



Opposing organizing forces of deposit-feeding marine communities

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Abstract

We contend that a range of phenomena characterizing temperate deposit-feeding communities in low-energy environments is strongly organized by two principal opposing forces: (1) spatially localized inputs of detritus or new recruits, leading to a mosaic of initial patches, with subsequent impacts on spatio-temporal variation of species with limited mobility; and (2) the impact of mobile consumers, which move to spatially localized resources and thereby exert major controls over comparatively larger spatial scales. Surface deposit feeders react differently from deep feeders, in terms of spatio-temporal population change. The two opposing community control forces, combined with responses of deposit feeder functional groups, have potentially different effects on community structure. Mobile consumers, often acting as keystone species, may move to localized patches created by the bottom-up force of food input or by localized recruitment of prey. Their mobility, combined with predicted optimal foraging behavior, would usually produce a spatially homogenizing force, leading to reduced spatial variation in community composition. By contrast, spatially localized inputs of resources, if dominant, would always lead to strong spatial heterogeneity. Dominance of complex space–time variation in detrital enrichment would lead to strong spatio-temporal complexity in macrofauna if the response of recruiting larvae and rapidly growing small invertebrate populations was immediate and keyed to localized food input. The ability of mobile consumers to locate detritus, combined with the spatial distribution and overall input rate of detritus, should determine the balance of surface and deep-feeding deposit feeders. The opposing force approach can be applied to communities generally.

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1. Introduction

1.1. The stability-trophic structure hypothesis

Levinton (1972) argued that the spatial and temporal variability of resources exerted a short-term, but major, influence on the structure of marine benthic communities. In particular, Levinton argued for a dichotomy between communities dominated by suspension feeders and those dominated by deposit feeders. Sanders (1958) had outlined a set of nearly mutually exclusive conditions that favored dominance by either suspension feeders or deposit feeders, so it made sense to search for distinguishing features between the two community types. Suspension-feeding communities were hypothesized to live in a trophically more varying environment and, additionally, a resource-independent environment. By contrast, deposit feeders were thought to live in a trophically more stable environment, with resource limitation being more common than in suspension feeding communities.

The overall hypothesis predicts more spatial constancy and resource limitation in deposit-feeding communities relative to suspension feeding communities. Such a hypothesis can be tested by comparing population densities of a common deposit-feeding species over a number of areas. This was done in a number of studies of the deposit-feeding genus *Hydrobia* and a remarkable consistency of density was found in many localities, suggesting resource limitation. The effects of population density on growth were mirrored by size variation in field populations (Levinton and Bianchi, 1981). Similarly, some comparative studies of European tidal and shallow subtidal environments support the increased spatial variance of suspension feeding populations, relative to deposit-feeding populations (Beukema et al., 1983; Kamermans et al., 1992) and the comparatively greater occurrence of food limitation in deposit feeders, as contrasted with suspension feeders (Kamermans et al., 1992; Olafsson, 1988). The prediction of frequent lack of food limitation of benthic suspension feeders has not been tested systematically, although one particularly well-done study produced contradictory results (Peterson and Black, 1987).

While these results are encouraging, our perception of deposit-feeding has changed markedly since Levinton (1972). Two arguments at that time supported the apparent constancy and resource limitation of deposit-feeding populations. First, deposit feeders were more abundant in fine-grained sediments, which contained more organic matter than the coarser-grained sediments, which are more usually dominated by suspension feeders (Sanders, 1958). Second, deposit feeders were found to digest and assimilate microbial organisms from the sediment with much greater efficiency than the more refractory particulate organic matter usually found in temperate intertidal and subtidal sediments (Fenchel, 1970; Hargrave, 1970; Lopez and Levinton, 1987; Lopez et al., 1977; Newell, 1965). If microbial abundance was a limiting factor, then microbial growth rate and standing stock in equilibrium with grazing would determine food availability and food limitation (Levinton, 1979b; Levinton and Bianchi, 1981). Furthermore, a balance between sediment pelletization and pellet breakdown also contributed to resource limitation in cases where pellets were not ingested until they had broken down to constituent particles (Levinton and Lopez, 1977). In the case of *Hydrobia*, laboratory studies suggested that resource limitation and spatial interactions appeared to limit densities to ca. 2 snails mm^{-2} (Levinton, 1979a). Bacteria appeared to be relatively

unimportant, so it was the rate of recovery of benthic microalgae that might limit *Hydrobia* population growth. This was substantiated by laboratory microcosm experiments of assimilation and growth limitation (Kofoed, 1975; Levinton and Bianchi, 1981).

