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Methods for ecological monitoring: Biological interactions in a rocky subtidal community

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ABSTRACT: Whilst both abiotic and biotic factors affect communities, biological interactions are widely believed to be the most important factors structuring subtidal communities. Among the potential biological interactions a few "key" species may regulate species fluctuations. A rocky subtidal community in the Oslofjord (Norway) has been investigated using stereophotography, field experiments and manipulations (settlement plates, scraping, cages). The purpose was to develop a method for biological monitoring of chronic pollution effects. Around 60 species were identified in the community. The most permanent occupants were *Lithothamnion* sp. (25–30 % cover) and *Pomatoceros triqueter* (ca. 20 % cover). The most important fluctuation was induced by the rapid growth of the hydroid *Laomedea longissima* to a 100 % cover in June and its rapid disappearance. Free space covered more than 30 % except in the period with large hydroid occurrence. The most active settlement period was in summer and autumn. The most important predators observed were *Coryphella* sp., *Asterias rubens* and *Psammechinus miliaris. Coryphella* grazed upon the hydroids and *Asterias* and *Psammechinus* foraged on settled organisms which resulted in an increase of free space. Predation and recruitment in that order are probably the two most important factors structuring the studied community. The "key" species were therefore the three predators. A monitoring programme should concentrate on these predators and their influence on the success of recruitment and the abundance of hydroids and free space, since these species control the natural fluctuations in the studied community. The stereophotographic method combined with simple settlement-plate experiments seems suitable for such a monitoring programme.

INTRODUCTION

Understanding the mechanisms producing natural fluctuations in communities is an essential prerequisite for assessing effects of chronic pollution stress; in ecological monitoring programmes eventually pollution effects must be separated from the variations produced by the natural community structuring factors. Lewis (1976) stated that monitoring fluctuations is easy, but without an understanding of causal mechanisms only the most obvious effects of pollution stress will be observed.

Both abiotic and biotic factors are important in structuring communities and producing natural fluctuations. In exposed areas, e. g. the intertidal, abiotic (physical) factors are believed to be of greatest importance, but in more protected or benign areas, e. g. the subtidal communities, biotic factors are widely believed to be the most important. Menge (1976) concluded that of mechanisms structuring communities in the intertidal, competition and predation were the most important and physical factors were of secondary importance. Yet a few species only, "key" species, are suggested as being important regulators of community structure (Paine, 1969; Dayton, 1972; Lewis, 1976).

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Little information, however, is available about structuring factors on natural rocky subtidal communities. Sutherland & Karlson (1977) and Anger (1978) found variation in larval recruitment on artificial substrates within a year and from year to year to be a major factor in controlling the development of such communities. Similar arguments had been used by Lewis (1964) who explained fluctuations by variations in seasonal recruitment, growth of species and differential mortalities of various plants and animals. However, on subtidal pilings, Karlson (1978) found that predators, notably echinoids and fish, were the most important structuring agents.

In communities exposed to severe physical conditions (such as the exposed intertidal), the importance of predation is reduced and interspecific competition for space is the dominant factor (Menge, 1976). These communities are often dominated by a single competitively dominant species, a situation which can also occur in communities in more sheltered areas where important predators are removed (Paine, 1966; Menge, 1976; Peterson, 1979).

Generally, in sheltered areas of the intertidal and especially in the subtidal communities, predation plays a dominant role. Predation provides free space available for new species to colonize (Paine, 1966; Dayton, 1971; Menge, 1976; Peterson, 1979), and by removing dominant competitors can give rise to communities with a greater amount of temporal and spatial heterogeneity or higher diversity (Paine, 1966; Peterson, 1979). In communities where predation seems to be the dominant biological factor, the most important predator is a "key" species (Paine, 1966, 1969).

Since there is little data available on rocky subtidal communities, an initial study on biological interactions has been concentrated on one community. The primary aim of the project is to evaluate the utility of the rocky subtidal as a suitable habitat for long-term ecological monitoring along the Norwegian coast.

