

Factors controlling marine and estuarine sublittoral macrofauna

D. J. WILDISH

*Department of the Environment, Fisheries and Marine Service, Biological Station;
St. Andrews, N. B., Canada*

ABSTRACT: The state of knowledge of marine and estuarine sublittoral benthic synecology may be said to be still in a descriptive stage of study. Much of the recent literature of the subject concerns either qualitative and quantitative descriptions of communities or associations, or concepts of such associations including diversity, stability and succession. It is the purpose of this paper to present a theory, based on a hierarchy of multiple limiting physical and biotic factors, for study of the controls governing community composition, biomass and productivity. Three major biotic factors are considered as qualitative and quantitative controls: food supply, supply of colonizing larvae, and interspecies competition. They are discussed and new techniques are suggested which may help in understanding the mechanisms of control.

INTRODUCTION

Two major themes may be found in the literature of estuarine and marine sublittoral macrofauna. The first is a description of animal associations based on numbers of individuals, species numbers and biomass (see review of Gray, 1974) in relation to sediments (Fager, 1964; Kinner et al., 1974; Christie, 1975; Ward, 1975) sedimentation (Moore, 1931), salinity (Newell, 1964; Wildish, 1970; Boesch, 1972; Wolff, 1974) and biotic factors (Dayton & Hessler, 1972; Campbell & Meadows, 1974; Moore, 1975). Productivity measurements for marine sublittoral macrofauna have also recently been made (Peer, 1970; Burke & Mann, 1974; Klein et al., 1975; Chambers & Milne, 1975). The second theme may be described as theoretical accounts of sublittoral macrofaunal associations in terms of community structure (see Watkins et al., 1973) or diversity (Sanders, 1968; Pianka, 1966) in terms of their successional stage (Leigh, 1965; Shugart, 1973) or stability/time relationships (Sanders, 1968). It is not the purpose here to review this work exhaustively but to present reasons for rejecting as working hypotheses, the currently popular concepts mentioned under theme two. A theoretical framework is suggested which will, I believe, direct field and laboratory experimental work towards a better empirical basis for the subject.

COMMUNITY CONCEPTS

Peters (1976) has recently crystallized the objections of a growing number of authors (see for example Goodman, 1974; Hurlbert, 1971; Jacobs, 1974; Livingston, 1976) to the use of community concepts such as diversity, succession, and stability/time relationships, at least as working scientific hypotheses. All three are considered to be ecological tautologies. A tautology is defined as a logical deductive argument based on premises which need not have observed empirical correspondence to real life and whose conclusions are implicit in the premises. An important property of tautology is that it cannot be empirically tested and is incapable of yielding predictions.

A second basis for rejection involves an enquiry as to whether such community concepts have been practically useful. The example used here is from the pollution biology literature. Macrobenthic fauna are recognized to be good indicators of point source pollution because they cannot move away from its source (Reish, 1973). In general, two problems are involved in work of this kind: a test to determine what spatial effect the pollutant may have had, and a temporal one to determine what pre- and post-operational effects occur at the same station.

In the last ten years considerable data on spatial testing have appeared (see for example, Crippen & Reish, 1969; Holland et al., 1973; Hendricks et al., 1974) and on temporal testing (Pearson, 1972; Rosenberg, 1972, 1973). Analytical methods used have relied heavily on community concepts, including diversity/stability and succession. Although it has been shown that pollution induced changes do occur and can be reversed, if the pollution source is stopped, no empirical base has appeared from which predictions could be made to other locations at other times. Each field observation or experiment involves high costs, and remains site specific in its results and applications.

MULTIPLE LIMITING FACTOR THEORY

Sublittoral macrofaunal community composition, biomass and productivity are controlled by multiple interactive physical and biotic factors. Major physical factors include: salinity, temperature, current speed, oxygen availability, sediments and water/sediment exchange phenomena. Major biotic factors include food supply, the supply of colonizing larvae and interspecific competition.

The rest of this discussion will be limited to the major biotic factors involved in controlling marine and estuarine sublittoral macrofauna.

