Recolonization and succession in soft-sediment infaunal communities: the spatial scale of controlling factors

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Abstract

Succession in marine soft-sediment habitats has been studied extensively and several general models of successional dynamics have been developed. However, few researchers have addressed how successional dynamics may change over different spatial scales. Here we extend a model that focuses on the factors that control recolonization and succession. These factors comprise three levels of a hierarchy which include environmental conditions, life history and population processes and biotic interactions. Using this hierarchical framework, we consider the spatial scales at which different factors operate, and argue that the relative mix and intensity of factors controlling succession change at different spatial scales. As a result, successional dynamics may vary considerably as the spatial scale of disturbance increases. At small scales, factors at each level of the hierarchy are important. The greater potential for biotic interactions at this scale may be particularly critical. At meso- to large scales, population processes and environmental conditions have the most influence on successional dynamics. Due to these differences, responses to small-scale ($\lesssim 1\ m^2$) as well as large-scale ($\gtrsim 1$ hectare) disturbances may be quite variable. Within this range ($\gtrsim 1\ m^2 \lesssim 1$ hectare), short- and long-term responses to disturbance may be relatively more predictable and conform to current models of succession in soft-sediment habitats.

Introduction

Disturbance is recognized as an important factor structuring marine and estuarine soft-sediment communities (Grassle & Sanders, 1973; Johnson, 1973; McCall, 1977; Woodin, 1981; Thistle, 1981). Because of its very nature, the physical fabric of soft-sediment habitats is relatively easily disturbed by a variety of processes over a broad range of spatial and temporal scales (Figure 1). It is not surprising then that recolonization and succession in soft-sediments have been studied fairly extensively (see Rhoads & Boyer, 1982; Probert, 1984; Thrush, 1991; Hall et al., 1994 for reviews, and references therein), and several models have been proposed that attempt to generalize these dynamics (discussed in more detail below). Moreover, this information plays a critical role in documenting

impacts and assessing ecological responses to human induced disturbance events.

Over the past several years, many ecologists have turned their attention to elucidating how ecological phenomena vary at different spatial and temporal scales (e.g. Dayton & Tegner, 1984; Schneider & Piatt, 1986; Wiens, 1989; Levin, 1992; Angel, 1994), including the dynamics of benthic communities (e.g. Barry & Dayton, 1991; Thrush, 1991; Dayton, 1994; Hall et al., 1994). In this paper, we focus on the dynamics of recolonization and succession in soft-sediment habitats at different spatial scales. There are several components of spatial scale that can be considered including spatial grain, or patch size, and spatial extent, or the area or distance over which specific phenomena occur. More specifically, we address two questions regarding these components of spatial scale.
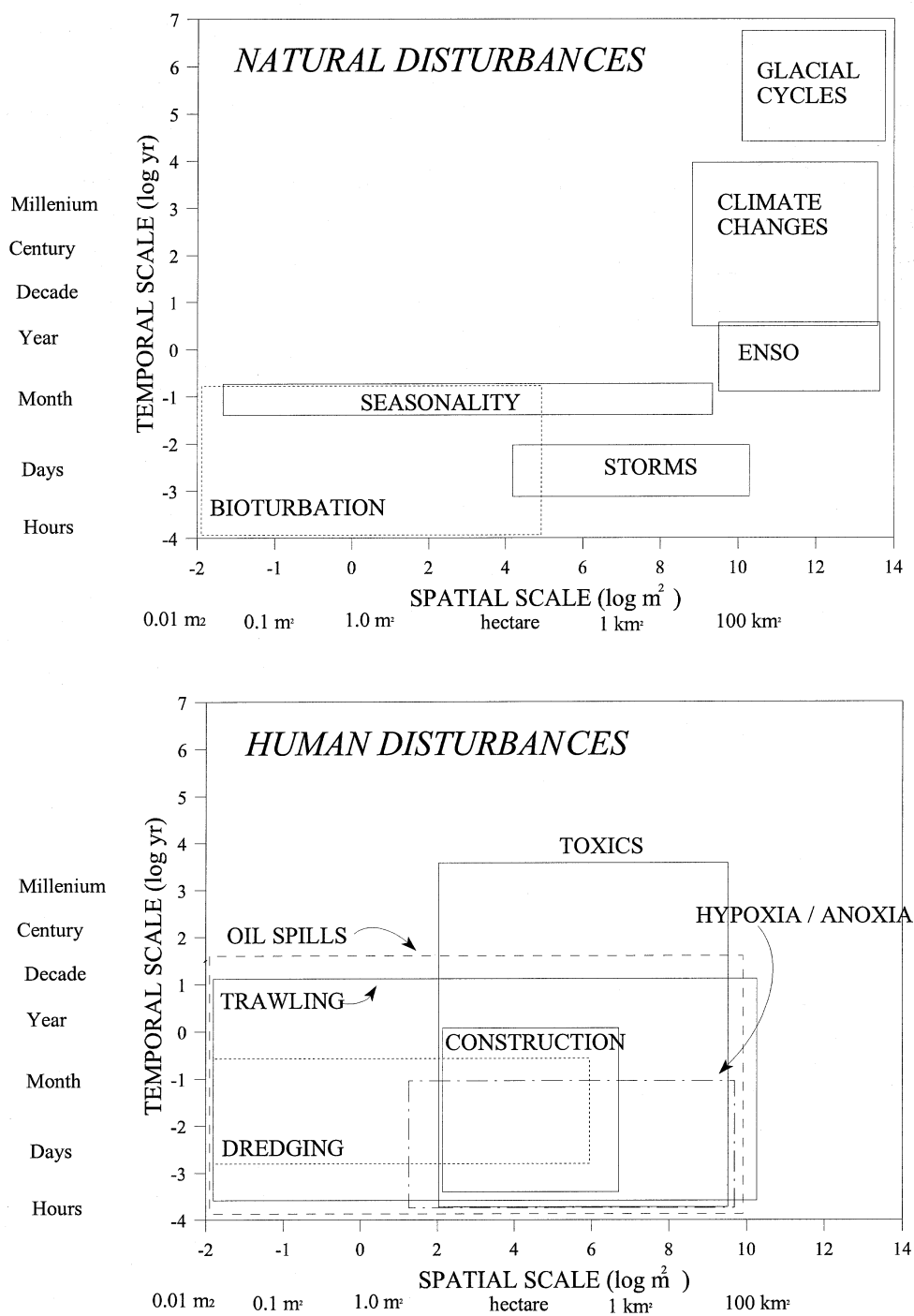
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Figure 1. Conceptual depiction of the spatial and temporal scales of different types of natural (top) and human (bottom) disturbances which impact soft-sediment habitats.

