Natural fluctuations in a rocky subtidal community in the Oslo Fjord (Norway)

Cycles
Predictions
Settling
Predation
Rocky-bottom

Cycles
Prédictions
Colonisation
Prédation
Substrat rocheux

Hartvig Christie
Institute for Marine Biology, P.O. Box 1064, Blindern, Oslo 3, Norway.

ABSTRACT

As part of a programme aimed at developing methods for ecological monitoring, a detailed analysis of a rocky community at 12 m depth was started. The study was based on nondestructive sampling using stereophotography, and additional experiments were done with settlement panels, predator exclusion and scraping of substrate to obtain further information about the dynamics of the community. Natural variations were found to be governed by key species which structured the community. Of more than 60 species found, ca. 10 were important in terms of abundance. Very few species exhibited stable abundance, and the community was dominated by annual cycles in populations mainly provided by seasonal settlement followed by predation and grazing, notably by *Asterias rubens*. Exclusion of this species lead to dramatic structural changes on artificial panels. Variation in abundance was analyzed using harmonic series plots. Models were produced for the most important species, and gave acceptable predictions when tested against the following year's data. Cyclic patterns appear annually, but suggestions of long term trends were found to slightly alter this annual cyclic stability.

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RÉSUMÉ

Variations naturelles dans une communauté infralittorale sur substrat rocheux du fjord d'Oslo, Norvège

Une analyse détaillée d'une communauté sur substrat rocheux, à 12 m de profondeur, a été entreprise ; elle fait partie d'un programme visant au développement de méthodes de surveillance écologique. L'étude a été basée sur une méthode d'échantillonnage non destructrice (la stéréophotographie) ; des expériences complémentaires ont également été effectuées, afin d'obtenir davantage d'information sur la dynamique de la communauté : colonisation de panneaux, exclusion de prédateurs, dénudation de substrats.

Il a été constaté que les variations naturelles semblent être gouvernées par les espèces-clés qui, de plus, structurent la communauté. Parmi les quelque 60 espèces trouvées, environ 10 sont importantes en termes d'abondance. Très peu d'espèces présentent une abondance stable, et la dynamique de la communauté est dominée par les cycles annuels quantitatifs des populations, principalement déterminés par une colonisation saisonnière suivie de prédation et de broutage, notamment par *Asterias rubens*. L'exclusion de cette espèce entraîne des changements structuraux très importants sur les panneaux artificiels.

Les variations d'abondance ont été analysées à l'aide de séries harmoniques. Des modèles sont présentés pour les espèces les plus importantes ; ils ont fourni des prédictions acceptables si on les compare aux données de l'année suivante. Des variations cycliques se produisent annuellement, mais il est suggéré que des tendances à long terme existent également et modifient légèrement cette stabilité cyclique annuelle.

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INTRODUCTION

Aimed at developing a survey programme for ecological monitoring, investigation on natural fluctuations and their structuring factors was started in 1978. Lewis (1976) suggested that it was necessary to know the causal mechanisms in a community so that one might distinguish the natural variations from changes caused by human activities (*e.g.* pollution).

Results obtained from 3 to 4 years of detailed investigation on a rocky subtidal community are presented here. After one year of study, Christie (1980) suggested that the observed seasonal variations were governed by a summer settlement followed by predation. Seasonal variations are the most common natural variations. The mechanisms giving rise to the seasonal variations and the communities' predictability (if the same seasonal cycles returned annually) are important factors in a monitoring context. Attention is paid to the most abundant species and « key species » (*see* Paine, 1969; Dayton, 1972; Lewis, 1976), but longterm trends are looked for as far as the data permit.

If the same seasonal events occur year after year, the community would have high stability. Sutherland and Karlson (1977) believed from their study that fouling community structure would undergo different changes from year to year, resulting in a community either changing dynamically or changing stepwise with multiple stable points (Sutherland, 1974). However, stability and predictability of rocky communities are dependent on organizing factors, for example communities organized by predators which then provide space for new settlement (Paine, 1966; Dayton, 1971; Menge, 1976; Karlson, 1978; Peterson, 1979). Where the role of predators are unimportant (Keough, Butler, 1979), competition will normally govern the community structure. Exclusion of predators (both natural and by design) will in some cases lead to total dominance by a dominant competitor (Paine, 1966; Menge, 1976), a stable point, such as the populations resistant to recruitment found by Sutherland (1974; 1978). Natural long term changes in abundance of important species could lead to very unpredictable community structures, and must also be dealt with before one can distinguish pollutants as a positive organizing factor.

METHODS

The community studied is on a smooth, nearly vertical rocky wall, at 12 m depth at Drøbak in the Oslofjord. Seasonal changes in temperature were found to vary between 0 °C in winter and ca. 15 °C in summer. Salinity ranged between 24 and 34 ‰.

