time when suspension-feeding) than when deposit-feeding. Only one of the two closely related species, however, grew as well or better on the suspended material — a biological response that is counter-intuitive and underscores the complex relationships among feeding physiology, the nature of food, and rate of food supply.

Aside from the issue of quality of organic matter, there is some controversy over whether deposit-feeders utilize primarily detritus or the microbes attached to it (Levinton 1979, Cammen 1989), with a larger body of literature suggesting that most detritus is not utilized (Newell 1965, Fenchel 1970, Hargrave 1970, Lopez et al. 1977). This may be a function of detrital composition, however, because some organic matter may be more readily digestible by deposit-feeders (Findlay & Tenore 1982), perhaps in part because of the interacting effects of food quality, ciliate fragmentation of detritus, and bacterial activity (Briggs *et al.*, 1979). Several other studies have suggested that microbial carbon alone may be insufficient to support infaunal communities (Tunnicliffe & Risk 1977, Cammen et al. 1978).

A number of deposit-feeders living in muddy sediments will suspension-feed in response

to suspended sediment flux (Taghon et al. 1980, Levinton 1991), and some species once thought to be suspension-feeders actually utilize deposited sediment as well (Mills 1967, Tenore et al. 1968, Hughes 1969). Thus, generalizing about feeding mode and sediment organic content is probably premature. Because obligate suspension-feeders generally depend more on flux of organic matter than on sedimented material, measurements of static amounts of organic matter in sediments is likely to relate only indirectly to species' distributions. Distributions are more likely related to flow regime, which in turn is related to sediment type (discussed below, p. 146) and thus organic content.

Clearly, many infaunal organisms respond to organic matter, both actively and passively, and as larvae, juveniles, and adults. Current issues concerning the quality, as well as the quantity, of organic matter as food for both deposit- and suspension-feeders, plasticity in feeding mode, the specificity of feeding types to sediment types, and boundary-layer flow regime as a covariate of sediment type (discussed further later, p. 146) render premature the development of a unifying principle regarding the organic content of sediments as the causal factor determining patterns of infaunal distributions.

Micro-organisms (including bacteria and microalgae)

The relatively large surface area of fine sediments undoubtedly contributes to the higher microbial abundance observed in fine relative to coarse sediments (Newell 1965, Cammen 1982, Yamamoto & Lopez 1985), and infaunal response to microbial populations could result in specific animal–sediment relationships. Growth rates of the microbial food of deposit-feeders may also depend on grain size (Taghon et al. 1978, Doyle 1979, Cammen 1982), perhaps through effects of porosity on nutrient flux through the sediment (Bianchi & Rice 1988).

Depending on the organisms involved and the source of organic matter, microbial populations may be the dominant source of nutrition for deposit-feeders living in muddy sediments. It has been suggested that some infaunal species, such as the polychaete *Nereis succinea*, obtain a portion of their nutrition from microbes and the remainder from plant detritus (Cammen 1980). Other species, such as *Capitella "capitata"*, may utilize microbes on refractory plant detritus such as marsh grass, but rely more on plant detritus itself when it is easily digestible (Findlay & Tenore 1982). Elevated bacterial activity and growth in the faeces of benthic detritivores (Newell 1965, Fenchel 1970, 1972, Hargrave 1970, Juniper 1981) may quickly replenish a depleted food resource; selective pressure would, however, tend to favour foraging strategies that minimize the probability of re-ingestion of fresh (i.e., microbially depleted) faeces (Miller et al. 1984, Miller & Jumars 1986), as demonstrated also for the deposit-feeding polychaete *Amphicteis scaphobranchiata* (Nowell et al. 1984).

Deposit-feeders living in sandy environments, however, can probably satisfy only a minor portion of their nutritional requirements with sedimentary bacteria alone (Plante et al. 1989). Low microbial biomass is well documented in sandy sediments (Meadows & Anderson 1968, Steele & Baird 1968, Steele et al. 1970, Weise & Rheinheimer 1978, Jonge 1985, Jonge & van der Bergs 1987) and has been attributed to abrasion effects in this highly dynamic sediment-transport environment (Munro et al. 1978, DeFlaun & Mayer 1983, Miller 1989). Thus, the microbial content of sands is probably not important as a food source, but this does not necessarily suggest that the microbial flora of sand is unimportant to colonizing fauna.

A number of studies have suggested that microbial biomass in marine sediments influences

the distribution of adult infauna. Laboratory experiments, for example, indicate that meiofauna respond to differences in bacterial availability (Gray 1966, 1967a, 1968). Field population densities of the gastrotrich *Turbanella hyalina* were correlated with a bacterial species having a particular type of cell wall, and still-water selection experiments suggested that the gastrotrichs actively selected sediments containing this bacterium (Gray & Johnson 1970). Harpacticoid copepods have also been shown to respond actively to microbial enrichment in field experiments (Kern & Taghon 1986), and partitioning of bacterial and phototrophic resources is important in the coexistence of three species of benthic copepods (two harpacticoids and one cyclopoid) (Carman & Thistle 1985). Several meiofaunal species have been shown to respond to microbially enriched sediments in field and laboratory experiments (Kern 1990), the proposed mechanism being differential migration following passive deposition.

Biological structures in sediments, such as tubes and seagrass shoots, enhance the local boundary shear stress and fluid flux to the bed (Eckman & Nowell 1984). Enhanced nutrient flux apparently leads to increased bacterial biomass near the structure (Eckman 1985) resulting, for example, in a local increase of harpacticoid copepod densities (Thistle et al. 1984). A mechanism involving enhanced nutrient availability may also explain observations of elevated bacterial and metazoan densities around burrows (Hylleberg 1975, Aller & Aller 1986, Reise 1987). Moreover, stimulation of microbial growth by feeding and irrigation ("microbial gardening") may be a mechanism by which deposit-feeders increase their own food supply (Hylleberg 1975, Miller et al. 1984, Grossmann & Reichardt 1991). Finally, the presence of micro-organisms, rather than a given physical characteristic of the sediment, has been shown to induce larval settlement in several infaunal species (Smidt 1951, Wilson 1955, Scheltema 1961, Gray 1967a; see also reviews by Gray 1974, Scheltema 1974).

Thus, the microbial community is a very important aspect of bottom sediments, particularly as a food supply to deposit-feeders in muds, and has been shown to influence infaunal distributions. In a more detailed review of the rôle of microbes as food for deposit-feeders, Lopez & Levinton (1987) conclude, however, that only in intertidal mudflats, where benthic microalgae are extremely abundant (Cammen 1982), would microbial food alone satisfy nutritional requirements. Moreover, microbial activity is only a crude correlate of sediment type and recent studies of interactions between microbial growth and deposit-feeders (Jumars & Wheatcroft 1989, Plante et al. 1989, 1990), as well as boundary-layer flow and sediment-transport effects on microbial populations (Miller et al. 1984, Grant et al. 1986a, b, Grant & Gust 1987, Miller 1989, Dade et al. 1990), suggest that understanding the factors that control the distribution, growth rates, and biomass of sediment micro-organisms will continue to be an important and complex subject of future studies.

"Stability" and amensalism

Sediment "stability" has been defined in a number of different ways throughout the years. In benthic ecology, the concept may have been launched by Fager's (1964) observation that an unusually dense assemblage of the tube-building polychaete *Owenia fusiformis* and the burrowing anemone *Zaolutus actius* "had a profound stabilising effect on the bottom sediment" in a shallow, sandy region of La Jolla Bay, California. Physical evidence for a local, stabilized substratum within this sandflat was the lack of ripple formation or resuspension in the worm-tube bed. Biological evidence of stabilization included presence of other animals that "would appear to require a stable substrate" and that did not occur

elsewhere on the sandflat, as well as growth of a diatom film normally found at deeper depths where there was considerably less wave surge activity. Fager (1964) did not speculate on the mechanism by which the bed was stabilized, but recent laboratory flume experiments suggest that stabilization was probably due to mucous-binding of the sediments, rather than to a purely hydrodynamic "skimming flow" effect (Eckman et al. 1981, Eckman 1985). Numerous field studies (Galtsoff 1964, Mills 1967, Young & Rhoads 1971, Daro & Polk 1973, Bailey-Brock 1979, McCall & Fisher 1980) document similar observations of dense concentrations of a variety of surface-evident biological structures, such as seagrass shoots and animal tubes, that purportedly produce sediment-stabilizing effects similar to, although perhaps not as dramatic as, those observed by Fager (1964). None of these studies, however, delineated the objective or quantitative criteria by which "stability" was assessed (*sensu* Nowell et al. 1981, Grant et al. 1982, Jumars & Nowell 1984a).

It was the experimental field study of Rhoads & Young (1970), and their novel interpretation of their results in terms of "amensalistic interactions" (discussed below) that introduced to benthic ecology the concepts of classifying sediments as "stable" or "unstable" and benthic assemblages as "stabilising" or "destabilising". Based on the premise that deposit-feeders tend to dominate muddy sediments and suspension-feeders tend to dominate sandy sediments, Rhoads & Young (1970) proposed that sediment reworking by deposit-feeders in muddy sediments increases resuspension and thus excludes suspension-feeders by inhibiting filtering activity and burying larvae. They called this the "trophic group amensalism" hypothesis. Like Sanders (1958) and Sanders et al. (1962), Rhoads & Young (1970) argued that deposit-feeders are poorly represented in sandy areas because of an inadequate food supply due to the high rates of horizontal sediment flux (advantageous for suspension-feeders) and low rates of deposition of organic matter. Support provided by Rhoads & Young (1970) for trophic group amensalism in Buzzards Bay, Massachusetts were observations of increased water content and erodibility of sediments reworked by deposit-feeders, and reduced growth rates of the suspension-feeding bivalve *Mercenaria mercenaria* when transplanted close to the bottom in a muddy habitat.

Rhoads & Young's field study represented one of the first attempts to determine experimentally the underlying mechanism for observed animal–sediment associations. Their study had a profound influence on the field of benthic ecology, and was a major force in bringing manipulative field experimentation into soft-sediment ecosystems. Surprisingly, however, subsequent studies motivated by results of Rhoads & Young were still largely correlative — that is, even more concentrated efforts to quantify animal distributions in relation to sediment characteristics. Thus, Rhoads & Young's (1970) important experiments largely resulted in acceptance and "reconfirmation" of amensalism through correlative sampling, rather than stimulating critical experimentation to test specific hypotheses. This was particularly unfortunate because of several major shortcomings in the original study. For example, they provided no direct evidence for the burial of larvae of suspension-feeders in muddy sediments, or of food limitation of deposit-feeders in sandy sites. Furthermore, Dayton & Oliver (1980) later pointed out that whereas growth rates of *M. mercenaria* were lower in Rhoads & Young's (1970) transplants just above the muddy bottom compared with transplants suspended higher in the water column, the near-bottom animals still had growth rates similar to those of animals in the sandy controls. Dayton & Oliver (1980) suggested that enhanced growth with distance above the muddy bottom may be due to higher rates of horizontal food flux because flow speed increases with distance above the bed.