Table 1. Ecological characteristics of Stage I and Stage III type species. The characteristics of Stage II species are intermediate between Stages I and III. Table adapted from McCall (1977).

Stage I	Stage III
1. Opportunistic Species	1. Equilibrium Species
a. Many reproductions per year	a. Few reproductions per year
b. High recruitment	b. Low recruitment
c. Rapid development	c. Slow development
d. Early colonizers	d. Late colonizers
e. High death rate	e. Low death rate
2. Small	2. Large
3. Sedentary	3. Mobile
4. Deposit Feeders	4. Deposit and Suspension
(mostly surface feeders)	Feeders
5. Brood Protection;	5. No Brood Protection;
Lecithotrophic Larvae	Planktotrophic Larvae

First, do factors controlling recolonization and succession in soft-sediment habitats operate across similar spatial scales (i.e. their spatial extent)? Second, how might any differences in the operational scale of the controlling factors affect patterns of recolonization and succession relative to the scale of disturbance (i.e. the size of the disturbance patch)?

We feel that these are important questions for several reasons. Experimental studies of recolonization and succession in soft-sediment habitats have been conducted primarily at small scales (on the order of < 5 m^2), and only a small number have considered spatial scale explicitly (Smith & Brumsickle, 1989; Ruth et al., 1994; Thrush et al., 1996). The extent to which we can use this information to predict the pace and pattern of succession at larger scales will be dependent on our understanding of how the controlling factors studied in these experiments scale up. This is especially critical in trying to elucidate the effects of large-scale human disturbances such as dredge disposal and trawling. In addition, current recolonization and succession models do not explicitly consider changes in spatial scales. By considering the scales over which controlling factors operate we hope to extend current models so that testable predictions can be developed for a variety of situations when disturbance impacts soft-sediment habitats.

Consideration of spatial scale in soft-sediment succession models

Several models of recolonization and succession in soft-sediment communities have been developed based on both experimental and observational studies. Two of the most commonly cited are those of Pearson & Rosenberg (1978) and Rhoads et al. (1978). These models predict a specific sequence of successional stages following disturbance (Figure 2). The stages are comprised of species with particular life modes and life histories that they are differentially adapted to conditions within each successional stage (Table 1). As given, neither of these models explicitly consider the spatial scales over which we might expect the predicted community changes to occur. However, examination of the data used to develop the models, and information from similar studies, provides some insights as to the robustness of the models relative to changes in the scale of disturbance.

Rhoads et al. (1978) developed their model based on small-scale (0.1 m^2 defaunated boxes) experimental disturbances (McCall, 1977) and on monitoring of community responses following dredge spoil disposal which disturbed an area approximately 29 000 m^2. There were differences in the timing and extent of recolonization among the two sites. For example, in the experimental boxes, there was a very rapid (10 d) and high influx of opportunistic species, whereas in the disposal area the influx of opportunistic species was not as great and occurred over an extended period of time (200 d). These differences were attributed to several factors, including location differences (shallow vs. deep for the experimental and disposal site, respectively) affecting the potential supply of larval colonists, year to year variability in larval availability, potential toxic leachate effects on larval settlement at the dumpsite and differences in methodology (e.g. the use of different sieve sizes). Although there were differences, groups of species with particular characteristics representing different stages were found, forming the basis for the model (Figure 2, Table 1). Thus, we may hypothesize that there were similar factors controlling recolonization and succession following these disturbances, but that these were operating differentially with respect to the size and location of the disturbance to cause the varying responses.