1.2. The importance of detrital supply

While microbial growth and pelletization rates and selectivity may indeed limit surface algal grazers to certain food types (Connor and Edgar, 1982; Kofoed, 1975; Levinton and Bianchi, 1981; Pace et al., 1979), it has become apparent that variable detrital enrichment exerts important influence on the trophic ecology of intertidal and subtidal deposit-feeding communities. This makes for a far more dynamic situation than argued by Levinton (1972). Most subtidal detritus derives from sedimenting phytoplankton, although some shallow water macroalgae can travel downslope to the deep sea (Levin and Smith, 1984); intertidal detritus is probably a combination of phytodetritus, decomposed macroalgae and to a lesser extent, seagrasses, and land derived sources (Mann, 1988). While microbial food sources are usually more digestible (Fenchel, 1970; Levinton, 1985; Levinton et al., 1984), detrital organic material is nevertheless very abundant in sediment and even a relatively low deposit feeder assimilation efficiency will extract significant nitrogen and carbon from the sediment (Cammen, 1980b; Cammen et al., 1978; Levinton et al., 1984). Although microbial intermediate routes are possible, stable isotope analysis demonstrates direct connections between detrital sources and deposit feeders (Findlay and Tenore, 1982; Peterson et al., 1985, 1986). Detritus derived from seaweeds can be spatially localized and correlated with deposit feeder abundance (Levinton and McCartney, 1991). Late winter–early spring deposition of detritus apparently fuels the sediment with deposit feeder food and opportunistic annelid populations rapidly increase as spring temperatures increase (Cheng et al., 1993; Marsh and Tenore, 1990). Furthermore, detrital supply, especially phytodetritus, can also be shown to be strongly positively correlated with pulses of benthic animal activity on subtidal shelves (Aller et al., 2002; Elmgren, 1984; Gerino et al., 1998; Stead and Thompson, 2003; Thompson and Nichols, 1988).

Laboratory studies of detrital supply suggest the combined role of detrital enrichment and temperature on opportunistic annelid deposit-feeding species, with indirect effects on the microbial component. Detrital input can be shown to enhance the growth of short generation time deposit feeders such as polychaetes and oligochaetes (Cheng et al., 1993; Tenore, 1977), which may intercept nutrients that might be exploited by other species (Alongi and Tenore, 1985). Higher temperature interacts with food supply by increasing metabolic cost and increasing the probability that opportunistic annelid populations will crash sooner in the early summer, when food supply is diminishing and temperature is increasing (Cheng et al., 1993; Levinton and Stewart, 1988). Not only does such detrital input positively affect the annelid populations, it also subsidizes benthic microalgal growth, which further provides highly digestible food for annelid consumers (Levinton and Stewart, 1988).

1.3. The spatially homogenizing effect of mobile consumers

Many marine communities are strongly affected by mobile and potent consumers that exert strong top-down effects. Examples include starfish and urchins on rocky

shores (Menge, 1976; Paine, 1966; Seed, 1969), herbivorous fish and urchins on coral reefs (Ogden et al., 1973; Sammarco, 1982), sea otters in kelp beds (Duggins, 1980; Estes and Palmisano, 1974; Harrold and Reed, 1985), lobsters and urchins in shallow subtidal and low intertidal habitats (Robles et al., 1990; Vadas and Steneck, 1995), and fish in seagrass beds (Heck et al., 2001). A classic in this area is the study by Schneider (1978), which showed that compensatory feeding and movement to new prey-rich patches by shorebirds resulted in equalization of prey numbers along soft-bottom shores. Robles et al. (1995) showed that the seastar *Pisaster ochraceus* moved surprisingly large distances along the shallow subtidal shore in response to localized high recruitment of mussels. After clearing these mussels away, they soon departed. Mobile zooplanktivorous fish would exert much the same effect by moving between major zooplankton patches, cropping them down and thus providing a similar equalizing force.

In soft-sediment communities, we suggest that mobile gastropods, echinoids, and sea cucumbers can locate new depositions of detritus and, through feeding and bioturbation, may equalize abundances of local surface-feeding deposit feeders. Fiddler crabs, for example, often move in packs to areas of high food abundance (Crane, 1975) and may strongly affect localized meiofaunal populations (Hoffman et al., 1984). The important feature of these mobile organisms is their ability to move to new patches of abundant food. Optimal foraging arguments suggest that such mobility is to be expected (Hughes, 1993; Stephens and Krebs, 1986) although the rules for spending time in a patch may vary with efficiency of foraging (e.g., Weissburg, 1992). The net effect of this mobility is the pruning down of localized patches of resources, followed by movement to other patches. Our experimental and field evidence (see below) shows that individuals of the mud snail *Ilyanassa obsoleta* move to patches of newly dead seaweed, resulting in rapid changes of density and spatial arrangement. These consumers are often also biological bulldozers and exert other negative effects on small deposit feeders of lower mobility (Kelaher et al., 2003; Levinton et al., 1985).

