Incorporation of soft-sediment systems into a model of marine benthic community regulation

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Abstract. This review (1) describes important regulating forces in soft-sediment systems, (2) outlines existing models of community regulation, and (3) revises a model of community regulation to incorporate soft-sediment systems. The Menge and Sutherland (MS) model of community regulation and its refinements were developed for hard-bottom habitats, but can be modified for soft-sediment systems. This 'consumer stress model' posits that mobile consumers feed ineffectively in harsh environments, and that the relative importance of physical disturbance, interspecific competition and predation varies predictably with the magnitude of recruitment, environmental conditions, productivity and trophic position. The MS model predicts that interspecific competition for a resource depends directly upon the level of recruitment, though it does not explicitly address the joint effects of recruitment and resource availability, which are important in soft-sediment communities. The model is here revised to incorporate hard-bottom and soft-sediment systems by changing the recruitment axis to a 'recruitment:resource ratio', whereby the effect of a given level of recruitment depends on resource availability. The potential utility of the revised model is illustrated in a hypothetical contrast of the effect of recruitment:resource ratios on community regulation for a mussel-dominated assemblage in hard-bottom habitats and an infaunal clam-dominated system in soft sediments.

Extra keywords: Community structure, diversity, predation, interspecific competition, physical disturbance

Introduction

Community ecologists seek to characterize patterns in abundance and distribution of species, the key interactions between these species, and the relative importance of physical and biological processes to community regulation. Structuring forces include both physical or physiological factors (e.g. stressors that exceed physiological tolerances such as desiccation associated with exposure and high temperatures), as well as biological processes including interspecific competition, predation and recruitment (Menge and Sutherland 1987). Although the importance of biological and physical processes in community organization has been documented and modelled for terrestrial and marine hard-bottom and coral reef communities (Hairston et al. 1960; Connell 1961a, 1961b; Paine 1966; Dayton 1971; Menge 1974; Gaines and Roughgarden 1985; Underwood and Fairweather 1989), this material has not been incorporated into a model of community regulation for soft-sediment marine communities, which differ substantially from the others (Wilson 1991).

Differences between soft-sediment and hard-bottom communities may alter the relative impact of biological and physical factors. For instance, soft-sediment communities are characterized by small infaunal species which have an intimate relationship with their habitat — ‘they eat it, they lick it, they move through it’, and they modify it in many ways (Dayton 1984). Hence, many physical, geological and biological process in soft-sediment estuaries are affected by the activities of benthic infauna (Day et al. 1989). The three-dimensional nature of soft sediments may allow infauna a refuge from predation and an associated reduction in prey encounter rate when contrasted with that in a two-dimensional habitat (Peterson 1979). Interspecific competition in soft-sediment habitats may be reduced because of the abundance of three-dimensional space (Wilson 1991). Physical factors also affect benthic communities significantly (e.g. oxygen deficiency, Rosenberg 1977; El Niño, Warwick and Clarke 1993; salinity gradients, Seitz 1996) and must be incorporated into models of community structure (e.g. Menge and Sutherland 1976, 1987).

A thorough review of the importance of both predation and interspecific competition to soft-sediment community structure concluded that ‘a unifying theory of soft-sediment community structure does not appear attainable at our present level of understanding’ (Wilson 1991). However, some consistent patterns have emerged from soft-sediment experiments in shallow systems (Peterson 1979; Wilson 1991) which are herein incorporated into a revised model of community regulation derived from hard-bottom systems (i.e. Menge and Sutherland 1987).

Forces regulating soft-sediment communities

The importance of biotic regulating forces (predation, interspecific competition, recruitment) to soft-sediment systems has been documented and extensively reviewed
Recruitment may be an important biological factor to consider in its own right (Underwood and Denley 1984), although its interaction with interspecific competition in controlling community structure is emphasized herein (e.g. Menge and Sutherland 1987). In their review, Olafsson et al. (1994) conclude that recruitment is not the major determinant of spatial and temporal patterns in soft-sediment systems. The effect of elevated recruitment (typically associated with increased interspecific competition) may be minimal because in soft-sediment systems the three-dimensional nature of the sediment and apparent abundance of food promotes coexistence of species (Peterson 1979). Thus, recruitment does not act similarly in hard-bottom and soft-sediment systems and may only increase interspecific competition in hard-bottom systems (Olafsson et al. 1994).