Based on studies of macrofaunal responses to organic pollution, Pearson & Rosenberg (1978) developed a model of benthic succession that shares many of the same elements as that proposed by Rhoads et al.
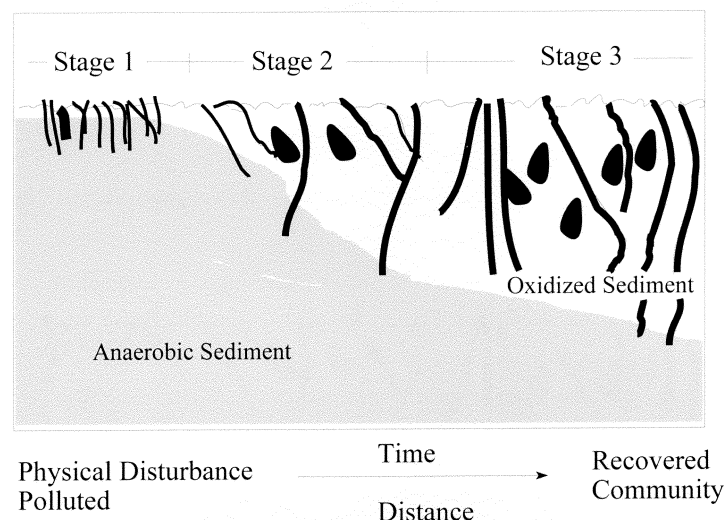
Figure 2. Model of soft-bottom community responses to disturbance / pollution gradients. Stage 1 represents early successional communities following disturbance or communities in polluted habitats. Stage 3 communities represent successional endpoints or communities in non-polluted habitats. Stage 2 are intermediate in both scenarios. See text for more details. The figure is redrawn from Rhoads et al. (1978). The characteristics of species dominating particular stages are given in Table 1.
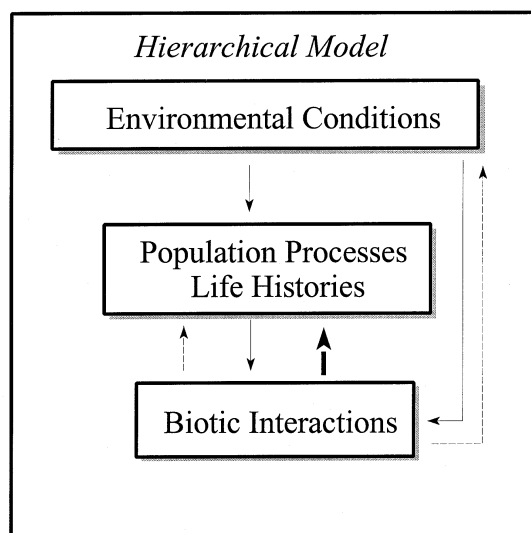

Figure 3. Hierarchy of factors controlling successional processes as proposed by Zajac and Whitlatch (1985). The thin solid lines indicate the flow of information on ecological time scales. Although information flows primarily from higher levels to lower ones, the dotted arrow lines reflect the possible upward flow of information (e.g. biotic interactions may alter sediment characteristics). Information can also flow on evolutionary time scales (as suggested by the thick arrow).

(1978). A critical aspect with respect to the themes being discussed here is that the model is based on studies of primarily large impacted areas, including portions of lochs and fjords. This suggests that the factors controlling successional dynamics following large-scale pollution abatement are similar to those operating in the small-scale disturbances such as conducted by McCall (1977) and in meso-scale disturbances such as dredge spoil disposal (Rhoads et al., 1978).

Taken together, these studies support the notion that successional dynamics are fairly similar over different spatial scales as well as the critical factors controlling these dynamics. However, results from other studies indicate that successional dynamics do not always conform to the predictions of these models and can be quite variable (e.g. Kaplan et al., 1975; Van Blaricom, 1982; Zajac & Whitlatch, 1982a, 1982b; Elmgren et al., 1983; Smith & Brumsickle, 1989; Thrush et al., 1991, 1996). It is still not clear then to what extent successional dynamics change over different spatial scales and in different situations (i.e. the type of disturbance and habitat), and what are the critical factors controlling succession at different spatial scales.

The scales at which factors controlling recolonization and succession operate

Zajac & Whitlatch (1985) suggested that the factors controlling soft-sediment succession can be viewed as a hierarchy comprised of three interacting levels:

Table 2. Examples of how factors controlling recolonization and succession change over different spatial scales. This list is not exhaustive and is meant to illustrate scale differences among the hierarchical levels shown in Figure 3. Larger dots indicate that a factor will likely be more important at the given scale than at others. Open positions in the table indicate that the factor does not control succession at the given scale. Questions marks indicate uncertainty as to the whether the factor operates at the given scale or not. See text for details.

Factors	Spatial scale		
	Small ($\lesssim 1$ m^2)	Meso (1 m^2–1 hectare)	Large ($\gtrsim 1$ hectare)
Environmental conditions			
Temperature	•	●	●
Salinity	•	●	●
Sediment type	•	●	●
Food resources	●	●	●
Hydrodynamics			
* Larval transport	●	●	●
* Sedimentary and food resource effects	●	●	●
* Interactions with boundary layer affecting larval settlement	●		
Life history and population processes			
Life span		●	●
Generation time		●	●
Population growth rate		●	●
Reproductive mode[1]	●	●	●
Larval development mode[2]	●	●	●
Active adult motility	●	•	
Feeding mode	●		
Biotic interactions			
Tolerance	•	●	●
Facilitation	●	?	
Inhibition	●	?	
Predation	●	•	

[1] Semelparity versus iteroparity.
[2] Direct development versus planktonic stage.

environmental conditions, species life histories and biotic interactions (Figure 3). The environmental level is comprised of factors such as temperature, salinity, sediment characteristics, hydrodynamics and food levels. The life history level is comprised of species traits such as life span, generation time, reproductive periodicity and output, mode of larval development, feeding mode and level of motility. The biotic interaction level comprises all the possible types of interactions that may occur, including facilitation, tolerance and inhibition (Connell & Slatyer, 1977) predation, and others (e.g. Woodin, 1983). These levels are quasi-independent, but to some extent each successive level sets the boundary conditions for the next level depending on circumstances (see examples in Zajac & Whitlatch, 1985). Also, we do not intend to suggest that natural processes are exactly structured in a hierarchical manner. Our model is meant to be used as

way of exploring the interactions among different sets of factors and processes and their relative influence on infaunal succession under different circumstances.