METHODS

A test area was chosen with a fairly smooth rocky surface at 12-m depth, ca 45° slope, at Drøbak in the Oslofjord (Norway). Drøbak lies in a sound between an inner polluted and an outer less polluted part of the fjord. Strong daily currents pass in and out of this sound and influence the upper water layer down to the community at 12 m. Water temperature fluctuates from ca 1 °C in winter to 15 °C in summer, and salinity varies between 24 ‰ and 34 ‰.

The sampling technique chosen for the subtidal rocky communities was largely based on stereophotogrammetry (Lundälv, 1971; Torlegård & Lundälv, 1974). Lundälv (1971) considered that stereophotographic recordings were a suitable and practical method for monitoring epibenthic communities. The stereophotographic method used is somewhat different from that described by Lundälv (1971); here two Nikonos III with 15-mm objectives were used as paired synchronized cameras (Kvalvågnæs et al., 1976).

Sampling design. All sampling was carried out by SCUBA-diving. A permanently fixed (marked) test area covering 3.0 m^2 has been recorded monthly using stereophotographic methods since March 1978. Of this area, 2.0 m^2 was used as a control area, 0.5 m^2 was scraped to remove the fauna and 0.5 m^2 was covered by cages. Two cages were used, one of fish net with mesh size of 10 mm and the other of nylon net with mesh size of 3 mm. The nets were fitted to the rocky surface with a thin rubber seal which was moored by small plugs driven into holes drilled in the substrate. The nets were raised from the substrate by means of wire hoops.

The control area gave data on the natural community structure and its fluctuations, the scraped area on recolonisation sequence, and the cages on effects of predation.

In addition to the photographic recordings, samples were taken from the community close to the test area. A settlement experiment was done with ceramic plates. In spring (March 1978) 12 plates were put out, of which one was recovered each month, and also at each month one plate was put out and then taken up the next month.

Analysing techniques. For picture analysis (of the control area, the scraped area and the caged area) a stereoscope (up to 40 × magnification) was used. To analyse each picture, two independent sets of 100 random points were counted in order to estimate the percent cover of the different organisms. Tests were done and 100 points were found to give small variances in percent cover of the occurring organisms.

Under each point the occurrence of animals on primary space, secondary space (epizoism) and canopy was recorded. Since recordings were made in the different layers the sum of estimates of species-specific percentage cover can exceed 100 %. By counting each picture twice, the estimates of % cover of the species on the control area were calculated from 1600 counts for each sampling date. Colonies or solitary individuals of larger plants and animals were counted directly and numbers extrapolated to m^{-2}.

The settlement plates were analysed by presence/absence of organisms. The difficulty of identifying some of the organisms in the pictures was overcome by identifying organisms sampled close to the photographic test area. This sampling also gave an idea of the fauna not available in photographic sampling.

RESULTS

By analysing the pictures, 34 different taxa of animals and plants were identified on the test area during the year. An additional 28 species were found on the settlement plates and in the samples from the nearby area giving a total of 62 species. The species list is given in Table 1.

Analysis of control area

The results from point sampling indicated that the control area was dominated by few species (Fig. 1). The encrusting *Lithothamnion* showed a stable occurrence (25–30 % cover) throughout the year, and together with *Hildenbrandia rubra*, the encrusting rhodophyceans occupied about 30 % of the primary space. The tube-building polychaete *Pomatoceros triqueter* covered around 20 % most of the year with an increase during the settling period (to 30 %).

The percentage occurrence of free primary space decreased through the spring and increased through autumn and winter. This fluctuation could be inversely correlated with the fluctuation of the hydroid *Laomedea longissima* (Figs.1, 2a). At the end of June *Laomedea* covered almost the whole community (primary, secondary space, and canopy) and obscured other organisms, making identification difficult. After *Laomedea*, *Tubularia* sp. entered the community, but in smaller amounts, and the occurrence of hydroids through autumn and winter is mostly represented by old remains of *Laomedea.*