The concept of classifying organisms in "functional groups" was refined and developed

further in Rhoads's (1974) review, but there are a number of legitimate criticisms of this concept, including the following.

(a) There is very little evidence (discussed earlier) for the generalization that deposit-feeders are restricted largely to muddy sediments and suspension-feeders to sandy sediments. Furthermore, given recent observations of feeding and mobility of infauna under realistic flow and sediment-transport regimes (discussed in detail below), categorizing infaunal organisms into simple functional groups such as deposit- or suspension-feeders, irrespective of the hydrodynamic and sediment-transport regime, is no longer meaningful. Sanders (1958), for example, originally suggested that almost 66% of the individuals in his typical "sand community" were suspension-feeders and over 80% of the fauna in his typical "mud community" were deposit-feeders. Using up-dated information on the feeding biology of his characteristic species (Table 3), we find that approximately 64% of the dominant infauna (those species representing >1% of total infauna, which is approximately 48% of total individuals) in the mud community were deposit-feeders. The sand community, however, contained 65% deposit-feeders and only about 12% suspension-feeders (of the species that represent >1% of total infauna, which is 46% of total individuals). Furthermore, of the 12 dominant taxa characterizing Sanders's sandy habitats, only two are now unequivocally accepted as obligate feeders on suspended material.

There are other studies correlating trophic groups with sediment type that have, in our estimation, also found no clear relationship. Pearson (1971), for example, divided fauna into a number of groups, including suspension-feeders, surface deposit-feeders and "deposit-swallowers", and found a significant positive correlation between surface deposit-feeders and the silt content of the sediment. There were no significant correlations, however, between suspension-feeders or "deposit-swallowers", and any of the sediment parameters that he measured. In the study of Bloom et al. (1972), densities of suspension- and deposit-feeders were not significantly correlated with mean particle size of the habitat. The density of deposit-feeders was significantly negatively correlated with the density of suspension-feeders, but the correlation was weak ($r = -0.41$). A stronger negative correlation was observed between percentage of the total fauna that were suspension- compared with deposit-feeders ($r = -0.825$), but this is to be expected because the sums of the percentages of these two feeding types must be close to one. Another example of co-occurring deposit- and suspension-feeders is Peterson's (1977) study of infaunal communities in Mugu Lagoon, California, where although suspension-feeders were five of the six numerically abundant species in the sand community, they were also four of the five numerically abundant species in a muddy-sand community and three of the five numerically abundant species in a mud community. In all three communities, other numerically dominant species were deposit-feeders. Thus, there is good evidence from a variety of habitats that species utilizing different trophic modes can co-occur in large numbers, and that distributions of suspension- and deposit-feeders are not mutually exclusive.

(b) There is little evidence for the generalization that muddy sediments are detrimental to larval and adult suspension-feeders. For example, in Hines et al.'s (1989) study of the effects of high densities of a suspension-feeding bivalve (*Mya arenaria*) and a "deposit-feeding" bivalve (*Macoma balthica*) on colonizing macrofauna, there was no consistent pattern relative to functional groups (i.e. they did not find, for example, negative impact of *M. balthica* on colonizing suspension-feeders). Then again,

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Table 3 A re-evaluation of distribution of feeding types in sandy and muddy habitats in Sanders' (1958) original study. Groupings are based on recent sources where behavioural observations were made. In many instances, the source for Fauchald & Jumar's (1979) conclusions was Sanders (1958) or Sanders et al. (1962), however the more recent source discusses feeding in the context of other studies on related species. Sanders suggested that the "suspension-feeding" community was comprised of >66% filter-feeders and the "deposit-feeding" community was comprised of >80% deposit-feeders. [1] Closely related species are known to be predacious, so classification as deposit-feeders is tentative. [2] Feeding is somewhat intermediate in that the animal resuspends and then ingests sediment. Nonetheless, deposited, rather than horizontally transported organic matter is presumed to be the dominant food source. [3] Conclusions on feeding mode were drawn from observations on closely related species. We were unable to find data on feeding in the species in question.

Dominant species in Sanders "deposit-feeding" mud community					Dominant species in Sanders "suspension-feeding" sand community				
Species	% of total	Suspension-feeder?	Deposit-feeder?	Reference	Species	% of total	Suspension-feeder?	Deposit-feeder?	Reference
Nucula proxima[3]	23.83		X	Lopez & Cheng 1983	Ampelisca spinipes	18.59		X[2]	Mills 1967
Nephthys incisa	17.13		X[1]	Fauchald & Jumars 1979	Byblis serrata[3]	11.31	Flow dependent		L. Watling (pers. comm.)
Turbonilla sp.[3]	9.21	Unable to determine			Cerastoderma pinnulatum[3]	10.17	X		Swanberg 1991
Nerinedes (=Scolelepis) sp.?[3]	6.85	Flow dependent, mostly suspension		Dauer 1983	Ampelisca macrocephala	6.31		X	Mills 1967
Retusa caniculata[3]	6.00	Predator[3]		Berry & Thomson 1990	Glycera americana	5.47		X[1]	Fauchald & Jumars 1979

Species	Value	Feeding type	Reference
Cylichna oryza[3]	4.56	Predator	Shonman & Nybakken 1978
Ninoe nigripes	3.01	X[1]	Fauchald & Jumars 1979
Ampelisca spinipes	2.92	X[2]	Mills 1967
Unciola irrorata[3]	1.85	Flow dependent	L. Watling & L. Schaffner (pers. comm.)
Lumbrinereis tenuis[3]	1.52	X[1]	Fauchald & Jumars 1979
Tharyx acutus[3]	1.08	X	Fauchald & Jumars 1979
Proportion of each feeding type	0	47.97	

Species	Value	Feeding type	Reference
Nephthys bucera[3]	4.47	X[1]	Fauchald & Jumars 1979
Tellina tenera[3]	3.29	X	Levinton 1991
Ninoe nigripes	2.97	X[1]	Fauchald & Jumars 1979
Lumbrinereis tenuis	2.69	X[1]	Fauchald & Jumars 1979
Nephthys incisa	1.99	X[1]	Fauchald & Jumars 1979
Unciola irrorata[3]	1.65	Flow dependent	L. Watling & L. Schaffner (pers. comm.)
Molgula complanata?[3]	1.85	X	Bingham & Walters 1989
	12.02	45.78	

M. balthica has long been known to feed also on suspended material (Brafield & Newell 1961), and although Hines et al. (1989) acknowledged this feeding behaviour, its potential effect on experimental results was not discussed. Theoretical survival curves constructed from size-frequency histograms of dead shells of bivalves collected in Long Island Sound, Connecticut, suggested very high juvenile mortality of the suspension-feeding bivalve *Mulinia lateralis* in muddy sediments (Levinton & Bambach, 1970), but this result is inconclusive because curves were not also constructed for shells collected from sandy habitats. Curiously, Levinton & Bambach (1970) noted that this species "seems to prefer muddy habitats in New England waters", but argued that this pattern may be a function of larval availability. In fact, dense populations of this opportunistic species frequently occur in organic-rich, low-oxygen situations (Stickney & Stringer 1957, Jackson 1968, Levinton 1970, Boesch 1973, Boesch et al. 1976, Holland et al. 1977, Virnstein 1977, Rhoads et al. 1978a, Reid 1979, Oviatt et al. 1984, Walker & Tenore 1984a), and larvae actively selected organic-rich muds over low-organic alternatives in still water and laboratory flume flows (Grassle et al. 1992b). Sediments dominated by mud, however, had a negative effect on growth rates of adults of the filter-feeding bivalve *Rangia cuneata* (Tenore et al. 1968). In contrast, larvae of the suspension-feeding bivalve *Mercenaria mercenaria* exposed to various concentrations of silt showed enhanced growth at low concentrations, but death occurred at high concentrations (Davis 1960). Growth rates of juvenile *M. mercenaria* were slower in high silt concentrations (Bricelj et al. 1984). Pratt & Campbell (1956) also found reduced growth of adult *M. mercenaria* in trays of mud relative to adjacent trays of sand placed in the field. In none of these studies, however, was the presence of deposit-feeders required to reduce growth. Furthermore, a reduction in growth rates in muddy compared with sandy habitats does not necessarily explain the absence of an organism from muddy areas.

(c) In studies where trophic-group amensalism was invoked to account for the results, other explanations were equally likely, as indicated in our earlier discussion of Rhoads & Young's (1970) experiments. Another example is the distribution of suspension-feeding corals in a Jamaican coastal lagoon (Aller & Dodge 1974), where regions with low numbers of suspension-feeders were attributed to high sediment resuspension that supposedly inhibited settlement and growth. This study provided the alternative explanation that it was zooxanthellae production (see Goreau 1961), not the corals *per se*, that were negatively affected by high water turbidity.

(d) The trophic-group amensalism hypothesis has been extensively modified and qualified to explain various observations, particularly in cases where deposit-feeders and suspension-feeders coexist. The coexistence of suspension- and deposit-feeders in Cape Cod Bay, Massachusetts, for example, was attributed to unusually high tolerance of the suspension-feeders to turbidity (Young & Rhoads 1971) and to the spatial scale of bioturbation effects (Rhoads & Young 1971). They proposed that feeding activities of the deposit-feeding holothurian *Molpadia oolitica* create unstable depressions, but that the faecal cones built by this species stabilize sediments in which suspension-feeders may survive. This heterogeneity, they argued, would result in small-scale favourable and unfavourable areas for suspension-feeders within a muddy habitat. Faecal cones, however, would provide little refuge from sediment resuspended from adjacent sediments without cones and would also elevate the suspension-feeders into a faster flow where they may receive enhanced horizontal food flux (Dayton & Oliver 1980). Stabilization of sediment by polychaete tube mats

was also proposed as a means of allowing functional-group coexistence (Young & Rhoads 1971). Moreover, an invasion of suspension-feeders into a muddy habitat following an oil spill was attributed to sediment stabilization by the oil, and subsequent mass mortality of these suspension-feeders was attributed to destabilization of the sediment as the oil dissipated (Rhoads & Young 1970). Similarly, coexistence of suspension-feeding sabellid polychaetes and a variety of deposit-feeding polychaetes in a Jamaican lagoon was attributed to the presence of binding algae or protective corals (Aller & Dodge 1974). Likewise, enhanced recruitment of *Sanguinolaria nuttallii* (a suspension-feeding bivalve) in the absence of *Callianassa californiensis* (a deposit-feeding ghost shrimp) in Mugu Lagoon, California, was attributed to trophic-group amensalism (Peterson 1977), although he also acknowledged that suspension- and deposit-feeders co-occurred in large numbers in some of the sites sampled and that more complex species interactions were necessary to explain the patterns observed. Finally, Myers (1977) invoked the trophic-group amensalism hypothesis to explain the absence of suspension-feeding bivalves from a sandy (not muddy!), coastal lagoon in Rhode Island as a result of the intense mechanical agitation of the near-surface sediments by the resident fauna. There were, however, a few abundant suspension-feeders at the site, which were tubicolous, "stabilizing species" that could persist, according to Myers (1977), only when fish predators were absent and water temperature was low.