Although a general association of environmental factors, population processes and biotic interactions with characteristic spatial and temporal scales can be inferred (e.g. Hall et al., 1994), the model did not address the question of scale explicitly. In this section, we elaborate on the model by assessing the spatial extent over which factors at each level of the hierarchy may operate relative to successional dynamics. After doing, so we address the question of which spatial scales each of the factors are likely to exert their most influence on recolonization and succession relative to the scale of the disturbance.

Environmental factors

It is well known that physical and chemical environmental factors, such as temperature and salinity, respectively, can vary over many spatial scales (Table 2). For example, in intertidal habitats, pits (on the order of < 1 m^2) dug by crabs and other foraging organisms can collect water during low tide and temperature and salinity in the pits may vary from exposed surrounding sediments. Such small-scale differences may affect local recolonization patterns, but it is easier to envision differences in these factors influencing responses to disturbance at larger scales. For example, salinity gradients in estuaries result in differential distribution of organisms (e.g. Boesch, 1977) and in turn alter the suite of species that may colonize following a disturbance (Zajac & Whitlatch, 1982a). Other physical and chemical factors are also likely to have their most pronounced effect at meso- to large scales, although certain chemical constituents released by infauna may have effects primarily over small scales (e.g. Woodin, 1991).

Infauna have various degrees of sediment type fidelity (Gray, 1974; Rhoads, 1974), and it is reasonable to assume that differences in sediment type will affect recolonization and succession by controlling which species settle is a disturbed patch with particular sediment characteristics. Unfortunately, there is surprisingly little experimental work that has been done to test sediment effects on recolonization and succession. Zajac & Whitlatch (1982a, 1982b) showed that there were few differences in initial recolonization among small-scale (0.229 m^2) sand and mud experimental disturbances for estuarine communities, although differences were more apparent in longer-term succession plots. At large scales, changing sediment characteristics within a disturbed area, specifically increasing deposition of fine sediment particles, appeared to be responsible for successional changes after severe flooding in a subtropical estuary (Moverley et al., 1986).

In contrast, other physical factors may have significant influences on succession over a range of spatial extents. Key among these is hydrodynamics, which can affect larval settlement and transport at several scales (e.g. Eckman, 1983; Butman, 1987; Palmer, 1988; Günther, 1992; Keough & Black, 1996). Hydrodynamics also affect the distribution of food resources which may have a critical role in shaping successional dynamics in soft-sediment habitats (Thistle, 1981).

Life history and population processes

The roles life history and population attributes play in shaping recolonization and succession in soft sediments have received much attention (e.g. Grassle & Grassle, 1974; McCall, 1977; Pearson & Rosenberg, 1978; Rhoads et al., 1978; Levin, 1984; Zajac & Whitlatch, 1991) and form much of the basis of the models discussed above (Figure 2, Table 1). For this level of the hierarchy, we propose that characteristics most closely associated with an individual will be more critical at small scales, whereas those which integrate population demography and species life history operate over larger spatial extents. The former include, for example, feeding mode and adult motility. The latter group includes, for example, population growth rate (as a function of population patterns in survivorship and fecundity), life span, generation time and the meta-population characteristics of species in the region. In addition to these factors, there are two critical attributes, reproductive mode and larval development mode, which operate and are likely critical to species responses to disturbance across all spatial scales.

As far as is known, most adult infauna have limited active motility (e.g. Günther, 1992; and references therein). Tubiculous forms are generally sedentary but can relocate over distances on the order of centimeters. Errant species move to a greater extent but most of these movements are over small scales. Some species, however, can actively enter the water column as adults and be transported by currents over distances of meters to kilometers (e.g. Dean, 1978; Dauer et al., 1982). Apart from active movements, storms (e.g. Dobbs & Vozarik, 1983) and near bottom flows (Emerson & Grant, 1992; Committo et al., 1995; Shull, 1997) can passively suspend adult infauna into the water column, causing them to be transported also over large distances.

Average life span, generation time and population growth rate set the pace of population processes. Differences in life span will expose individuals in populations to different suites of temporal changes, whereas differences in generation time will have the same affect but in the context of different cohorts of individuals. Generation time can also have significant effects on population growth rate. Population growth rate establishes the potential for populations to maintain themselves in particular habitats and to respond to various environmental conditions (Zajac & Whitlatch, 1991). We suggest that the greatest variability in these population characteristics likely occurs at meso- to large spatial scales. However, few studies have ad-

Table 3. Hypothesized scales of dispersal and relative differences in exposure to varying environments and period of exposure of species with different combinations of reproductive and larval development modes. See text for further discussion.