Other organisms covered around 10 % throughout the year. In spite of this low %

Table 1. Species found in the tested community by different sampling designs

Species (or substrate)	Picture analysis	Settlement plates	Samples
Unoccupied rocky substrate	x		
sediment	x		
Lithothamnion sp.	x		
Hildenbrandia rubra	x		
Cyanophyceae (*Dermocarpa* sp.)	x	x	x
Delesseria sanguinea	x	x	x
Phycodrys rubens	x		
Bonnemaisonia hamifera	x		x
Cruoria pellita	x		x
Cibicides lobatulus		x	
Porifera indet. *(encrusting)*	x		
Hydrozoa indet.	x		
Laomedea longissima	x	x	x
Tubularia sp.	x	x	x
Eudendrium sp.	x		x
Campanularia sp.			x
Actinaria indet.	x		
Tealia felina	x		
Alcyonium digitatum	x		
Nematoda indet.			x
Nemertina indet.			x
Pomatoceros triqueter	x	x	x
Hydroides norvegica			x
Spirorbis borealis		x	
Nereis sp.			x
Polynoidae indet.			x
Serpalidae indet.			x
Hesionidae indet.			x
Phyllodosidae indet.			x
Terebellidae indet.			x
Siratulidae indet.			x
Polyplacophora indet.	x		
Acmaea sp.	x		x
Buccinum undatum	x		x
Gibbula sp.	x		
Prosobranchia indet. (juv.)		x	x
Coryphella sp.	x	x	x
Modiolus modiolus	x	x	x
Mytilus edulis (juv.)		x	x
Saxicava arctica	x	x	x
Anomia ephippium		x	
Balanus balanus			x
Copepoda Harpacticoidae indet.		x	x
Amphipoda Gammaridae indet.			x
Caprella linearis		x	x
Corophium sp.			x
Isopoda indet.			x
Galathea sp. (juv.)			x
Eupagurus bernhardus			

Table 1 (Continued)

Species (or substrate)	Picture analysis	Settlement plates	Samples
Hyas araneus			x
Carcinus maenas	x		
Electra spp.		x	
Asterias rubens	x	x	x
Ophiura albida	x		x
Ophiopholis aculeata			x
Psammechinus miliaris	x		x
Strongylocentratus droebachiensis	x		x
Styela rustica	x		x
Corella parallelogramma	x		x
Ciona intestinalis			x
Botrylloides leachi	x		x
Ascidiacea indet.			x
Pomatochistus pictus	x		
Microstomus kitt	x		