These examples compromise the generality of the concept of trophic-group amensalism. In fact, one of the few studies to test experimentally an aspect of this hypothesis showed that resuspension, simulated by sediment additions to aquaria, reduced survival in several tube-building, deposit-feeders (Brenchley 1981). Tube-builders were also negatively affected by mobile deposit-feeders and mobile suspension-feeders, suggesting that mobility was more important than trophic group in structuring benthic communities. High-density assemblages of tube-builders may prevent the establishment of burrowers that could destabilize the sediment (Woodin 1974; but see also criticisms of the interpretation of Woodin's results, based on subsequent experiments, in Dayton & Oliver 1980), whereas low-density assemblages would be more susceptible to colonization and, thus, sediment destabilization by burrowers. Additional support for mobility-group amensalism is lacking, however, except where the mobile organism is much larger than the sedentary organisms (Posey 1987). Survival of a sedentary, tubicolous polychaete (*Streblospio benedicti*), for example, was unaffected by a subsurface, deposit-feeding oligochaete, *Monopylephorus evertus*, although growth rates of *Streblospio benedicti* were somewhat reduced (McCann & Levin 1989).

The trophic-group amensalism hypothesis provides generalizations regarding animal–sediment relationships not at the population or species level of organization, but at the level of functional groups of organisms. The concept of functional groups relative to organism effects on sediments is problematic, however, because it is often difficult to categorize the effects of a given species as either sediment stabilizing or destabilizing (Jumars & Nowell 1984a). A species can have more than one effect on the sediments, as suggested by Rhoads & Young (1971) for *Molpadia oolitica* (discussed earlier, p. 138). Moreover, when effects of individual organisms within a community are tested separately, and rigorous criteria are used to evaluate their effects on the boundary-layer flow and sediment-transport regime (Nowell et al. 1981, Rhoads & Boyer 1982), it is the integrated effect of the entire benthic community that determines whether sediments are more or less susceptible to transport than they would be in the absence of the fauna, flora, and microbiota (Grant et al. 1982).

Furthermore, sediment "stability", in most cases, has not been clearly defined. Rhoads

(1974), for example, referred to muddy bottoms as being "unstable" due to the sediment-reworking activities of deposit-feeders. Yet, in most instances, muddy bottoms are depositional areas that experience much lower boundary shear stresses than sandy bottoms. Using a physical criterion for "stability" based on the boundary shear stress required to initiate particle motion (τ_{cr}) (Shields 1936, Miller et al. 1977) muds are unstable relative to sands if flow conditions in the sedimentary habitats are comparable and exceed τ_{cr} of the muds. Some biological effects, such as mucous-binding, may tend to increase τ_{cr} (Mantz 1977; Self et al. 1989, Dade & Nowell 1991), and others, such as pelletization and direct burial may tend to decrease the supply of fine sediments to the water column (Jumars et al. 1981). Storm events would tend to erode and transport far more sediment in a muddy habitat than in a sandy environment. The physical effect evidently referred to by Rhoads (1974) was the relative amount of sediment in suspension, which is generally higher above a muddy than a sandy bottom, and the highly mobile "fluff" layer characteristic of many bioturbated beds (Rhoads & Boyer 1982, Beier et al. 1991, Stolzenbach et al. 1992). Interestingly, this is a definition based more on water-column than bed characteristics, and has contributed to confusion in the literature concerning the stability of sediment beds.

In summary, physically meaningful and consistent definitions generally have not been used by benthic ecologists for the terms "stable" and "unstable" with regard to bottom sediments. In addition, the designation of simple, functional groups of organisms based on still-water observations of feeding or mobility is no longer meaningful; if the concept of functional groups is to be useful, it must be modified to include considerations of organism behaviour within the context of the flow and sediment-transport regimes in which they reside. Finally, there is very little concrete support for the trophic-group amensalism hypothesis as a rigorous explanation for animal–sediment associations; the tenet has been sufficiently modified to account for so many "special" cases that it is now so general an explanation that it is not very useful. Because of these modifications, trophic-group amensalism cannot be considered a rigorous, predictive explanation for animal–sediment relationships.

Two case studies

The complexity of animal–sediment associations, and the intimate relationship among the various factors that may produce them, can be illustrated by summarizing current information on the distributions of two relatively well-studied infaunal species and the factors that may determine these distributions. The bivalve, *Mercenaria mercenaria*, was one of the key species studied by Rhoads & Young (1970) in the formulation of their trophic-group amensalism hypothesis, and there is a relative wealth of both distributional and experimental studies on this organism because of its commercial importance. The polychaete, *Owenia fusiformis*, is relatively well-studied for a non-commercial species, and provides an interesting contrast to *Mercenaria mercenaria* in two regards. First, *Owenia fusiformis* is known to switch between deposit- and suspension-feeding depending on flow conditions. Secondly, *O. fusiformis* has been studied largely for the purpose of understanding its potential stabilizing effects on sediments, as opposed to the alternative (i.e. effects of sediment "stabilization" on its distribution).

Mercenaria mercenaria

The hard clam, *Mercenaria mercenaria*, (hereafter called *Mercenaria*) is probably the best studied infaunal, suspension-feeding bivalve in terms of its distribution and ecology, including a large number of both observational (i.e. field distributions) and experimental studies. It came to be considered a classical infaunal suspension-feeder that is restricted to relatively coarse sediments following Rhoads & Young's (1970) transplant experiments (described earlier, p. 134) to test their trophic-group amensalism hypothesis. In this study, Rhoads & Young also quantified the abundances of suspension- and deposit-feeders relative to sediment type along two transects in Buzzards Bay, Massachusetts, and although they mentioned several species of deposit-feeders that dominated the muddy sites, they did not provide species-specific information for the suspension-feeding communities at the sandier sites. The station locations were not far from some of Sanders's (1958) Buzzards Bay transects, yet *Mercenaria* was not mentioned at all by Sanders. Furthermore, as we pointed out previously, few of the species Sanders classified as suspension-feeders in the late 1950s would still be classified as such today (Table 3, p. 136), and thus Rhoads & Young's sandy sites may have likewise contained very few species that were actually suspension-feeders. We shall return to the issue of sediment specificity of suspension-feeders like *Mercenaria* at the end of this section (p. 144).

Assuming, for the moment, that *Mercenaria* is less successful in muddy than sandy environments then, according to the trophic-group amensalism hypothesis, this distribution may be attributed to the reworking activities of deposit-feeders in muds effecting lower growth rates and/or high mortality of suspension-feeding juveniles (Rhoads & Young 1970). Furthermore, according to Sanders (1958), suspension-feeders should be associated preferentially with sandy sediments because of the relatively high horizontal flux of suspended food in these environments. If there were strong selective pressure for confinement of suspension-feeders to coarse sediments, then *Mercenaria* larvae might have been expected to select actively for sandy sediments.

The relatively long-lived (several weeks), planktotrophic larvae of *Mercenaria* do not appear to require a specific sediment cue to induce metamorphosis, and in the laboratory will settle on a variety of substrata, including sediments, plastics and glass (Loosanoff & Davis 1950). Laboratory experiments by Carriker (1961) indicated that newly recruited juveniles (byssal plantigrade stages) tended to settle on sediment with particle sizes smaller than their own shells, as opposed to coarser substrata, and that they preferred organic-rich, fine sediment. In 2-day, still-water experiments, Keck et al. (1974) found, however, that *Mercenaria* larvae preferred sand over mud. But, given the relatively long duration of their experiments, it is unclear whether this pattern reflected larval selectivity (i.e. initial settlement) or post-settlement redistribution. We suspect the latter, given results of the very short-term (4 h), still-water experiments of Bachelet et al. (1992), where larvae showed no sediment preference. It should be noted that Bachelet et al. (1992) also re-evaluated the earlier, still-water experiments of Butman et al. (1988b), where there was active selection by *Mercenaria* larvae for a low-organic over a high-organic sediment in still water. Because of a potential problem with preservation of the larval shell in the high-organic treatment in that study, and because Bachelet et al. attempted to replicate precisely the methods used by Butman et al. (1988b) and found no statistically significant selection, Bachelet et al. (1992) concluded that *Mercenaria* larvae must be considered non-selective, at least over 4 h in still water. Butman et al. (1988b) also demonstrated very low settlement and no active selection by *Mercenaria* larvae in a slow, turbulent flume flow.

If *Mercenaria* larvae do not actively select sandy over muddy sediments at settlement, then perhaps the pattern results from enhanced passive larval supply to sandy compared with muddy habitats, or to differential post-settlement survival or migration. In nature, higher densities of young and old individuals of *Mercenaria* have been observed in silty sand within seagrass beds compared with purer sand in adjacent "bare" sandflats (Peterson et al. 1984, Irlandi & Peterson 1991). Peterson (1986) compared size-frequency distributions of *Mercenaria* in a seagrass bed and a bare sand area and found that essentially all sizes of *Mercenaria* were more abundant in the seagrass bed, but the pattern was amplified in the larger size classes. Thus, the pattern may have been established at settlement (although newly-settled larvae were not sampled in this study) and was enhanced subsequently via post-settlement processes (e.g. differential survival or migration resulting from competition or predation). The depositional environment of the seagrass bed, which results in passive accumulation of silt particles, may also passively accumulate larvae, whereas currents may be sufficiently strong to preclude high settlement in more exposed sandy areas. Thus, passively settling larvae should accumulate in higher numbers in areas of relatively low boundary shear stress, and not in the high shear stress regimes that typically characterize sandy sites. Pratt (1953) suggested that *Mercenaria* larvae settle passively in local micro-depositional sites created by rocks and shells protruding from an otherwise flat substratum. Supporting this hypothesis, Carriker (1961) observed that post-larvae (and adults) were often concentrated around, and with their byssal threads attached to, shells projecting above the bottom.

To our knowledge, there is no information on larval supply and post-settlement distribution of this species in the field, although many of the bivalves sampled by Wilson (1990) may have been *Mercenaria* because adults of this species are abundant in similar habitats nearby (Peterson et al. 1984, Peterson 1986, Irlandi & Peterson 1991). Using traps largely buried within the bed and that were designed to collect settling or resuspended larvae, Wilson (1990) collected, on average, about 50% more bivalves inside a seagrass bed than in the adjacent sandflat. At times of high larval availability, he also collected significantly higher numbers of post-larvae in the seagrass bed than in the sandflat. This suggests that settlement may determine the pattern of higher abundances in the seagrass bed, either through active habitat selection or passive deposition. Wilson's study was not designed to distinguish between these alternative hypotheses, but sediment volume collected was actually higher in traps located in the sandflat than those located in the seagrass bed, making passive deposition doubtful. If *Mercenaria* was the dominant bivalve species sampled by Wilson (1990), and if the seagrass bed that he studied was a local, depositional site for silts as demonstrated for a nearby seagrass bed (Peterson et al. 1984), then Wilson's results would also refute preferential selection of relatively sandy sediments by settling larvae.