	Reproductive mode		
	Monotelic	Polytelic	Semi-continuous breeders
Larval development mode			
Planktonic			
Dispersal	Multi-scale	Multi-scale	Multscale
Environmental exposure	Wide array	Wide array	Wide array
Exposure period	Shorter	Shorter	Extended
Benthic			
Dispersal	Small to mesoscales	Small to mesoscales	Small to mesoscales
Environmental exposure	Local	Local	Local
Exposure period	Shorter	Shorter	Extended

dressed variation in population processes of benthic fauna across a range of spatial scales, so it is difficult to assess the extent to which this supposition is accurate. Zajac & Whitlatch (1988, 1989) found populations of the polychaete *Nephtys incisa* exhibited significant variation in individual growth, size-structure and fecundity among sites 200 to 3 km apart, but that despite these differences the populations formed a relatively coherent demographic unit having similar population growth rates. Alon & Stancyk (1982) found significant variation in life history traits among two populations of grass shrimp (*Palaeomenetes pugio*) among estuaries with different salinity regimes approximately 15 km apart. In contrast, Olive & Morgan (1984) found that populations of several *Nephtys* species in widely separated beach areas in the British Isles had similar age-structures, and suggested that they may have similar population dynamics which are keyed into periodic recruitment failures. Although our focus here is on spatial variation, it should be noted that there can be significant short-term temporal differences in the demographic characteristics of local infaunal populations (e.g. Levin & Hugget, 1990; Zajac, 1991) which may be of greater magnitude than spatial differences.

Infauna exhibit a variety of reproductive and larval development modes, and their population dynamics may vary considerably over different spatial scales depending on the combination of these two traits. Infaunal species can divided into three broad groups based on their reproductive modes: monotelic, polytelic and semi-continuous breeders (Olive & Clark, 1978). Monotelic species reproduce once and die, polytelic species usually have one major reproductive event per year over their lifetime, and semi-continuous breeders reproduce on a continuous basis upon reaching sexual maturity that may be interrupted by, for example, seasonal changes in environmental conditions. Larval development can likewise be split into two general groups, planktonic and benthonic, but there are many species which brood larvae to some advanced stage and then release them into the plankton for various periods of time (e.g. Olive & Clark, 1978).

Although a detailed discussion is not feasible here, Table 3 presents general combinations of these traits and possible key impacts on dispersal and the degree and extent to which populations will be exposed to different environmental conditions. In general, these two traits operate over the full array of spatial scales relevant to soft-sediment environments, but the range of scales for species with particular traits are different. The greatest difference occurs between species with semi-continuous reproduction relative to other combinations of these traits.

Planktonic development puts larvae up into the water column where they can be carried by currents over a wide range of distances. Thus, monotelic and polytelic species with planktonic development, may disperse over a similar range of scales and be exposed to a wide array of environmental conditions. The major difference here is that the larval cohort in any one particular year is comprised from the reproductive efforts of several adult cohorts for polytelic species, and just by one cohort of adults reaching sexual maturity
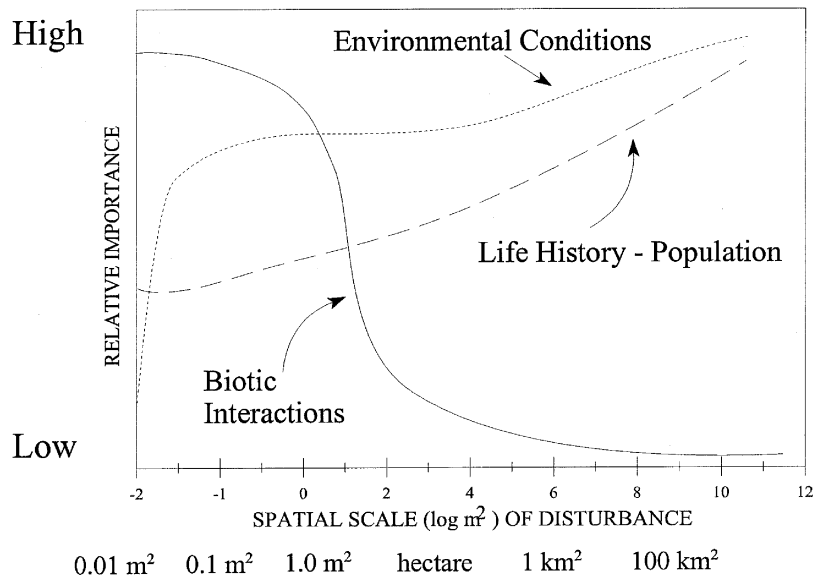
Figure 4. Predicted relative levels of importance of each level of the hierarchy (Figure 3) in controlling successional dynamics over different scales of disturbance.

for monotelic species. In both cases, release of larvae usually takes place over a short period of time once during a year. This reduces the exposure period and, depending on the duration of larval development, will affect the array of environments the larvae are exposed to. The degree of exposure of larvae to different environments (locally and at larger scales) will determine the probability of larvae encountering a disturbed patch and the chances of colonization, relative to the timing of competency and settlement. In comparison, semi-continuous breeders with planktonic larvae will also be dispersed broadly over a wide array of habitats, but this will occur over an extended period of time.

Benthic development likely leads to dispersal over relatively smaller distances, although dispersal may be somewhat greater under high flow conditions. Thus, individuals of species with benthic development will be exposed to more local environments. We see these conditions applying to both semelparous and iteroparous species with benthic development. Exposure periods are also shorter given the short-term periodicity of reproduction noted above. The situation will be similar for semi-continuous breeders except that the exposure period will be extended.

Biotic interactions

We consider biotic interactions within the context of three broad groups which were suggested as mecha-

nisms for successional change by Connell & Slatyer (1977). Facilitation comprises interactions in which one group of organisms enhances the establishment of another. Inhibition results in groups of organisms preventing or significantly reducing the establishment of another group. This may occur via competition for resources such as food and/or space. Tolerance represents the null situation in which organisms establish populations in an area depending primarily on their ability to live within prevailing environmental conditions. To this set of interactions we also add predation.