Physical and physiological stresses are prevalent in soft-sediment systems (Boesch 1977; Bonsdorff 1989; Mattila 1992), but their influence on the importance of biological factors remains unclear. In hard-bottom systems, severe stress is likely to reduce the influence of biological processes such as predation or interspecific competition on community structure (Paine 1966; Menge and Sutherland 1976), and similar effects may occur in soft-sediment systems. For example, shallow soft-sediment areas are characterized by great seasonal variation in abiotic factors, such as temperature and wave action (Boesch 1977; Rennie and Nielsen 1991; Mattila 1992), which may change the impact of predation and other biological processes in community regulation. For example, feeding efficiency of estuarine predators is reduced in sub-optimal salinity zones (Remane and Schlieper 1971). Changes in salinity during a tidal cycle in the upper York River, Chesapeake Bay, can be as high as 5 (psu) within 12 h, whereas a change of <3 is common in the down-estuary areas (Boesch 1977). In addition, temperature at the mouth of the York River is more stable than in the rest of the river because of the relative proximity to oceanic influence (Boesch 1977). Changes in physical or physiological characteristics are likely to have profound effects on the activities of resident fauna, such that lower salinity areas are more stressful, especially in estuaries where many species are of marine origin (Remane and Schlieper 1971). For example, though the predatory blue crab is characterized as euryhaline, below suboptimal salinities (~27 psu) respiration rate and metabolic expenditures increase (Colvocoresses et al. 1974; Mangum and Tote 1977) and vary inversely with salinity due to higher energy demands of osmotic regulation at low salinity (Findley et al. 1978). On the basis of this limited number of investigations, stress emerges as an important structuring force in soft-sediment systems on a local scale.

Productivity may be equally important in driving community dynamics, because environmental gradients along which community structure can vary include both environmental stress and productivity (Menge et al. 1996). Productivity can be inserted into models of community regulation where low productivity equates to high stress. Model predictions are similar to environmental stress models (e.g. Menge and Sutherland 1987); however, food web structure additionally increases with high productivity or decreases with low productivity. For example, during El Niño, nutrients in eastern Pacific waters are depleted when upwelling fails. Subsequently, phytoplankton, zooplankton and higher trophic levels are dissipated (Glynn 1988).
Theoretical models

Conceptual models offer a heuristic tool to either explain or predict patterns in community structure (e.g. species diversity). Stochastic variation, such as that influencing recruitment, may, however, limit predictive capabilities (Underwood and Denley 1984). Gaps in our understanding of the effects of interspecific competition and predation on the structure of soft-sediment communities have thus far precluded a unifying theory of community regulation (Wilson 1991), but theoretical models from terrestrial and hard-bottom communities may provide a starting point for understanding regulation in soft-sediment systems (Menge and Olson 1990).

Early interspecific competition and predation models

The first models of community structure were developed for terrestrial systems (Hairston et al. 1960) and suggested that competitive exclusion occurs only in the absence of predation. In food chains with two levels (grazers feed on primary producers), primary producers are regulated by herbivores, which thereby preclude interspecific competition between producers. In food chains with three levels (carnivores feed on grazers which feed on primary producers), grazer abundance is controlled by carnivores, and primary producers consequently compete interspecifically. Predator and prey are regulated by different factors (Oksanen et al. 1981); top carnivores are resource limited, whereas plants are controlled by grazers in two-level food chains and by interspecific competition for resources in three-level systems. Thus, the importance of structuring forces differs depending on trophic complexity and linkages within the community.