The issue of differential growth or post-settlement survival under conditions of high compared with low suspended silt concentration that characterizes muddy compared with sandy habitats, respectively, has been relatively well studied for larvae and adults, but not juvenile *Mercenaria*. Laboratory studies on the effect of resuspended silt on larvae indicate that levels of turbidity less than $750 \, mg \cdot l^{-1}$ may enhance growth, although decreased growth was observed at concentrations greater than $1 \, g \cdot l^{-1}$ (Davis 1960). Even at silt levels of $4 \, g \cdot l^{-1}$, however, Davis (1960) observed no significant larval mortality. Likewise, for suspended sediment concentrations of 0, 56, 110, 220, 560 and $2200 \, mg \cdot l^{-1}$, Huntington & Miller (1989) could detect no differences in larval survival, and growth was significantly reduced only at the highest silt concentration tested. It is possible that settled juveniles are more sensitive to suspended silt than are planktonic larvae, given that reduced

growth of juveniles was observed at silt concentrations of only $44\,mg\cdot l^{-1}$, but not at $25\,mg\cdot l^{-1}$, for juvenile *Mercenaria* (Bricelj et al. 1984). Thus, there could be a recruitment "bottleneck" in high suspended silt environments. The significance of these laboratory results to natural populations is unclear, however, given that the highest silt levels observed within 3 m of the bottom in a "silt-clay basin" containing deposit-feeders were only $10–35\,mg\cdot l^{-1}$ (Rhoads 1973). Likewise, Grizzle & Lutz (1989) measured concentrations of suspended inorganic particulate matter of $51–111\,mg\cdot l^{-1}$ over sediments ranging from mud to sand, and known to contain adult *Mercenaria*. In the Indian River Bay, Delaware, where *Mercenaria* is abundant, Huntington (1988) measured suspended sediment concentrations of $10–570\,mg\cdot l^{-1}$, with an average of about $60\,mg\cdot l^{-1}$. Thus *Mercenaria*, at least in these cases, appears to be distributed widely with respect to suspended sediment concentration.

Data on growth rates of adult *Mercenaria* are somewhat inconsistent among studies. In cases where adult growth rates were compared in adjacent sandy and muddy plots, lower growth rates were found in the finer sediment treatment in some instances (Pratt 1953), but not in others (Kerswill 1949, Grizzle & Morin 1989). The sandy and muddy plots in Pratt's (1953) study were both within a muddy habitat, however, and thus it seems likely that resuspension from the ambient, muddy sediment would have a comparable impact on both treatments. This observation suggests that it is some component of the bottom sediment and not the sediment in suspension that conferred lower growth rates in Pratt's muddy plots. In contrast, Pratt & Campbell (1956) found faster growth rates for clams living in sand-filled as opposed to mud-filled boxes within a site, yet for a given sediment treatment, growth rates in their silty environment were often higher than those in the sandier environment. This result suggests that both bottom sediment type and depositional regime are important. Rhoads & Young (1970) found no differences in growth between clams suspended above the bottom turbid layer at a muddy site and those at their "control" (sandy) site, but as mentioned earlier, higher growth rates observed in trays of clams sufficiently elevated above the muddy bottom (compared with those placed within the bottom turbid layer) may have simply reflected higher horizontal food supply due to higher current speeds above the bottom (Dayton & Oliver 1980). Peterson et al. (1984) observed higher growth rates of clams inside, compared with outside, seagrass beds, and the experimental field study of Irlandi & Peterson (1991) confirmed this observation. In addition, when seagrass was clipped at the base, clam growth and survival was higher in intact than in clipped beds (Irlandi & Peterson 1991). They attributed their results either to predation (seagrass as a refuge), hydrodynamics (seagrass as a baffle to enhance vertical flux of food), sediment stability (seagrass beds as sediment stabilizers in the sense of reducing resuspension), or epiphytic algae (which are more abundant in seagrass beds). Of these explanations, there is probably more support for the hydrodynamic baffling hypothesis, particularly given that food capture by *Mercenaria* has been shown to increase with increasing suspended food concentration (Walne 1972). All of these studies, taken together, indicate that growth of adult *Mercenaria* is not necessarily higher in sandy sediments. In fact, the seagrass studies suggest higher growth rates in depositional sites that usually have a substantial silt fraction in the sediment. The studies have not separated, however, the importance of sediment type compared with flow regime.

One explanation for inconsistencies in growth rates across sediment types may be variations in the flux of organic matter (as food) contained within the suspended material. Greater differences in growth rates of *Mercenaria* have been observed in comparisons between different flow environments than between different sediment treatments, and growth rates were positively correlated with horizontal flux of particulate organic matter,

bottom current speed, and suspended chlorophyll concentration (Grizzle & Morin 1989). This association corroborates results of other field (Haskin 1952, Greene 1979) and laboratory (Hadley & Manzi 1984, Manzi et al. 1986) studies showing that *Mercenaria* growth is positively related to current speed, particularly when suspended food concentration is held constant (Grizzle et al. 1992). These results support the hypothesis that food supply (horizontal flux of suspended organic material) is an important factor determining *Mercenaria* distributions. In the study of Irlandi & Peterson (1991), for example, a strong leading-edge effect (higher growth rates in upstream animals) was observed in a seagrass bed with asymmetrical tidal flow, suggesting both that food was limiting within the seagrass bed and that within this depositional locale, horizontal food flux determined individual growth rates. A study that directly manipulated near-bed currents in the field, however, showed no difference in *Mercenaria* growth rates over the modest range of currents produced (Judge et al. 1992). Even though food depletion evidently did not occur over these *Mercenaria* beds, such that increased horizontal food flux resulted in no added benefit, this result is not necessarily inconsistent with the hypothesis that advective-diffusive processes that control suspended food concentration can limit the distribution of this and other benthic suspension-feeders (Fréchette et al. 1989).

We propose that sediment type alone is actually a poor predictor of *Mercenaria* distributions and suspended food supply seems a more likely causative factor. Sediment type may, in some cases, be a correlate of food supply to suspension-feeders in that sandy sediments will, on average, be sites of higher advective fluid flux, but the dynamics of food supply to suspension-feeders clearly are not as straightforward as originally suggested by Sanders (1958). Food supply is a function of both vertical mixing and advective processes, as well as of upstream food concentration and feeding rates of the animals (Fréchette et al. 1989, Shimeta & Jumars 1991). Furthermore, in reviewing the literature on the distribution of *Mercenaria* populations relative to sediment type, we found no support for the contention that this species is restricted to relatively coarse sediments. Adult abundances are known to be higher in fine sediments containing some coarse (>2mm) material such as sand (Walker & Tenore 1984b) or shells and gravel (Pratt 1953, Wells 1957, Carriker 1961, Walker & Tenore 1984b), and densities in relatively pure sand may be comparable with those in relatively pure mud (Pratt 1953). In fact, Grizzle & Lutz (1989) collected *Mercenaria* off the New Jersey coast from a variety of sediment types ranging from sand to mud, although they provided no density estimates. High population abundances have also been reported in relatively high-flow regions, such as in the vicinity of outlets to salt-water ponds (Wells 1957, Carriker 1961, Mitchell 1974). Furthermore, although mature individuals of *Mercenaria* may be found in sandflats (Peterson et al. 1984), they were more abundant in an adjacent seagrass bed consisting of silty-sands (Peterson et al. 1984, Peterson 1986, Irlandi & Peterson 1991).

In summary, neither Sanders's (1958) generalizations on animal–sediment relationships nor Rhoads & Young's (1970) trophic-group amensalism hypothesis appear to be supported by existing data on the distribution and ecology of *Mercenaria*, even though the obligate suspension-feeding mode and short siphon of this species make it an ideal candidate for the proposed amensalistic relationship. Existing data indicate that this species is not distinctly associated with a particular sediment type. There is neither consistent evidence that larvae actively select sandy over muddy sediments, nor that growth and survival of recruits are higher in sandy sediments. There are, however, many studies suggesting that *Mercenaria* distributions may be related directly to the suspended particulate and near-bed flow regimes above a given sediment. Clearly, relatively high suspended particulate concentrations and

relatively high flow speeds are advantageous in terms of food flux to suspension-feeders, but the issues of seston quality and the physiological limits of the performance of the filtering apparatus must also be considered, in addition to biological interactions with other species (see review by Arnold 1984, Hunt et al. 1987). Understanding the distribution of this commercially important and widely distributed species has suffered from a lack of rigorous predictive theory (see review by Fréchette et al. 1993). This situation should improve with, for example, the recent development of hydrodynamic models of food supply to suspension-feeders (Fréchette et al. 1989, Monismith et al. 1990, Cloern 1991, O'Riordan et al. 1993) together with experiments that directly test model predictions (Cole et al. 1992, Butman et al. in prep.) and thus reveal other important biological determinants of suspension-feeder distributions.

Owenia fusiformis

Owenia fusiformis (hereafter called *Owenia*) is a tube-building polychaete that commonly occurs in dense assemblages in fine and muddy sand (Fager 1964, Shimek 1983, Dauvin & Gillet 1991). Although predation has been proposed as an important structuring mechanism for *Owenia* populations (Fager 1964, Shimek 1983, Dauvin & Gillet 1991), there does not appear to be evidence that it results in higher densities of this species in certain sediments (i.e. we are unaware of evidence that *Owenia*'s predators are restricted in terms of sediment type).

Larvae of *Owenia* are planktotrophic, and will metamorphose quickly in the presence of fine sand (Wilson 1932). Although fine sand appears to be the best inducer of metamorphosis, some individuals will metamorphose in response to mud or will metamorphose spontaneously in the absence of sediment (Wilson 1932). Settlement behaviour in flow has not been evaluated, but recently settled individuals in nature have been recorded in sediments ranging from coarse sand to mud, and their occurrence on the bottom may be a function of water-column transport (Thiébaut et al. 1992). Although active vertical migration by larvae may aid in their retention within a suitable area (Thiébaut et al. 1992), Fager (1964) suggested that dense beds of *Owenia* may develop in the shallow subtidal from passive accumulation of larvae in sediments located at the heads of rip currents. Larvae can and do settle in high densities in muddy sediments (Yingst 1978, Dauvin & Gillet 1991); however, higher post-settlement mortality may occur in mud compared with adjacent muddy sand (Dauvin & Gillet 1991). Nonetheless, patches of *Owenia* may persist in a variety of sediment habitats (Dauvin & Gillet 1991). Thus, larval selectivity does not appear to account for the occurrence of *Owenia* in fine and muddy sand and we are unaware of fine-scale measurements demonstrating differences in larval availability above adjacent sand and mud habitats.