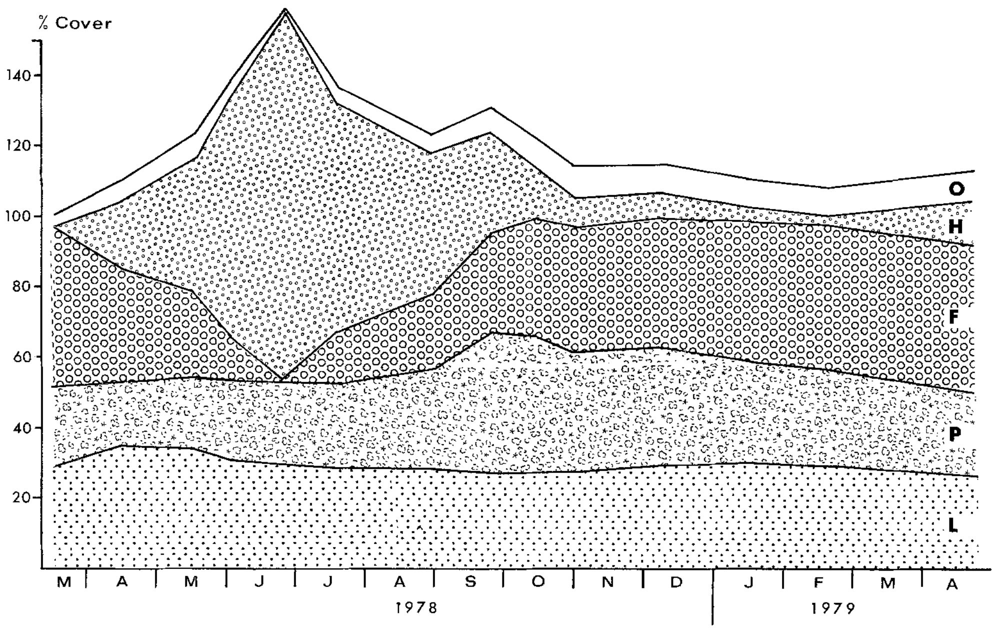

Fig. 1. Variation in cumulative percent cover of: L = encrusting rhodophyceans (mostly *Lithothamnion*), P = *Pomatoceros triqueter*, F = free space, H = hydroids (mostly *Laomedea*), O = other organisms recorded by point sampling

cover, some species occurred more or less permanently in high densities. Rhodophyceans, *Alcyonium digitatum*, *Coryphella* sp., *Asterias rubens* and *Psammechinus miliaris* were numerous; less frequent were some actinarians, *Acmaea* sp., *Strongylocentrotus*

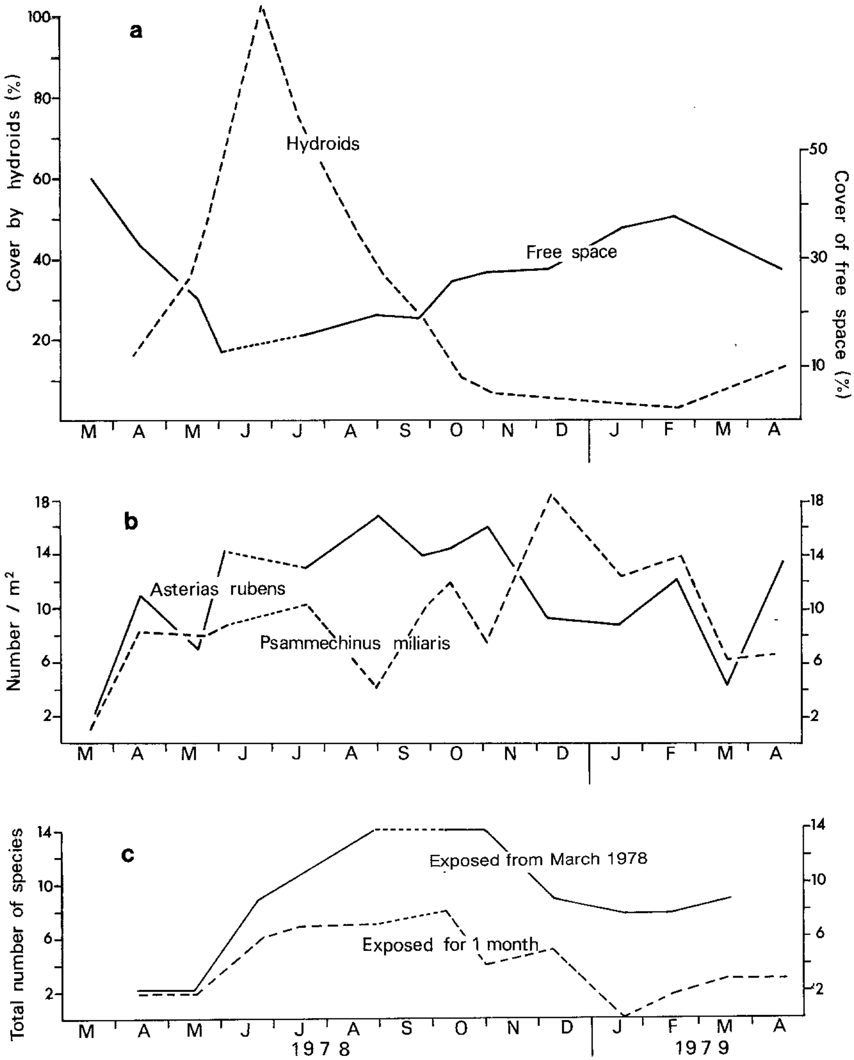

Fig. 2. Variations through the year. a = percent cover of hydroids compared to free space. b = densities of *A. rubens* and *P. miliaris*. c = total number of species settled on two series of settling plates with different exposure times. Dotted lines = unsuccessful recordings

droebachiensis, Ophiura albida, and the ascidians *Styela rustica, Botrylloides leachi* and *Corella parallelogramma.*

The occurrence of *P. miliaris* and *Asterias rubens* is shown in Figure 2b. They are presumed to be important predators in the community, and were observed throughout the year at densities above ca 10 m^{-2}. Most of the *A. rubens* and *P. miliaris* present were represented by individuals smaller than 50 mm and 30 mm, respectively.