Of course no generalization applies universally and we emphasize that our claim refers to large-bodied consumers that are mobile, relative to the grain of environmental heterogeneity in a given habitat. Depending on this scale of mobility relative to spatial variation in prey density, mobile consumers might decrease or increase among-site variance (Schneider, 1992). Localized recruitment of important consumers that are less mobile, such as limpets and predatory snails, can increase patchiness (e.g., Menge, 1995). Even mobile consumers may arrive at dense patches and consume all local prey, thus increasing spatial variance (Fairweather, 1988; Schneider, 1992). Indeed, it is the fact that such variation can occur that we need both experimental and sampling approaches to understand the balance between mobile consumer activities and localized bottom-up inputs.

1.4. The spatially diversifying effect of localized food input and recruitment

The input of food supply often acts quite differently from the expected homogenizing effect of mobile, top-down consumers. Food inputs are often spatially patchy, especially when they involve deposition of detritus. For example, benthic green seaweeds are often

spatially discontinuous on sand and mud flats and their deposition can strongly affect population response of benthic surface deposit feeders (Levinton and Stewart, 1982; Raffaelli and Milne, 1987). Using photosynthetic pigment markers, (Levinton and McCartney, 1991) showed that the inputs of seaweed detritus into a sand flat, even with vigorous flow, were highly localized, and most deposition occurred immediately adjacent to the seaweed beds. In the mud flats of Flax Pond in Old Field, New York, patches of *Ulva* are apparent and these often lead to localized decomposition and inputs of detritus and formation of bacterial mats (Fig. 1). Localized patches of food and resident infauna create a complex spatial mosaic of positive and negative cues for settling larvae and immigrating adults (Woodin et al., 1998). Burrowing activities within invertebrate beds, which can be very localized (e.g., *Clymenella* and other deeper burrowing polychaete beds), can affect horizontal bedload and deposition of eelgrass seeds (Luckenbach and Orth, 1999). On western rocky shores of South Africa, localized deposition of seaweed detritus derived from kelp beds was a major bottom-up structuring force, causing strong spatial variance in limpet densities (Bustamante and Branch, 1996; Bustamante et al., 1995; Menge, 1995). There has been more recent appreciation of the role of local food inputs in affecting rocky shore communities (Menge et al., 1997).

The understanding of the balance of these two organizing forces is crucial in general explanations of community ecology but also has strong relevance to an emerging understanding of major changes now occurring in the coastal ocean, involving the removal of major top-down and highly mobile organizing elements of communities (e.g., Jackson et al., 2001; Newell, 1988) combined with the increased input of nutrients from pollution and the great enhancement of the dominance of inputs from bottom-up forces (e.g., overgrowth of nuisance algal blooms and high abundances of phytobenthos) on community organization. For example, removal of top predators and consumers such as urchins may result in rapid overgrowth of species in lower trophic levels, although complications can develop from multiple trophic levels (Estes and Palmisano, 1974; Peterson and Estes, 2001). The overharvesting or invasion of bivalve mollusks in coastal and estuarine systems has resulted in major shifts of water column communities (Newell, 1988; Officer et al., 1982).

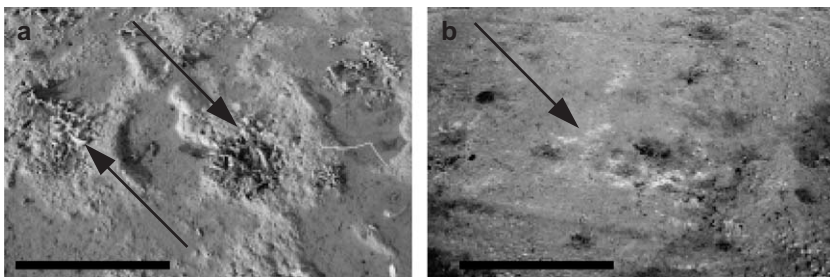


Fig. 1. Spatially patchy occurrence of the green seaweed *Ulva rotundata*, on a mudflat at Flax Pond, New York, USA. (a) Live *Ulva* patches; (b) one patch that has decomposed in situ, with the sediment now covered (in Spring) by *Beggiatoa*. Scale = 25 cm.