Feeding in *Owenia* may range from surface deposit-feeding to filter-feeding, depending on flow conditions (Dales 1957). Given the plasticity in feeding mode, there is no clear expectation of distribution pattern based on trophic-group amensalism, although the ability to deposit-feed renders unlikely amensalistic exclusion from muddy habitats. Dauvin & Gillet (1991) suggested that *Owenia* could not occur in substrata where there was not a significant fine-sediment fraction. Growth rates of *Owenia* individuals in muddy sediments were comparable with those in muddy sand (Dauvin & Gillet 1991), yet there was higher mortality in pure muds. This result suggests that amensalistic interactions cannot explain the distribution of this species, and it is likewise difficult to imagine how a facultative deposit-

feeder that may stabilize bottom sediments can fit into the trophic-group amensalism paradigm. Feeding plasticity also clearly does not fit into Sanders's (1958) animal−sediment dichotomy.

We do not mean to suggest that the interplay between feeding mode and particle flux does not influence distributions of this and other infaunal species, but that existing paradigms based on functional groups are unsuitable for the complex feeding behaviours that are observed in infaunal species under realistic flow conditions. The higher mortality that has been reported for *Owenia* in mud may reflect post-settlement processes (Dauvin & Gillet 1991), such as predation, but again this possibility fails to explain why predators might be limited to this (muddy) environment, and why *Owenia* appears to be somewhat sediment-specific in its distribution. In fact, dense tube mats of this species may result from hydrodynamic concentrating mechanisms operating at the time larvae are competent to settle, much as Fager (1964) originally envisaged. The probability of survival of a passively deposited, dense aggregation of *Owenia* would depend on both food supply and predators within the depositional locale. The dense tube mat may serve to enhance the food value of sediment within the mat via enhanced microbial activity (Eckman 1985). Tests of such scenarios are now technologically possible in large laboratory flumes and could, likewise, be done through field experiments.

Processes that determine the sedimentary environment

The boundary-layer flow and sediment-transport regime play a critical rôle in a variety of benthic ecological processes; after a decade or so of experimentation both in the field and in laboratory flumes, this fact is now established. Although previous reviews of animal−sediment relationships (i.e. Purdy 1964, Gray 1974, 1981, Rhoads 1974, Pérès 1982, Probert 1984), and the studies on which they were based, often acknowledged interactions between sediment type and flow regime, they could not adequately incorporate considerations of the dynamic nature of bottom sediments and the associated near-bed flow regime that have evolved in the last decade.

Boundary-layer flow

As a fluid moves across a fixed surface such as the sea floor, frictional drag retards the motion of the fluid such that velocity is zero at the sediment surface. As a result, horizontal velocities very close to the sediment are much lower than at distances further up in the water column. Increase in velocity with increasing height above bottom is referred to as shear, and the shear region adjacent to the bottom is referred to as the bottom boundary layer. In "depth-limited" boundary layers in shallow water, the effect of bottom drag (and thus enhanced mixing) extends all the way to the water surface. In deeper water, however, boundary drag affects only a portion of the water column. The boundary-layer thickness (i.e. the region of shear) is a function of the turbulent mixing in the flow (discussed below) and the periodicity of the force driving the flow. Thus, currents, tides, and waves may all contribute to boundary-layer formation, flow characteristics and thickness.

The boundary layer can be divided into three regions based on the shape of the velocity profile (Fig. 1). At the sediment-water interface is a region called the "viscous sublayer"; this region is of paramount relevance to benthos because it is the interface between the water column and the sediment. Thus, settling organic material, sediments, and larvae are transported
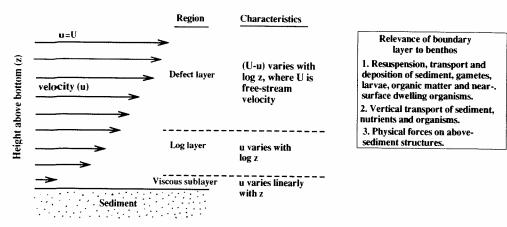
Figure 1 Boundary-layer flow

along and must pass through this layer en route to the bottom. This is also a region where vertical shear in velocity is highest; this has important ramifications for the horizontal transport of organic matter (Muschenheim 1987a, b) and larvae (Jonsson et al. 1991). Directly above the viscous sublayer is a region referred to as the "log layer". Because the viscous sublayer is very thin (of the order of millimetres), the log layer is also extremely important for transport of materials to and from the benthos. It is often convenient to characterize the boundary-layer flow environment by the boundary shear velocity (u_*), which is a measure of the magnitude of turbulent mixing in the flow and is directly related to the shear. The shear velocity is proportional to the square root of the boundary shear stress (τ), the tangential force per unit of bottom area. Because u_* roughly characterizes vertical mixing within the boundary layer, vertical transport of materials increases with increasing u_*. General descriptions of the basic features of hydrodynamic and sediment-transport processes within the bottom boundary layer, particularly with respect to potential effects on benthic organisms, can be found in Nowell & Jumars (1984), Muschenheim et al. (1986) and C. A. Butman (1987). More rigorous descriptions of bottom boundary-layer flows in the ocean can be found in Wimbush (1976), Komar (1976a), Madsen (1976), Nowell (1983), and Grant & Madsen (1986), and of sediment-transport processes on continental shelves in McCave (1972), Sternberg (1972, 1984), Smith & Hopkins (1972), Komar (1976b), Drake (1976), Smith (1977), Nowell (1983), B. Butman (1987b) and Cacchione & Drake (1990). In this section we briefly discuss results of recent boundary-layer flow and sediment-transport studies that have changed the way in which the sedimentary environment is viewed. Although some repetition is inevitable, we tailor this discussion to be complementary to those of Nowell (1983), Jumars & Nowell (1984a, b), Nowell & Jumars (1984) and Miller & Sternberg (1988). The purpose of this section is to summarize for benthic ecologists recent conceptualizations of the physical regime in soft-sediment habitats, and to identify processes that are still poorly understood.

The distribution of sediments

Surficial sediment distributions are determined by (a) the sediment source (relict or modern), (b) interactions between sediment particles (including adsorption of chemicals), (c) the hydrodynamic regime, and (d) biological effects. All four of these factors can

potentially determine whether sediment remains in the bed or is transported by the flow. Regardless of sediment type, the sediment mixture within a given locale generally is not static but is in dynamic equilibrium with flow conditions at that site. Surface particles, ranging from sand to clay, are constantly being removed (through resuspension or burial) and added (through deposition or regeneration from depth in the bed). In a purely physical sense, i.e. ignoring, for the moment, factors (a), (b), and (d) above, the sediment is generally a reflection of the near-bed flow regime. Thus, relatively coarse beds generally occur in regions that regularly experience high u_* (where fine sediments are prevented from settling onto the bed) and, likewise, relatively fine sediments occur in regions that rarely experience high u_* (where deposition of fine particles can occur). Although sediments at any given locale generally reflect the "average" near-bed flow regime, this applies only to long-term averages and, even so, it is an over-simplification. In fact, physical processes operating at different temporal and spatial scales transport sediments in differing amounts and directions, sometimes resulting in dramatic temporal changes in the nature of bottom sediments at a given site. For example, in some instances, wave-generated boundary shear stress is a more effective means of resuspending bottom sediments than the shear stress generated by steady currents (Grant & Madsen 1986, Cacchione & Drake 1990). In regions with significant wave activity, as well as traditional measurements of the "steady" currents, adequate characterization of the boundary-layer flow and sediment-transport regimes requires measurements of currents within the wave boundary layer (of the order of centimetres thick) and of the wave field (Grant & Madsen 1986).

From long time-series measurements of the flow and sediment-transport environment on Georges Bank, Massachusetts, for example, B. Butman (1987b) identified at least four physical processes responsible for sediment movement; tides, storms, internal waves, and warm-core Gulf Stream rings. Each process operates at a characteristic temporal and spatial scale, and the processes may occur simultaneously or separately. The amount of sediment transported, as well as the direction of transport, also varies as a function of the physical forcing. Infrequent storm events may greatly influence sediment transport in a given habitat (Hollister & McCave 1984, B. Butman 1987a) and geological events have resulted in some exceptions to modern sediment-flow equilibrium relationships. Thus, the local availability of different sediment types may determine sediment-flow equilibria. For example, the HEBBLE site off Nova Scotia, Canada, which is an area where large amounts of fine sediments have been transported over geological time, is a site where fine sediments occur despite very high near-bed velocities (Hollister & McCave 1984). Similarly, fairly coarse sediments could occur in areas of weak bottom flow if there is no source of fine sediments.

Sediment transport can be divided into two steps, the first of which involves overcoming particle inertia such that the particle begins to move (called "initiation of motion"); the second step is actual transport. Heavy particles, such as coarse sand grains, begin to roll, hop or saltate along the bottom as "bedload" transport once the shear velocity exceeds that required to initiate motion; this u_* is often referred to as "u_* critical" (u_{*crit}). At higher shear velocities, coarse particles make higher and longer excursions into the water column until they remain largely in suspension; the shear velocity at which this transition occurs is often referred to as "u_* suspended" (u_{*susp}). Even at high shear velocities, however, there still is considerable exchange of particles between the water column and the bed. Very light particles, such as clays, also have thresholds for sediment motion, but u_{*susp} is less than u_{*crit} so once motion is initiated, particles go directly into suspension rather than first moving as bedload. Determining u_{*crit} and u_{*susp} for a given sediment, as well as the hydrodynamic conditions where u_* of the environment exceeds u_{*crit} and u_{*susp}, is of great interest

to those studying sediment transport, and has relevance to animal–sediment relationships.

The bulk of information on initiation of sediment motion comes from empirical, laboratory studies where u_{*crit} was determined from visual observations of a thin layer of mono-dispersed sediment. Shields (1936) synthesized observations made on a variety of sediment sizes and types into a single predictive curve, called "Shields curve", which relates two dimensionless quantities composed of fluid, flow, and sediment variables. Miller et al. (1977) up-dated this curve for measurements made since Shields (1936), and they used only those measurements taken under a restricted set of meaningful laboratory conditions, con-siderably reducing scatter in the data. Thus, for a given size and specific gravity of sediment, and a given fluid viscosity, u_{*crit} can be determined from Miller et al.'s (1977) modified Shields curve. Numerous other investigators have constructed similar curves that vary primarily in the range of application and the parameters used to plot the data (see review in Nowell et al. 1981). Each curve is also constrained in applicability by limitations of the methods, which are often severe in terms of relevance to marine sediments (Miller et al. 1977, Nowell et al. 1981). That is, measurements were made primarily on single size classes of particles distributed in a thin layer, or even a monolayer, on the observation surface, and most measurements have been made on relatively large (e.g. coarse silt and sands), abiotic, non-cohesive particles. Results for muddy, cohesive sediments are much more complex (Mantz 1977, Dade & Nowell 1991, Dade et al. 1992), and biologically reworked sediments yield widely varying results (e.g. as reviewed in Nowell et al. 1981).