The hydroid-eating nudibranch *Coryphella* sp. was numerous during winter and spring, but as adult totally absent through summer and autumn while eggs and juveniles were found during the summer months (Fig. 3). Løyning (1922) found a similar pattern in *Coryphella rufibranchiales* from the same area.

Occasionally, sediment deposits were observed on the rocky surface, mostly among remains of old hydroids.

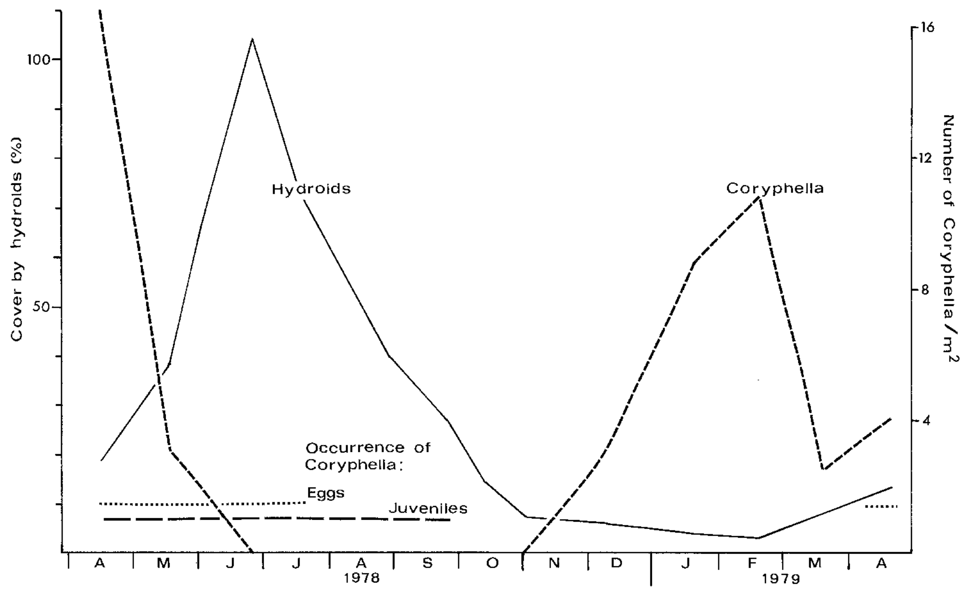

Fig. 3. Fluctuations in the hydroid populations compared with occurrence of *Coryphella* (density of adults, time when eggs and juveniles are observed)

Analysis of scraped area

After scraping, unoccupied primary space covered more than 80 % of the substrate. The remaining occupants were *Lithothamnion* (less than 20 % cover) and a few *P. triqueter* left in small crevices.

Total recolonisation of this area was not observed after one year. Figure 4 shows the abundance of unoccupied primary space on the scraped area compared with the control area. Successful recruitment of *Laomedea longissima* (ca 110 % cover in June) and settled *Pomatoceros triqueter* (ca 20 % cover in September-October) almost disappeared and unoccupied space dominated the area (ca 65 % cover) before the next hydroid colonisation was observed in April 1979. *Lithothamnion* increased slightly in % cover during the first months. Other organisms which settled were small colonies of *Cruoria pellita* and *Botrylloides leachi* and some motile predators entered the area (e g. *Acmaea* sp., *Coryphella* sp., *P. miliaris* and *A. rubens*). The densities of these were always less on the scraped area than on the control area, except for *P. miliaris* and *A. rubens* which occurred in higher densities (ca 20 m^{-2}) in the period July-September on the scraped area.