FOOD LIMITATION

A convenient way of classifying macrobenthic associations is by their method of feeding. Thus, Pearson (1971) described five trophic groups: motile predators, algal scrapers, surface deposit feeders, deposit swallows and suspension feeders. The first two groups are quite specialized and make up only a small proportion of the total.

The bulk of species are either suspension or deposit feeders. In many cases, trophic relationships of given groups are inferred and experimental observations on methods of feeding have yet to be made. Of particular interest in this is the degree to which a particular species may be facultative for suspension or deposit feeding.

In the trophic group amensalism hypothesis, Rhoads & Young (1970) suggest that there are interactions between the two trophic groups causing inhibition of one group, the suspension feeders, by re-suspended sediments which clog the filtering mechanism and by prevention of larval settlement due to the absence of a suitable substrate for filter feeding epifauna.

Rhoads & Young (1970) recognized that the amensalism hypothesis could not explain why predominantly suspension and deposit feeding associations develop in soft sediments. To do so, I propose the trophic group mutual exclusion hypothesis. It states (1) that sublittoral macrofaunal community composition, biomass and productivity are food limited; (2) the basic exclusion mechanism is a physical factor: the current speed through its control on the supply of suspended food and its inhibitory effect on the development of the later stages of deposit-feeding associations by control of oxygen exchange between sediment and bottom water and by removing biogenically re-suspended sediments.

The food of macrobenthic animals is mainly aerobic, heterotrophic microorganisms (see Newell, 1965; Fenchel, 1969) or small meiobenthic animals such as nematodes, ciliates, etc. which depend trophically on microorganisms. In inshore areas, autotrophs may also provide a relatively small proportion of food directly to suspension feeders or to deposit feeders from a diatom sediment surface film. A major factor considered to control numbers of bacteria, and hence availability of macrobenthic food, is sediment particle surface area (Zobell, 1946). Experimental evidence for this consists either of determination of bacterial numbers by classical methods in cultures containing sediments of known particle diameter (see Zobell, 1946; Fenchel, 1970; Krumbein, 1970, 1971a) or determination of organic carbon and nitrogen in relation to sieved sediment fractions (Newell, 1965; Longbottom, 1970). All of these results suggest that with decreasing particle diameter and hence increasing particle surface area, the numbers or biomass of bacteria increase proportionately. Newell (1970) has summarized the evidence that bacteria do attach firmly to sediment surfaces and that this enables adsorption of particulate or dissolved nutrients necessary for bacterial growth. Ionic concentration of sea water is known to be important for the attachment process (Meadows, 1965). These data apply mainly to deposited sediments but similar conclusions apparently apply to detritus: bacteria associations in the water column (see Jørgensen, 1966). The experimental data to support this contention are not yet convincing (see Banse, 1974). In bottom water, carbon or other nutrients could be limiting to bacterial growth.

According to the trophic group mutual exclusion hypothesis the proportion of suspension to deposit feeding species which develop on a vacant sediment is decided primarily by the current speed spectra in the bottom water immediately above it. Sanders (1956), Pearson (1971) and Krumbein (1971b) emphasized the importance of current speed; the latter author indicates that bacterial numbers of surface sediment and bottom water depended on the direction and intensity of tidal currents. Observa-

tional data on bottom currents, which include tidal, wave induced or reaction currents, are generally not reported with macrobenthic distribution data, so a test of this cannot be made with existing data. Nevertheless, the hypothesis could explain apparent anomalies of sediment: animal associations recognized by McNulty et al. (1962), Rhoads & Young (1970), Levinton (1972), Pearson (1971) and in my own data from the Bay of Fundy (Wildish et al., in preparation). Most workers report that deposit feeding associations are associated with fine grained sediments less than $63 \mu\text{m}$ and low current speeds and that mixed sediments contain a higher proportion of suspension feeders. Sediment distribution usually is related directly to the contemporary current speed immediately above it (see Hjulström, 1939). The effect of macrobenthos, such as algae, in preventing sediment scouring and stabilizing the sediment: water interface is emphasized in recent work (see Rhoads, 1974). Thus, in L'Etang Inlet, Canada, a suspension feeding association is associated with a sediment of median particle diameter 10 to $15 \mu\text{m}$. The sediment surface is stabilized by surface microflora and the contemporary current speed is high (maximum 95 cm/sec) although not reaching a critical velocity to cause erosion. In a sandy sediment (median particle diameter 0.325 mm) a polychaete deposit feeding association is present with a lower current speed of 35 cm/sec maximum in which velocities sometimes caused erosion.