1.5. Deep versus shallow deposit feeders

Of necessity most detrital input to soft sediments comes from the overlying water as phytodetritus or from the surface as the result of decomposition of seaweeds and seagrasses (Lopez and Levinton, 1987). Surface feeding annelids and gastropods are poised to take advantage of this input and much benthic secondary production, even in parts of the deep sea, probably depends on detrital additions (Christensen and Kanneworf, 1986; Duggins and Eckman, 1997; Elmgren, 1984; Tenore and Hanson, 1980; Thiel et al., 1988; Thompson and Nichols, 1988). Surface feeders range from deposit feeders that directly ingest sediment and detrital material to those that collect particles saltating in the bedload (Taghon et al., 1980) or even suspension feeders that depend on resuspended bottom detritus and benthic microalgae (Judge et al., 1993). While much of this material is probably consumed or decomposes at the surface, it is the ultimate supply for a variety of deposit feeders, principally polychaetes that live and feed mostly beneath the surface (Bianchi, 1988; Hylleberg, 1975; Longbottom, 1970; Rhoads and Stanley, 1965; Weinberg, 1988). Deep feeders can draw surface-deposited organic matter down rapidly below the surface, subjecting it to further decomposition and ingestion by deeper feeders (Mayer and Rice, 1992). Burrowing and feeding activities of this functional group convert often refractory organic matter into animal flesh either by direct consumption or by stimulating or enabling sediment bacterial activity by attracting deposition of organic detritus (Retraubun and Evans, 1996; Rice and Rhoads, 1989). While many deposit-feeding invertebrates are efficient at stripping microbial organisms from sediments and digesting labile detrital material, deep-feeding annelids may be especially capable, owing to the presence of strong solubilizing potential in the gut, which is partially enabled by strong surfactant activity (Mayer et al., 1997).

Deep feeders are not restricted to feeding entirely below the surface. For example, the usually deep feeding bamboo worm *Clymenella torquata* will emerge and feed at the surface if fresh detritus is deposited there (Weinberg, 1988). Deep feeders are often ecologically connected to the surface by virtue of their burrowing and irrigation activities, which exert strong feedbacks and sometimes subsidy of microbial activities and abundance at the sediment surface (Bianchi et al., 1998). Deep-feeder activity may also exert negative effects on surface zoobenthos requiring a stable living position, such as burrowing amphipods (Flach, 1992).

Deep feeders are usually dependent upon the material that is not consumed at the surface by decomposing organisms and surface deposit feeders. On the other hand, their large size provides them with higher throughput (Cammen, 1980a), longer gut residence times and likely greater total digestive capacity (Mayer et al., 1995). Their sub-surface habitat, moreover, places them out of direct contact with a variety of visual predators, such as shorebirds. We hypothesize that the sum of these features tends to reduce mortality and increases population stability. We predict therefore that temporal variability of this functional group should be less than for surface deposit feeders.

1.6. Impacts on spatial variance of community structure

We need a systematic approach to the understanding of the balance of these forces and the impacts of these changes on spatial–temporal variation in community structure.

Because natural communities are so variable, the importance of a statistical framework to such studies cannot be overstated. Soft-sediment communities are dynamic in space and time and yet we still know little of how they generate patterns of population change at different spatial scales (Thrush, 1991; Zajac, 2001). It is clear that simple relationships between sediment and animal assemblages are insufficient to explain distributions; more complex algorithms are necessary (Snelgrove and Butman, 1994) and require an accounting of the effects of spatial scale (Zajac et al., 1998). We believe that our overarching hypothesis of interactions between spatially discontinuous inputs and top-down effects of mobile consumers is a key to much of this variation. We hypothesize that much of this variation is generated by localized asynchrony of seasonal cycles, owing to spatial differences in times of disturbance, which may be erratic and unpredictable, or may be due to spatial differences in the temporal initiation of processes that follow overall a similar seasonal cycle, such as deposition of phytodetritus and other organic detritus from the spring phytoplankton bloom (Beukema et al., 1983; Elmgren, 1984). Previous work on salt marsh mudflat communities demonstrated a shift in life history of the dominant annelid species toward a swimming morph, when food was exhausted. This led to the inference that local areas must have consisted of a patchwork of sites in various states of a food “boom and bust” cycle, which provided an adaptive explanation for swimming away from a locally depleted patch (Nilsson et al., 2000).

The concept of a *spatial–temporal mosaic of patches* was pioneered by Johnson (1970), who argued that subtidal soft-sediment communities normally undergo a predictable successional sequence following a disturbance. The sea bed consisted of a spatial landscape of patches with different elapsed periods since a disturbance. It was this spatial patchwork of disturbance histories that explained the spatial variance in community structure. Our evidence (discussed below) from studies of intertidal mudflats demonstrates that such a spatial mosaic is real, and we have been able to demonstrate site-specific asynchrony in cycles of flushes and crashes of surface deposit-feeding invertebrates