The influence of predation on community structure varies depending on its intensity (Virststein 1977; Reise 1985; Menge and Sutherland 1987). In the rocky intertidal zone, high local diversity is often maintained by moderate levels of predation, whereby selective predation prevents competitive dominants from monopolizing food or space (Paine 1966, 1971, 1974). In the ‘intermediate disturbance’ hypothesis, species diversity is highest at intermediate levels of predation (Connell 1978). ‘Keystone’ predators can keep in check other species that would otherwise dominate the system. The impact of these predators is disproportionately large compared with their abundance (Power et al. 1996). In soft sediments, however, the lack of a competitive dominant reduces the potential for alterations in diversity due to variation in predation intensity (Peterson 1979; Wilson 1991). Typically, predation acts to increase diversity by (1) reducing the density of competitive dominants and thereby allowing competitively inferior species to coexist and prosper, (2) reducing most species densities to a level below that promoting interspecific competition, and (3) creating patches with lower densities at different stages of succession to hypothetical climax communities (Paine 1966, 1971; Virststein 1977; Reise 1985; Mattila 1992). Extremely high predation pressure, alternatively, may decrease diversity by causing local extinctions of relatively rare species.

Theories on community regulation, originally developed in hard-bottom systems, have emphasized the importance of predation (Paine 1966; Menge and Sutherland 1976, 1987; Glasser 1978, 1979; Bayne 1981; Oksanen et al. 1981; Schoener 1982; Connell 1983; Menge and Olson 1990). The relative effects of interspecific competition, predation and physical disturbance as major regulating forces in rocky intertidal communities (Connell 1961a, 1961b; Paine 1966; Dayton 1971) contrast with results from experiments in marine soft sediments (Woodin 1974; Reise 1977; Peterson 1979). Although predation is clearly important in structuring soft-sediment systems (see Peterson 1979; Wilson 1991), other aspects of previous models must be amended for incorporation of soft-sediment dynamics. For instance, in soft sediments, processes involving interspecific competition, such as trophic group ammensalism and adult–larvae interactions, are difficult to demonstrate and may only be important at extremely high infanual densities (Rhoads and Young 1970; Woodin 1976, 1978; Peterson and Andre 1980). For example, in a limited number of experiments, physical reworking of sediments by tube building infauna did not allow subsequent settlement of suspension-feeders (Woodin 1974), though the effects were on density and not diversity. Although this has been interpreted as competition for space (Woodin 1974), others challenge this interpretation citing settlement of larvae irrespective of tube-builder abundance (see review Wilson 1990).

Environmental stress models

The effect of environmental stress on an organism and community structure can be through either physical (e.g. wave-induced dislodging of individuals) or physiological (e.g. desiccation, temperature, salinity) mechanisms (Menge and Sutherland 1976, 1987; Menge and Olson 1990). There are many models incorporating gradients in environmental stress in marine systems for hard-bottom habitats such as the rocky intertidal (Menge 1976; Menge and Sutherland 1976, 1987; Menge and Olson 1990). There are many models incorporating gradients in environmental stress in marine systems for hard-bottom habitats such as the rocky intertidal (Menge 1976; Menge and Sutherland 1976, 1987; Menge and Olson 1990). The outcome of stress depends on whether predators or prey are more seriously affected, and this yields either prey or consumer stress models.

Prey stress models

In prey stress models, prey species are more severely affected by environmental stress than are predators, such that prey defences are weakened more than the consumer’s activity.
(Menge and Olson 1990). At low levels of environmental stress, predators and prey are equally affected. At increased levels of stress, the activity of predators is little reduced, whereas that of prey falls markedly, thereby increasing the importance of predation and potentially reducing diversity. These models typically apply to plant control by herbivores.

**Consumer stress models**

These posit that consumers are more severely affected by environmental stress than are the prey. Where environmental stress inhibits predators, prey abundance increases, consequently increasing interspecific competition. Under low stress, predation intensity is high, and prey abundance is controlled by predators, thereby reducing interspecific competition (Menge and Olson 1990). Depending on the level of interspecific competition, at low environmental stress, species diversity could be enhanced if there is no competitive dominant or it could be reduced if there is one. A corollary of this model states that in ‘severe’ and ‘unpredictable’ environments adaptations are to the physical environment, but in ‘benign’ or ‘predictable’ environments adaptations are to other organisms and the community is controlled biologically (Sanders 1969).