Given the relatively small size of most infauna and their limited motility, it is generally assumed that direct biotic interactions occur over small distances. Experimental studies of competition in soft sediments have primarily been conducted at small scales using cores of manipulated densities and cages (see Wilson, 1990 for a review). Based on this body of work there is ample evidence that competitive interactions can shape infaunal communities at these scales by inhibiting settlement and establishment of individuals. Studies which have focused on recolonization and succession, using similar approaches have also shown that inhibition and facilitation can shape responses to small scale disturbances (e.g. Gallagher et al., 1983; Whitlatch & Zajac, 1985).

The extent to which biotic interactions extend beyond the ambit of direct individual-to-individual interactions depends on the size and nature of patches formed by particular species, their density within the patch and the nature of the interactions. For example, Thrush et al. (1996) found that sediment stabilization by tube-building polychaetes was an important factor structuring sandflat communities. Recovery in large disturbance patches (3.24 m^2) in this community was slower than in smaller patches (0.203 m^2) because of greater sediment instability in the larger patches and the lack of facilitation provided by an established tube bed. Most studies of biotic interactions in soft-sediments provide measures of population densities, however, few provide information on the characteristics and sizes of patches where the interactions take place. To assess how biotic interactions might extend over larger scales it is important to obtain this type of information (e.g. McArdle & Blackwell, 1989; Thrush et al., 1989), and then assess interactions amongst such patches (e.g. Peterson & Black, 1987).

Predatory interactions among infauna may inhibit the establishment of individuals and shape community structure (Ambrose, 1991). Predation on infauna by epifauna, can also be an important structuring force in infaunal communities (e.g. Virnstein, 1977; Woodin, 1981; Knieb 1985; Riese, 1985 and references therein). As with inhibition and facilitation, it is fairly well known that predatory interactions take place at small scales in soft-sediments. This may be particularly the case with respect to interactions among infauna. With respect to epifauna, predatory interactions can occur over multiple scales depending on the foraging area and abundance of the predator. For example, individual epibenthic predators such as shrimp, crabs and fish forage locally, and their effects are easily quantified by assessing reduction of infauna in foraging pits. At high densities their populations may significantly affect large areas of soft-sediment habitats. Examples of large-scale predatory effects on soft-sediment populations include foraging by over-wintering birds on mudflats (Wilson, 1988, 1989) and whale feeding on soft-sediment infauna (Oliver & Slattery, 1985).

How the scale of controlling factors may affect recolonization and succession

Based on the above discussion, we hypothesize that the relative importance of each level of the hierarchy

in controlling recolonization and succession changes as the spatial scale of the disturbance changes. In general, environmental factors exert control over multiple scales, life history and population processes are critical at primarily meso- to large scales, whilst biotic interactions have the most effect at small scales (Figure 4). These differences may be significant in shaping the dynamics of recolonization and succession relative to the size, and possibly type, of disturbance.

Disturbances affecting infaunal communities occur at a variety of scales (Figure 1) (Hall et al., 1994). Yet as noted above, models predicting successional dynamics in soft-sediments do not explicitly consider spatial scale. Can the models developed by Rhoads et al. (1978) and Pearson & Rosenberg (1978) be augmented by incorporating spatial scale? We do so by considering several components of recolonization and succession, including the predictability of the various stages of succession, the rate of recovery and the relative abundances of different types of species during succession (i.e. opportunistic vs. non-opportunistic species) in relation to the spatial scale (extent) of controlling factors and the scale (size) of disturbance.

The models shown in Figure 2 predict a successional sequence comprising an initial recolonization by opportunists (Stage I) followed by a progressive re-establishment of climax type species (Stage III). However, the predictability of these stages and the relative abundance of different species types during succession may change as the scale of disturbance changes (Figure 5). [The nature of the disturbance, i.e. polluted vs. non-polluted, may also be a critical factor as discussed below.] At small spatial scales (< 0.1 m^2), particular factors at the life history – population processes level of the hierarchy will be primarily in play, causing the predictability of any particular successional stages to be relatively low and the relative variation in the mix of species type to be high. Specifically, adult motility plays a key role here, as well as the availability of competent larvae for settlement. Since the disturbance scale is small, the relative probability of various species colonizing the disturbance patch is similar, depending on the characteristics of the community set by prevailing environmental factors. Key among these may be small-scale flow patterns, whereas factors such as salinity, temperature and sediment type have little effect on influencing succession.