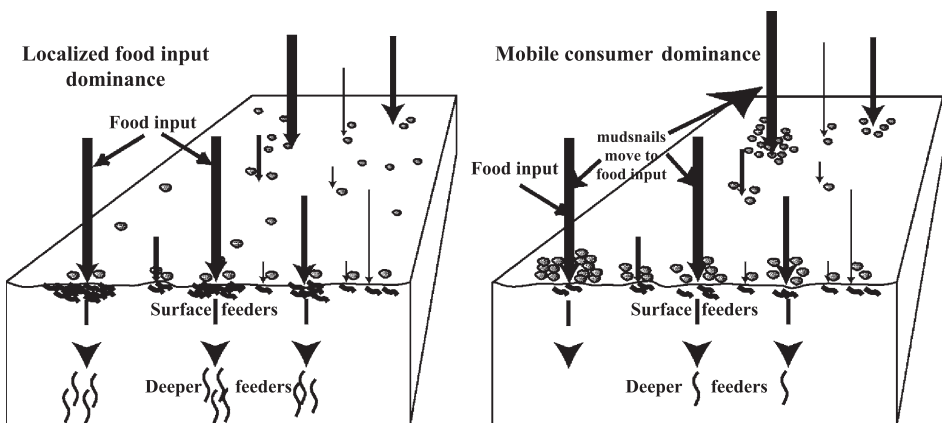


Fig. 2. Benthic processes can be conceived as resulting from the opposing forces of mobile consumers finding and affecting localized inputs of detritus and detritivores that respond to those inputs.

(Kelaher and Levinton, 2003). A later development of Johnson's model was formulated by Rhoads et al. (1978) who argued that earlier surface-feeding species would be succeeded by later deeper-feeders. In our experience, these two types tend to coexist in the same habitats in southern New England communities.

Fig. 2 is a visualization of our spatial–temporal model of opposing forces, applied to salt marsh soft-sediment communities of southern New England. Detrital inputs are argued to be spatially discontinuous and temporally asynchronous. This force stimulates population increase of surface-feeding deposit feeders. Those with short distance

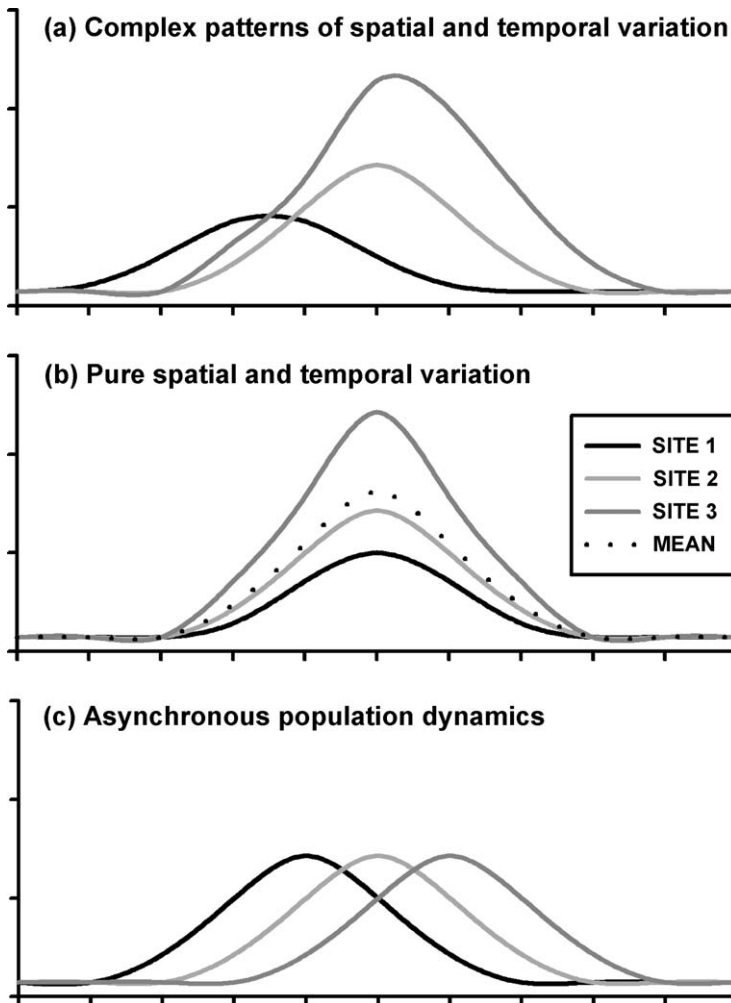


Fig. 3. Inputs of detritus that are spatially and temporally localized should result in a spatio-temporal mosaic of localized population growth by rapid-responding deposit-feeding annelid populations. This should hypothetically result in asynchrony among local sites, separated by distances on the order of 10s of meters.

adult movement (e.g., *Hydrobia*, *Streblospio*, *Paranais*, *Capitella*) respond by either short-distance movements to localized sites of food abundance (*Hydrobia*), increasing population abundance in situ (*Paranais*), or by larval recruitment and growth (*Streblospio*, *Capitella*). These localized responses are countered by movement of mobile consumers, such as the deposit-feeding gastropod *I. obsoleta* and the fiddler crab *Uca pugnax*, which can locate patches of detritus and consume both detritus and negatively affect patches of locally growing annelids. If the area is dominated by detrital input and surface feeder responses, then we expect spatial variability in population growth rate. Given that detrital inputs are not likely to be simultaneous throughout the trophically heterogeneous area, we also expect between-site temporal variability. The sum of these two processes will result in high spatio-temporal variation among sites for the surface feeders (Fig. 3). Deeper feeders depend on the organic matter that they can draw down into the sediment, but they are not as affected by surface mobile consumers, be they detritivores or predators. They therefore are expected to have less patchy population distributions and less temporal variability than the surface detritivores.