**Recruitment models**

The effect of recruitment limitation on community structure in soft sediments has only recently been addressed (Summerson and Peterson 1984; Peterson 1991; Peterson and Summerson 1992), and has been eliminated as a main determinant of spatial and temporal patterns in soft-sediment systems (Olafsson et al. 1994). The Menge and Sutherland Model (MS) (1987), incorporates recruitment density (influx of new individuals into the population) into an environmental stress model (Fig. 1). The level of recruitment alters the importance of interspecific competition and predation; at low recruitment, interspecific competition is often reduced, whereas at high recruitment it is intensified (Gaines and Roughgarden 1985; Underwood and Fairweather 1989). In a two-dimensional rocky intertidal system, where space is limiting, higher recruitment exacerbates interspecific competition for that limiting resource.

**Nutrient/Productivity models**

These models have been developed for systems varying in productivity (Fretwell 1977; Oksanen et al. 1981). In these models, plants in relatively unproductive systems do not produce enough energy to support the herbivores in the community, there are many basal species, and the community is thereby controlled by interspecific competition. In productive systems, energy is sufficient to support both herbivores and carnivores, consequently increasing the importance of predation in community regulation. Thus, these models predict the alternating importance of competition and predation with changes in length of the food chain (assuming omnivory is absent or trivial, Fretwell 1977; Oksanen et al. 1981). In this case, nutrient or productivity levels (rather than environmental stress) determine trophic complexity (Menge and Olson 1990). A more recent model (including omnivory) posits that competition and predation do not alternate. Rather, with long food chains, predation controls lower trophic levels and the strength of the interaction increases with increasing productivity (Menge et al. 1996). Again, effects of productivity on survival of benthic infauna are inconclusive, although there is some evidence for food limitation of growth and fecundity in both deposit- and suspension-feeding infauna (see review in Olafsson et al. 1994).

![Model of community regulation at intermediate trophic level](image)

**The Menge and Sutherland 1987 Model**

Intertidal hard-bottom communities are easily manipulated and have been extensively studied, yielding a synthetic model of community regulation, the Menge and Sutherland Model (Fig. 1). This ‘consumer stress model’ posits that mobile consumers are excluded from, or feed ineffectively in, harsh environments, and that the relative importance of physical disturbance or physiological stress, interspecific competition and predation varies predictably with the magnitude of recruitment (Menge 1991), environmental conditions, and trophic position (Menge and Olson 1990). Moreover, diminished primary productivity (i.e. food availability) may have similar qualitative effects on community structure, acting as an environmental stressor (Menge et al. 1996). Under extreme environmental stress or low productivity, physical factors are most important in determining community structure; predation becomes significant when environmental conditions are less severe (Menge and Sutherland 1987), or productivity is sufficient to maintain higher trophic interactions (Menge et al. 1996). In sum, the...
model predicts that at low environmental stress, predation is important, and at high recruitment and intermediate environmental stress and predation, interspecific competition is most important (Menge and Sutherland 1987). Low primary production can stress the community; therefore, similar predictions result when primary productivity gradients are incorporated (Menge et al. 1996).

There is extensive experimental evidence to suggest that the MS model works well for many hard-bottom systems. When predator efficiency is affected by stress (see Menge and Denley 1984), predation generally increases in benign environments and is the dominant structuring force (Paine 1969, 1971, 1974; Connell 1975; Menge 1976; Menge and Lubchenco 1981; Gilinsky 1984), but only when the effectiveness of predators is reduced substantially by stress (Underwood and Denley 1984). For instance, in rocky intertidal habitats the efficiency and effect of predators is greater at lower, more benign levels on a shore (Connell 1961a; Paine 1966; Dayton 1971; Feare 1971; Menge 1974) or when productivity is moderate to high (Menge et al. 1996).

The model states that interspecific competition increases at intermediate predation levels. Although benthic abundance usually increases when predators are reduced or removed (Connell 1975), interspecific competition can subsequently act only where resources are limiting (Dayton 1971; Paine 1971, 1974; Menge 1976; Lubchenco 1978; Lubchenco and Menge 1978). Consequently, interspecific competition is not always exacerbated with predator removal (Koehn and Butler 1979; Sousa 1979); sometimes it does not lead to a change in community structure (Creese 1978; Creese and Underwood 1982; Underwood and Denley 1984).