Diagnostic of the early stages of deposit feeding associations are low current speeds which if they occur on a fine sediment with particle diameters less than $63 \mu\text{m}$ develop into an intensively reworked deposit feeding association dominated by bivalves of the kind described by Rhoads & Young (1970). On sandy sediments with low current speeds a deposit feeding association dominated by polychaetes develops and here biogenic reworking is less evident. Biogenic reworking involves burrowing, increasing the surface water content, reducing the stability of the mudwater interface and allowing resuspension by weak currents. Coprophagy of the large number of fecal pellets may involve "seeding" of the pellets to increase colonization by microflora (Fenchel, 1970). Hylleborg (1975) describes the "gardening" activities of the lugworm, *Abarenicola pacifica*, which ingests sediment and utilizes attached bacteria. Fecal matter is enriched to support the growth of further bacteria as food. One functional purpose of biogenic reworking from the point of view of the deposit feeder is to increase oxygen availability and optimize the food available to them, thus resuspended sediments provide a large surface area for attachment of microflora in sea water containing nutrients and oxygen. Of course it is not of value to the deposit feeder to resuspend particles which are then swept away by tidal currents. Mills (1969) provides an example of the dynamic balance between an amphipod, *Ampelisca abdita*, and the sediment in which it lives. The tube-living, sediment-ingesting *Ampelisca* occurs in large numbers on the shore during summer, reducing the grain size of surface sediments by its trophic habits which eventually causes sediment-tidal current instability and washout of the *Ampelisca* tubes.

By contrast, suspension feeding associations develop in areas with higher current speeds and, at least in those developing on soft sediments, may involve some means of stabilizing the sediment-water interface. In warmer climates this stabilization may take the form of coral reefs and here symbiosis with autotrophs becomes a prominent feature increasing the suspension feeding association productivity. Hildreth & Crisp

(1976) show that current speed and particulate matter concentration does not affect the filtration rate of suspension feeding bivalve molluscs. Removal of suspended matter from water depends simply on the particulate matter concentration and current speed. There are inherent, probably species specific, natural limits to this relationship for both particulates and current beyond which further increases do not enhance growth or are injurious (Galtsoff, 1964; Kirby-Smith, 1972). Kirby-Smith (1972) has shown that, at low current speeds, growth of the bay scallop is reduced because of lack of food. This is in spite of the fact that phytoplankton-food removal efficiency was 63 % compared with 30 % removal at the higher, optimum current speeds for growth. These experimental results are consistent with field observations (see Hildreth & Crisp, 1976) in that dense communities only develop where currents are high because of the efficient removal of microbial food by such molluscs. In temperate-water marine sponges food removal efficiency was 44 to 77 % and bacteria were sufficient as food (Reiswig, 1975).

Within the last ten years a biochemical method has been adapted by Holm-Hansen & Booth (1966) to monitor adenosine 5'-triphosphate (ATP) universally present in living organisms of sea water and sediments. ATP determination by firefly bioluminescence assay is a simple, sensitive and reproducible measure linked to living microbial biomass which may be crucial in laboratory and field experiments to test the trophic group mutual exclusion hypothesis. Major interfering effects in the firefly bioluminescence assay (Wildish, 1976) include ionic inhibition or enhancement by anions or cations in solution and light emission stimulation by non-adenylate nucleotides. Both these difficulties can be overcome by suitable modifications involving liquid chromatographic column pretreatment to remove ions (Hodson et al., 1976) and analytical methods which consider the first few seconds of light emission (Wildish, 1976). The method is considered to be additional to classical methods of determining total and viable microbial numbers and biomass. The strong point of classical methods is that they are taxon specific although often poorly reproducible.