2. *Spartina* salt marsh mud-flat annelid communities: a case study

We will illustrate some of the claims made above by discussing our recent work on salt marsh *Spartina* mud flats on the north shore of Long Island, New York, USA. These flats are dominated by deposit-feeding gastropods, oligochaetes, and polychaetes. In spring, a conspicuous flush-crash cycle is dominated by surface-feeding annelids, dominated by the oligochaete *Paranais litoralis*, which reproduces in this area exclusively asexually by means of naidian paratomy (Cheng et al., 1993; Levinton and Stewart, 1988; Nilsson et al., 2000). Other annelids, such as *Streblospio benedicti*, may follow in abundance, but a spring population increase usually peaks in May and crashes by early summer (Cheng et al., 1993; Kelaher and Levinton, 2003). The deeper-feeding *Leitoscoloplos robustus* is also common throughout Flax Pond mud flats. Finally the mobile gastropod *I. obsoleta* is quite common and has been previously shown to exert negative effects on other deposit feeders (Levinton and Stewart, 1982; Levinton et al., 1985) and to have strong effects on even otherwise poorly digestible components of the sediment (Levinton and Stewart, 1982).

2.1. Spatial–temporal variation

As argued above, inputs of detritus should be an organizing force in deposit-feeding communities. This should be especially true if surface-feeding species exhibit localized cycles with strong among-site spatio-temporal variation. We tested this by following seasonal variation at a number of sites, using an orthogonal design with random factors that could distinguish components of spatial and temporal variance for different deposit-feeding functional groups. For surface-feeding annelids, the spatio-temporal component of variance dominated over the purely spatial (among-site) component of variance (Kelaher and Levinton, 2003). This can be illustrated by a plot of temporal variation of

the dominant oligochaete *P. littoralis* studied in an unpublished Spring 2002 field investigation at four sites (Fig. 4). The flush-crash cycles are evident at all three sites but the time of peak abundance is clearly non-synchronous. It is not clear why abundance increases or decreases at different times in the different sites. Similar spatial–temporal variation was discovered for surface feeders in the work of Kelaher and Levinton (2003). On the other hand, deep feeder variation exhibited no clear patterns of spatio-temporal discordance (Fig. 5), suggesting perhaps lowered response to winter deposition of detritus.

In our studies of salt marsh mudflats, deeper-feeding species in the same sites do not exhibit strong flush-crash cycles and the spatial component of variation is far smaller than for the surface feeders.

2.2. The opposing force of a mobile consumer

In Flax Pond mud flats, the main mobile consumer is the deposit-feeding gastropod *I. obsoleta*. Previous work at our field sites suggests that this gastropod can have variable mobility, depending especially upon microhabitat (Levinton et al., 1995). *I. obsoleta* can have very strong negative effects on resident species, often causing emigration of mobile forms (DeWitt and Levinton, 1984; Levinton et al., 1985). We were interested to characterize the ability of *I. obsoleta* to locate patches of detrital resource and the effects that such abilities might have on the smaller-bodied and less mobile surface-feeding deposit feeders.

Fig. 6 demonstrates that the mobile consumer *I. obsoleta* moves toward local patches of food input. After 1 month, *Ilyanassa* densities were far higher in patches that had been enriched with ground *Ulva* detritus. Furthermore, experimentally contrived high densities of snails exerted negative effects on populations of both surface and deep feeders (Kelaher et al., 2003). Using Multidimensional scaling (Fig. 7), there was a striking similarity between annelid assemblages under low snail densities and open uncaged conditions,

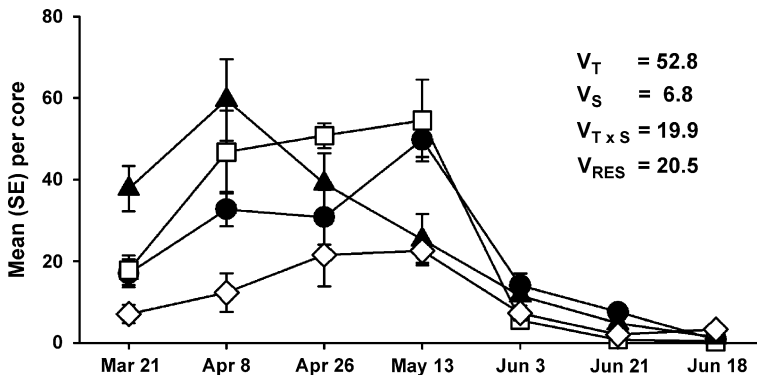


Fig. 4. Seasonal variation of abundance of the near-surface-feeding oligochaete *P. littoralis* at four sites in a salt marsh mudflat at Flax Pond, during the spring–summer of 2002 (unpublished data). Listed are variance components: V_T (time), V_S (among-site-spatial), and $V_T \times S$ (space–time interaction).

