LARVAL SETTLEMENT OF SOFT-SEDIMENT INVERTEBRATES: THE SPATIAL SCALES OF PATTERN EXPLAINED BY ACTIVE HABITAT SELECTION AND THE EMERGING RÔLE OF HYDRODYNAMICAL PROCESSES[1,2]

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INTRODUCTION

While Robertson Davies (1985) was not discoursing on the mechanisms controlling larval settlement of soft-sediment invertebrates when he wrote the poignant phrase, ". . . science is the theology of our time, and like the old theology it's a muddle of conflicting assertions", a perusal of the literature on larval settlement from the last half-decade probably would only fortify this point of view. Since the alternative hypotheses of active habitat selection and passive deposition were identified, an adverse relationship between these mechanisms has been perpetuated in the literature with, seemingly, "conflicting assertions" as to which process is actually responsible for creating the observed distributions of postlarval and adult infauna. There are several notable exceptions, however, where a truce in the war between alternative hypotheses has been proposed by discussions of the space and time scales likely to be associated with each process and the implications to settlement. The present review expands on this theme. The process-orientated literature on larval settlement (primarily studies of active habitat selection) is summarized in terms of the scales of distribution that can be explained. The emerging rôle of bottom boundary-layer flows during settlement is discussed, again with a focus on the applicable scales of the processes. The intention is to illustrate that active habitat selection and passive deposition need not be competing, but are likely complementary, hypotheses by providing examples or proposed scenarios where both mechanisms would be operating, but separated in space and time. Thus, in retort to Davies' somewhat pessimistic view of the rigour of scientific explanations, I hold that when seemingly conflicting assertions are closely scrutinized they may all be valid replies but, in fact, to different questions.

The rôle of larval settlement in determining the distribution and abundance of soft-substratum organisms is still largely unknown (see Connell, 1985, for similar conclusions regarding the hard-substratum case). While factors

[1] In honour of the contributions of Douglas P. Wilson.
[2] Contribution No. 6303 from Woods Hole Oceanographic Institution.
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responsible for inducing larval settlement and metamorphosis have been identified primarily through laboratory experiments in still water, the importance of these factors as causative agents creating the observed infaunal distributions in the field can only be deduced. Little is known about how initial patterns of larval settlement relate to the eventual distributions of adults. Field studies to determine mechanisms controlling benthic community structure usually did not consider larval settlement phenomena. Even when larval settlement was included in analyses, the studies were rarely designed so that differential larval settlement could be distinguished from differential post-settlement mortality. Studies designed to determine mechanisms controlling larval settlement overwhelmingly favour the active habitat selection hypothesis; most of these studies did not, however, consider or test the alternative hypothesis that larvae are passively deposited onto the sea bed. Whether or not larval settlement sites in the field are determined, even in part, by boundary-layer flow processes has been largely a matter of data interpretation. The few field studies which experimentally explored the rôle of physical processes during settlement, however, demonstrate that hydrodynamical hypotheses are feasible alternative explanations for patterns of larval settlement and infaunal recruitment.

This paper reviews the process-orientated literature on soft-substratum larval settlement to establish the scales of observed pattern of infaunal distribution which can be explained by a given process. From this organization of the existing data, some new working hypotheses concerning the rôles of biology and physics during settlement are generated. In addition, conceptual and research gaps in the literature are identified. This is not an examination of the specific cues demonstrated to affect or effect settlement and metamorphosis (Table I), but is designed to complement other larval-settlement reviews by focusing on the scales of pattern and processes.

This review is limited to settlement of larvae of soft-sediment infaunal invertebrates, but the literature on hard substrata is tapped periodically to illustrate a particular point that has not been studied in a soft-substratum system. Aspects of the settlement of larvae onto soft and hard substrata may be similar, but there are sufficient differences or potential differences in biological and physical features of these habitats, to which the larvae may respond, that separate discussions are warranted. Hard substrata are basically two-dimensional and organisms must attach to the surface, while sediments are three-dimensional and organisms can escape flow forces and other surface phenomena by burrowing into this third dimension (see Woodin & Jackson, 1979). In addition, characteristics of flows over soft substrata may differ from flows over hard substrata because of the nature of the roughness elements and because moveable-bed effects (*e.g.* Smith & McLean, 1977; Grant & Madsen, 1982) apply only to sediments. Crisp (1984) and Connell (1985) provide recent reviews of factors controlling settlement onto hard substrata although there is not yet a formal treatment of the rôle of hydrodynamical processes (but see Nowell & Jumars, 1984; Wethey, 1986).

The physical behaviour of planktonic stages of organisms in fluid flows is probably segregated more by size and taxonomic position than by the nature of the substratum on or in which the organisms live. For example, crustacean larvae generally swim an order of magnitude faster than polychaete larvae (see reviews of Mileikovsky, 1973; Chia, Buckland-Nicks & Young, 1984).

TABLE I

Reviews of factors (e.g. cues) affecting or inducing settlement or metamorphosis of benthic organisms

Reference	Group or taxa reviewed
Thorson (1957, 1966)	Soft-substratum organisms
Wilson (1958)	Soft- and hard-substratum organisms
Bergquist, Sinclair & Hogg (1970)	Demosponges
Meadows & Campbell (1972a)	Soft- and hard-substratum organisms, as well as freshwater organisms
Campbell (1974)	Cnidarians
Crisp (1974, 1976, 1984)	Soft- and hard-substratum organisms, with special emphasis on barnacles
Fell (1974)	Sponges
Gray (1974)	Soft-substratum organisms
Scheltema (1974)	Soft- and hard-substratum organisms
Berrill (1975)	Tunicates
Schroeder & Hermans (1975)	Polychaetes
Beeman (1977)	Opisthobranch gastropods
Chia & Bickell (1978)	Coelenterates
Eckelbarger (1978)	Sabellariid polychaetes
Hadfield (1978a)	Molluscs
Lewis (1978)	Cirripedes
Strathmann (1978)	Echinoderms
Switzer-Dunlap (1978)	Aplysiid gastropods
Andrews (1979)	Oysters
Pearse (1979)	Chitons
Sastry (1979)	Bivalves (excluding oysters)
Guérin (1982)	Soft- and hard-substratum organisms
Burke (1983)	Hard-substratum organisms
Day & McEdward (1984)	Soft- and hard-substratum organisms

Concerning the effects of flow physics on sinking and settlement of larvae, the size of the organism and its fall velocity are the most important considerations (see Hannan, 1984a). Thus, in discussions of physical processes, I often include studies of any organism within the size range of infaunal larvae.

For clarity, the definitions of some terms commonly used in larval studies are reiterated here. Planktonic larvae of infaunal invertebrates undergo larval development in the water column during the dispersal phase of their life history. Dispersal is entirely a water column phenomenon; larvae are generally considered to be developing and not ready to settle during large-scale dispersal. Dispersing planktonic larvae are easy to identify in certain groups, such as the Crustacea, where several distinct larval stages precede a final larval form that can settle onto the substratum. In other groups, such as the Polychaeta, larval development usually involves the gradual addition of segments and loss of ciliation; cessation of planktonic development, and thus, of the dispersal phase, may be more difficult to identify in these groups.

Dispersal is largely regarded as passive transport by water currents because the scales of horizontal water motion are so much greater than the swimming

speeds of larvae (Mileikovsky, 1973). Active behavioural and physiological responses of larvae (e.g. phototaxis, geotaxis, and responses to salinity changes) may, however, displace them vertically into water masses where fluid motion may not be large compared with the movements of the larvae (Mileikovsky, 1973, but see also Butman, 1986a). Thus, there is an active component to dispersal in many organisms because they can make vertical migrations into particular water masses (e.g. see review by Sulkin, 1984, for decapod larvae). The relative contribution of active larval behaviours compared with passive transport processes for the retention of larvae in estuaries has been debated for several decades (see Kennedy, 1982, for recent papers on this topic); contemporary ideas on larval dispersal processes can be found in the overview by Scheltema (1986).

   Planktonic larval development was separated into two periods for the gastropod, *Nassarius obsoletus*, by Scheltema (1967): a development period during which growth and differentiation of the larva occurs and a delay period during which there is a gradual decrease in growth and the larva is physiologically capable of metamorphosis. During metamorphosis, an organism undergoes certain morphological changes that "portend a new way of life" (Scheltema 1974, p. 263). For organisms with a planktonic larval stage, settlement is defined as "the termination of a pelagic, larval existence and the assumption of a sessile or nonsessile sedentary life", Scheltema (1974, p. 263). Usually larvae considered available for settlement include only larvae that have entered the delay period of their planktonic development and, thus, are competent to metamorphose. For many species this is difficult to determine, except *ex post facto*; even in laboratory experiments, discerning if an unmetamorphosed larva is capable of metamorphosis is difficult because once the organism has passed through the development period, it may require a specific cue for metamorphosis to occur (see reviews listed in Table I). None the less, in this review larvae considered to be available for settlement are only those within the delay period of their planktonic larval development (*i.e.* competent larvae).

   It is important to distinguish clearly between metamorphosis, settlement, and recruitment. Metamorphosis may precede, coincide with, or follow settlement and refers to an irreversible set of anatomical and physiological changes in the organism presumably "coordinated through an endocrine mechanism" (Scheltema, 1974, p. 263). Metamorphosed larvae are referred to as postlarvae in this review. Settlement "denotes a responsive behaviour" and is "presumed to be under nervous control" (Scheltema, 1974, p. 263). While this definition could imply an active choice by the larva to settle, the interpretation used here is that, during settlement, the organism takes up activities or behaviours (*e.g.* burrowing and tube building) which are indicative of the benthic life history stage. Thus, whereas metamorphosis involves morphological and physiological changes from a larval to a postlarval form, settlement involves a change in venue from a planktonic to a benthic existence. Unfortunately, this definition of settlement implies that once settled, the organism will not re-appear in the water column but will reside entirely in or on sediments. In this regard, Scheltema's (1974) definition of settlement must be modified because there are mounting records of the occurrences of postlarval and adult benthic organisms in the water column (see Table II), exclusive of swarming behaviour for spawning and reproduction.

TABLE II

Observations of benthic postlarval and adult polychaetes, molluscs, and meiofauna in the water column: some studies may have collected larval forms along with immature and adult organisms; this information usually was not given in the paper; when information on the state of maturation of the collected organisms was given in the paper, the name of the organism is followed by: A = adult, F = female with eggs, I = immatures, NE = not epitokous, NS = non-spawners, PM = post-metamorphic, S = some individuals may have been spawning; all species listed are polychaetes, unless noted as B = bivalve

Reference	Method of observation	Organisms observed
Bayne (1964)	Plankton tows	*Mytilus edulis* (B)
Emery (1968)	Plankton tows; suction devices	Nereids and other polychaetes
Williams & Porter (1971)	Plankton tows	*Ensis directus* (B, PM) *Tagelus divisus* (B, PM) *Solemya* (= *Solenomya*) *velum* (B, PM) *Solen viridis* (B, PM) *Donax variablis* (B, PM) *Petricola pholadiformis* (B, PM) *Spisula raveneli* (B, PM)
Seymour (1972)	Laboratory observations, but cites Fage & Legendre (1927) for field observations	*Arenicola marina* (NS)
Thomas & Jelley (1972)	Emergence traps	*Eteone lactea* *Glycera dibranchiata* *Nereis succinea* (I, A, S) *Nereis virens* (I, A, S) *Pherusa affinis* *Scoloplos fragilis* (F, S)
Beukema (1973)	Plankton tows	*Macoma balthica* (B)
Porter (1974)	Plankton tows	Polychaetes (A)
Hobson & Chess (1976)	Plankton tows	Polychaetes
Alldredge & King (1977)	Emergence traps; plankton tows	Polychaetes from the families: Syllidae, Orbiniidae, Opheliidae
Porter & Porter (1977)	Emergence traps	Polychaetes
Porter, Porter & Batac-Catalan (1977)	Emergence traps	Polychaetes
Dean (1978a)	Direct observations of surface waters at night with search-light; specimens collected with dipnet	*Nereis virens* (I)
Dean (1978b)	Direct observations of surface waters at night with search-lights; buoyed and anchored nets	*Glycera dibranchiata* (I) *Glycera capitata* (I) *Eteone longa* (F) *Nephtys discors* *Glycera* sp. (I) *Nereis virens* *Pherusa affinis*

TABLE II–*continued*

Reference	Method of observation	Organisms observed
Graham & Creaser (1978)	Buoyed and anchored plankton nets	*Glycera dibranchiata* (A, NS)
Beukema & DeVlas (1979)	Plankton tows	*Arenicola marina* (I)
Hobson & Chess (1979)	Emergence traps	Polychaetes
Alldredge & King (1980)	Emergence traps	*Brania* sp. (F, S)
		Sphaerosyllis hystrix (F, S)
		Armandia brevis (A, NE)
		Aricidea sp. (A)
		Prionospio heterobranchiata newportensis (A)
		Pseudoeurythoe sp. (A)
		Gyptis brevipalpa (A)
		Protodorvillea gracilis (A)
		Nematonereis unicornis (A)
Hammer & Zimmerman (1979)	Emergence traps	Syllidae, sp. A
		Alciopidae, sp. A
		Autolytus sp.
		Diopatra ornata
		Eunoe sp.
		Exogone sp.
		Lumbrineris sp.
		Odontosyllis sp.
		Schistomeringos longicornis
		Platynereis bicanaliculata
		Meiofauna
Bell & Sherman (1980)	Samples of water overlying sediments	Meiofauna
Dauer, Ewing, Tourtellotte & Barker (1980)	Plankton tows; direct observations of surface waters	*Scolecolepides viridis* (I, A, S)
Santos & Simon (1980a)	Containers filled with sediment raised 0·5-m above bottom	*Nereis succinea* (A)
		Gyptis vittata (A)
		Parahesione luteola
		Stylochus sp.
Bhaud, Aubin & Duhamel (1981)	Near-bottom sediment traps	*Phyllodoce* sp. (I or A)
		Polydora antennata (I or A)
		Spio martinensis (I or A)
		Amphictenidae (I or A)
		Polyophthalmus pictus (I or A)
		Ophryotrocha sp. (I or A)
		Lamellibranchs (B, I or A)
Hagerman & Rieger (1981)	Sediment traps	Meiofauna
		Meiobenthic polychaetes
Hammer (1981)	Emergence traps	*Schistomeringos longicornis*
		Minuspio spp.
		Odontosyllis sp.
		Hesionids
Levin & Greenblatt (1981)	Plankton tows	*Loimia* sp. (I)

TABLE II–*continued*

Reference	Method of observation	Organisms observed
McWilliam, Sale & Anderson (1981)	Emergence traps	*Exogone* sp. (I) *Armandia* sp. (I) Other polychaetes
Tranter *et al.* (1981)	Downward-directed light traps	Polychaetes
Ohlhorst (1982)	Emergence traps	Polychaetes
Dobbs & Vozarik (1983)	Filtrate from power plant cooling system	Polychaetes (47 species) Bivalves (7 species) Gastropods (12 species)
Levin (1984)	One-gallon plankton jar samples	*Exogone lourei* (A, S, F) *Odontosyllis phosphorea* (A, S) Harpacticoid copepods
Hannan (1984b)	Near-bottom sediment traps	*Mediomastus ambiseta* (A, I)
Palmer & Gust (1985)	Pump samples of near-bottom water	Meiofauna
Levin (1986)	One-gallon plankton jar samples	*Streblospio benedicti* (I) *Rhynchospio arenincola* (I)

In contrast to dispersal, metamorphosis, and settlement, recruitment is not a physiologically or behaviourally distinct stage in the life history of the organism, but is observer-defined; the organisms surviving to a size collected by the sampler are considered recruited individuals (Keough & Downes, 1982). Because recruitment generally is defined by the sieve screen size and the sampling interval in infaunal studies, recruited organisms can be unmetamorphosed larvae, postlarvae, juveniles, or even adult organisms. Note, however, that settlement refers only to larvae or, when larvae metamorphose prior to settlement, postlarvae.