As the scale of disturbance increases to around 1 m^2, we hypothesize an increase in the relative predictability of successional stages and that the variation in the relative abundance of non-opportunistic species
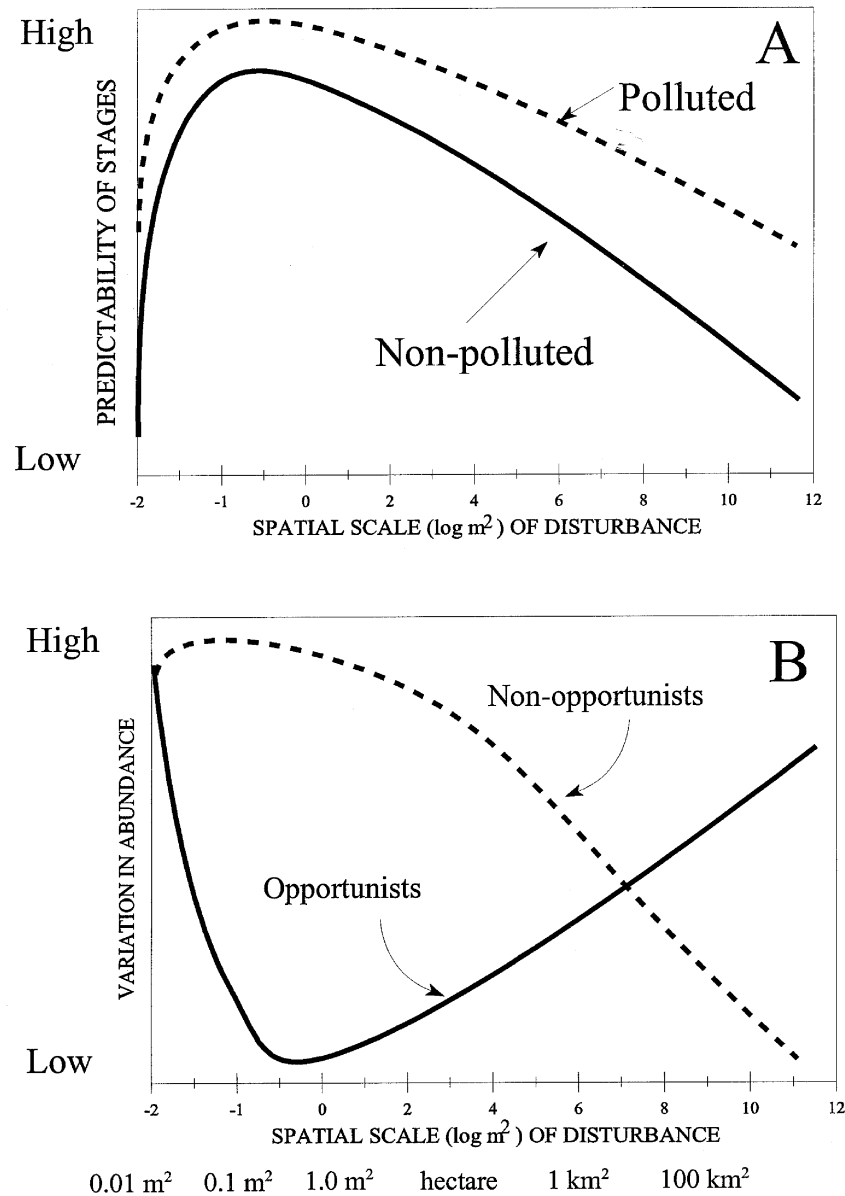
Figure 5. Predicted changes in A) the relative predictability of successional stages shown in Figure 2 relative to the spatial scale of disturbance, and B) the variation in the abundance of opportunistic (Stage I like) and non-opportunistic (Stage III like) species relative to the spatial scale of disturbance. In 5A, the curve noted non-polluted refers to natural disturbances or human disturbances that do not involve potentially toxic materials; polluted refers to human disturbances that involve potentially toxic materials including high levels of organic loading.

will decline. We base this prediction on the results of experimental work presented in support of the model (e.g. McCall, 1977) and the interaction of certain hierarchical factors. As disturbances approach this scale, the ambit of active adult motility is exceeded on the most part, and recolonization is shaped by the availability of settling infauna and the hydrodynam- ics of the area that can deliver both larvae via the water column and any adults that may be moved by bedload transport. This results in the settlement of primarily small, opportunistic-type species, setting up the potential for successional sequences as shown in Figure 2.
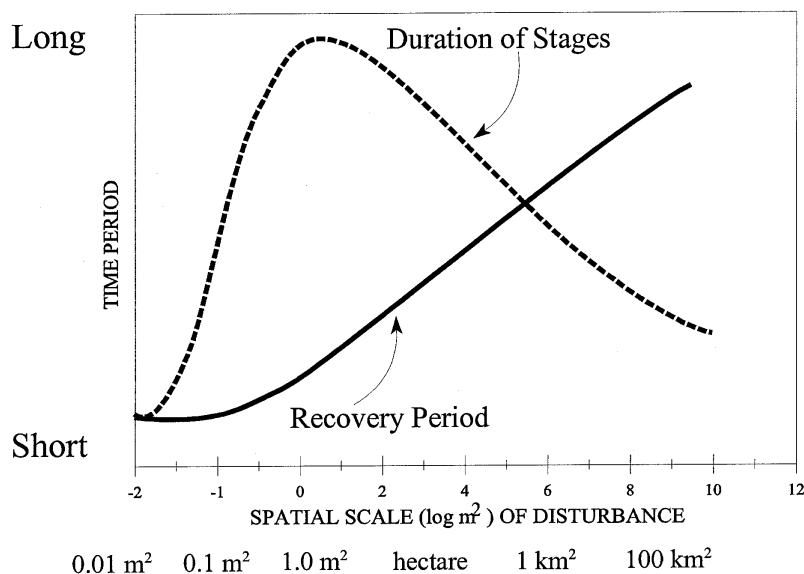
Figure 6. Predicted changes in the duration of successional recovery (solid line) and the duration of particular stages (dotted line), relative to the spatial scale of disturbance.

At spatial scales from approximately 1 m² to > a hectare, we hypothesize a decline in the predictability of successional stages, an increase in the variability of opportunistic responses and a decline in the variation of colonization by non-opportunistic species (Figure 5). At these spatial scales, many more environmental factors begin influencing succession as large-scale differences in, for example, sediment type and flow affect the distribution of source populations providing colonists to initiate recolonization, and their population dynamics to advance successional changes. Differences in demographic characteristics and population growth rates among source populations and within the disturbed area itself are also likely to be greater. Adult motility has little effect, and successional dynamics will depend on variable transport of larvae of a greater mixture of species.