Laboratory flume studies on effects of individual benthic organisms (Nowell et al. 1989), groups of individuals of the same species (Rhoads & Boyer, 1982), and cores of sediment containing natural macrofaunal (Rhoads et al. 1978b, Luckenbach 1986, Grant et al. 1982) and meiofaunal (Palmer & Gust 1985, Palmer 1988b) communities indicate substantial biological effects on sediment transport. Similarly, diatom films (Grant et al. 1986a), mats of purple sulphur bacteria (Grant & Gust 1987), and exopolymer adhesion (Dade et al. 1990) can significantly affect the entrainment of sand. Studies of individual or species-specific effects compared with whole-community effects have their strengths and weaknesses (see discussion in Nowell & Jumars 1987); at the least, however, these studies indicate that benthic biological processes can significantly increase or decrease u_{*crit} of marine sediments, relative to the abiotic case and, in some instances, the result is non-intuitive (Nowell et al. 1981). For example, Daborn et al. (1993) showed that migratory birds can affect sediment stability by feeding on deposit-feeding bioturbators (the amphipod *Corophium volutator*). Diatoms within the sediment excrete polysaccharides that bind the sediments, but the amphipods graze on diatoms; thus, removal of the amphipods through bird predation results in increased sediment stability.

Initiation of motion of natural marine sediments is germane to this discussion of animal–sediment relationships because, (a) the condition where u_* exceeds u_{*crit} is one useful way to define objectively sediment "stability" (Grant et al. 1982), which has been proposed as a determining factor in the distribution of trophic groups (Rhoads 1974); and (b) animals, plants and microbes can respond to and directly affect sediments and sediment transport. Moreover, because these effects can vary both temporally (Rhoads et al. 1978b, Grant et al. 1982, Rhoads & Boyer 1982) and spatially (Nowell et al. 1981), relationships between organisms and the sediments in which they reside may be very complicated indeed. Unfortunately, the development of a universally predictive relationship (or set of relation-ships), such as Shields curve, for biologically altered sediments is still in its infancy. This subject should receive considerable attention in the future because field observations of sediment transport cannot be predicted using the theoretical and empirical relationships

developed for abiotic sediments alone, and discrepancies may be resolved by inclusion of benthic biological effects (Drake & Cacchione 1985, 1989, B. Butman 1987b, Lyne et al. 1990a, b).

As the ability to evaluate u_* in different sedimentary environments improves, it may be possible to use this parameter to classify the "stability" of habitats. Stability may be defined in terms of the frequency and duration of sediment-transport events. Thus, environments where u_{*crit} was frequently exceeded for a considerable time could be termed "unstable", whereas environments where u_{*crit} was rarely exceeded, and then only for brief intervals, could be termed "stable". This kind of classification is not without problems. For example, muddy sediments may be problematic because there can be a surficial "fluff" layer of light, flocculent material that is so easy to erode that it virtually remains just barely suspended above the bottom in most flows (Stolzenbach et al. 1992), but the underlying, bioturbated mud may be tightly bound by mucous secretions such that it is much more difficult to erode than abiotic, muddy sediment. Even given such difficulties, defining sediment stability based on an objective criterion such as u_{*crit} would avoid the present terminological ambiguity (see also Jumars & Nowell, 1984a). Alternatively, sediment stability could be defined in terms of actual vertical profiles of suspended sediment concentration and sediment flux. This would indicate that the amount of material transported as suspended load compared with bedload may be much more meaningful to the ecology of infaunal organisms. In practice, the field measurements required for this kind of classification may be difficult, but new technological developments may soon make such measurements feasible.

Sediment transport rates and directions determine the horizontal flux of food and larvae; however, it is not just the total flux of material in suspension that may be relevant to animals living in the seabed, but the distribution of this material as a function of height above the bottom (Muschenheim 1987b, Fréchette et al. 1989). Sediment moving as bedload rather than suspended load, for example, may be an important factor determining animal distributions (see next section, pp. 150–158). Moreover, as with the initiation of sediment motion, benthic organisms can directly affect suspended sediment concentration profiles, for example, by pelletizing the bed and changing the transport characteristics of the particles (Taghon et al. 1984, Komar & Taghon 1985), by directly ejecting particles into suspension (Rhoads 1963), and by affecting the vertical distribution of grain size within the sediment through their feeding activities such that surficial sediments differ from the sediment mixture deposited originally (Rhoads & Stanley 1965, Rhoads 1967).

Dynamic variables that correlate with sediment type and that may determine infaunal distributions

Given that the bottom sediment, for the most part, reflects the boundary-layer flow and sediment-transport regime, correlations between animal and sediment distributions may be caused not by any particular aspect of the sediment itself, but by the physical processes that created that particular sediment environment. In this section, the potential rôle of hydrodynamic regime is discussed with regard to larval supply and food supply, and how these variables may contribute to the establishment and maintenance of animal–sediment relationships.

Hydrodynamic regime

There is mounting evidence for plasticity in feeding mode as a function of the flow and sediment-transport regime. Many species of surface deposit-feeders, for example, are now known to be facultative suspension-feeders (Hughes 1969, Buhr & Winter 1977, Fauchald & Jumars 1979, Salzwedel 1979, Dauer et al. 1981), evidently in response to flow and elevated fluxes of suspended particulates (Taghon et al. 1980, Ólafsson 1986, Thompson & Nichols 1988, Levinton 1991, Taghon & Greene 1992). Switching between deposit- and suspension-feeding can occur over a tidal cycle, as observed for the bivalve *Macoma balthica* (Brafield & Newell 1961). Switching can also occur within a single, bedload-transporting flow regime, depending on the location of the organism relative to ripple geometry, as observed for the spionid polychaete *Pseudopolyora kempi japonica* at slow ripple migration rates (Nowell et al. 1989). Furthermore, the extensive, detailed observations of Miller et al. (1992) of the feeding behaviour and motility of 16 species of soft-substratum invertebrates from five phyla in a laboratory flow tunnel indicate various kinds of responses to oscillatory flow. These responses are correlated not simply with feeding mode, but more specifically with the functional morphology of the appendages used for particle capture. In fact, of the 16 species, which came from habitats ranging in depth from the intertidal to the continental shelf, only one did not change feeding behaviour in response to oscillatory flow (the only burrowing species examined — the predatory starfish *Astropecten americanus*). Epifaunal gastropods also showed changes in motility with increasing oscillatory flow and sediment transport. The conventional concepts of "feeding guilds" (*sensu* Fauchald & Jumars 1979) and "functional groups" (*sensu* Rhoads & Young 1970) therefore must be revised to account for behaviour as a function of the flow and sediment-transport regime (Jumars & Nowell 1984a, Nowell et al. 1989, Okamura 1990, Shimeta & Jumars 1991, Turner & Miller 1991a, Miller et al. 1992).

The boundary-layer flow regime may also directly affect animal distributions through drag and lift forces on above-ground structures, such as tubes, or on the animals themselves. The drag on a structure in turbulent flow is proportional to the frontal surface area (i.e. relative to the flow direction) of the structure and velocity squared, such that relatively small increases in velocity result in much larger increases in drag. Although the size, shape, and stiffness of tubes and appendages of benthic organisms, for example, are likely to have evolved to withstand drag forces in the environment, there may be structural or biological limits to tube and appendage stiffness and morphology, and animal distributions may reflect these limits. That is, there may be an upper limit to flows in which tube-dwellers can reside, due to the drag on feeding appendages, as well as on tubes. To our knowledge, this possibility has not been explored for infaunal organisms, but the studies of Koehl (1977a, b, c), for example, on the distribution of sea anemones relative to the flow forces they encounter suggest that animal distributions can, in fact, be determined, at least in part, by the fluid dynamic environment (see also Koehl 1984). Lift forces are likewise a function of velocity squared and may affect animal distributions, as suggested by O'Neill (1978) for sand dollars.

Passive, suspension-feeding tube-dwellers are also known to utilize the flow regime to enhance food capture. (The broader subject of food supply to suspension-feeders as a function of boundary layer flow is discussed later, p. 156.) In a steady flume flow, Carey (1983) showed that tubes of the terebellid polychaete *Lanice conchilega*, which project above the sediment surface, create a characteristic vortex pattern downstream. The upward motion associated with the vortices may increase particle resuspension in the lee of the tube,

particles that may then be captured as food by the tentacular crown of the worm. Likewise, Johnson (1990) suggested that the spacing of individuals within a bed of phoronids enhances the incorporation of benthic food items into their diets through passive entrainment by the flow. In addition, some tube-dwellers are known to orientate tube openings relative to flow direction (Brenchley & Tidball 1980, Vincent et al. 1988), a strategy that may decrease the energy required for particle capture.

Very dense assemblages of tube-dwellers can potentially enhance particle retention time within the tube bed via skimming flow (described earlier, p. 134), although the densities required may rarely occur in natural populations (Eckman et al. 1981). The flow regime associated with tubes protruding above the bed may indirectly result in a stabilized sediment bed (in the sense of decreasing the probability of sediment erosion) via enhanced nutrient flux to and thus microbial growth within the sediments (Eckman 1985). This more stable bed may then facilitate the existence of species that otherwise could not occur within that flow and sediment-transport regime.

The exchange of pore waters, and thus, the depth within the sediment that is oxygenated, is related to the near-bed flow regime and the geometry of pore spaces, both of which correlate with sediment size. Microbial population growth is another potentially important variable that is strongly correlated with near-bed flow (reviewed by Nowell & Jumars 1984). For example, intermediate current velocities at the HEBBLE site off of Nova Scotia resulted in stimulation of microbial growth and removal of metabolites (Aller 1989). Other aspects of pore-water chemistry (e.g. sulphide concentrations) may similarly be controlled by the near-bed flow regime (Ray & Aller 1985) and limit species distributions.

Small, near-surface-dwelling organisms that are susceptible to erosion, such as some meiofaunal species (larval supply is treated elsewhere) may be transported directly by the near-bed flow regime. Palmer & Gust (1985, see also Bell & Sherman 1980) have shown, for example, that meiofauna can be resuspended and transported by everyday tidal flows on intertidal mudflats. There appears to be a behavioural basis for meiofaunal taxa that are susceptible to passive transport (Palmer 1984). Depth distributions of meiofauna within the sediment bed are also known to be both taxon-specific and a function of flow regime (Palmer & Molloy 1986, Fegley 1988). The broader topic of marine meiofaunal dispersal and distributions as a function of the boundary-layer flow regime has been reviewed recently by Palmer (1988a).

The hydrodynamic regime also may be utilized by animals to enhance the probability of fertilization during spawning, or to otherwise facilitate gamete dispersal. Barry (1989) suggested that a reef-building tube-worm spawns in response to big storms, evidently to enhance zygote dispersal. Tidally-timed spawning behaviour has also been demonstrated for several invertebrate species (Stanczyk & Feller 1986).