By these definitions, in order to study settlement, the first larval stages to reach the sea bed and begin living as benthic organisms must be sampled; to emphasize this, I often refer to these as "initially settled larvae" in this review. As Keough & Downes (1982) and Connell (1985) recently elucidated for hard-substratum organisms, most studies which claim to measure larval settlement have actually measured recruitment.

PATTERNS OF JUVENILE AND ADULT DISTRIBUTION

Research on factors that determine settlement sites for infaunal larvae was motivated by early documentation (*e.g.* Petersen, 1918) of distinct faunal assemblages that vary spatially. The procession of benthic survey studies which followed further revealed that species distributions are often well correlated with distributions of particular sediment grain sizes (Table III and summaries of the early work by Thorson, 1955, 1957; but see also conclusions of McNulty, Work & Moore, 1962b; Santos & Simon, 1974). The spatial

TABLE III

Benthic survey studies where infaunal communities and sediment grain sizes were documented over areas of the sea floor: the intention of this table is to give a historical perspective of the sampling scales, sampling intervals and sieve sizes used in a selection of survey studies where benthic communities and sediments were sampled simultaneously; the list is intended to be illustrative, not exhaustive; minimum distances between stations were usually estimated from plots of station locations on maps of the study sites; NG = information not given in the reference; sampled once = each station was sampled once only and not necessarily simultaneously with the sampling of the other stations

Reference	Location of study	Depth (m)	Sieve screen size (μm)	Minimum sampling interval	Minimum distance between stations (m)
Ford (1923)	Plymouth, England	NG	"series of screens"	Sampled once	123
Spärck (1933)	Franz Joseph Fjord, East Greenland	27–780	NG	Sampled once	730
Stephen (1933)	Northern North Sea, Scotland	0–200	1500, 2000	Sampled once	NG
Thorson & Ussing (1934)	Scoresby Sound Fjord Complex, East Greenland	20–530	NG	Sampled once	1760
Holme (1949)	Mouth of Exe Estuary, England	Intertidal	1000	Sampled once	30
Sanders (1956)	Long Island Sound, NY	6–31	300, 2000	2 months	3220
Sanders (1958)	Buzzards Bay, MA	7–20	500	Sampled once	1850
Wieser (1959)	Puget Sound, WA	Intertidal	Not sieved	Sampled once	NG
McNulty, Work & Moore (1962a)	Biscayne Bay, FL	2–10	1000	Sampled once	230
Sanders, Goudsmit, Mills & Hampson (1962)	Barnstable Harbor, MA	Intertidal	Unscreened, 750	1 yr	NG
Buchanan (1963)	Coast of Northumberland, North Sea	10–90	NG	Sampled once	1800
Wigley & McIntyre (1964)	South of Martha's Vineyard, MA	40–567	74, 1000	Sampled once	1800
Cassie & Michael (1968)	Manukau Harbor, North Island, New Zealand	Intertidal	2500	Sampled once	800

Gray (1968)	Eagle Cove, San Juan Island, WA	Intertidal	"fine plankton net"	1·5 months	10
Lie (1968)	Puget Sound, WA	12–200	1000	2 months	2000
Gibbs (1969)	Plymouth Sound, England	2–12	500	Sampled once	50
Lie & Kisker (1970)	Juan de Fuca Strait and off Washington coast, USA	13–317	1000	Sampled once	1800
Nichols (1970)	Port Madison, Puget Sound, WA	2–34	1000	Sampled once	75
Day, Field & Montgomery (1971)	Beaufort Shelf, NC	0–200	1000	2 months	1110
Hughes & Thomas (1971)	Biddeford River, Prince Edward Island, Canada	Intertidal	500	Sampled once	5
Johnson (1971)	Tomales Bay, CA	0–18	1500	NG	NG
Pearson (1971)	Lochs Linnhe and Eil, Scotland	0–>90	1000	Sampled once	250
Bloom, Simon & Hunter (1972)	Tampa Bay, FL	Intertidal	1000	4 months	20
Gage (1972a,b)	Lochs Etive and Crenan, Scotland	0–117	1000	Sampled once	710
Hughes, Peer & Mann (1972)	St. Margarets Bay, Nova Scotia	18–>60	800	Sampled once	175
Eagle (1973)	Liverpool Bay, England	5–11	500, 1000	5 months	310
Gage & Geekie (1973b)	Loch Etive, Scotland	20–60	1000	Sampled once	100
Santos & Simon (1974)	Tampa Bay, FL	Intertidal	500	3 months	90
Crumb (1977)	Delaware River, NJ	Intertidal	500, 1000	1 month	4000
Mountford, Holland & Mihursky (1977)	Chesapeake Bay, MD	3–9	1000	3 months	280
Tyler & Banner (1977)	Oxwich Bay, Bristol Channel, Wales	5–20	1000	Sampled once	55
Whitlatch (1977)	Barnstable Harbor, MA	Intertidal	250	1 month	65
Larsen (1979)	Sheepscot Estuary, ME	0–9	1000	Sampled once	NG
Flint & Holland (1980)	Gulf of Mexico, TX	22–131	500	1 month	6390
Shin & Thompson (1982)	Coastal waters of Hong Kong	13–70	400	2 months	500
Maciolek & Grassle (in press)	Georges Bank, MA	38–168	300	3 months	500

scales (tens of metres to tens of kilometres) separating distinct assemblages and sediment types were, in part, dictated by the manoeuvrability of the sampling vessel and the accuracy of shipboard-operated navigational equipment; minimum distances between subtidal stations ranged from 50 m to 64 km, while intertidal communities could be sampled at closer intervals of 5 m to 800 m (Table III). In addition, once a relationship between species and sediment composition was observed, delimiting species distributions in relation to sediment type became the primary purpose of most benthic surveys, so relatively large distances between stations were desirable, since significant differences in bulk properties of sediments (*e.g.* grain size) could be easily detected at these spatial scales.

As the topic of organism-sediment relations was experimentally dissected through the years, nearly all of the field and a good portion of the laboratory research was on the favourability of particular habitats to adults and on the interactions between different trophic and mobility types (Gray, 1974; Rhoads, 1974). Detailed studies of the feeding and mobility types of the infauna revealed that functional groups of organisms occurred in distinct types of sediment. Most authors did not speculate on larval settlement mechanisms which could have produced these patterns of distribution (in fact, larval settlement is not discussed at all in Rhoads', 1974, review), but only discussed the favourability of these particular habitats to adults. Initially, the most popular explanation for these assemblages concerned the availability of food resources. For example, Sanders (1958) hypothesized that deposit-feeders dominate clays because these sediments are also rich in organics and microbes, while filter-feeders occur in sandier environments because the higher near-bottom flows deliver suspended particulates to the organisms at faster rates.

Later experimental manipulations showed that interactions between functional groups are also important. Rhoads & Young's (1970) classic "trophic group amensalism" hypothesis, for example, states that activities of deposit-feeding organisms interfere with the establishment and maintenance of populations of suspension-feeders and that such amensalistic interactions are intimately related to the nature of the sedimentary environment (*e.g.* the degree of substratum motion). Recently, more complex interactions between the feeding and locomotive activities of benthic organisms and the structure of the bottom boundary-layer flow and sediment-transport regimes have been identified, stipulating a re-evaluation of the effects of functional groups on sediments and sediment transport (Jumars, Nowell & Self, 1981; Jumars & Nowell, 1984a) and of fluid- and sediment-dynamic effects on community structure (reviewed by Jumars & Nowell, 1984b).

Few of these studies considered how the functional groups of organisms are initially established. The studies usually did not ask if the distinct assemblages resulted from differential larval settlement or differential post-settlement mortality, nor did they consider how the mechanisms controlling larval settlement (*e.g.* active habitat selection or passive deposition) would affect the establishment and maintenance of the assemblages (see also Dayton & Oliver, 1980). The licence to focus primarily on adults may have resulted because, concurrent with the early survey studies, a relatively small core of biologists (*e.g.* see studies cited in Table V, see pp. 128–9) conducted meticulous laboratory experiments on infaunal larvae and meiofauna, demonstrating that

the organisms can actively choose between microhabitats. Thus, the rôle of larval settlement in creating the observed organism-sediment relations was generally assumed to be through active habitat selection (*e.g.* Thorson, 1957; Wilson, 1958; Meadows & Campbell, 1972a; Gray, 1974), even though scant direct evidence from the field was available to support this tenet (see later discussion, pp. 139–141). In fact, passive deposition of larvae also could have produced the observed patterns of organism distribution if, (1) larvae were deposited over broad areas, but differentially survived only in hospitable adult habitats (corresponding to particular sedimentary environments), or (2) species-specific larval fall velocities corresponded with particular sediment fall velocities so that hydrodynamically similar particles and larvae were deposited in the same environment.

Interpreting the importance of amensalism or other interactions between established infauna and the flow or sediment environment to benthic community structure requires knowledge of the rôle of larval settlement processes (see also Jumars & Nowell, 1984b). For example, the trophic group amensalism hypothesis requires that initial distributions of larvae on the sea bed result from differential larval settlement, due to active habitat selection, or to differential post-settlement survival. If differential larval settlement results from passive deposition (*i.e.* settlement patterns depend on larval fall velocities and on the near-bottom flow regime), then it may not be necessary to evoke complex amensalistic interactions to explain the distributions of the adults. Thus, for example, suspension-feeders may not co-occur with deposit-feeders simply because the two functional groups have larvae with different fall velocities that are passively deposited in different fluid-dynamic environments.

In both the survey and the process-orientated studies of soft-bottom community structure, the importance of larval ecology cannot be assessed *a posteriori* because larvae were rarely quantitatively collected in samples (Tables III and IV). Two methodological problems have especially prohibited an adequate consideration of the larval stages; Dayton & Oliver (1980), Santos & Simon (1980a), and Williams (1980) have discussed these problems. (1) Field sampling was usually too infrequent (monthly or even biweekly) to record initial settlement prior to post-settlement interactions. (2) The sieve screen size (500 μm) commonly used in recent benthic studies is too large to retain newly settled larvae of most invertebrate species. Even though the sieve screen size used in faunal surveys has decreased over time (note that Thorson, 1966, defined macrofauna as those organisms retained on a 2-mm sieve and meiofauna was originally defined by Mare, 1942, as organisms with body lengths between 0·2 and 2·0 mm), so that 300-μm screens are used in some contemporary survey studies (*e.g.* Grassle *et al.*, 1985; Thistle, Yingst & Fauchald, 1985; Maciolek & Grassle, in press), 60- or 100-μm screens often are required to retain newly settled larval (or postlarval) stages (Eckman, 1979; Gallagher, Jumars & Trueblood, 1983; Hannan, 1984a).

THE RÔLE OF LARVAL SETTLEMENT

In most discussions of the rôle of larval settlement in soft-substratum community ecology (*e.g.* Thorson, 1946, 1950, 1957, 1966; Smidt, 1951; Muus,

TABLE IV

Process-orientated field studies of factors controlling soft-substratum com-munity structure: studies are arranged by the process under investigation; included in this table are studies of processes structuring macrofaunal com-munities, but not studies of single species populations; this list includes the commonly cited studies in the English literature and is not intended to be comprehensive; NS = some of the samples were not sieved

Reference	Minimum sampling interval	Sieve screen size (μm)
Colonization, succession, response to disturbance		
Grassle & Grassle (1974)	3 days	297
Boesch, Diaz & Virnstein (1976)	3 months	500, 1000
Dauer & Simon (1976)	1 month	500
McCall (1977)	10 days	297, 1000
Rees, Nicholaidou & Laskaridou (1977)	1 month	1000
Rhoads, Aller & Goldhaber (1977)	2 months	300, 1000
VanBlaricom (1982)	1 wk	500
Woodin (1978)	1 month	1000
Oliver *et al.* (1980)	1 month	500
Santos & Bloom (1980)	1 month	500
Santos & Simon (1980a)	1 wk	250, 500
Santos & Simon (1980b)	1 month	500
Arntz & Rumohr (1982)	2 months	125, 500, 1000
Zajac & Whitlatch (1982a,b)	2 wk	297
Gallagher, Jumars & Trueblood (1983)	2 days	63
Watzin (1983, 1986)	7 days	63
Ambrose (1984b)	2 months	500
Levin (1984)	3 days	250
McGrorty & Reading (1984)	6 months	500
Predation		
Young, Buzas & Young (1976)	1 month	1000
Reise (1978)	2 wk	500, 1000, NS
Virnstein (1978)	2 months	500
Arntz (1980)	2 months	1000
Holland *et al.* (1980)	2 months	500
Hulberg & Oliver (1980)	2 months	250, 500
Mahoney & Livingston (1982)	1 month	500
Animal-sediment relations		
Rhoads & Young (1970)	1 month	500, 1000
Young & Rhoads (1971)	Sampled once	1000
Levinton (1977)	1 yr	2000
Myers (1977a,b)	1 wk	500
Orth (1977)	1 month	1000
Wilson (1979)	1 month	500
Brenchley (1981)	7 days	500
Wilson (1981)	15 days	500
Competition		
Woodin (1974)	1 month	500, 1000
Peterson (1977)	1 day	2300
Weinberg (1979)	1 month	500
Peterson & Andre (1980)	55 days	2300
Wilson (1983)	1 wk	500

TABLE IV-*continued*

Reference	Minimum sampling interval	Sieve screen size (μm)
Temporal variability		
Muus (1967)	1 month	700, 1000, NS
Lie (1968)	2 months	1000
Dauer & Simon (1975)	3 months	500
Peterson (1975)	4 months	3200
Holland & Polgar (1976)	3 months	1000
Holland, Mountford & Mihursky (1977)	3 months	1000
Whitlatch (1977)	1 month	250
Buchanan, Sheader & Kingston (1978)	2 months	500
Ziegelmeier (1978)	6 months	3200

1973; Gray, 1974; Woodin, 1976, 1979, 1985; Oliver, 1979; Woodin & Jackson, 1979; Dayton & Oliver, 1980; Watzin, 1986), active habitat selection by larvae is the favoured mechanism for establishing benthic communities. Support for this hypothesis comes primarily from the numerous laboratory experiments where larvae were given a choice of substrata in which to settle (Tables I and V). Post-settlement mortality may also determine (*e.g.* Levinton & Bambach, 1970; Luckenbach, 1984) or further restrict the distribution of adults (*e.g.* Thorson, 1966; Muus, 1973; Oliver, 1979; Peterson, 1986; Watzin, 1986).