Furthermore, the model posits that environmental harshness structures communities by eliminating sensitive species, such as on wave-swept shores where animals are killed by intense wave action (Harger 1970; Connell 1972, 1975; Menge 1978a, 1978b; Moran 1980). Similarly, reduced productivity can act as a stressor, eliminating all but the hardiest species and thereby reducing diversity (Menge et al. 1996).

The importance of various factors (e.g. effects of predation) may be similar for soft-sediment as for hard-bottom systems, whereas other aspects of the MS model may need modification to incorporate soft-sediment systems (e.g. effects of interspecific competition). The main drawback of the MS model is that it does not recognize that soft-sediment habitats may have extremely high recruitment densities without interspecific competition becoming important (Olafsson et al. 1994), in contrast to hard-bottom, space-limited habitats.

**Revised model of marine benthic community regulation**

The MS model (Menge and Sutherland 1987) is a comprehensive and potentially useful model of community regulation for incorporation of soft-sediment systems (Fig. 1). For instance, the relative effects of structuring forces on species diversity are depicted in Fig. 2.

![Fig. 2. Remake of Menge and Sutherland’s (1987) synthetic model of species diversity which is derived mainly from hard-bottom data. The left mode of the diversity curve is the intermediate (physical)-disturbance model and the right mode is the predation model of species diversity. A gradient in productivity may be substituted for that of environmental stress, such that the effect of high environmental stress may be compared with that of low productivity (Menge et al. 1996).](image-url)
However, at extremely high recruitment, resources are still not limiting and the effect of interspecific competition will not be as great as in hard-bottom systems. Interspecific competition may be moderately important, leading to exclusion, reducing diversity, and causing a slightly bimodal diversity curve (Fig. 3) with a less severe dip than in hard bottoms (Fig. 2). Instead of using two models, one each for hard- and soft-sediment systems (Figs 2 and 3), both systems can be incorporated in one model if the relationship of recruitment to resource availability is considered.

To apply the MS diversity model to soft-sediment as well as hard-bottom systems, it helps to conceptualize variation in the importance of interspecific competition with resource availability across recruitment values for these different systems (Fig. 4). When recruitment is low, the importance of interspecific competition is necessarily low throughout a range of systems with differing magnitudes of resource availability (Roughgarden 1986; Menge and Sutherland 1987). When recruitment is high and resources are high (as is typical in three-dimensional soft-sediment systems; Fig. 4, front face), the importance of interspecific competition rises slowly to a modest upper asymptote. When recruitment is high and resources are low (such as in hard-bottom systems limited by space; Fig. 4, back face), the importance of interspecific competition rises quickly to an upper asymptote well above that for high resource availability (e.g., in soft-sediment systems). The overall effect is a reduced importance of interspecific competition in areas with high resource availability, despite high recruitment. Such variation in the importance of interspecific competition with differing resource availability leads to a need to incorporate the joint effects of recruitment and resource availability into the MS diversity model.

The MS diversity model can be modified to apply to any benthic system by changing the recruitment axis to a recruitment:resource ratio (hereafter $R_c:R_s$ ratio; Fig. 5). At high environmental stress (Fig. 5, left side), the revised model predicts that physical factors limit species diversity, whereas at intermediate environmental stress and low $R_c:R_s$ ratios (Fig. 5, middle of front face), the importance of both physical factors and predation will be minimal, leading to increased diversity. In more benign environments, the importance of predation increases, thereby decreasing diversity (Fig. 5, right side). At low $R_c:R_s$ ratios, interspecific competition should not be important and a unimodal curve of species diversity applies (Fig. 5, front face), but at high $R_c:R_s$
ratios and intermediate environmental stress, interspecific competition reduces diversity (Fig. 5, middle of back face). Whereas Menge and Sutherland’s (1987) diversity model states that a unimodal diversity curve may result at low recruitment or when competitive mechanisms permit coexistence (coexistence competition), in my revised model, a unimodal curve can occur in the absence of competition and at high recruitment (e.g. in soft-sediment systems). Though both models produce the same outcome, the underlying mechanisms differ fundamentally. The revised model allows examination of diversity in systems with varying resource availability as well as a continuum in recruitment magnitude, and it encompasses habitats where competition is not important. In this revised model, as in Menge et al.’s (1996) revision, food limitation enters the model as a stressor. A food-limited system would lie on the left side of the model (Fig. 5), where diversity is low at any level of recruitment. As food availability increases, diversity initially increases, then decreases as more trophic levels are supported and predation becomes important (Fig. 5, right side).