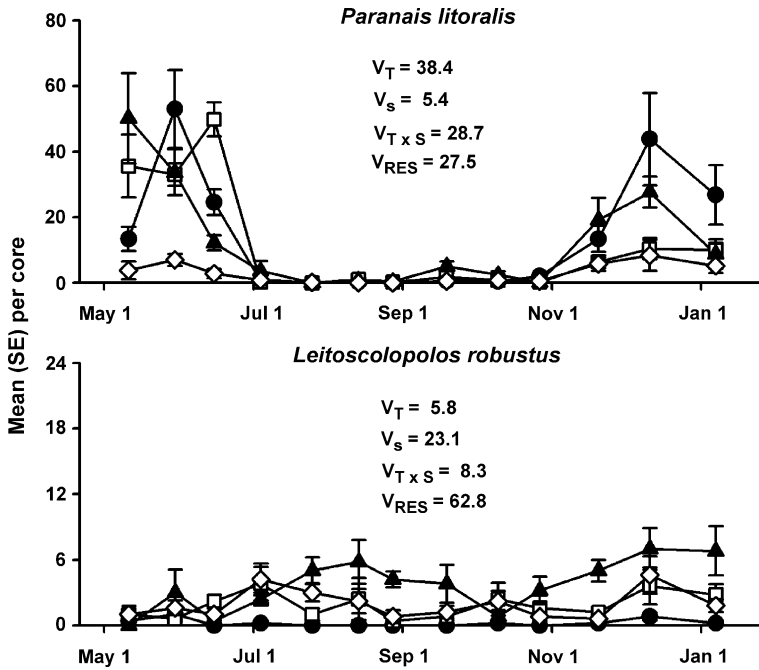


Fig. 5. Spatio-temporal variation of population abundances of the boom-and-bust species *P. litoralis* as compared to the variation of the deeper-feeding *L. robustus*. The temporal fluctuations of population abundance V_T and the time*spatial variance $V_{T \times S}$ components of the latter are both very low relative to those of surface feeders that respond to the late winter input of food.

whose snail densities approximated the low experimental snail densities (Kelaher and Levinton, 2003). We thus have direct evidence that our overarching hypothesis, that a competition between mobile consumers and localized inputs of food determines commu-

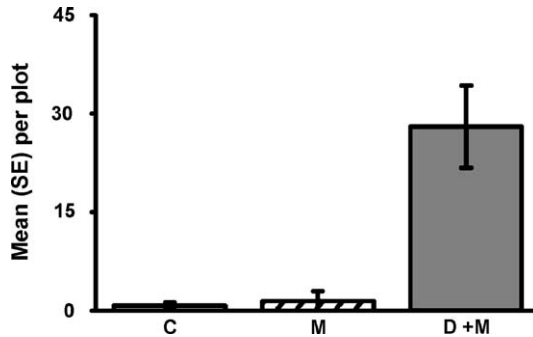


Fig. 6. Attraction of *I. obsoleta* to localized patches of detritus. Mean (S.E.) density in untouched control plots with added *Ulva* detritus and manual disturbance (D+M) and with manual disturbance only (M). Treatments are significantly different (ANOVA, $F_{2,7} = 27.43$, $P < 0.01$). Tukey HSD tests indicated by lower case letters above bars. Treatments labeled with different letters are significantly different ($P < 0.05$) (from Kelaher and Levinton, 2003).