It is not surprising that active habitat selection has been the favoured larval-settlement process because the clear evidence from the early laboratory studies (see Table V) is difficult to ignore. In a few notable discussions, however, reservations were raised regarding the application of these laboratory results, where experiments were conducted at very small scales and in still water, to the field, where the scales of processes are much larger. While Thorson is frequently credited as an early advocate of active habitat selection, because of his observations of settling larvae associated with particular sediment types in "bottle collectors" (Thorson, 1946), he was, in fact, consistently cautious when applying results of laboratory experiments in still water to the field. For example, regarding the choice experiments of Wilson (1952, 1953a,b), Thorson (1966, p. 275) noted that the experiments were done, ". . . in petri-dishes, where the larvae by swimming 1 or 2 centimeters only had a chance to discriminate between heaps of sand which might be more or less attractive, neutral or more or less repellent to them as a future substratum. In nature, the larvae will *not* get a similar opportunity to compare a series of substrata by swimming a short distance only. . . . Far from questioning Wilson's main thesis: That the larvae may discriminate between attractive and non-attractive substrata, a fact shown so convincingly that it can be accepted as a 'biological rule', we have, however, to find out what will happen in *nature*, when a larval swarm ready to metamorphose and drifting along the bottom will for the first time meet a substratum which they might 'accept', although it is far from ideal for their settling. The larvae cannot know, that if they continued to drift over the bottom for perhaps 10–20 kilometers more,

they might meet a much more attractive substratum. It seems reasonable to assume, that such larvae, at least if they have already postponed their metamorphosis for some time and are in their less critical phase, will accept and accordingly settle in a bottom substratum much less attractive than the one they would have preferred, had they been given a 'free choice'.

"The consequence of this must be, that the distributional pattern of larvae on the natural bottom substrata must be much less delicate, i.e. much more coarse, than in the experiments undertaken in the laboratory." Thorson was impressed with the behaviour of dispersing and settling larvae, but he also acknowledged that test sites for larvae on the sea bed were probably dictated by near-bed currents, so he tended to under- rather than over-state the rôle of active habitat selection. The evidence that larvae can test the substratum and have preferred habitats simply indicates that ". . . their chance of finding a suitable place for settling is much better than hitherto believed" (Thorson, 1950, p. 36).

One of the most lucid commentaries on the extent to which active habitat selection determines the distribution of benthic marine organisms is the brief (and infrequently cited) paper by Moore (1975), which was written in response to the views of Meadows & Campbell (1972a,b) and Meadows & Mitchell (1973). Moore (1975) proposed "habitat availability" and "ecological opportunity" as alternative arguments to active habitat selection and animal behaviour for explaining the "local" distribution of organisms in the sea. He re-emphasized one of Thorson's (1966) points, that organisms may not have the same kinds of "free choices" in the field as they have been given in the laboratory. During dispersal, planktonic larvae are restricted to particular localities by passive transport processes so that larvae may never even encounter preferred substrata (as determined in laboratory experiments) in the field. Post-settlement mortality or passive deposition of larvae may then shape species distributions. Moore (1975) also reiterates the postulate of Pratt (1953; discussed more later, see pp. 141–3) that correlations between the composition of soft-substratum communities and sediment type may also result from passive sorting of both larvae and sediments by hydrodynamical processes. Furthermore, Moore (1975) emphasizes the importance of scale in directly applying the habitat-selection results to the field, stating that "local" to a behaviouralist (e.g. Meadows & Campbell, 1972a,b; Meadows & Mitchell, 1973) may refer to a much smaller scale (i.e. on-the-order-of the organism) than the "local" of an ecologist, which generally refers to more geographical-type scales; the disparity between these scales decreases, however, with increasing organism size and their ability to independently traverse large distances. His concluding remarks (Moore, 1975, p. 100) raise questions that are still relevant, and largely unanswered, today: "Re-examining the generality of Meadows and Campbell's statement that habitat selection largely determines the local distribution of animals in the sea, a number of issues appear conditional, (i) how is 'determine' construed? (ii) how is the concept of 'local' envisioned? and (iii) which type of 'animal' is involved with reference to (ii)? But in any circumstances, to regard habitat selection as 'largely' determining local distribution would seem to be an overstatement of the case."

A small number of benthic studies (e.g. Baggerman, 1953; Pratt, 1953; Fager, 1964; Tyler & Banner, 1977) have favoured the passive deposition,

rather than the active habitat selection, hypothesis to account for some or all of the observed patterns of infaunal species distribution. Curiously, the passive deposition hypothesis was suggested to these authors by the same kinds of correlations between sediment and species composition, that led most other authors (cited previously) to conclude that larvae actively select for particular sediment or sedimentary environments. Support for the passive deposition hypothesis was largely correlative in these early studies (but see later discussion of experimental manipulations by Baggerman, 1953). Later studies have, however, shown that hydrodynamical null hypotheses are feasible explanations for the observed patterns of distribution; Jumars & Nowell (1984b) review some of this work.

Now that the stage has been set with the alternative hypotheses of active habitat selection compared with passive deposition for creating observed patterns of species distributions, it is fruitful to examine closely the data base substantiating each of these views to determine the plausibility and scales of cause and effect.

THE ACTIVE HABITAT SELECTION HYPOTHESIS

Laboratory experiments on larval settlement can be divided roughly into two groups: (1) studies of habitat selection (*i.e.* where larvae were given a choice of substrata) and (2) studies of environmental or biological factors that induce metamorphosis. Results from experiments in the first category can provide direct evidence of habitat selection, while selection is only implied by results from experiments in the second category. There is some confusion in the literature as to which studies actually provide direct evidence of habitat selection (through choice experiments), so these are listed in Table V and will be discussed separately from the metamorphosis experiments.

All laboratory studies of active habitat selection (*i.e.* the choice experiments) were done in still water, except one (Cuomo, 1985), so that relevance of these results to settlement in field flows is at present obscure. The response of settling larvae to water motion was qualitatively investigated in the laboratory for several infaunal larvae and meiofauna species. The polychaete larvae of *Ophelia bicornis* and *Polydora ciliata* were stimulated to attach to sand grains when subjected to water motion ("squirting" water on larvae placed in a Petri dish in the case of Wilson) in the studies of Wilson (1948) and Whitelegge (1890), respectively. Wilson (1948) also reported that *Ophelia* could "use" the current in order to detach from an unpreferred substratum to re-enter the flow. Wilson (1968) and Eckelbarger (1975, 1976) induced settlement of larvae of sabellariid polychaetes which live in habitats subjected to waves as adults, by stirring the water in the experimental container. Boaden (1963, 1968) and Gray (1966b) observed behaviour of meiofauna in water flowing through a small space between parallel plates and through clear tubing. They found that, at low current speeds, some species were rheotactic, moving upstream toward the source of the current, but all of the organisms were simply washed downstream above some higher current speeds.

These studies of water motion relative to some aspects of the behaviour of settling infaunal larvae or meiofauna were not designed to mimic a particular, realistic boundary-layer flow regime. At most, the mean current speed (*i.e.*

TABLE V

Laboratory experiments on substratum selection by soft-substratum invertebrate larvae, juvenile or adult macrofauna, epifauna and meiofauna: dimensions of treatments and distances between treatments are rough estimates, taken from the information available in the reference; A = archiannelid; B = bivalve; C = cumacean; CR = crab; G = gastrotrich; GA = gammarid amphipod; H = harpacticoid copepod; I = isopod; L = lancelet; LO = lobster; N = nematode; O = ophisthobranch gastropod; P = polychaete; S = shrimp; T = turbellarian; TO = tubificid oligochaete; TP = thin partition between adjacent sediment treatments; NG = information not given in paper

Reference	Organism(s) studied	Maximum dimension of experimental container (cm)	Maximum dimension of treatment (cm)	Maximum distance between treatments (cm)
Studies of macrofauna or epifauna larvae				
Wilson (1948)	*Ophelia bicornis* (P)	9·0	1·5	4·5
Wilson (1952, 1953a,b, 1954, 1955)	*Ophelia bicornis* (P)	7·0	0·75	"a few cm"
Wilson (1970a)	*Sabellaria alveolata* (P)	6·5	1·7	3·0
Wilson (1970b)	*Sabellaria spinulosa* (P)	6·5	1·7	3·0
Wilson (1977)	*Lygdamis muratus* (P)	6·5	2·3	2·0
Keck, Mauer & Malouf (1974)	*Mercenaria mercenaria* (B)	NG	NG	NG
Botero & Atema (1982)	*Homarus americanus* (LO)	55·0	27·5	TP
Cuomo (1985)	*Capitella* sp. I (P)	60·0	7·5	3·0
J. P. Grassle (pers. comm.)	*Capitella* sp. I and II (P)	13·3	3·9	5·5
McCann (in press) and L. A. Levin (pers. comm.)	*Streblospio benedicti* (P)	25·5	7·6	1·0
Studies of meiofauna				
Wieser (1956)	*Cumella vulgaris* (C)	NG	NG	NG
Gray (1966a)	*Protodrilus symbioticus* (A)	7·0	1·0	5·0
Gray (1966b)	*Protodrilus symbioticus* (A)	15·0	NG	NG
Gray (1966c)	*Protodrilus symbioticus* (A)	7·0	1·0	5·0
Gray (1967a)	*Protodrilus rubropharyngeus* (A)	7·0	1·0	5·0
Gray (1967b)	*Protodrilus hypoleucus* (A)	7·0	1·0	13·0
Jansson (1967a)	*Parastenocaris vicesima* (H)	NG	0·8	NG
Jansson (1967b)	*Coelogynopora schulzii* (T) *Aktedrilus monospermatecus* (TO)	NG	0·8	NG

Reference	Species			
Gray (1968)	*Leptastacus constrictus* (H)	7·0	1·0	5·0
Gray & Johnson (1970)	*Turbanella hyalina* (G)	15·0	1·0	13·0
Jensen (1981)	*Chromadorita tenuis* (N)	10·0	10·0	6·0
Klauser (1986)	*Convoluta* sp. (T)	5·0	1·0	3·0
Studies of macrofauna or epifauna				
Teal (1958)	*Uca minax* (CR)	75·0	37·5	TP
	Uca pugilator (CR)			
	Uca pugnax (CR)			
Webb & Hill (1958)	*Branchiostoma nigeriense* (L)	24·0	7·5	10·6
Williams (1958)	*Penaeus setiferus* (S)	243·0	45·7	137·2
	Penaeus aztecus (S)			
	Penaeus duorarum (S)			
Meadows (1964a)	*Corophium volutator* (GA)	9·0	9·0	16·0
	Corophium arenarium (GA)			
Meadows (1964b)	*Corophium volutator* (GA)	34·0	17·0	TP
Meadows (1964c)	*Corophium volutator* (GA)	12·0	6·0	TP
	Corophium arenarium (GA)			
Croker (1967)	*Parahaustorius longimerus* (GA)	"Large finger bowls"	"Divided in half"	TP
	Neohaustorius schmitzi (GA)			
	Lepidactylus dytiscus (GA)			
	Haustorius sp. (GA)			
	Acanthohaustorius sp. (GA)			
Lewis (1968)	*Fabricia sabella* (P)	9·0	6·4	TP
Sameoto (1969)	*Haustorius canadensis* (GA)	9·5	6·7	TP
	Neohaustorius biarticulatus (GA)			
	Acanthohaustorius millsi (GA)			
	Parahaustorius longinerus (GA)			
	Protohaustorius deichmannae (GA)			
Hadl *et al.* (1970)	*Microhedyle milaschewitchii* (O)	6·0	1·5	0·2
Jones (1970)	*Eurydice pulchra* (I)	"Large circular tank"	"Crystallizing dishes"	"At equal intervals around perimeter"
	Eurydice affinis (I)			
Morgan (1970)	*Pectenogammarus plancrurus* (GA)	15·2	2·5	10·2
Gray (1971)	*Scolelepis fuliginosa* (P)	30·0	7·5	15·0
Phillips (1971)	*Callianassa jamaicense louisianesis* (S)	32·0	16·0	TP
	Callianassa islandgrande (S)			

from the average fluid-discharge rate) was measured. Relevant aspects of the boundary-layer flow regime (*e.g.* the shear or boundary shear stress, see pp. 145–8) were quantified, relative to settlement, in only one published study to date, that of Crisp (1955) on barnacle cyprids. The experiments were conducted in clear glass tubing and the animals were stimulated to attach over a range of low shear (the change in velocity with distance above the surface), but were prevented from attachment beyond some threshold value. All the water flow compared with attachment or settlement observations mentioned above indicate the potential sensitivity of larvae to moving fluid and the likelihood of passive transport very close to the sea bed, although the limiting values of boundary-layer flow parameters for which this would occur have yet to be quantified for soft-substratum organisms (but see theoretical calculations of Butman, 1986a).