A fixed site was permanently marked off with plugs (*see* Christie, 1980). By using a reference system, the exact same area was sampled nondestructively by the underwater stereophotography technique introduced by Lundälv (1971). The equipment we used was described in detail by Green (1980). A comprehensive survey programme connected to the stereophotographic sampling is described by Christie *et al.* (in press). In the present study 2 m^2 of the bottom were used as a control area, and another 0.5 m^2 was scraped at the start in 1978. A settlement experiment started in 1978 with ceramic plates (15 × 15 cm) submerged for 2 months. Four PVC plates (40 × 40 cm each) were put out in March 1981 and another plate (100 × 35 cm) was hung on a rope ca. 2 m above the bottom to avoid benthic predators.

All sampling was carried out by SCUBA diving, approximately once a month.

All stereoslides are analysed with a stereoscope (*see* Green, 1980; Christie *et al.*, in press) by counting colonies or solitary individuals or by estimating abundance as percentage cover by point sampling (Christie, 1980). Settling plates were qualitatively analysed by presence/absence of species.

In calculating curve fitting models of fluctuations, harmonic series analysis (Fourier series) was used (Bliss, 1970, p. 219; Gray, 1981, p. 75).

RESULTS

Although more than 60 species were found to occur in the community (Christie, 1980), only the most important species are treated in this paper. The species selected are those of greatest abundance or those of greatest importance in structuring the community.

Figure 1 shows data obtained through 1978-1980 of free space (unoccupied by organisms) and of important organisms. By using the method of Bliss (1970, p. 219) to create curves with the best fit to the seasonal fluctuations, the observed data from 1978 and 1979 produced cyclical curves which, as a series of sine functions, serve as predictions for the seasonal variation patterns of the different species for 1980. In Figure 1 the observed fluctuations from 1980 are compared to the predictions.

For all species the comparison shows a similar pattern of variation through 1980 as the predicted model. However, the models consider only annual patterns, and not long-term trends which occur in most species or as a phase displacement compared to annual cycles as seen in Figure 1 *G*. Using the data for three or four years, models can be calculated taking into consideration both linear increase or decrease and eventually phase displacement. The curves with the best mathematical fit are drawn in Figure 2. All species presented fluctuate in a 12 month cycle, except the erect red algae (Fig. 2 *G*) which had the best fit to a periodicity of 10.2 months. However, this species shows a stable trend in abundance, while the hydroid *L. longissima* (Fig. 2 *B*) decreased and the others showed an increase. Other patterns of long-term trends are not assessable after only 3 or 4 years of study.

A few species occurred as stable populations throughout the sampling period. The most important are the encrusting *Lithothamnion* sp. and *Pomatoceros triqueter* (Fig. 3). Species of less importance (abundance) but also occurring in stable populations all through the sampling period are represented by *Alcyonium digitatum* and *Tealia felina*.

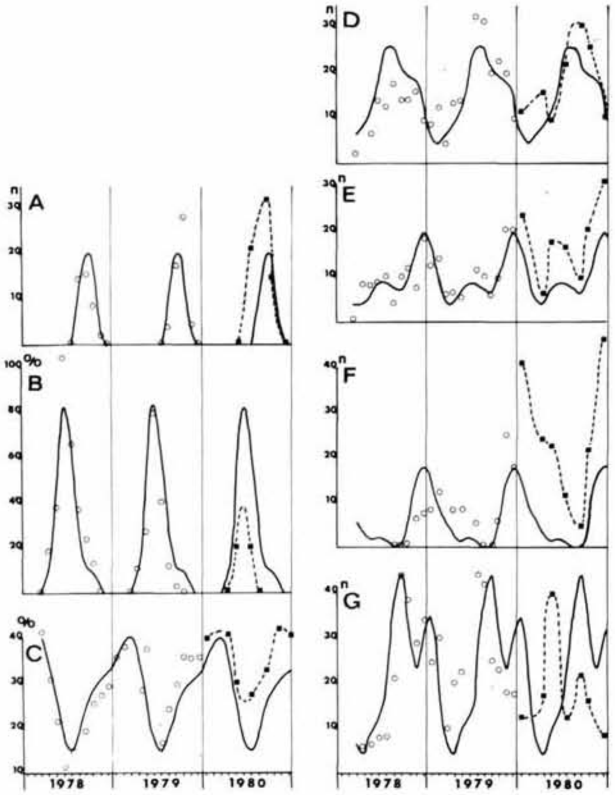

Figure 1

Seasonal cycles of free space and important species. The observed data from 1978 and 1979 (○) are basis for the calculations of annual cyclic curvefitting models (solid line) which also are plotted as predictions for 1980. The observed fluctuations from 1980 (■----■) are plotted for comparison to the predicted curves. Abundance in numbers m^{-2} (n), or in percent cover (%).
A) Tubularia *sp.;* B) Laomedea longissima*;* C) *free space;* D) Asterias rubens*;* E) Psamechinus miliaris*;* F) Acmaea *sp.;* G) *erect red algae.*