Typically in soft-sediment systems, resources are not limiting, because of the three-dimensional nature of the substratum, the \( R_c : R_s \) ratio is low to moderate, and the diversity curve would be expected to be unimodal. In contrast, at high \( R_c : R_s \) ratios, species diversity is bimodal (i.e. intense interspecific competition may pertain at intermediate levels of environmental stress where neither physical factors nor predation are intense). A bimodal diversity curve may characterize hard-bottom systems, where resources are often limiting and interspecific competition is important. The revised model of community regulation permits incorporation of a variety of soft-sediment habitats, from the coastal ocean to the deep sea, although its predictions remain untested.

As an example of the application of the model, consider the potential community effect of competitive exclusion by numerically dominant bivalves, such as the mussel *Mytilus* in hard-bottom habitats (Paine 1974) and the infaunal clam *Macoma balthica* in soft sediments (Seitz 1996). If 1000 infaunal clams (a numerical dominant in the community) recruited and survived to adulthood in 1 m², they could penetrate about 30 cm into the sediment (Seitz 1996). The resource available would be 300 000 cm³, yielding a \( R_c : R_s \) ratio of 1000 clams per 300 000 cm³, i.e. 0.003 (recognizing that the \( R_c : R_s \) ratio would be inflated somewhat by other infaunal species). Given this relatively low \( R_c : R_s \) ratio, there would probably not be interspecific competition for space or food in the assemblage, and the community would be expected to lie on the back face of Fig. 5 or be unimodal across a gradient in environmental stress or productivity (Fig. 6a). In contrast, if 1000 mussels, similar in size to the clams, recruited to 1 m² of hard-bottom habitat, and given that the substratum is two-dimensional (conservatively, 1 cm thick), the volume of resource available would be 10 000 cm³.

This yields a \( R_c : R_s \) ratio of 1000 mussels per 10 000 cm³, i.e. 0.1, a higher \( R_c : R_s \) ratio by nearly two orders of magnitude. At such a ratio, along a gradient in environmental stress, one would expect community diversity to lie on the back face of Fig. 5 or be bimodal (Fig. 6b). Additionally, if recruitment were low (100 individuals) on the same hard substratum (Roughgarden 1986), the \( R_c : R_s \) ratio would be lower (0.01) by an order of magnitude, and interspecific competition would probably be unimportant, resulting in a unimodal curve (Fig. 6a). Thus, the use of a recruitment : resource axis accommodates patterns and processes in community structure of hard-bottom habitats and soft sediments.

### Summary

Experiments on controlling forces in soft-sediment systems have advanced our knowledge substantially, although a unifying model of community regulation applicable to hard and soft substrata alike remained elusive (Wilson 1991). The Menge and Sutherland (1987) model can be modified to incorporate both systems with the inclusion of the notion that all habitats do not have equivalent resource availability relative to similar levels of recruitment. Thus, the effect of recruitment on community parameters will differ depending
on whether resources are limiting. This concept can be incorporated into the MS model by changing the recruitment axis to a recruitment:resource ($R_c:R_s$) ratio. In soft sediments, where food and space are rarely limiting, the $R_c:R_s$ ratio will typically be low and interspecific competition will be of little importance. In contrast, in hard-bottom habitats where space is limited, when recruitment is high, the $R_c:R_s$ ratio will also be high, leading to interspecific competition. The different $R_c:R_s$ ratios lead to different predictions for the importance of structuring forces in various systems, an idea that can be evaluated experimentally.

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