As a final note on hydrodynamic regime and benthic communities, it is very likely that intertidal, subtidal and deep-sea habitats are impacted by bottom flow in very different ways. For example, depressions on the seafloor in deep-sea, soft-sediment habitats, which may persist for several years (Snelgrove, pers. obs.), may accumulate detritus (Aller & Aller 1986, Thiel et al. 1988) and display elevated biological activity (Aller & Aller 1986). In muddy, subtidal habitats, structures may persist for periods of weeks or less, as biological modification and storm events obliterate patches (B. Butman 1987a). Accumulation of macroalgae and settling larvae has been observed in artificial depressions compared with flush sediments in this type of habitat (Snelgrove 1994); however, in intertidal and high-energy subtidal communities, accumulation of organic matter and/or organisms has been noted in some studies (VanBlaricom 1982, Savidge & Taghon 1988) but not in others

(Reidenauer & Thistle 1981, Oliver et al. 1985, Hall et al. 1991). The inconsistency in results for high-energy environments may reflect the complex interaction between high-energy flow and the particle trapping characteristics of depressions (Yager et al. 1993), and the short-lived nature of the accumulation. In this type of habitat, structure may be obliterated over a single tidal cycle (Sun et al. 1993) or persist for days to weeks (VanBlaricom 1982, Savidge & Taghon 1988, Hall et al. 1991). Thus, hydrodynamic effects, through transport of sediment, larvae and organic material, may affect intertidal, subtidal and deep-sea, soft-sediment communities in different ways, and at different scales. It has been suggested, in fact, that temporal and spatial scales of patchiness may be responsible for fundamentally different types of communities in shallow-water and deep-sea habitats (Grassle & Sanders 1973, Snelgrove et al. 1992).

Larval supply

The last decade has seen a surge of interest in larval ecology, particularly from the standpoint of how supply may influence spatial pattern (Lewin 1986). The recognition of the importance of larval availability is not new (see Young 1987), however, and annual fluctuations in larval availability have long been thought to contribute to temporal variation in local species pattern (Thorson, 1957). Nonetheless, the linkage between physical and behavioural aspects of larval dispersal and settlement over realistic spatial scales is changing our perception of how patterns are initially established (C. A. Butman 1987). Indeed, the present view of larval dispersal is very different from Petersen's (1913) perception of a "rain of larvae" to the sea floor followed by differential mortality.

Early small-scale, sediment-selection studies conducted in still water (Table 2, p. 124) led to a general acceptance of the notion that habitat specificity in species distributions may be the result of active habitat selection by larvae. These experiments, as well as the scales at which they were conducted, are discussed in detail by C. A. Butman (1987) and will be treated here only briefly. A number of the species tested displayed some form of habitat selectivity in still water (Table 2); these studies have demonstrated that active habitat selection is probably important on at least some scale for most species. It is unclear, however, how selective behaviour operates in nature because very few choice experiments were conducted in realistic flow regimes. For at least some soft-sediment species, mean horizontal flow speeds greater than their maximum horizontal swimming speeds occur at heights of only several body lengths above the bottom (Butman 1986). Thus, hydrodynamics are likely to affect larval settlement at least at some spatial scale. Correlations between distributional patterns of early recruits and sediments have been interpreted both as an active response to sediment type (including grain size) and as a result of passive deposition (reviewed by C. A. Butman 1987).

Laboratory flume studies designed to test directly the relative importance of passive deposition compared with active selection over scales of centimetres in slow, turbulent flows suggest that both passive and active processes contribute to settlement patterns. In flow- and still-water experiments, *Capitella* sp. I selected a particular sediment type on a fine spatial scale although sediment choice appeared to be hydrodynamically constrained by flow direction (Butman et al. 1988b, Butman & Grassle 1992, Grassle et al. 1992b). Larvae of *Mulinia lateralis* were also capable of habitat selection in still water and flow (Grassle et al. 1992a); selection in flow was, however, more consistent among replicate experiments, suggesting that near-bottom currents may facilitate selection by transporting these relatively

poor swimmers across different sediment environments for their perusal. Experiments testing selectivity of *Mulinia lateralis* and *Capitella* sp. I transported over small depressions containing different sediment types indicated that larvae were entrained in depressions like passive particles, but were generally able to escape if the substratum was unsuitable (Snelgrove et al. 1993). In all of these studies, larvae were evidently delivered to the bed passively, and then actively elected to stay or to leave. The recent flume study of Jonsson et al. (1991) indicated that bivalve pediveliger dispersal may be constrained by near-bottom flows. They suggested that as pediveligers swim upwards in a characteristic helical motion, the vertical shear within the viscous sublayer in hydrodynamically smooth, turbulent flow may induce torque on the larvae. This could make swimming above the sublayer impossible, thus confining pediveligers to the water immediately (i.e. millimetres) above the sediment. Thus, flume studies suggest that hydrodynamics as well as behaviour, are important, but admittedly relatively few studies have been done and it would be premature to try to draw generalizations based on these studies alone.

One of the few early field studies to consider hydrodynamics within the context of larval transport and settlement was Pratt's (1953) survey of *Mercenaria mercenaria* distributions in Narragansett Bay. Adult densities were highest in fine sediments with shell and rock. Pratt suggested that roughness features might provide microhabitats of low velocity suitable for settling in high-flow areas, which would be advantageous feeding environments for the suspension-feeding adults. Enhanced sand dollar settlement has also been noted on cobbled sand compared with a sandflat, with a similar possible explanation (Birkeland et al. 1971). Furthermore, Tyler & Banner (1977) noted a correlation between fine sediment and adult ophiuroid density, and attributed it to hydrodynamic effects on larvae – larvae might be sorted and deposited similarly to fine sediments in low-energy areas.

Results of efforts to conduct field sampling on a fine scale have also suggested that hydrodynamics may impose considerable constraints on distribution and eventual settlement site. Fine-scale sampling of larvae in estuaries (see review by Stancyk & Feller 1986) suggests that distributions are constrained by physical processes. Meroplankton distributions in Kiel Bay, Germany, appeared to be tied to the water masses in which spawning took place (Banse 1986), suggesting that these organisms behaved as passive, neutrally buoyant particles. Cameron & Rumrill (1982) found that sand dollar larvae on the California coast were advectively transported as a patch over sand-dollar beds and less suitable habitats (Cameron & Rumrill 1982), again suggesting passive transport and deposition. Larvae of the polychaete, *Pectenaria koreni*, showed vertical stratification in the water column in the western Bay of Seine, France, when turbulence was low, but they were homogeneously distributed when turbulence was high, suggesting passive mixing during high turbulence but possible active migration during low turbulence (Lagadeuc 1992). A similar effect was observed in *Owenia fusiformis* larvae (Thiébaut et al. 1992); however, only early stages were vulnerable to passive mixing and the resulting seaward transport. Older stages were able to migrate to water column strata which promoted retention in the Bay. Tidal transport of larvae may also be an important dispersal mechanism: Levin (1986) found ten-fold variations in larval abundance in Mission Bay, California, and suggested that a large patch of larvae was oscillating across the mudflat with flood and ebb tides. Unfortunately, extensive time-series measurements of larval distributions over large areas are relatively rare in non-estuarine habitats. Particularly needed are large-scale, simultaneous measurements of larval distributions and initial larval settlement to compare with subsequent recruitment and survival to reproduction.

Several studies have observed comparable settlement over adjacent areas with different

sediment types (Smidt 1951, Muus 1973) or biological structures (Luckenbach 1984), suggesting that larvae of at least some species may be non-selective or, if they settled passively, that the depositional regime was similar among the different sampling locales at the time of settlement. In two recent studies where differences in abundances of newly-settled recruits of the bivalves *Macoma balthica* (Günther 1991) and *Mya arenaria* (Günther 1992) were documented along a sediment gradient, both active biological and passive transport processes may have been responsible. In none of these studies, however, was variability in larval supply (i.e. flux from the water column) across sediment types measured, although the spatial scale of sampling was generally small.

Experimental field manipulations designed to evaluate the importance of flow and larval distribution have suggested that fine-scale hydrodynamics may be important in larval supply. Eckman (1979) found differential recruitment in intertidal species of tanaid crustaceans and direct-developing polychaetes near simulated animal tubes, suggesting that the distribution of benthic larvae was influenced by fine-scale hydrodynamics. In a later study (Eckman 1983), tube spacing and density were also shown to influence recruitment, confirming that hydrodynamics can have a very large impact on organism distribution. It is unclear, however, whether the patterns observed reflected passive deposition or an active response by larvae to some aspect of the different flow environments or to something that correlates with fine-sediment distributions, such as organic matter. Field experiments by Kern & Taghon (1986) on passive accumulation near epibenthic structures, where an enrichment treatment was also tested, indicated that both active behavioural responses and physical transport processes determined small-scale recruitment patterns. Similarly, Savidge & Taghon (1988) demonstrated enhanced settlement in depressions compared with flush sediment, suggesting passive accumulation. Utilizing biases in sediment-trap collection efficiencies, Butman (1989) showed that traps with higher collection efficiencies for passive particles tended to collect higher numbers of most taxa of larvae compared with traps with lower passive collection efficiencies, suggesting that larvae may be passively transported and deposited like sediment particles.

Given that flow may determine where larvae are transported, the potential importance of hydrodynamics in distributions of infaunal species becomes obvious. Larvae may be sorted like passive particles, and thus may be associated with a given sediment type for this reason alone. Predicting the onset of larval competency is a critical issue in larval ecology at present (Pechenik 1990, Bachelet et al. 1992); however, it is known that some lecithotrophic species may delay metamorphosis without any detrimental effect on survival, growth and fecundity (Pechenik & Cerulli 1991 and J. P. Grassle, pers. comm. for *Capitella* sp. I) whereas some planktotrophic species have a relatively narrow window where selective settlement is possible (Grassle et al. 1992b for *Mulinia lateralis*). Short development times to competency increase the probability of at least staying within the vicinity of the habitat of the adult, which may be favourable. A short competency period for a species that is highly habitat specific may decrease the likelihood of settlement on a suitable substratum, particularly if the larvae are vulnerable to passive hydrodynamic deposition. An extended development time in the plankton, however, might increase the likelihood of dispersal away from the parental habitat, perhaps to unfavourable sites (Jackson & Strathmann 1981). This is an important subject area for future research.

Flow may also redistribute settled individuals and this may be an important means of dispersal, particularly for direct developers (Sigurdsson et al. 1976). Post-larval transport has been noted for a number of species, including *Cerastoderma edule* (Baggerman 1953), *Mya arenaria* (Matthiessen 1960, Emerson & Grant 1991), and *Macoma balthica* (Günther

1991). Given that fall velocities of competent polychaete and bivalve larvae are within the range of fine silts (Butman et al. 1988a, Grassle et al. 1992b), and that post-larvae of at least one bivalve species (*Mercenaria mercenaria*) are within the range of sands (Peterson 1986, C. M. Webb & C. A. Butman unpubl. data) the probability of passive redistribution of settled individuals would be higher in high-energy environments, and may therefore be important to animal–sediment associations in sandy, erosional areas.