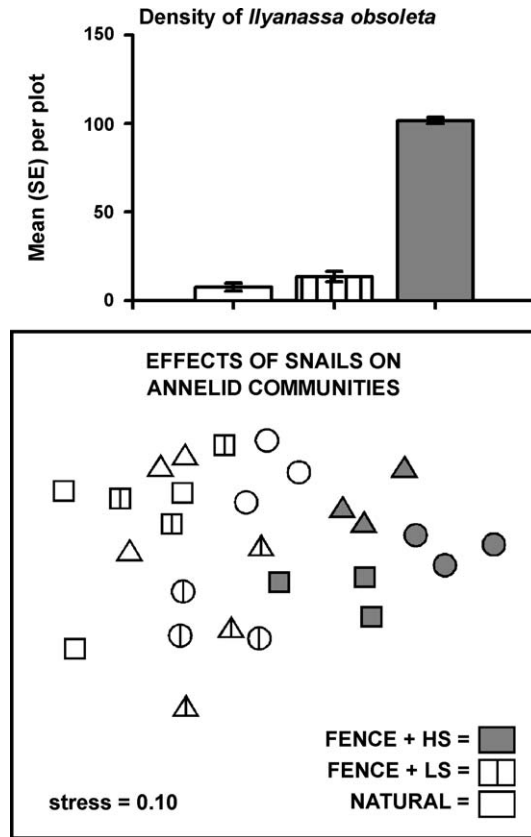


Fig. 7. Effect of *I. obsoleta* density on annelid communities at Flax Pond. Upper diagram shows experimental high and low snail densities as compared to densities in uncaged field sites. Lower diagram shows MDS plot of annelid assemblages for the three experimental conditions (from data presented by Kelaher et al., 2003).

nity structure, is a key player in determining temporal and spatial aspects of benthic community structure in tidal mud flat deposit-feeding communities.

3. Discussion

The purpose of this paper is to understand the consequences of the two opposing ecological forces that operate on different spatial scales. The most notable feature of communities is the strong spatial variation of species composition, to the point that it is difficult to make simple inferences about predictability of community structure. These differences are especially accentuated on a mesoscale of 10–100 m between sites (Kelaher and Levinton, 2003). We contend that such differences in quiet-water mud flats dominated by deposit feeders result from spatial–temporal patterns generated by localized resource inputs interacting with mobile consumers.

Localized detrital inputs are obvious features of quiet water mudflats and even some flats of higher energy (Levinton and McCartney, 1991). On the scale of 10^{-2} – 10^{-1} m, pits, fecal mounds, and low points between ripple crests are local sites of higher organic matter; such sites are sinks for low density particles, which are typically organic rich (Billheimer and Coull, 1988; D'Andrea et al., 2002; Mayer et al., 1993; Yager et al., 1993). On the larger scale of 10^1 – 10^2 m, areas may be devoid or covered with seaweeds, particularly green seaweeds such as *Ulva* and *Enteromorpha*. In False Bay, San Juan Island, Washington, inputs from *Ulva* detritus are considerable and a large fraction of this input is processed eventually by deeper-feeding polychaetes (Hylleberg, 1975; Hylleberg and Riis-Vestergaard, 1984). However, spatially, coverage is far from uniform and especially high coverage by *Ulva* is localized to beds (Levinton and McCartney, 1991). Our experimental evidence suggests that such detrital inputs stimulate population growth of asexually reproducing oligochaetes and appears to attract settling larvae of *Streblospio* and *Capitella* (Kelaher and Levinton, 2003). It may be that localized patches of sediment rich in detritus must be of a certain minimum size to attract concentrations of settling larvae. Our unpublished work (Junkins et al., in preparation) suggests that food-rich patches of 63 cm² are colonized no more frequently by swimming oligochaetes than food-poor patches of the same size. Presumably larger patches, such as the ones (ca. 1 m²) can be detected more predictably by larvae encountering and saltating along the bottom (Kelaher and Levinton, 2003).

Mobile consumers are defined as those consumers that can move large distances relative to the average distance between peaks of abundant resource input. If the consumers can locate patches, they will tend to move toward them and forage preferentially, from the point of view of the spatial array of resources. Such movements have the expected effect of equalizing the spatial distribution of prey numbers, which can be justified empirically (Schneider, 1978) or theoretically from the point of view of optimal time-in-patch models (Pyke, 1984; Weissburg, 1993). This equalizing force opposes the spatially diversifying force of localized inputs mentioned above.

Finally, the spatio-temporal force can be explained by different times of input in different sites or perhaps different initial amounts of input in different sites, which may give sites with larger detrital input a “head start” on causing population growth or attraction of settling larvae. Thus, in places where local detrital input dominates over the ability of mobile consumers to equalize abundances spatially, we predict the dominance of a spatio-temporal component of variation in explaining abundance patterns over all sites, relative to a purely spatial component of variation.

This model, of course, ignores several important potential additional components in deposit-feeding and other marine communities. Predation of course can be a potent force in all communities, although our current evidence suggests that it is not important in regulating Flax Pond surface feeders (Cheng et al., 1993). In some cases, the movement of predators will approximate the role of mobile consumers. While such predators may not be competing with locally expanding deposit-feeding populations, they still will obviously also be equalizing the spatial variance of such developing patches of local animal abundance. We also ignore a number of other factors, such as bedload transport, which may be a major source of movement of especially shallow-burrowing animals in high energy environments or after storms (Palmer and Gust, 1985; Schaffner et al., 2001;

Thistle et al., 1991), and spatial variation in chemical attractants and repellents (Woodin, 1991; Woodin et al., 1998). Finally, any realistic spatial model must move to a comparison of multiple and larger spatial and regional scales (Thrush et al., 1997; Zajac, 2001), which will be a major challenge in the future.

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