LABORATORY STUDIES OF HABITAT SELECTION

Laboratory choice experiments of settling larvae were pioneered by Wilson in an extensive series of substratum-selection experiments on *Ophelia bicornis* (Wilson, 1948, 1952, 1953a,b, 1954, 1955). The studies were done in small Petri dishes (3–9 cm in diameter), where larvae were allowed to choose between small piles (0·75–1·5 cm in diameter) of sediment separated by several centimetres. These are the smallest-scale experiments conducted on active habitat selection. A similar experimental design was used by Wieser (1956), Gray (1966a,b,c, 1967a, 1968), Croker (1967), Gray & Johnson (1970), Hadl, Kothbauer, Peter & Wawra (1970), Wilson (1970a,b, 1977), and Klauser (1986) (see Table V). Similar-sized dishes were used in the studies of Wilson (1948), Meadows (1964a), Lewis (1968), and Sameoto (1969), with the various treatments separated into pie-shaped sections by narrow vertical barriers (*e.g.* glass slides), so they were essentially adjacent. Very small-scale experiments also appear to have been done in the studies of Jansson (1967a,b), but only the treatment dimension (0·5 cm^3) is given in the paper. The experiments were done in a "simple alternative chamber" made of plastic tubing, where the treatment patches were placed in either end.

In all the studies cited above, the entire experiment was conducted at the scale of centimetres: in containers $\leqslant 9$ cm in diameter (except, perhaps, Jansson, 1967a,b), with maximum treatment dimensions of < 7 cm, and maximum distances between treatments of $\leqslant 5$ cm (Table V). In the remaining choice studies (Table V), containers and distances between treatments were of the order of tens of centimetres, except for one experiment (Williams, 1958) conducted in a relatively large chamber (a trough 243 cm long by 61 cm wide), with five adjacent sediment treatments. The studies by Meadows (1964b,c), Gray (1966b, 1971), Gray & Johnson (1970), Jones (1970), and Morgan (1970) were similar to the Wilson design, but in dishes of larger diameter (12–34 cm). Webb & Hill (1958), Phillips (1971) and J. P. Grassle (pers. comm.) conducted experiments in shallow, square or rectangular containers subdivided into equal-sized compartments which contained the sediment treatments. The studies of Teal (1958), Botero & Atema (1982), and McCann (1986) were done in aquaria. The sediment treatments were separated in the vertical by Jensen (1981); a dish was suspended 2 cm below the

water surface in an aquarium and different sediment treatments were placed in the dish and on the bottom of the aquarium. Finally, Cuomo (1985) continuously supplied polychaete larvae to a sea-water table containing square dishes, 15 of each of two sediment treatments. This is the only study where larvae entered the treatment area *via* moving fluid, although the experiments were not designed to mimic any particular field flow regime.

The direct choice studies generally have shown that the organisms preferentially settle or accumulate in sediment treatments that characterize their natural adult habitat. Some of the specific attractive elements of a particular sediment treatment have been reduced by experimentation. The "attractive factors" are, for example, the microorganism population on the sediment particles (Wilson, 1955) or the cement secreted by conspecific adults (Wilson, 1970a,b). Thus, the potential for organisms actively to select preferred habitats is established by these (except Cuomo, 1985) laboratory experiments in still water, but only over spatial scales of centimetres to tens of centimetres (and up to ≈ 200 cm in the case of Williams, 1958). Note, also, that most of the experiments were on meiofauna and postlarval macrofauna or epifauna. Choice experiments for settling larvae were limited to studies of only eight infaunal species and lobster larvae (Table V).

LABORATORY STUDIES OF METAMORPHOSIS

The first experiment to induce metamorphosis of a planktonic larva was conducted by Mortensen (1921) on echinoderm larvae, but again Wilson was responsible for much of the detailed work on infauna which immediately followed (*e.g.* Wilson, 1932, 1937, 1948, 1951, 1953a,b, 1954, 1955, 1958, 1968, 1970a,b; Day & Wilson, 1934). From these experiments, larvae competent (*i.e.* physiologically capable) of settlement were introduced into separate dishes containing various sediment and water-column treatments. After a period of time, the dishes were scored for the number of metamorphosed larvae. While these kinds of experiments do not directly demonstrate habitat selection, they are useful for resolving the specific components of the attractive factors. For example, using dialysis membranes, Highsmith (1982) and Suer & Phillips (1983) determined the approximate molecular weight of the "scent" promoting metamorphosis in a sand dollar and an echiuran worm, respectively, allowing further characterization of the chemical nature of the substance. Most factors that promote metamorphosis are organic and often they are species-specific (Burke, 1983; Crisp, 1984). Cuomo (1985), however, recently showed that dissolved hydrogen sulphide originating from sediments or in the water column strongly promotes settlement and metamorphosis of *Capitella* sp. I larvae.

Many organisms which metamorphose in response to a particular treatment will delay metamorphosis in the absence of that factor (see especially the reviews of Strathmann, 1978, and Crisp, 1984). Crisp (1984) attributed a revolution in the way of thinking about the rôle of larval settlement in establishing benthic communities to the discovery of delayed metamorphosis because it indicates that certain species are not "forced" to settle in an inhospitable environment, but have time to search for a preferred habitat. Since research in invertebrate zoology in the 1930s was primarily on embryology and development, Crisp (1984) noted that the importance of tem-

perature- and time-dependent processes overshadowed the potential rôle of external factors in the developmental sequence. Thus, the discovery of delayed metamorphosis invoked the participation of the environment, and of the ecologist, in the process of larval settlement. Now, however, we may have come full-circle, as the rôle of developmental constraints on the duration of pelagic life is again being stressed. Pechenik (1980) suggested that a limit to the delay period for dispersing larvae may be programmed into development so that larvae would be capable, for example, of delaying metamorphosis for a longer time in cold water. Subsequent experiments on the relationship between development, metamorphosis and temperature (*e.g.* Jackson & Strathmann, 1981; Pechenik, 1984; Lima & Pechenik, 1985) lend support to this hypothesis. In addition, there are reports of deterioration or regression of the larva (Henderson & Lucas, 1971; Caldwell, 1972; Yamaguchi, 1974) and a decline in selectivity (*e.g.* Scheltema, 1961; Gray, 1967a; Caldwell, 1972; Grassle, 1980) over the delay period and some species metamorphose in the water column (Day, 1937; Thorson, 1946; Rasmussen, 1956; Baggerman, 1953; Sarvala, 1971; Lacalli, 1980; Peckenik, 1980; Levin & Greenblatt, 1981). Recently Kempf & Hadfield (1985) found, however, that the lecithotrophic larvae of a nudibranch will eventually feed in the plankton if they are deprived of a settling stimulus for a sufficiently long time; thus, they extend their competent period and enhance the probability of encountering a suitable settlement cue. Furthermore, Richmond (1985) has shown complete reversible metamorphosis in the planula larva of a coral species in response to disturbance, with subsequent re-settlement and successful metamorphosis.

SITE PERUSAL, CUE DETECTION, AND SITE SELECTION

The procedure used by a larva to select a habitat and the method of cue detection are still largely the subject of speculation for infaunal organisms. There has been considerably more research on the chemosensory response for hard-substratum (and especially, fouling) organisms (Crisp, 1984); even so, Burke (1983) concluded that there is still only "circumstantial evidence" for the involvement of particular sensory structures in perceiving cues which induce metamorphosis, and that while a neurological and behavioural model of stimulus and response can be ascribed to the induction of metamorphosis, there is still no substantive information on how various neural and endocrine mechanisms actually control the metamorphic sequence.

Crisp & Meadows (1963) coined the phrase "tactile chemical sense" to describe the process of chemoreception in settling barnacles, where the cyprid must make direct contact with the chemically treated surface to detect the cue; presumably an organ in the antennules is the site of the chemoreceptors in this group (*e.g.* Gibson & Nott, 1971). A tactile requirement for perception of the chemical cue is also supported by most of the data available for infaunal and epifaunal larvae. Observations of the behaviour of the organism during settlement generally indicate that the larva must contact the surface to per-ceive the cue (*e.g.* Wilson, 1968; Caldwell, 1972; Eckelbarger, 1978; Rice, 1978); some animals actually burrow into the substratum, without meta-morphosing, and then swim away (*e.g.* Wilson, 1955; Rice, 1978). Eckelbarger (1978) discusses the potential sensory function of anterior ciliary tufts on sabellariid polychaetes just prior to settlement, during the searching stage.

The results of Suer & Phillips (1983) directly support the tactile chemical sense in an infaunal organism (the echiuran, *Urechis caupo*) because the chemical factor promoting metamorphosis was effective only if it was absorbed onto a surface.

The chemotaxis hypothesis (here meaning movement toward or away from a waterborne cue) has received only intermittent support through the years. As Crisp (1974) reiterated, dilution of the cue in the water as it diffused and was mixed by flow turbulence above the bed, is an obvious problem with this hypothesis. Organisms would have to perceive the relatively undiluted cue while they were practically sitting on the sea bed (*e.g.* see Crisp & Meadows, 1962; Butman, 1986a) to settle in close proximity to the source; otherwise, once they perceive the diluted cue at some distance away from the bed, settlement could occur over a broad region of the bottom which may or may not contain the source of the cue. Reports of organisms responding to cues "at a distance" from the bed are rare (Crisp, 1974), although much more research is needed. Most of the evidence for the chemotaxis hypothesis is circumstantial: the larvae metamorphosed when a substance was added to the water (Crisp, 1974). To be direct evidence of chemotaxis, it must be shown that the substance added did not adhere to a surface (*e.g.* the walls of the container) that the larva then tested; for example see the criticisms of Scheltema's (1961) study in Crisp (1974) and Scheltema (1974). The chemotaxis hypothesis is supported by the recent experiments of Cuomo (1985), who suggested that a threshold concentration of hydrogen sulphide in the water above the sediment was responsible for eliciting the settlement response in a capitellid polychaete. The nuchal organ may be the site of chemoreception, as speculated by Bhup & Marsden (1982). In addition, Highsmith (1982) showed that surface textures or films were not involved in eliciting metamorphosis in the sand dollar, *Dendraster excentricus*, and suggested that the larvae can detect a concentration gradient of the inducer, released from the adult sand dollar bed. Further substantiation of a waterborne inducer for metamorphorsis in this species is given in Burke (1984), where > 90% metamorphosis occurred in aqueous extracts from water overlying the sand in which the adult pheromone was released, but only 5% metamorphosis occurred in extracts overlying sand outside the sand dollar bed.

Like the direct choice studies and the metamorphosis experiments, the logistics of active habitat selection whether by the tactile chemical sense or by chemotaxis, are poorly explored for infaunal larvae settling in moving fluid; all experiments have been done in still water. If an entirely waterborne cue can elicit the response while the larva is still in the plankton, as the results of Highsmith (1982), Burke (1984), and Cuomo (1985) suggest, then it is particularly critical to do laboratory studies in simulated field flows. As mentioned earlier, by the time cues advected and mixed by flow turbulence are perceived by a planktonic larva, the organism may end up on the sea bed in a habitat from which the cue did not emanate (*e.g.* Cameron & Rumrill, 1982).

Doyle (1975) proposed a settlement model for active habitat selection where the probability of a larva responding to a given cue in the water can be only zero or one, *i.e.*, a threshold level of the stimulus evokes the response. This is an attractive theory, particularly if the competent larvae drift in water very close to (*i.e.* within centimetres of) the sea bed during the cue-

detection stage, because it minimizes errors in site selection and requires a relatively simple behaviour response. While accurate site location would be improved if a larva could swim upstream along a cue concentration gradient, this possibility appears to be limited to very weak near-bed flow regimes, due to the relatively slow swimming capabilities of most infaunal larvae (Mileikovsky, 1973; Mann & Wolfe, 1983; Chia, Buckland-Nicks & Young, 1984) compared with velocities very close to the sea bed (Butman, 1986a). Even if cues must be adsorbed to a surface that the larva can test, as the bulk of the evidence to date suggests, test sites also may be specified by bottom boundary-layer flow conditions (Butman, 1986a; see later discussion, pp. 148–51). Thus, while larvae of many infaunal invertebrates are clearly capable of discriminating between microhabitats and metamorphosing in response to specific cues, the field conditions wherein active habitat selection actually determines patterns of recruitment are unknown.

FIELD EXPERIMENTS ABOVE OR ON THE SEA FLOOR

Field studies on active habitat selection may have the advantage of being realistic from a fluid-dynamic point of view, but other aspects of field conditions are limiting to experimentation. For example, it is nearly impossible to sample initial settlement onto the sea bed and to measure subsequent early postlarval mortality in soft-substratum systems. Even in hard-substratum systems, the newly settled stages have been identified and followed for only a few species (Connell, 1985). Experimental studies in the field can be classified either as manipulations above the bottom or direct manipulations of the sea floor. The literature is reviewed with the primary emphasis on identifying the spatial scales involved in the experiments and on separating cases where habitat selection actually was demonstrated in the study from indirect or inconclusive evidence of selection.

    While experiments generally are required to determine processes, direct sampling of the unmanipulated sea floor has also provided useful information on patterns of recruitment and significant correlates, especially when sampling was both frequent (days to weeks) and rigorous (using appropriately small sieves to sample newly settled organisms) and when the water column was sampled simultaneously (e.g. Muus, 1966, 1973; Oliver, 1979; Hannan, 1980; Luckenbach, 1984; Webb, 1984). Results of the detailed field study of Muus (1966, 1973) on bivalve larval availability in the plankton (e.g. from Fosshagen, 1965, which overlapped with the first year of Muus' study) and recruitment in two localities (at 18 m and 27 m), indicate that both habitat preferences in settling larvae and early postlarval mortality shape adult distributions. This is a somewhat unusual study in that the two field sites were separated by only ≈ 1 km and differed markedly in faunal composition, but differences in the bottom sediments (dominance by the 64 to 250-μm fraction at the 18-m site and dominance by the 64 to 125-μm fraction at the 27-m site) probably were not hydrodynamically meaningful (i.e. did not represent a large enough change in bed roughness to alter the structure of the near-bed flow; see pp. 148–54. These relatively small sediment differences certainly may be biologically meaningful. Muus acknowledged that observed patterns of recruitment imply active habitat selection only if the supply of larvae to the two sites was equivalent, but provides reasonable arguments,

based on known circulation patterns in the Øresund, that "the same water masses and same larval swarms" probably pass over the two localities (Muus, 1973, p. 103).