The adsorption of a monomolecular layer of nitrogen at liquid nitrogen temperatures and use of B.E.T. equations (Brunauer et al., 1938) or by measurement of ethylene glycol vapor adsorption (Marin & Jacobs, 1964) could be used to accurately measure sediment surface areas. Slabaugh & Stump (1964) have shown that marine sediments measured in this way have surface areas one or two orders of magnitude greater than calculations based on their median particle diameters. The difference apparently is due to shape irregularities and micropores of the particles. The geological origin of the particle also influences the surface area: glauconites had a greater surface than quartz sediments. In freshwater-lake sediments studied by Banin et al. (1975) the 0 to 2 μm clay fraction contributed 98 to 99 % of the surface area.

The two methods mentioned provide considerable promise in testing the trophic group mutual exclusion hypothesis. Experimental tests possible include: (1) A definitive test with sediments of known surface area to determine microbial biomass and productivity maxima where nutrients and oxygen are not limiting. (2) Field observations of microbial ATP, current speed and suspended sediments just above the sediment surface in a typical deposit and suspension feeding association. The study should be on a seasonal and tidal basis and would require use of special sampling methods to

take water samples a known distance above the sediment (see Smith, 1971; Joyce, 1973). (3) Laboratory experiments, particularly with deposit feeders, to determine the extent to which gut microflora contribute to the trophic requirements of the animal. Schwarz et al. (1976) have suggested that such microorganisms may play a significant role in deep sea animals. (4) To determine the role of bacterioplankton as food for suspension feeders.

COLONIZING LARVAL SUPPLY AND COMPETITION

The colonization of a vacant sediment will depend on the supply of larvae which reach it and their suitability to live in it. Factors which influence larval supply include the species composition of larval donors, nearness of the donors to the vacant site, current direction and velocity (Bousfield, 1955), and the temporal nature of the supply including the survival time of the larvae in plankton. Besides this it is known that benthic larvae may delay settling and select certain sediments (Fenchel, 1975; Moore, 1975) based on the bacterial content or presence of pheromones (Campbell & Meadows, 1974).

Species competition is probably most important at the settling stage as suggested by Rhoads & Young (1970) in the amensalism hypothesis. An inverse relationship was found between recruitment of *Macoma* and the abundance of *Pontoporeia* by Sergestråle (1973) probably because the amphipods eat the newly settled spat. Other authors such as Woodin (1974), Fenchel (1975) and Aller et al. (1974) provide empirical support for interspecific competition at the settling stage affecting species composition.

DISCUSSION

A central question of sublittoral macrofaunal synecology concerns the nature of the controls regulating community composition, biomass and productivity. Community concepts are considered as unlikely to provide hypotheses which lead to an empirically testable base for the reasons given above. Whether future hypotheses based on a hierarchy of multiple limiting factors, as suggested here, can do so still remains to be seen. In both field and laboratory experiments it should be possible to isolate the factors involved if the parameters are properly chosen or controlled.

Colonizing larval supply and interspecific competition are the major factors controlling community composition if temperature and salinity differences are removed. The major factor controlling biomass and productivity is the food supply. The potential for productivity of suspension feeders can be assessed from uptake efficiency measurements and current speed times microbial biomass content of the water. Potentials for deposit feeders should be given by the sediment microbial biomass content, inclusive of biogenically resuspended sediments, efficiency of removal of microflora and possibly the sediment oxygen which may limit macrofaunal activity as well as production of microbial food. Of considerable interest in this is the turnover rate or production of the microbes themselves which has been determined by measuring rates

of incorporation of labelled substrates (see Carney & Colwell, 1976; Herbland & Pages, 1976) or from oxygen uptake studies (Pamatmat & Banse, 1969).

Although suspension feeding and deposit feeding associations are contrasted here – they may be regarded as extremes in a gradient from one type to the other. Actual macrobenthic associations consist of mixtures of each trophic type. The potential productivity of each type can be measured in the same way as suggested above and the two values summed in proportion to the percentage of each trophic type present.

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Author's address: Dr. D. J. Wildish
Department of the Environment
Fisheries and Marine Service
Biological Station
St. Andrews, N.B. EOG 2X0
Canada