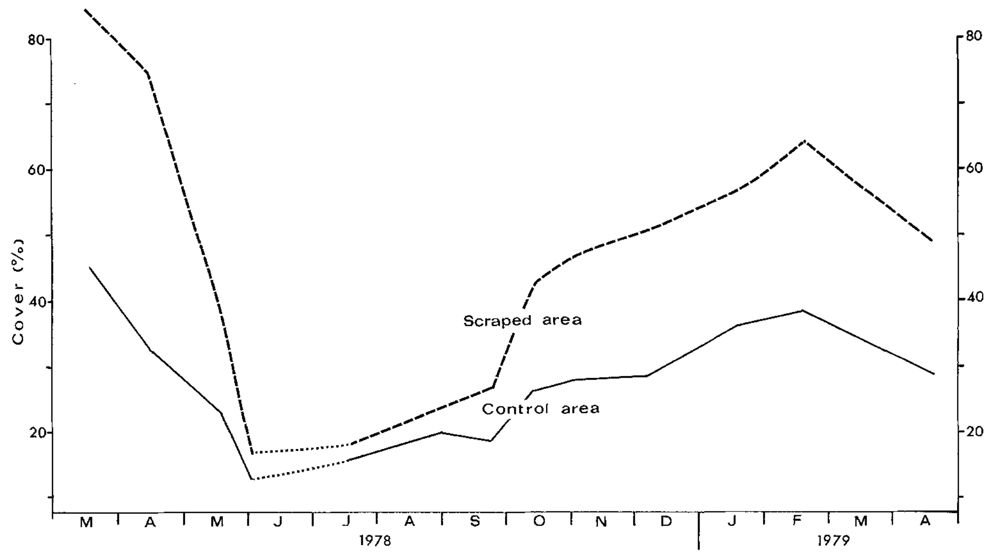

Fig. 4. Variation in percent cover of free space on control area and scraped area. Dotted line = unsuccessful recordings

Cage experiment

In order to study the effect of predators on the community a predator exclusion experiment was done. From comparison with the control area, the most common predators observed were *Coryphella*, small *Asterias* and *Psammechinus*. Even though removed from the cages once a month, these small predators nevertheless managed to reenter. Analysis of the community inside the cages showed no significant difference compared with the control area during the 8 months the cage experiment lasted (April-December 1978).

The experiment then did not directly show any effect of the above-mentioned predators, but perhaps indicated that other predators such as fishes and crabs do not play a large role in structuring this community since they were excluded. Conclusions, however, are not easy to draw from cage experiments as the cage itself leads to changes in physical factors by reducing current flow and light, and increasing sedimentation. Satisfactory cage experiments are more difficult to do in the subtidal than the intertidal.

Settlement plates

Figure 2c shows the number of species settled on the two series of plates. The complete species list settled on the ceramic plates is shown in Table 1.

The most active settling period was during summer and autumn. There was little or no settlement in winter and limited settlement during spring. The foraminifer *Cibicides lobatulus* and the polychaete *Spirorbis borealis* were found to settle almost throughout the year. Polyzoans of the genus *Electra* were found to settle at different periods of the year. Of the species with seasonal settling the hydroids were the first to appear in spring.

The most numerous settling organisms during the summer were the molluscs (*Mytilus edulis, Modiolus modiolus, Saxicava arctica*, and unidentified prosobranchs). *Pomatoceros triqueter* dominated the plates during the autumn. Vagile species observed were juveniles of *Coryphella, Asterias* and sea urchins.

Some species observed in the picture analysis on the test area were scarce or not found on the ceramic plates. Among the rhodophyceans and ascidians found colonizing the test area only one *Delesseria sanguinea* and one *Corella parallelogramma* were found on the plates. These species seem to settle and grow in small crevices, close to old hydroid stipes or other irregularities on the substrate.

Removal of specimens

There are always some species never observed on picture analysis but which were found in samples removed and examined in the laboratory (see Table 1). These species are called "secondary species", and although there are many such species they are of little importance in controlling community structure (Lewis, 1976). During summer, samples included high numbers of settled molluscs which were also found on the settlement plates.