To avoid problems associated with direct sampling of the sea bed (*e.g.* processes operating at the sediment-water interface that may obscure initial settlement patterns), several manipulative field studies have been done in structures raised above the sea floor (Table VI). In nearly all cases, larval settlement differed among the various treatments deployed simultaneously and the authors concluded that larvae actively select their settlement sites. All field studies which compared collections in artificial structures with collections from the natural sea bed may, however, have suffered from "trapping arti-facts"—physical, chemical, and biological differences between the micro-environment of the trap and the natural bottom—which complicate interpret-ation of the results (Oliver, 1979; Hannan, 1981). Unless the collection characteristics of the traps for passive inert particles (*e.g.* sediments) can be defined (Hargrave & Burns, 1979; Gardner, 1980; Butman, 1986b; Butman, Grant & Stolzenbach, 1986), collections resulting from biological processes (*e.g.* active habitat selection behaviours of the larvae) cannot be separated from collections resulting entirely from hydrodynamical processes. Hannan (1981) was unable to distinguish between these possibilities to account for the differences (orders of magnitude) in numbers of postlarvae collected in traps placed ≈ 1 m above the sea bed compared with those in cores of the natural bottom. Oliver (1979; some results are also reported in Dayton & Oliver, 1980) used relatively "tall" and "short" plastic cups filled with the same amount of sediment (to the rim of the short cup) to simulate physical conditions of deposition and resuspension, respectively. Relatively more "*Capitella capitata*" (the sibling species, *sensu* Grassle & Grassle, 1976, may be similar to *Capitella* sp. Ia, as in Hannan's, 1981, study conducted nearby) were collected in the tall than in the short cups, while another polychaete species, *Armandia brevis*, was not differentially collected by the two trap designs. Oliver (1979) suggested that *Capitella* actively selected the depo-sitional environment in the short traps, but that *Armandia* was less selective in its settlement requirements; both behaviours are consistent with the dis-tributional patterns of the adults and the responses of the populations to disturbance (Oliver, Slattery, Hulberg & Nybakken, 1980). Passive accumu-lation of *Capitella* larvae or postlarvae in the depositional environment is, however, also consistent with the results. Differences between species in hydrodynamic properties (*e.g.* fall velocities), swimming abilities, and periods of larval availability relative to flow processes, could account for the different patterns of collection by the traps for the two species. In the only study (Hannan, 1984a,b) where hydrodynamical properties of larvae and collection characteristics of traps (Butman, 1986b) were defined in the laboratory before field deployments, nearly all of the abundant infaunal organisms (in three invertebrate phyla) were collected in the relative abundances predicted for passive particle collections by traps.

It is valid to compare collections in different sediment treatments placed in the same type of artificial structure raised above the sea floor, when the treatments are exposed to the same flow regime (*e.g.* Oliver, 1979; Levin, 1981, 1984; Watzin, 1983, 1986), but considerations of possible "edge effects" and other differences between treatments due to position within the structure

TABLE VI

Field experiments on larval settlement or early recruitment of infauna: experimental studies where sampling intervals were > 1 month or sieve screen sizes ⩾ 1 mm are not included in this table because initial settlement or early recruitment are unlikely to be detected with these methods; distances and dimensions were estimated, when possible, from the information given in the paper; * = in studies where settlement into one type of box, tray or trap (usually containing defaunated sediment) was compared with settlement onto the natural sea bed, the distance between "treatments" would be between the structure and where the sea bed was sampled; this usually was not given in the study but probably is no greater than tens of centimetres or metres; NG = information not given in the paper; NA = not applicable to this study; OSO = one station only was sampled; P = polychaete; B = bivalve

Reference	Experimental approach	Organisms studied	Minimum sampling interval	Sieve screen size (μm)	Minimum distance between stations (m)	Maximum treatment dimension (cm)	Maximum distance between treatments (cm)
Thorson (1946)	"Bottle collectors" moored above sea bed; plankton and bottom samples	All infauna	6 wk for bottles, 2 wk for plankton	NG for bottles, 83 for plankton	NG	Bottle dimensions not given	NG*
Baggerman (1953)	Manipulations of the sea bed	Bivalves	12 h	500	OSO	45	NG
Reish (1961)	"Sediment bottle collectors"	All infauna	28 days	246	710	"Gallon jar" dimensions not given	NG
Hermans (1964)	Different substrata placed in suspended bottle collectors	*Armandia brevis* (P)	2 wk	NG	OSO	"Thorson" bottles, dimensions not given	NG
Richter & Sarnthein (1977), but technical layout in Sarnthein & Richter (1974)	Different substrata placed in trays moored above sea floor	Molluscs	2 wk	63	80	71	118
Grassle & Grassle (1974)	Boxes of defaunated sediment made flush with the sea bed; bottom samples	All infauna	3 days	297	4600	100	NG*
Guérin & Massé (1978), Massé & Guérin (1978)	Different substrata placed in three designs of collectors moored on the bottom or above the bottom	Polychaetes and molluscs	1 month	1000 "on diagonal" (= 700 if mesh is square)	NG	8·6	180

McCall (1977)	Boxes of defaunated sediment placed on the sea bed; bottom samples	All infauna	10 days	297	9000	3700	NG*
VanBlaricom (1978)	Containers with thin layer of sediment moored above the sea bed; bottom samples	All infauna	13 days for containers, 1 month for bottom	250 for containers, 500 for bottom	OSO	10 for containers	NG*
Eckman (1979)	Manipulations of the sea bed	All abundant infauna	11 days	61	OSO	100	700
Oliver (1979), Dayton & Oliver (1980)	(a) different treatments filled containers held in racks above sea bed; bottom samples	Polychaetes	(a) 6 days	(a) 250 for containers, 500 (250 for "a few cores") for bottom	(a) OSO	(a) 14 for containers	(a) 42 for containers
	(b) manipulations of the sea bed		(b) 1 month	(b) 500 (250 for "a few cores")	(b) 1000	(b) 2000	(b) NG
Santos & Simon (1980a)	Containers filled with sediment placed in rack above sea bed; plankton and bottom samples	All infauna	7 days for containers, "irregularly" for plankton, 1 month for bottom	OSO	250 for containers, 144 for plankton, 500 for bottom	5 for containers	NG*
Williams (1980)	Manipulations of the sea bed	Tapes japonica (B)	7 days	149	OSO	150	750
Bhaud, Aubin & Duhamel (1981)	Collectors filled with sediment placed above sea bed; bottom samples with epibenthic sledge	Polychaetes and bivalves	5 days	NG	OSO	"2 litre capacity" collectors, dimensions not given	NG*
Hannan (1981)	Collectors with thin layer of sediment moored above sea bed; bottom samples	Armandia brevis (P), Capitella spp. (P), Nothria elegans (P), Prionospio pygmaea (P)	7 days	250	400	10	NG*
Levin (1981)	Different sediment treatments filled containers placed directly on sea bed; bottom samples	Streblospio benedicti (P), Pseudopolydora paucibranchiata (P)	2 wk	Worms were visually counted under dissecting microscope	OSO	9	26
VanBlaricom (1982)	Manipulations of the sea bed	All infauna	7 days	500	OSO	30	NG
Zajac & Whitlatch (1982a)	Buckets of defaunated sediment made flush or protruding above the sea bed; bottom samples	All infauna	14 days	297	620	48	NG*
Eckman (1983)	Manipulations of the sea bed	All abundant infauna	2 days	61	OSO	30	1970

TABLE VI–*continued*

Reference	Experimental approach	Organisms studied	Minimum sampling interval	Sieve screen size (μm)	Minimum distance between stations (m)	Maximum treatment dimension (cm)	Maximum distance between treatments (cm)
Gallagher, Jumars & Trueblood (1983)	Manipulations of the sea bed	All abundant infauna	2 days	63	OSO	3·7	500
Watzin (1983, 1986)	Different sediment treatments filled containers held in racks raised above sea bed	All infauna	7 days	63	OSO	14	50
Hannan (1984a,b)	Different sediment trap designs, with known passive particle collection characteristics, moored above sea bed	All abundant infauna	1 day	100	OSO	14·7	2400
Levin (1984)	Manipulations of the sea bed; containers filled with sediment placed on sea bed; plankton samples	Polychaetes	3 days for manipulated sediments, 1 month otherwise	250 for containers and sediments, 63 for plankton	100	63 for bottom, 9 for containers	100
Luckenbach (1984)	Sampled four areas of sea bed representing natural sediment treatments; plankton and bottom samples for initial availability	*Mulinia lateralis* (B)	1 day for initial availability; 4 days for initial settlement; 1 month for recruitment	105	OSO	10	NG*
Bonsdorff & Österman (1985)	Trays filled with sediment placed on sea bed; bottom samples	All infauna	2 wk	500 for macrofauna; 500, 200, 63 for meiofauna	OSO	40	NG*
Whitlatch & Zajac (1985)	Different sediment treatments in cores held in racks above sea bed	All infauna	10 days	180, 300	OSO	5	100
Woodin (1985)	Different sediment treatments in cores implanted in bottom	Spionid polychaetes	9 days	250	OSO	11	1500

must be carefully analysed (see Nowell & Jumars, 1984). While it may not be possible to define the hydrodynamic conditions above these sediment treatments, as long as conditions are constant among treatments, between-treatment differences in settlement or recruitment can be assessed.

Results of the field manipulations above the sea floor are strongly suggestive of active habitat selection by many infaunal larvae or postlarvae on scales of tens of centimetres to metres (Table VI), with the caveat that hydrodynamic alternative hypotheses usually were not considered or tested. Data from many of these manipulative field studies will remain equivocal until the possibility of differential passive deposition or accumulation between structures or between structures and the bottom can be discounted. The strongest results are for studies where hydrodynamic conditions were held constant among treatments, although the physical characteristics of the flows over these sediments are undefined.

Directly manipulating bottom sediments to test the active habitat selection hypothesis alleviates the problems with structures. If the bottom roughness scales remain unchanged between manipulated and control sediments, then flow characteristics should be similar for all treatments (see Nowell & Jumars, 1984). The results of such studies (*e.g.* Oliver, 1979; Williams, 1980; Gallagher, Jumars & Trueblood, 1983) show that recruited postlarvae are associated with distinct habitats on the scale of metres (Table VI). Because of problems in sampling initially settled larvae and subsequent early mortality, mentioned above, it is not clear if the pattern results from active selection when the larvae first reach the sea floor or from a re-distribution of the postlarvae after initial settlement; it is also possible that observed distributions resulted from very early postlarval mortality of settled larvae that were originally evenly distributed among the sediment treatments. In cases where bottom sediments were manipulated specifically to change the nature of the near-bed flow regime, with accompanying *a priori* predictions of hydrodynamic effects on recruiting infaunal postlarvae or meiofauna (Eckman, 1979, 1983; Hogue & Miller, 1981), the hydrodynamic null hypotheses could not be falsified (see pp. 141–5).

PATTERN OF DISTRIBUTION AND ACTIVE HABITAT SELECTION: A PROBLEM OF SPATIAL SCALES

The spatial scales (centimetres to tens of centimetres) for which active habitat selection has been conclusively demonstrated in laboratory experiments in still water (Table V) are one to six orders of magnitude smaller than the spatial scales (tens of metres to tens of kilometres) over which species and sediment composition are significantly correlated in the field (see Table III, pp. 120–1). Thus, the process of active habitat selection, as demonstrated by these laboratory results, cannot account for the observed field distributions, due to the mismatch in spatial scales. Field experiments on processes controlling larval settlement were conducted at spatial scales of tens of centimetres to tens of metres (Table VI); while active habitat selection was strongly implied by the results of many of these studies, this interpretation remains

equivocal because the alternative hypothesis of passive deposition was usually neither considered nor tested.

When patterns of community composition and structure have been delimited at small spatial scales, *e.g.* of the order of 1 to 10 m in Jones (1962), of 0·1 to 1 m in Angel & Angel (1967) and Grassle *et al.* (1975), of 0·01 to 1 m in Reise (1979), of 100 cm in Gärdefors & Orrhage (1968) and Jumars (1976), of 10 m in Gage & Geekie (1973a), and of 10 cm in Olsson & Eriksson (1974), sediment samples were not taken at each infaunal sampling location, except in one case (Angel & Angel, 1967). The entire area sampled in these small-scale dispersion studies was usually considered homogeneous in its bulk sediment characteristics, based on one to a few sediment samples from the area. Thus, the spatial patterns and scales of diversity detected in these studies were usually attributed to processes other than those directly related to bulk properties of sediments.

The small-scale patterns of species distribution and diversity detected in these studies are the only patterns to which results of habitat selection experiments can be applied directly. Even though bulk properties of sediments were presumed to be constant within the areas sampled in these studies, Angel & Angel (1967) and Jumars (1976) briefly discussed the potential importance of small-scale variability in sediment characteristics; Jumars & Eckman (1983) provide a more detailed discussion of this topic. Local heterogeneity in sediment topography (*e.g.* due to geological or biological processes) can cause significant small-scale (centimetres to metres) variations in sediment grain size because of local changes in the near-bottom flow regime; patchiness in infaunal distributions at these small scales can be attributed to this sediment heterogeneity (*e.g.* Rhoads & Young, 1970; Eckman, 1979, 1983; Thistle, 1983). In addition, detailed analyses of sediment characteristics using microscopic methods and staining techniques (*e.g.* Whitlatch & Johnson, 1974) indicate that bulk sediment analyses obscure variation in sediment properties (*e.g.* protein, carbohydrate, and lipid contents, as well as grain size) to which organisms may respond (Whitlatch, 1974, 1980). Many laboratory studies of habitat selection have demonstrated that there are chemical and biological substances (*e.g.* chemical conditioning of sediments by adults or the abundance and composition of bacterial populations) in sediments which augment grain size as attractive factors to stimulate or enhance larval settlement. Thus, within an area of homogeneous sediment type (based on analysis of grain size), larvae may actively select for microhabitats based on these other aspects of sediments. For example, Thistle, Reidenauer, Findlay & Waldo (1984) and Eckman (1985) have shown that there is local enhancement of bacterial abundances around vertical protrusions (seagrass shoots or animal tubes) from the sea bed and that infauna are concentrated in these regions.

In summary, larvae may select for microhabitats at small spatial scales (centimetres to tens of centimetres) based on sediment characteristics other than just grain size (as determined from bulk sediment analyses). The capability of larvae to distinguish between and actively select for habitats with distinctly different grain sizes and separated by large distances (tens of metres to tens of kilometres) is yet to be demonstrated. The passive deposition hypothesis may resolve this problem because it specifies that larvae are deposited at the same spatial scales as apply to sediment transport and deposition (see p. 144). At this time, passive deposition of larvae represents

the simplest and most feasible mechanism for creating initial large-scale distributions of larvae in the field. Active habitat selection may be confined to only very small spatial scales.