In summary, the hydrodynamic factors that determine the sedimentary composition of an environment may similarly determine the larval supply to that habitat. Although there is experimental support for passive deposition operating at several spatial scales, results may be confounded by, for example, active selection by some species for organic-rich sites where fine particles accumulate. Thus, larval supply is an indirect correlate of sediment type that could result in what appear to be consistent animal–sediment associations. Sorely needed are field experiments specifically testing the passive deposition and active habitat selection hypotheses, including quantification of larval supply as well as subsequent survival of recruits within their depositional (or actively selected) locales.

Food supply

Food supply to benthic organisms is heavily dependent on local flow conditions, which we have shown to be a primary determinant of sediment distributions. Muddy sediments generally have a higher organic content than sandy sediments because organic matter tends to be more closely associated with the lighter, depositional sediment fraction that accumulates in low-flow areas. Within such flow environments, rates of particle transport tend to be low in the horizontal and high in the vertical. In sandy environments, fine particles may still deposit, but they tend to resuspend easily and are transported both vertically (upward mixing) and horizontally, resulting in little accumulation of fine sediment and organics. Thus, the organic content of sediment is affected by the large-scale flux of particulate matter and differential binding to sediment particles.

Even within a sedimentary regime, hydrodynamics influence sedimentary organic content and thus the infauna. This may be illustrated by summarizing studies on effects of small-scale topographic variation on the distribution of organic matter and infauna. In a variety of habitats, ranging from shallow water (VanBlaricom 1982) to the deep sea (Grassle & Morse-Porteous 1987), organic material has been observed to accumulate in small (tens of centimetres) depressions, as a direct result of their trapping characteristics. Not surprisingly, in different flow environments, coarse (Nelson et al. 1987) or fine sediment (Risk & Craig 1976) may also accumulate in depressions, although this would not be expected in habitats with homogeneous sediments. Variation in topography and organic content has been related to faunal distributions in a variety of habitats. Intertidal amphipods tend to accumulate in ripple troughs (Sameoto 1969), which may be an active response of the organisms to enhanced detrital accumulation in troughs; however, in some instances, amphipods (Grant 1981) and nematodes (Hogue & Miller 1981) have been shown to occur in greater abundance in ripple crests than troughs. Organisms may respond actively to elevated organic levels resulting from material accumulating in troughs during low tide, followed by passive burial in the following high tide by migrating ripples. Higher densities of colonizers have been observed in depressions compared with defaunated flat areas (Savidge & Taghon 1988), and passive advection was postulated as a probable explanation. Diatom films on the surface of the sediment may also vary across topographic features. Under calm flow conditions, thicker

films may be found in ripple troughs and slopes (Grant et al. 1986a). Such differences in film thickness may be an important source of food variation. Detritus, worm tubes and algae have all been observed to accumulate in pits created by ray foraging (VanBlaricom 1982), and changes in carbon to nitrogen ratios have suggested that initial detritus was colonized by bacteria and algae, and then by macrofauna. Although this has the potential to be an important source of heterogeneity in some habitats, other habitats, such as walrus feeding pits, have elevated organic content but very modest faunal differences compared with adjacent undisturbed flat areas (Oliver et al. 1985). Thus, the magnitude and types of responses to small-scale variation in organic content, be they active or passive, are almost certainly a function of the ambient faunal composition and the local flow regime.

These studies indicate that fine-scale flow variation may result in a variety of different types of food patches and infaunal responses. Unfortunately, they fail to clarify whether colonizers are passively entrained with the organic matter, which they may then utilize, or whether they are actively responding to it. These studies do illustrate how the same small-scale hydrodynamics that can influence sedimentary composition may also influence food availability and result in faunal responses (be they active or passive).

The availability of food in suspension may also be limiting to the distribution of many organisms. Because many suspension-feeders depend on the horizontal transport of organic matter, their distributions may be confined to areas of relatively high fluid velocity (Sanders 1958, Wildish 1977); such high-flow areas also tend to be dominated by relatively coarse, low-organic sediments. Rates of suspension-feeding and growth are a function of food supply in a variety of taxa (Muschenheim 1987b, Grizzle & Lutz 1989, Grizzle & Morin 1989, Peterson & Black 1991, Turner & Miller 1991b), clearly influencing distributions of organisms. Resuspension of bottom material may augment phytoplankton as food for some suspension-feeding bivalves (Grant et al. 1986b, 1990), although other species have shown decreased growth in relatively high turbidity (Bricelj et al. 1984, Murphy 1985, Grizzle & Lutz 1989, Huntington & Miller 1989, Turner & Miller 1991b). Moreover, as discussed earlier, suspension-feeding is not necessarily limited to those animals living in relatively coarse sediments.

The process of filter-feeding is complex, however, because there are a variety of different particle-trapping mechanisms (Rubenstein & Koehl 1977, LaBarbera 1984, Shimeta & Jumars 1991), and the type of suspension-feeder may range from flow-dependent, facultative suspension-feeders (Taghon et al. 1980, Miller et al. 1992), to organisms that resuspend depositional material for feeding (Mills 1967), to active and passive suspension-feeders (Jørgensen 1966). Thus, the relationship between suspension-feeder distribution and flow regime may be extremely complex.

Suspension-feeders become proportionally less abundant with increasing water depth, perhaps as a result of a decrease in flux of organic matter where currents are generally weaker (Sanders et al. 1965, Jørgenson 1966). Passive suspension-feeders may also be confined to flow environments with greater horizontal fluid flux than active suspension-feeders, although the dichotomy of feeding type may be better described as a gradient (LaBarbera 1984). Flume studies have shown that the polychaete, *Spio setosa*, filter-feeds several centimetres above the bottom, which may be a response to the higher organic seston flux at this height compared with the higher proportion of dense inorganic particles closer to the bed (Muschenheim 1987b), again suggesting that horizontal flux is important. It is difficult, however, to imagine a mechanism by which infaunal organisms can detect and respond to a dynamic quantity such as food flux; it seems more likely that the biological response is to a scaler variable, such as suspended food concentration (Fréchette et al. 1993).

Historically, there has been a tendency to think of food supply to suspension-feeders in terms of either horizontal or vertical food flux, but horizontal advection and vertical mixing occur simultaneously and cannot be decoupled in nature. Models of the effects of vertical mixing alone on food supply to benthic suspension-feeders are unrealistic for the field because horizontal advection is also important for replenishing the food supply to an area (Fréchette et al. 1989). Higher growth rates of *Mercenaria mercenaria* have been observed in seagrass beds compared with adjacent sandflats (Peterson et al. 1984, Irlandi & Peterson 1991), for example, despite the lower horizontal food flux through the seagrass. In this case, the higher growth likely resulted from enhanced total particle flux (i.e. horizontal and vertical) created by the seagrass baffling. We suggest that, in all environments, it is important to consider the three-dimensional nature of fluid and particulate flux because horizontal and vertical flux are not, in fact, separable in nature (Fréchette et al. 1989).

Suggestions for future research

Although fauna and sediment grain-size distributions in many benthic habitats have been at least crudely characterized, subsequent sampling should be hypothesis driven and conducted over appropriate spatial and temporal scales. How the many different interactive variables that characterize a sandy or muddy habitat may contribute to faunal patterns can only be determined through controlled experimentation and sampling. Central to the problem of understanding animal–sediment relationships is the paucity of data on the natural history of organisms, particularly under realistic flow conditions. The feeding ecology within simulated or natural flow regimes is known for only a few species, and even less is known about feeding under simulated or natural sediment-transport conditions. Similarly, the behaviour of settling larvae under natural and simulated flow conditions has been studied in very few species. The development of new technology for observing animal behaviour under simulated natural conditions in the laboratory, such as sea-water flumes (Taghon et al. 1984) and water tunnels (Miller et al. 1992), high-speed movie cameras, low-light and high-resolution video cameras (Jonsson et al. 1991), and automated motion analysers (Butman et al. 1988a), now permits meaningful studies on how flux of organic matter, sediment, and larvae may contribute to spatial pattern in the benthos. Techniques now exist to allow precise measurement, and in some cases manipulation of, sedimentary variables such as grain size, composition and amount of living and non-living organic matter (Mayer & Rice 1992), and pore-water chemistry (Ray & Aller 1985), either *in situ* or in laboratory experiments. In some cases, it may also be possible to use passive tracers such as glass beads (Wheatcroft 1992) or rare-earth tags (Levin et al. 1993) to follow these variables over time and thus to establish how they interact with living organisms.

Equally important are field studies designed to address well-defined hypotheses on distributions of benthic species. For example, we are unaware of a successful attempt to track a cohort of soft-sediment larvae from fertilization to settlement, admittedly a difficult task but one that is now possible (see methods reviewed by Levin 1990) and well worth the effort. Similarly, frequent monitoring of larval supply over adjacent, contrasting habitats and evaluating initial settlement (before potential biological interactions take place) relative to recruitment would also help determine the rôles of hydrodynamics and larval selectivity

under natural circumstances. Studies on settlement and colonization have often suffered from insufficient resolution in temporal sampling, thus introducing a number of potential confounding factors. *In situ* and laboratory manipulation of sedimentary variables such as grain size (Zajac & Whitlatch 1982), pelletization (Miller & Jumars 1986), porosity and water content (Rhoads & Young 1970), stability (Grant et al. 1982), and sedimentary correlates such as organic content (Snelgrove et al. 1992), bacteria and algae (Kern & Taghon 1986, Kern 1990), will clarify the relative effects of these confounding factors. Similarly, bottom flow can be manipulated in the laboratory (Ertman & Jumars 1988, Snelgrove et al. 1993) and in the field (Eckman 1983, Butman 1989, Judge et al. 1992, Snelgrove 1994) by creating structures that alter flow in a predictable way. Manipulative experiments are now possible in virtually any habitat through use of SCUBA and manned and remotely operated underwater vehicles. The availability of this technology and other types of *in situ* visualization makes it possible to take more precisely placed samples where very detailed field observations of the hydrodynamic and sedimentary environment may be made. In the past researchers have had no means of evaluating the small-scale structure and variability of the habitat they were sampling, which may be an important determinant of the local benthos. Finally, instrumentation is now being developed that allows meaningful measurements of the sedimentary and flow regime within a given habitat at scales that are meaningful to individual organisms.

Although reductionist approaches have numerous drawbacks, they are an important tool for untangling the present web of ideas on animal–sediment associations. Existing paradigms to explain patterns in benthic communities have been derived from either very limited experimentation (trophic-group amensalism) or correlative field sampling (grain size, total organic carbon), and are clearly inadequate as explanations or predictive tools. Although no single variable or simple paradigm may be responsible for the spatial patterns that are observed in benthic assemblages, emerging technologies offer an opportunity to improve markedly on present understanding. Returning to the opening quote by Hutchinson (1953) regarding the concept of pattern in ecology, animal–sediment relationships probably are "a mere trivial expression of something we may learn to expect all the time", but that something or somethings are yet to be identified.

Acknowledgements

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