DISCUSSION

Natural fluctuations in communities are caused by the seasonal increase and decrease of populations (Lewis, 1964). The most important change found on the community investigated was the rapid growth of the hydroid *Laomedea longissima* and its disappearance (Fig. 1). Figure 2a shows a good negative correlation between free space and the abundance of hydroids. The rapid decline of the hydroid population was probably caused by *Coryphella* (Fig. 3) which feeds upon hydroids (Thompson & Brown, 1976). The hydroids occupied the free space available in the community, and when hydroids were cropped down, the amount of free space increased to 30–40 %.

The number of species settled also varied throughout the year (Fig. 2c). During the period of highest settling activity (summer and autumn) space was available for settling. The area of the unoccupied substrate increased from 15 to 30 % during this period, and if the encrusting *Lithothamnion* is considered as a possible substrate for settling, more than 50 % of the space should be available for settling. On the scraped area even 20–25 % more of the space was at times unoccupied (Fig. 4).

Predation is probably the reason settled organisms (except a few *Pomatoceros*) never grow to sizes big enough to be recorded on picture analysis. Among the predators observed, *Asterias rubens* and *Psammechinus miliaris* were probably the most important since they occurred most frequently and were active in the community throughout the year (Fig. 2b). On the scraped area *P. miliaris* and *A. rubens* were found in high densities at the most active settling period, and in lower densities during the rest of the year compared with the control area. Small individuals of these predators entered the cages in high densities during summer and autumn; this may explain why no differences between community structure in the cages and that in the control area were found. Since *Asterias* and *Psammechinus* played such a dominant role, other predators present not able to enter the cages (crabs, fishes and others) play at most a minor role in structuring the community. The results from the scraped area on *A. rubens* and *P. miliaris* suggest such organisms were abundant where prey individuals were abundant.

The factors important to this community were therefore the relatively high percent cover of free space maintained by *Asterias* and *Psammechinus*, the settling and growth of hydroids, and then predation on these by *Coryphella.*

A. rubens and *P. miliaris* are common and important predators in Norwegian waters. Thompson and Brown (1976) have stated that within a short time nudibranchs like *Coryphella* are able to crop hydroids to extinction. Paine (1976) found a relation between the size of prey and size of predator of the asteroid *Pisaster.* The small size of *Asterias* in the tested area suggests a small-sized prey. The high densities of small *Asterias* through summer and autumn probably forage upon newly settled organisms.

P. miliaris eats almost everything among attached and dead plant and small animals (Lawrence, 1975). Sea urchins also remove attached species from the substrate by a "bulldozer" effect when moving and *P. miliaris* is always found to carry fragments of plants or scales of animals as a cover or camouflage.

The role of predation as an important factor producing free space, and reducing dominant competitors (implying higher diversity) is found both from protected intertidal areas and in subtidal communities (Paine, 1966; Menge, 1976; Karlson, 1978; Peterson, 1979). *Modiolus modiolus,* which in some parts of the Oslofjord is totally dominant in communities (personal observations), was only present in low densities on the test area even though dense settling occurs, suggesting spat is rapidly consumed by *A. rubens* and *P. miliaris.*

Little information is available from this study on effects of physical factors on the different species. The sediments sometimes observed among attached animals could have, for example, some influence on recruitment.

As predation is presumed to be the most important factor structuring the tested community, the predators *Coryphella, Asterias* and *Psammechinus* are suggested as being the most important "key" species. In a rationalized monitoring programme, the factors monitored must be the abundance of these predators and their influence on the success of recruitment and the abundance of hydroids and free space.

The stereophotographic method is especially suited for nondestructive ecological monitoring of the same organisms over time on a two-dimensional surface. The method used seems from these preliminary investigations to be well suited as a method for monitoring on smooth, rocky subtidal communities. The stereophotographic recordings combined with simple settlement plate experiments give sufficient information for follow-up investigations and suggest reasons for natural fluctuations or those induced by other perturbing factors.

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