THE PASSIVE DEPOSITION HYPOTHESIS

To my knowledge, the passive deposition hypothesis was first formally proposed to account for patterns of initial larval settlement or recruitment of infaunal species in the studies of Baggerman (1953) and Pratt (1953). Prior to these, brief, qualitative discussions of the rôle, or potential rôle, of "currents" in controlling larval dispersal and in determining settlement sites were given in Orton (1937), Kreger (1940), Thorson (1946, 1950), and Verwey (1952). For hard-substratum habitats, experiments on the rôle of hydrodynamical processes in settlement occurred much earlier. Observations and experiments on flows which permit or inhibit settlement of fouling organisms date from the 1940s (McDougall, 1943; Smith, 1946; Doochin & Smith, 1951; Crisp, 1955; Wood, 1955) due, at least in part, to the important applied aspects of this problem (*i.e.* the commercial need for developing methods to inhibit biofouling). Likewise, probably the most extensive studies, to date, of the rôles of both biological and physical processes in the dispersal and settlement of any single species were done on barnacles (Bousfield, 1955; de Wolf, 1973).

   Strictly speaking, the passive deposition hypothesis stipulates that competent planktonic larvae initially reach the sea floor at sites where passively sinking particulates, with fall velocities similar to larvae, initially settle (Hannan, 1984a,b). As indicated in Hannan (1984b), this hypothesis does not specify that the deposited organisms will accumulate at these locales, as the geological definition of "deposits" implies, but refers only to the process controlling where the larvae will initially come to rest on the sea bed. Then, other biological or physical processes may re-distribute the organisms (see later discussion, pp. 154–5). Note also that, "deposited larvae may or may not have 'settled' according to the biological definition of Scheltema" (Hannan, 1984b, p. 1109). The passive deposition hypothesis has never been tested directly because it requires simultaneous sampling of initially deposited larvae and passive particles with fall velocities similar to larvae. This eventually may be possible in a laboratory flume, where realistic field flow regimes could be simulated (see Nowell & Jumars, 1987), and the distributions of inert particles with known fall velocities could be compared with the distributions of larvae or postlarvae when they first reach the bottom. The chances of testing the passive deposition hypothesis in the field seem remote, due to problems in actually sampling initial distributions of larvae and particles prior to interference by benthic biological and physical processes, and to problems of defining the fall velocities of initially settled particulates in their naturally occurring states (*e.g.* flocculated or biologically aggregated). Support for the passive deposition hypothesis comes from studies of passive accumulation, passive sinking, and passive resuspension and transport of larvae, postlarvae or meiofauna, which are discussed separately below.

   It is important to distinguish the passive deposition hypothesis from the earlier notion that larvae fall in a "random rain" onto the sea bed, which was

once considered the alternative hypothesis to active habitat selection (*e.g.* see discussion of these early ideas in Thorson, 1957). Random deposition explicitly states that there is an equal probability that individual larvae will fall onto any bed location. This hypothesis is synonymous with the passive deposition hypothesis only for a homogeneous suspension of larvae and particles falling through still water. In moving water, for an infinite water mass with a uniform particle supply distributed homogeneously in the water column, and with a steady and non-varying physical regime, the initial distribution of particles on the sea bed would be random. For temporally and/or spatially varying flow regimes, particle abundances, and particle distributions in the water column, the particles will not, however, fall at random onto the sea bed. In these cases, the sites for initial settlement of particles are determined by the hydrodynamical processes and the particle characteristics. Thus, for the physical regimes of interest in most marine studies, a random rain of larvae to the sea bed is not the appropriate null hypothesis for testing the importance of physical processes, since particle deposition is not expected to be random. In fact, a random pattern of initial larval settlement would, in most cases, falsify the passive deposition hypothesis. If larvae physically behave in a flow like passive particles, then it is their fall velocity and hydrodynamical processes which determine when and where the larvae will reach the sea bed. Thus, passive deposition is the appropriate physical null hypothesis against which biological (*i.e.* active habitat selection) hypotheses can be tested.

PASSIVE ACCUMULATION

The correspondence of distributional patterns of a cockle (Baggerman, 1953), two species of bivalve (Pratt, 1953), and several echinoderm species (Tyler & Banner, 1977) with modern fine-sediment distributions was attributed to the passive accumulation of settling larvae and fine sediments in similar locales. Illuminated by discussions with Baggerman, Verwey (1952) and Kristensen (1957) suggested that some bivalve populations may result from passive accumulation in "sheltered" or "weak current" areas. Orton (1937), Segerstråle (1960, but see also 1962), and Carriker (1961) also indicated the potential importance of strong near-bed currents maintaining larvae in suspension (*e.g.* in gyres or swift tidal channels) and weak currents allowing the spat to settle onto the bed. Fager (1964) attributed the presence of an unusually shallow, very dense, and oddly shaped (elliptical, with the long axis parallel to shore) bed of the polychaete, *Owenia fusiformis*, to such physical processes. He suggested that larval settlement was concentrated in this locale due to the coincidence of a water mass containing large numbers of competent larvae with a rip current at the site. The hydrodynamics associated with the rip would allow larvae to accumulate passively in the unusual bed configuration. On a much smaller scale, Birkeland & Chia (1971) suggested that early recruitment of sand dollars may be more successful in patches of sand within a cobble field compared with a sand flat, because the cobbles act like "breakwaters" for the flow over the sand; it is, however, unclear if the authors were implying passive deposition or enhanced retention in these slow-flow regions. In all of these studies, evidence of the rôle of hydrodynamical processes is largely correlative, but the novelty of these interpretations when other,

similar, correlative evidence invoked the active habitat selection hypothesis (see pp. 123–7), is striking.

The manipulative field experiments of Baggerman (1953), Eckman (1979, 1983), and Hogue & Miller (1981) provide substantive support for the passive accumulation hypothesis. Baggerman (1953) placed vertical barriers (screens) on the sea bed and sampled for cockle spat near and away from the screens. She also determined that a range in sizes of cockle spat were likely to be transported and deposited like fine sediments by showing that measured gravitational fall velocities of spat were similar to the measured fall velocities of the sediments transported at the study sites. She did not, however, determine, *a priori*, how the vertical screens would affect the near-bottom flow at her study sites; she assumed that the region of low flow developing in the lee of the screens would be sufficient to trap sediments and passively falling spat. Eckman (1983) made specific *a priori* hypotheses on how the artificial tubes he placed in sediments would affect both the fluid flux to the bed and the boundary shear stress because he did laboratory flume experiments to measure these physical effects. In another study, Eckman (1979) placed artificial tubes at regular intervals in sediments and, taking contiguous samples over the area, determined the spatial scales of organism distributions and compared them with the spatial scale of the physical effects resulting from this manipulation. Hogue & Miller (1981) repeated Eckman's (1979) experiments in a different intertidal area, but studied dispersion patterns of nematodes, rather than recruitment of infauna. In all these studies, recruitment patterns were consistent with predictions based on hydrodynamical criteria; that is, the null hypothesis of passive accumulation could not be falsified.

Indirect support for passive deposition and accumulation comes from the numerous reports of higher postlarval or adult infaunal abundances in depressions on the sea floor (*e.g.* Chapman & Newell, 1949; Pratt, 1953; Pamatmat, 1968; Sameoto, 1969; Howard & Dörjes, 1972; Farke, de Wilde & Berghuis, 1979; VanBlaricom, 1982; McLusky, Anderson & Wolfe-Murphy, 1983; Levin, 1984) or in seagrass beds that baffle water motion (*e.g.* Orth, 1977; Scheibling, 1980; Peterson, Summerson & Duncan, 1984) than in adjacent sandflats. The pattern of distribution for newly settled larvae has, however, yet to be measured.

These patterns of enhanced abundances in areas of relatively slow flow need not arise at the time of settlement, but may result from differential post-settlement mortality. To determine at what stage in the life history the pattern of enhanced abundances of the hard clam, *Mercenaria mercenaria*, in seagrass beds compared with adjacent sandflats is established, Peterson (1986) computed the ratio of organism densities between the two habitats for the 0-year class and all subsequent year classes. Because these ratios were considerably larger (by $\approx 4 \times$) for the older year classes, Peterson (1986) concluded that post-settlement phenomena, such as competition and predation, were at least as important as settlement phenomena in creating the pattern.

For all the passive accumulation studies, a problem with unambiguously interpreting the process responsible for the observed pattern of enhanced recruitment in regions of slow flow is that fine sediment and detritus also will accumulate in these areas. Thus, the alternative hypothesis that larvae actively select sites where fine sediments and detritus accumulate or preferentially survive in these areas cannot be discounted.

PASSIVE SINKING

Organisms are unlikely to be passively deposited onto the sea floor unless they sink through near-bottom waters like passive particles. Hannan (1984a,b) tested this passive sinking hypothesis for larvae falling through turbulent field flows using several groups of geometrically different sediment trap designs (see Table VI, p. 138). *A priori* predictions regarding the rank order that the various traps would collect larvae in the field were dictated from laboratory flume experiments to determine particle collection efficiencies of the traps in flows dynamically similar to average conditions at the field site studied. The flume flow was seeded with particles having fall velocities similar to those measured in the laboratory for non-swimming polychaete larvae. In these experiments, nearly all of the abundant organisms (polychaete, bivalve, and enteropneust postlarvae) were collected by traps in the patterns predicted for passive particle collections. Thus, the passive sinking hypothesis could not be falsified.

PASSIVE RESUSPENSION AND TRANSPORT

Indirect evidence that organisms living at the sediment surface may be resuspended and transported comes from studies where the water column and the sea bed were sampled simultaneously, or where the bottom was sampled intensively, throughout storm events (Hagerman & Rieger, 1981; Hogue, 1982; Dobbs & Vozarik, 1983); organisms either were missing from the sea bed or were present in the water column during the storms. The sampling studies of Bell & Sherman (1980) and Palmer & Brandt (1981) suggested that even tidal velocities may be sufficient to resuspend and transport meiofauna (but see also Grant, 1981). Palmer & Gust (1985) quantified this effect by measuring the bottom shear stress over a tidal cycle, when simultaneous water column and bottom samples also were collected. The *a priori* hypothesis was that meiofauna would be resuspended with the surface sediments only when the bottom shear velocity exceeded the critical erosion velocity for the sediments. They found that organism abundances in the water directly above (within tens of centimetres of) the sea bed were highest when the bottom shear velocity exceeded the threshold value. Furthermore, from laboratory experiments, Palmer (1984) showed that the organisms probably were not actively entering the water, although certain behaviours (*i.e.* remaining at the sediment surface rather than burrowing) increased a given organism's probability of being resuspended. Indirect support for passive resuspension and transport of surface- or near surface-dwelling infauna comes from the numerous reports of postlarval and adult organisms in the water column (see Table II, pp. 117–9) and of post-settlement migrations (*e.g.* Chapman & Newell, 1949; Baggerman, 1953; Kristensen, 1957; Sigurdsson, Titman & Davies, 1976; Farke *et al.*, 1979).

SUMMARY

The hypotheses that hydrodynamical processes determine accumulation, sinking or resuspension and transport of larvae, postlarvae or meiofauna could not be falsified in the experimental studies conducted thus far. These

results provide support for the passive deposition hypothesis, but direct tests for initially settled larvae are lacking. A limitation to interpreting results from the passive accumulation experiments is that fine sediments and detritus tend to accumulate in regions of slow flow so that the observed enhanced abundances of organisms in these areas, presumed to be the result of passive accumulation, could also result from active habitat selection for these detrital-rich zones or from enhanced early postlarval survival. Experimental manipulations are needed to distinguish among these possibilities.

LARVAL SETTLEMENT IN THE
BOTTOM BOUNDARY LAYER

Results of the passive accumulation, sinking, and resuspension and transport studies stipulate that physical processes cannot be discounted in considerations of larval settlement phenomena, so it is worthwhile to discuss briefly characteristics of the bottom boundary-layer flow environment, where settlement takes place. The near-bed flow regime determines the spatial scales applicable to passive deposition and also the hydrodynamical constraints for successful active habitat selection. Other discussions of bottom boundary-layer processes relevant to benthic ecology, and written for a general audience, can be found in Wimbush (1976), Vogel (1981), Nowell (1983), Nowell & Jumars (1984), and Butman (1986a); the recent review of Grant & Madsen (1986), written primarily for fluid dynamicists, summarizes many important aspects of boundary-layer flows in continential-shelf environments. The following discussion is limited to steady, uniform (in the horizontal) flow over a bottom which is also uniform over large horizontal distances, relative to the height off the bottom. The purpose is to provide some basic fluid-dynamical perspective on larval settlement, while retaining the essential physics.

GENERAL FEATURES OF BOUNDARY-LAYER FLOWS
OVER SOFT SUBSTRATA

As water flows over the sea bed, a region of shear (the slope of the velocity profile, $\partial u/\partial z$, where u is the horizontal velocity component and z is the perpendicular distance from the bed; see Fig. 1) develops as a result of the retarding effect (drag) of the boundary on the flow. This region of shear near the bed is called the boundary layer. Within the boundary layer, current speed goes from zero at the bed to the mean-stream velocity (U) at the top of the boundary layer (where $z = \delta$, the boundary-layer thickness). For heights exceeding $z = \delta$, the bottom no longer has a significant effect on the flow; this is called the region of potential or frictionless flow and, in the absence of other flow processes (e.g. surface wind stress or other sources of flow turbulence) and for a constant density, $u = U$ in this region. When the shear near the bed is sufficiently large, turbulent eddies are generated that mix lower-momentum fluid close to the bed with higher-momentum fluid away from the bed; this thickens the boundary layer and reduces the mean velocities at a given height above the bed (especially close to the bottom).

The shape of the velocity profile in the boundary layer depends on flow properties (e.g. the flow Reynolds number, the background turbulence and

accelerations), fluid properties (*e.g.* stratification induced by temperature, salinity and suspended sediment), and boundary characteristics (*e.g.* the bed roughness and the cohesiveness of sediments). Velocity profiles have been measured for controlled laboratory flows and their characteristics have been determined theoretically under certain conditions. For the steady, uniform flow case considered here, two shapes of the velocity profile are well known, a parabolic shape for laminar boundary layers and a logarithmic shape for turbulent boundary layers.
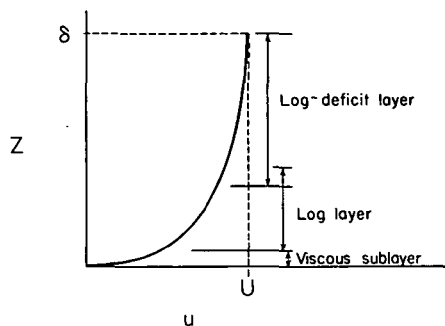
Fig. 1.—Diagram of a turbulent boundary layer plotted on a linear scale for both axes, showing the relative positions of the viscous sublayer, the log layer, and the log-deficit layer: taken from Butman (1986a).