In addition to shifts in successional characteristics at different spatial scales, we also suggest that there are changes in the duration of overall recovery and of particular stages (Figure 6). For very small disturbances (< 0.1 m²), recovery may be relatively fast, on the order of days to weeks, because of the potential for a rapid influx of adult, juvenile and larval colonists from surrounding sediments and the water column. Under these circumstances, if there are any discernable successional stages, they will occur over very short time periods. As the area of disturbance

increases to approximately 1.0 m², we suggest that the duration of recovery will increase, but the extent to which this occurs may depend on potential biotic interactions that are prevalent at this scale. Inhibition type interactions may increase particular successional periods as later arriving colonists cannot establish populations, whereas facilitation may shorten the recovery process by enhancing the settlement of later stage species. The absence of a critical interaction at this and larger scales may also extend the recovery period, as suggested by results presented by Thrush et al. (1996). At these scales, the duration of particular stages are also likely to be long relative to the overall duration of the succession. Disturbance areas are small enough so that they can be potentially colonized in high numbers by opportunistic species, but large enough to perhaps be beyond the scale of effective adult migration.

As the spatial scale of disturbance increases, the duration of successional recovery should increase (Figure 6). This may be a function of simply that the area undergoing recovery increasingly approaches, or eventually exceeds, the potential for source populations to supply colonists that can establish populations over short periods of time (months to a year). Succession will be dependent on factors that operate over large scales, including the mix of demographic characteristics of potential source populations and large-scale transport processes (Table 2). At these scales, we

also predict that the duration of particular seral stages may be shorter relative to the overall duration of succession. However, it is uncertain which stages will be extended and which might be abbreviated. For example, initial opportunistic stages may be transient and occur in small patches within the large disturbed area. As large-scale environmental factors alter the habitat and population processes come into play, this initial stage may be very short and an extended build up of later successional species may follow. In contrast, the opposite may occur, in large areas that were disturbed by pollution. Initial seral stages may last several years as environmental conditions both in the sediments and in the water column ameliorate until they are within the tolerance ranges of later stage organisms. In this case, the succession would be marked by an extended initial stage followed by shorter durations of later successional stages.

Conclusions

Much of our understanding of factors controlling recolonization and succession is based on experimental studies conducted at spatial scales of generally less than 1 m^2 (Hall et al., 1994). These have necessarily focused on a small portion of the suite of factors comprising the hierarchy shown in Figure 3. Our knowledge of disturbance, recolonization and succession relative to meso- and large scale controlling factors is rudimentary and observational / correlational in nature. In this paper we have strived to fashion a framework based on available information so that the study of soft-sediment successional processes might be effectively approached at these larger scales.

Based on our interpretations of the information available it appears that current succession models (Figure 2) are applicable to some small-scale natural disturbances and to large-scale cases of disturbance by organic pollution. Using the basic aspects of these models and the hierarchical framework, we suggest that successional dynamics may change considerably as the spatial scale increases. The mix and intensity of controlling factors changes at different spatial scales (Figure 4). At small scales, factors within all three levels of the hierarchy are important. The greater potential for biotic interactions at this scale may be particularly critical. At meso- to large scales, population processes and environmental conditions have the most influence on successional dynamics. Because of these differences, there may be spatial thresholds for partic-

ular types of successional dynamics. Specifically, we predict that variation in successional dynamics will be greatest at very small (< 0.1 m^2) and at meso- to large scales (> 1.0 hectare) and that successional dynamics between these two scales will be more predictable and conform more to the models shown in Figure 2. One difference in these predictions may involve succession following disturbance caused by organic pollutants. Successional dynamics in response to this type of disturbance may represent a specific case in which recovery and seral stages are governed primarily by the relative adaptations of infauna to environmental conditions caused by organic loading. Because the controlling factors are constrained by the type of disturbance to a smaller subset, successional dynamics will be more predictable (Figure 5A), following model predictions more closely (Figure 2). However even in this case, situations such as intermittent hypoxia may result in more variable successional dynamics depending on the timing, degree and duration of these events.

A potentially interesting aspect of changes in successional dynamics across different spatial scales is the relationship to the biodiversity of a particular region. In a species-rich region there may be a more diverse set of life histories and demographic dynamics displayed by resident species than in less diverse regions. If successional processes are keyed to the variation present in factors at different spatial scales, then we might predict that soft-sediment successional dynamics will be more variable as regional species richness increases. Unfortunately to our knowledge there are no studies that have addressed this possibility.

An important question facing benthic ecologists and those charged with managing and protecting sea floor habitats is, To what extent can we use small-scale experiments to predict larger scale responses? Our predictions suggest that this may not be possible because the relative mix of factors controlling successional process at different spatial scales may be fundamentally different. To gain a better understanding of successional processes in soft-sediments it will be necessary to push the spatial experimental envelop by simulating disturbances of various types at larger scales. This may be especially important and indeed practical for certain kinds of disturbances such as trawling. For situations when it is not practical, e.g. periodic hypoxia / anoxia, monsoons and large-scale dredging, specific sets of predictions and specific sampling designs should be formulated that address

multi-scale processes in order to tease apart the relative importance of environmental factors, population and life history processes and biotic interactions in controlling successional dynamics.

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