The boundary layer will be laminar or turbulent, depending on the flow Reynolds number, a dimensionless parameter which is the ratio of inertial forces to viscous forces in the flow. The Reynolds number (VL/v) depends on a length (L) and a velocity (V) scale for the flow, as well as on the fluid kinematic viscosity (v). Laminar boundary layers occur at low Reynolds numbers; molecular viscosity dominates as inertial forces are relatively unimportant for these conditions. Laminar boundary layers are very stable in the downstream direction; any disturbance to the layer (caused by flow over a bump, for example) will be quickly dissipated by viscosity, restoring the velocity profile to the undisturbed state. Thus, in laminar boundary layers, the flow is parallel to the bottom. Turbulent boundary layers occur at high Reynolds numbers and thus inertial forces (or turbulence) dominate over molecular viscosity. The velocity is composed of a mean component plus a fluctuating (turbulent) component. Transfer of mass and momentum within the layer is caused by these turbulent eddies. While the time-averaged flow velocity is in the horizontal, as in the laminar case, turbulent eddies have velocity components in all directions. Descriptions of laminar and turbulent boundary layers can be found in Clauser (1956), Schlichting (1979), and Yaglom (1979); features most relevant to problems in benthic ecology are indicated in Nowell & Jumars (1984). Laminar boundary layers are rare in the ocean, so that subsequent discussion will be for the turbulent case.

Turbulent flows are classified as smooth, rough, or transitional (*e.g.* Schlichting, 1979), depending on the roughness Reynolds number ($Re_* = u_* k_b/v$) which is, again, a dimensionless ratio of inertial to viscous forces in the flow, but in this case it depends on the shear in the flow (u_*, the bottom shear velocity, which is $\mu \, \partial u/\partial z$, where μ is the molecular viscosity of the fluid) and on the physical bed roughness (k_b), as well as on kinematic

viscosity. In the immediate vicinity of the bottom, molecular viscosity is primarily responsible for dissipating flow energy. Outside the viscous sublayer, turbulent eddies mechanically dissipate flow energy as they break down into smaller and smaller eddies until, ultimately, energy is again dissipated by viscosity. A pronounced viscous sublayer (see Fig. 1) may develop in the case of flow over hydrodynamically smooth bottoms occurring at low Re_* (e.g. Eckelmann, 1974). Over hydrodynamically rough bottoms (high Re_*), viscosity still acts at the boundary, but no distinct well-behaved sublayer forms and eddies may penetrate to within tenths of a millimetre of the bed; thus, in rough-turbulent flow, the velocity structure close to the bed is complicated (e.g. Nowell & Church, 1979) and not well known. For intermediate Re_*, transitional flow occurs, with characteristics intermediate between smooth- and rough-turbulent. In the field, smooth-turbulent profiles have been measured by Chriss & Caldwell (1982) and W. D. Grant (pers. comm., see Butman, 1986a) and rough-turbulent profiles by Smith & McLean (1977), Cacchione & Drake (1982), Gross & Nowell (1983), and Grant, Williams & Glenn (1984). At a given site, the flow can be smooth-turbulent under one flow condition and rough-turbulent under another, for example, due to changes in bed roughness by rippling during storms or by bioturbation (see Grant & Madsen, 1986).

Based on empirical studies and scaling arguments (Clauser, 1956), turbulent boundary layers can be divided into three regions (Fig. 1). Adjacent to the boundary, in the viscous sublayer, velocity (u) varies linearly with distance from the bottom. Above this, u varies with $\ln z$ in what is known as the log layer. The region farthest from the boundary is known as the log-deficit layer because the deficit velocity ($U-u$) varies with $\ln z$. The remainder of this discussion will focus on the qualitative and quantitative features of the log layer and the viscous sublayer, because their characteristics are relatively well known (e.g. Clauser, 1956; Yaglom, 1979; Nowell, 1983; Grant & Madsen, 1986) and they are the regions most relevant to larval settlement.

The total thickness of the bottom boundary layer depends on the bottom shear velocity (u_*) and inversely on the forcing frequency for the flow. On the continential shelf, at a latitude of 40°, for a flow periodicity stipulated by the Coriolis force, a u_* of about 1 cm·s^{-1}, and in the absence of stratification, the bottom boundary layer would be about 40 m thick (Grant & Madsen, 1986). The boundary layer grows all the way to the water surface in the smooth-turbulent, tidally driven flows at 10-m depth in Buzzards Bay, Massachusetts (U.S.A.), and for u_* between 0.4 and 0.6 cm·s^{-1} (flow speeds of about 10 to 15 cm·s^{-1} at $z = 50$ cm); the boundary layer fills half the water column for $u_* = 0.2$ cm·s^{-1} (a flow speed of about 5 cm·s^{-1} at $z = 50$ cm) (Butman, 1986a). Boundary layers resulting from forcing due to surface waves are very thin (centimetres to tens of centimetres), however, because of the high-frequency nature of these flows (Grant & Madsen, 1986). In the field, the log layer is known to be about 10–15% of the total boundary layer (Clauser, 1956; Nowell & Church, 1979; Grant & Madsen, 1986), so the log-layer thickness varies between centimetres (wave boundary layer) to about a metre (tidal boundary layer) to several metres (planetary boundary layer), in the examples above. For smooth-turbulent flows, the viscous sublayer can be estimated by 10 v/u_*; for u_* between 0.1 and 1.0 cm·s^{-1} (typical values for

smooth-turbulent flow) and $v = 0.01$ cm^2·s^{-1}, the viscous sublayer thickness will be from 0·1 to 1·0 cm.

In summary, a larva beginning its descent through the water column in the region of potential flow will experience a constant horizontal velocity until it reaches $z = \delta$ and then will experience a sheared flow, where the velocity decreases approaching the bed. At some distance close to the bottom, the horizontal velocity becomes vanishingly small (since $u = 0$ at the sea bed), so the organism would be free to manoeuvre in basically still water. A question relevant to larval settlement in general, and active habitat selection in particular, is: in what region above the sea bed are flow speeds sufficiently low such that settling organisms could effectively manoeuvre (*e.g.* swim among test sites)? Such hydrodynamical constraints for active habitat selection are discussed below. If the larvae sink through the water and are deposited onto the sea bed like passive particles, then parameters of the boundary-layer flow and the gravitational fall velocities of the organisms determine where they will initially reach the sea floor and where they are likely to accumulate. In this case, sediment transport theory can be used to predict depositional or accumulation sites for larvae on the sea floor. Physical considerations involved in such predictions are also discussed below.

HYDRODYNAMICAL CONSTRAINTS ON ACTIVE HABITAT SELECTION

Hydrodynamical constraints on active habitat selection depend on how settlement cues are perceived by the organisms (see pp. 132–4) and on their swimming behaviours and speeds. If larvae respond to waterborne cues, then the boundary-layer flow determines the extent of mixing (and thus, of dilution) of the cue by the time the larva perceives it. The manner in which the larva responds to the cue (*e.g.* does it suddenly quit swimming and sink or does it actively swim straight down to the bed?) and the structure of the near-bed flow regime determine how far the larva will be advected downstream before it reaches the bottom. If larvae must make direct contact with the sea bed in order to perceive a settlement cue then, again, potential test sites on the bed depend on how they conduct a search (*e.g.* do they swim horizontally among sites or do they swim or sink down to a site and then reject it by swimming straight up?) and on the boundary-layer flow regime. Most of the existing laboratory data suggest that larvae must make direct contact with a surface bearing the cue in order to perceive it; this sensing mechanism is assumed, for the sake of argument, in the following discussion.

To determine the flow velocities that larvae experience as they approach the sea floor, Butman (1986a) constructed boundary-layer velocity profiles, based on near-bottom current observations from a shallow (10-m depth), subtidal site in the coastal embayment of Buzzards Bay. The flows at this site are primarily driven by the semi-diurnal tides and current speeds measured one metre above the bottom ranged from 0 to 22 cm·s^{-1}. Velocity profiles in the log layer were calculated, assuming both smooth- and rough-turbulent flow, and for different flow speeds. These velocities were compared with the maximum horizontal swimming speed measured for polychaete larvae (from the review of Chia, Buckland-Nicks & Young, 1984).

The surprising result of this study was that horizontal flow velocities considerably exceed larval swimming speeds, even at only several larval body
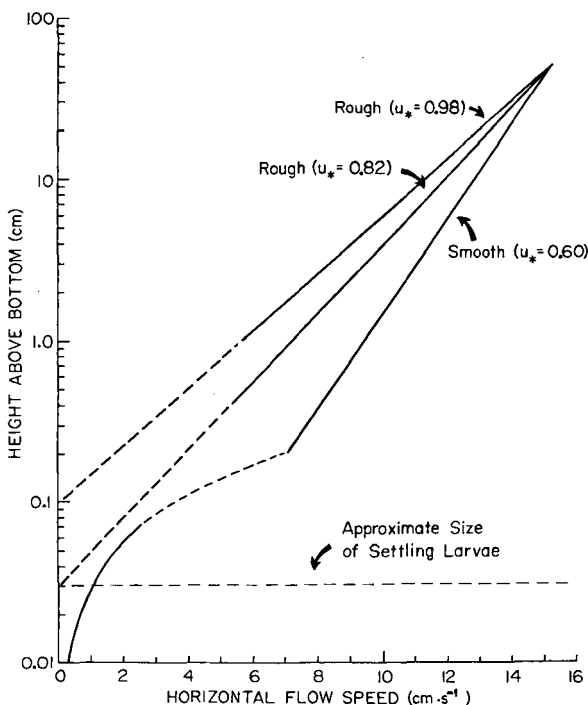
Fig. 2.—Turbulent velocity profiles constructed in Butman (1986a), plotted on a log-linear scale: for the rough-turbulent profiles, the dashed portion represents $(10)(z_0)$; below this level, the accuracy of predictions of velocity by the log-layer function are unknown; for the smooth-turbulent profile, the curved region is the viscous sublayer; the line is dashed at the interface between the log layer and the viscous sublayer because the actual function predicting velocities in this region is unknown; the profiles were constructed for a flow speed of $u = 15$ cm·s^{-1} at $z = 50$ cm, but for different values of bottom roughness (see Table I in Butman, 1986a).

lengths above the bed, for most of the flow conditions used in the analysis. At near-peak ebb or flood tide (when $u = 15$ cm·s^{-1} at $z = 50$ cm), the flow speed is 1 cm·s^{-1} at distances of about 300 μm (smooth-turbulent), 500 μm (rough-turbulent, $u_* = 0.82$ cm·s^{-1}) and 1500 μm (rough-turbulent, $u_* = 0.98$ cm·s^{-1}) above the bed (Fig. 2). Because maximum measured swimming speeds of polychaete larvae are only 5 mm·s^{-1}, they would have a difficult time manoeuvring horizontally (e.g. to swim between potential test sites) in any of these flows. Swimming full-speed against the flow at about two body lengths above the bottom, the larvae would still be advected downstream at 5 mm·s^{-1}! Plots of smooth-turbulent velocity profiles for various current speeds (stages of the tide for the Buzzards Bay case) (Fig. 3) indicate that larvae could effectively manoeuvre via horizontal swimming at distances of several body lengths above the bed during near-slack tide (line C in Fig. 3, where $u = 5$ cm·s^{-1} at $z = 50$ cm) and for slower forcing flows.

Figure 2 also shows that, at a given height above the bed and for the same

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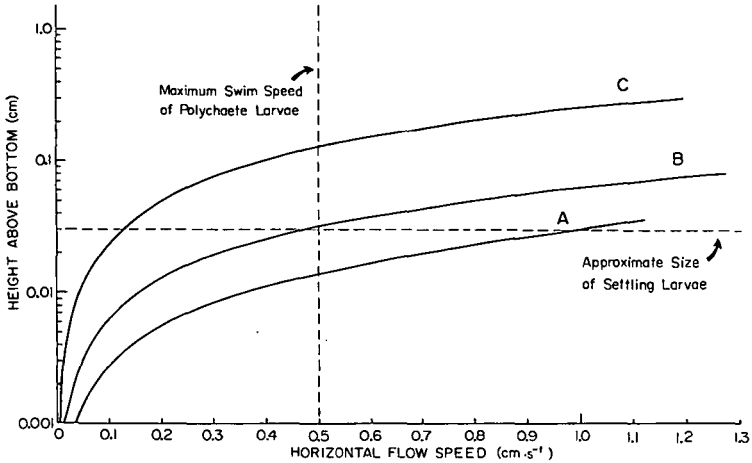
Fig. 3.—Smooth-turbulent velocity profiles for three flow speeds (repre-
senting three stages of the tidal cycle in Buzzards Bay), as constructed in
Butman (1986a) and plotted on a log-linear scale: only the viscous sublayer
is shown on the Figure; Line A is for $u = 15$ cm·s^{-1} at $z = 50$ cm; Line B
is for $u = 10$ cm·s^{-1} at $z = 50$ cm; Line C is for $u = 5$ cm·s^{-1} at $z = 50$ cm.

forcing flow at the top of the log layer, the mean horizontal velocity close to
the sea bed will be substantially slower in rough- than in smooth-turbulent
flow due to the more efficient mixing of high- and low-momentum fluid
by eddies in the rough-turbulent flow. Larvae experience, however, only
horizontal flow velocities within the viscous sublayer in smooth-turbulent
flow, whereas for rough-turbulent flow, they experience the mean horizontal
flow speed plus the fluctuating velocity components in all directions, as eddies
regularly penetrate the viscous sublayer. Thus, while a larva may encounter
unmanageable flow velocities for effective manoeuvring in the horizontal, it
can swim up and down unperturbed by vertical flow velocity within the
viscous sublayer for smooth-turbulent, but not for rough-turbulent flow.
    From this quantitative analysis of bottom boundary-layer velocity profiles
in a realistic field flow environment, it appears that polychaete larvae probably
do not actively swim horizontally among test sites, except under very low-
flow conditions (*i.e.* around slack tides in the Buzzards Bay case). It seems
more likely that larvae test habitats by sinking or swimming down to the bed
and reject a site by swimming back up into the water column, although the
potential effectiveness of this behaviour for rough-turbulent flow is unclear.
Since near-bed velocities would carry the larvae over a suite of potential test
sites, the habitats presented for their perusal are hydrodynamically
constrained. Note that while the sites that a drifting larva may inspect are
hydrodynamically determined, the larva may be carried over a wide range of
habitats (at 1 cm·s^{-1}, the larva is carried about 1 km·day^{-1}), much farther
than it can swim in the same amount of time. Sinking at a rate of 0·1 to 1·0
cm·s^{-1} (as measured in Hannan, 1984a,b), the larva would, however, hit
bottom after being advected only centimetres, so it would have to swim up
at speeds greater than or equal to its fall velocity to stay above the bottom
while drifting. It is possible that larvae do not select habitats by swimming

among them; once they reach the sea floor, they may simply crawl between microhabitats, in which case the spatial scales for active habitat selection are very small indeed.

Given that near-bed flow velocities over a relatively smooth, flat bottom may allow for very limited manoeuvring by larvae, any flow region with substantially lower velocities (*e.g.* in the lee of a relatively large roughness element, such as a rock or a tube, or in a dense canopy, such as a seagrass bed) may be particularly important to settling larvae. Whether they actively leave the flow (*i.e.* by swimming down or sinking) to enter such regions, or simply get deposited there (see pp. 151–4), they may be able to investigate actively such areas without significant interference from the flow regime.

The velocity profiles constructed in Butman (1986a) are discussed in detail here because they are unique to the present day literature in larval ecology; they represent, however, conditions for but one class of flow environment (steady, uniform, tidally driven flows in shallow, coastal embayments) and for one group of infauna (the polychaetes). Furthermore, the analysis is limited by the lack of biological information, for example, on how larvae actually peruse available sites even in still water (*i.e.* is it by horizontal or vertical swimming, or some combination of the two, and from what height above the bed?) and on the relative swimming speeds and fall velocities of the organisms and the changes in these speeds over their pelagic life. While it is clear that hydrodynamics may limit the active habitat selection options for settling larvae, the capabilities of the larvae to overcome or utilize these flow obstacles are not clear.

PASSIVE PARTICLE TRANSPORT AND DEPOSITION

The long-held tenets that larval dispersal is primarily passive, *via* ocean currents, but that larval settlement is controlled by active larval behaviours have assumed that flows very close to the sea bed (*e.g.* within the viscous sublayer) were sufficiently slow to allow for searching and active habitat selection by the larvae. The likelihood that larval settlement is controlled, at least in part, by hydrodynamical processes is strengthened by the results of Butman (1986a) that relatively large (compared with larval swimming speeds, but see also Herrmann, 1979, and Lee, 1984) horizontal flow speeds occur within larval body lengths of the sea bed. If boundary-layer flow processes are transporting and depositing larvae, then the body of literature on sediment transport and deposition can be used to generate *a priori* predictions of depositional and accumulation sites for the organisms on the sea bed.

The trajectory of a particle falling from the water surface to the bottom is determined by the horizontal displacement caused by the flow (advection) and by gravitational sinking of the particle. Once it reaches the bottom, the particle will settle on the sea bed if the bottom shear stress ($\tau_b = \rho u_*^2$, a force per unit bottom area, where ρ = fluid density) does not exceed the critical value for suspension of the particle. This critical stress is usually reported in units of velocity as u_{*s}, the critical suspension velocity. The ratio of particle fall velocity (w) to u_{*s} determines if the particle remains in suspension; when $w/\kappa u_{*s} < 0.8$ (where κ = von Karman's constant of 0.4), then the particle will move as suspended-sediment transport (Smith & Hopkins, 1972). For $w/\kappa u_{*s} > 0.8$, the particle will fall to the sea bed, but will move as bedload

transport if $u_* > u_{*c}$, where u_{*c} is the critical shear velocity for the initiation of particle motion. Bedload transport involves sliding, rolling or hopping of particles along the sea bed. From detailed laboratory measurements, curves have been constructed which allow prediction of u_{*c} for given particle characteristics (diameter and density) and fluid characteristics (density and viscosity). The most common relationship used is Shields' curve (Shields, 1936) or a subsequent modification (*e.g.* Miller, McCave & Komar; Yalin, 1977); these curves were, however, constructed from measurements on abiotic, non-cohesive sediments $\geqslant 100\ \mu$m in size and spread in homogeneous size classes (*i.e.* not size-class mixtures) on the bottom. Results for initiation of motion or suspension of fine, biotic or cohesive sediments and sediment mixtures (*e.g.* Nowell, Jumars & Eckman, 1981; Grant, Boyer & Sanford, 1982; Lick, 1982; McCave, 1985; Partheneides, 1986) have not yet been integrated into formal predictive functions, at the level of Shields' curve, for example.

The shear velocity of the flow (u_*) and the particle fall velocity (w) are involved in all estimates or predictions of particle deposition and transport. Measurements of w now are reliable and routine for a wide range of non-aggregated particles; as mentioned earlier, determining the fall velocities of naturally occurring aggregates is still, however, troublesome (but see new *in situ* techniques in Bartz *et al.*, 1985). Estimating u_* for the suite of complex flow environments occurring in the field has been a primary focus in sediment-transport modelling over the last decade (Grant, 1977; Smith, 1977; Smith & McLean, 1977; Grant & Madsen, 1979, 1982; Grant & Glenn, 1983; McLean, 1985). From detailed field measurements of velocity at several heights within the log layer, it is possible to estimate u_* from the slope of the line relating u and $\ln z$ (because, within the log layer, $u = u_*/\kappa \ln z/z_0$, where $z_0 =$ the bottom roughness parameter); the correlation between the two variables must, however, be extremely high (generally > 0.990) for reasonable limits (*e.g.* $< 20\%$) to the error in such u_* estimates (Gross & Nowell, 1983). This is because a well-behaved log layer generated from a single source of flow forcing is actually rare in the field. Instead, forcing from several sources (*e.g.* tides, internal waves, and surface waves generated by winds) occurs simultaneously to produce several log layers superimposed on one another. The effects are not simply additive between steady (due to currents) and non-steady (due to waves) flows, so a considerable theoretical modelling effort has been placed on predicting u_* from field data in these cases (Smith & McLean, 1977; Grant & Madsen, 1979, 1982).

The wide range of values which are possible for u_* in the field, even over time at a single location, means that particles may move almost continuously or intermittently, depending on the physical forcing. Bottom topography also plays a major rôle in determining the eventual accumulation sites for a given particle class, by altering the flow regime. Through these processes, the large-scale (tens of metres to tens of kilometres or more) distribution of sediment grain sizes are established. The sediment distributions documented by regional surveys generally reflect a long-term dynamic equilibrium between the physical processes which transport and deposit the sediments. A recent overview of the spatial and temporal scales of physical processes which produce various features of the sedimentary and sediment-transport environment at a single, well-studied locale (Georges Bank, Massachusetts, U.S.A.), and written for a general audience, is given in Butman (in press).

Smaller-scale (centimetres to metres) changes in sediment texture result from small-scale variability in bottom topography. The scale of the morphological feature in the sea bed sets the scale of sediment grain-size patchiness. For example, in an area of coarse sand, fine sediments often accumulate in the feeding pits of rays, which are tens of centimetres in diameter (Grant, 1981; VanBlaricom, 1982). For unevenly distributed flow obstacles (or relatively large roughness elements) such as rocks, biogenic mounds, or tubes of infauna which are relatively far apart, the sediment environment is affected at spatial scales of the order of the diameter of the obstacle (*e.g.* Eckman & Nowell, 1984). For more densely packed elements, effects on sedimentation are a function of the height and packing of the elements and of the flow regime (*e.g.* Wooding, Bradley & Marshall, 1973; Nowell & Church, 1979; Eckman, 1983), so that laboratory flume studies may be required to predict specific effects (see especially Eckman, 1983).

Passive deposition and accumulation of larvae is expected at the spatial scales which apply to sediments with similar fall velocities. The quantitative data for polychaete larvae indicates that their fall velocities (0·1 to 1·0 cm·s^{-1}) are within the range of fine quartz sediments (silts) 10–80 μm in diameter (Hannan, 1984a,b). Pratt (1953) and Tyler & Banner (1977) found that bivalve and echinoderm postlarval distributions were well correlated with distributions of the "fine" sediment fraction over spatial scales of kilometres. Settling larvae may thus accumulate in regions where fine sediments accumulate; *i.e.* both groups of "particles" are in dynamic equilibrium with the physical environment. On the largest scales (tens of metres to tens of kilometres), these accumulation zones are set by large-scale topography and the flow during the time of larval settlement. Settling larvae, however, differ from settling particulates in that they may become sticky once they reach the bed or they may burrow into it. If these factors are significant, then perhaps only the initial distribution of larvae on the sea bed would be determined by physical processes. Finally, larvae may also accumulate like passive particles on small spatial scales (centimetres to metres) due to microtopography effects, as suggested by the results of Baggerman (1953), Eckman (1979, 1983) and Hogue & Miller (1981).

In summary, the increasing literature on sediment transport allows predictions of erosion, transport, deposition, and accumulation of particles of a given fall-velocity class, given important information regarding the field flow regime. Such models can be used to generate predicted distributions for passively settling larvae, once the larval fall velocity is known. Both large- and small-scale patterns of initial larval settlement and subsequent accumulation could be explained by physical processes, since variability in sediment distributions can occur on several scales. It is, however, most intriguing that the observed correlations between infaunal species composition and bulk sediment distributions at large spatial scales (*e.g.* see Table III, pp. 120–1) may simply occur because larval settlement is determined by the same physical processes which maintain the distribution of sediments, which have fall velocities similar to larvae.

The passive deposition hypothesis may also explain some of the often extreme variability in larval settlement in different years. Although the surficial sediment distributions are the cumulative result of many sediment transport events over a long time, the larvae experience only a subset of these

events at the time of settlement. This wide range of flow events (storms, spring or neap tides, and run-off, for example) could change the 'average' deposition pattern for larvae by altering the advective, as well as the depositional regimes, for the short time that the organisms are in this critical stage of their life history. In addition, attractive characteristics of surface sediments depend, in part, on rates of sedimentation and the hydrodynamics of the region, such that appropriate settlement cues may be emitted from a given area only intermittently (Chia & Crawford, 1973). The sporadic availability of depositional environments or attractive surface sediments should be particularly important for species that have sharply limited, rather than extended, reproductive seasons. In fact, Todd & Doyle (1981) have proposed the "settlement-timing hypothesis" to account for the reproductive behaviour of benthic invertebrates, where the behaviour of a given species in a particular environmental settling is a compromise for that area, between the optimal time for spawning and the optimal time for settling, both of which are energetically constrained.

COMPATIBILITY OF THE ALTERNATIVE HYPOTHESES

Active habitat selection by and passive deposition of larvae need not be considered mutually exclusive alternative hypotheses. The processes may both operate, but over different scales of space and time. The relative importance of the two processes may also vary for different species (depending, for example, on the fall velocity and swimming capabilities of the organisms), for different flow environments, or depending on how long the organisms have been in the plankton. In addition, the composition of infaunal communities may be determined, in part, by dispersal and deposition (active or passive) of post-larvae or adults (but see also Santos & Simon, 1980a), as evidenced by the mounting records of benthic organisms in the water column (Table II, but see also Ambrose, 1984a). Surface or near-surface dwelling organisms may periodically enter the water with sediments during rigorous, storm-induced resuspension events (Hagerman & Rieger, 1981; Hogue, 1982; Dobbs & Vozarik, 1983), or regularly, during tidal resuspension (Bell & Sherman, 1980; Palmer & Brandt, 1981; Palmer & Gust, 1985). There is also indirect evidence (from sampling of the sea bed) that infauna or meiofauna actively or passively enter the water column to migrate to new locations (Baggerman, 1953; Trueman, 1971; Dauer & Simon, 1975; Farke, de Wilde & Berghuis, 1979; Grant, 1981). Thus, individual members of the infaunal community may be much more dynamic than heretofore believed.

Evidence from the literature on benthic ecology and considerations of physical phenomena suggest that larvae may be passively deposited and accumulate at the large spatial scales (tens of metres to tens of kilometres) which apply to sediment transport and deposition and that active habitat selection occurs over much smaller scales (centimetres to metres) within these broad, depositional areas. Local distributions of settling or settled organisms also could be determined by small-scale physical phenomena, such as changes in flow induced by microtopography of the sea bed. In addition, larvae may be permitted to select actively habitats over larger spatial scales during time

periods when flows near the bed are very slow (*e.g.* surrounding slack tide) or in areas of sluggish circulation, in general.

The extent to which organisms can actively select habitats within their flow environments depends on their method of perceiving, testing and locating habitats. Certain species, morphological types and/or developmental stages of larvae are more capable of controlling their position in the water column than others. Crustaceans, in general, possess much better swimming and position regulating capabilities than most other infauna (see Mileikovsky, 1973; Mann & Wolf, 1983; Chia, Buckland-Nicks & Young, 1984; Sulkin, 1984), so they may be expected to manoeuvre more effectively in flows. Likewise, during development swimming abilities may increase (*e.g.* Herrmann, 1979; Lee, 1984) or decrease (*e.g.* Konstantinova, 1969; Miller & Hadfield, 1986; author's unpubl. data), so larvae may become more or less effective in locating preferred habitats.

The evidence for decreasing substratum selectivity as competent larvae spend more time in the plankton suggests a finite period for active habitat selection, following which, passive deposition may occur. Delay of metamorphosis by many species may allow the organisms to be passively advected until they reach flow environments which are sufficiently sluggish that active searches for preferred substrata are possible. Species with developmental constraints on their pelagic period may only be capable of actively selecting habitats early in their competent period, if flows permit, whereas later on the organisms may be passively deposited as the larvae are "forced" to metamorphose and settle. Hadfield (1978b), however, reported an interesting case of "partial metamorphosis" in the larvae of an enteropneust, where the larvae lose all pelagic characteristics except the teletroch, which is retained for locomotion until the organisms reach a bottom habitat that is soft enough for burrowing.

These options for the compatibility of the active habitat selection and passive deposition hypotheses are posed to stimulate new research in this area. Certainly there are other options, in addition to the few proposed here. As technological advances increasingly provide biologists with the tools necessary to study organisms within their natural habitats (simulated in the laboratory or *in situ*), so we may expect advances in our ecological insight of how organisms perceive, cope with, and are controlled by their environment. Nearly thirty years ago, Wilson (1958) spoke of the interdisciplinary nature of larval settlement studies, urging interaction between biologists and chemists in defining attractive factors of sediments and other settlement cues. His remarks (Wilson, 1958, p. 96) are still relevant today, only "other sciences" now includes physics, as well : "As for the larval-settlement problems, so here the zöologist has been brought to the borders of other sciences, and without collaborators from these sciences to help him [and her] along he [and she] is [are] not likely to make much further progress."

ACKNOWLEDGEMENTS

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NOTE ADDED IN PROOF

Regretfully, most of the papers from the Proceedings of the Invertebrate Larval Biology Workshop held at the Friday Harbor Laboratories, University of Washington, 26–30 March 1985, and published in *Bull. Mar. Sci.*, **39**(2) in 1986, were not available to the author at the time this manuscript was written. Many of these papers are relevant to the ideas discussed in this review.