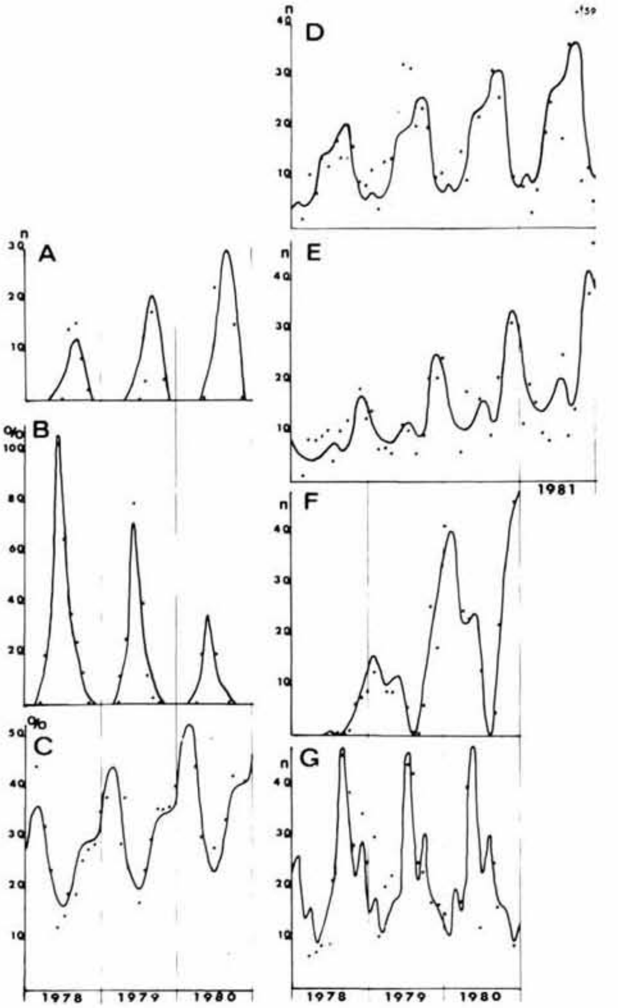

Figure 2

Calculated models for annual cycles added long term trends. Same species and abundance as in Figure 1.

Although they exhibit unpredictable variations, ascidians are also characteristic of these rocky communities. Of these, the most abundant were *Boytrylloides leachi*, *Styela* sp. and *Corella parallelogramma.*

The most important patterns on the scraped area are shown in Figure 4. Cycles of both free space (*A*) and *A. rubens* (*B*) have higher peaks compared to the control area. On the scraped area the settled organisms were more effectively removed by predators, and in the winter time the covering organisms (as the inverse to free space) are only represented by the stable populations of *Lithothamnion* sp. and *Pomatoceros triqueter*. In Figure 4 *C* results of the settlement plate experiment are plotted. There was a significant positive correlation between density of *A. rubens* and the number of species settled and a negative correlation between these two and the free space (Fig. 4). This pattern indicates that many organisms settle and occupy space throughout the summer, and that *A. rubens* was attracted by the food supply available, but would leave the areas when organisms were removed, as on the scraped area. From the various species found on settling plates (Fig. 4 *C*), most dense spatfall is found among the hydroids (*Laomedea longissima*, *Tubularia* sp.), bivalves (*Mytilus edulis*, *Modiolus modiolus*, *Hiatella arctica*) and the

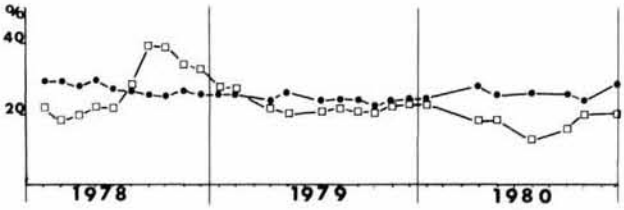

Figure 3

Percent cover of Lithothamnion *sp.* (●) *and* Pomatoceros triqueter (□) *during the sampling period.*

polychaete *Pomatoceros triqueter*. Eggs and juveniles of the nudibranch *Coryphella* sp. are found in high densities in the hydroid colonies. Some authors believe that grazing by this specie is an important factor in removal of the hydroids (Thompson, Brown, 1976; Christie, 1980).

The effect of predator exclusion is shown in Figure 5. Although predators (mainly *A. rubens*) to some extent invaded the panel, a monthly removal of predators leads to dramatic changes. The exclusion panel acquired

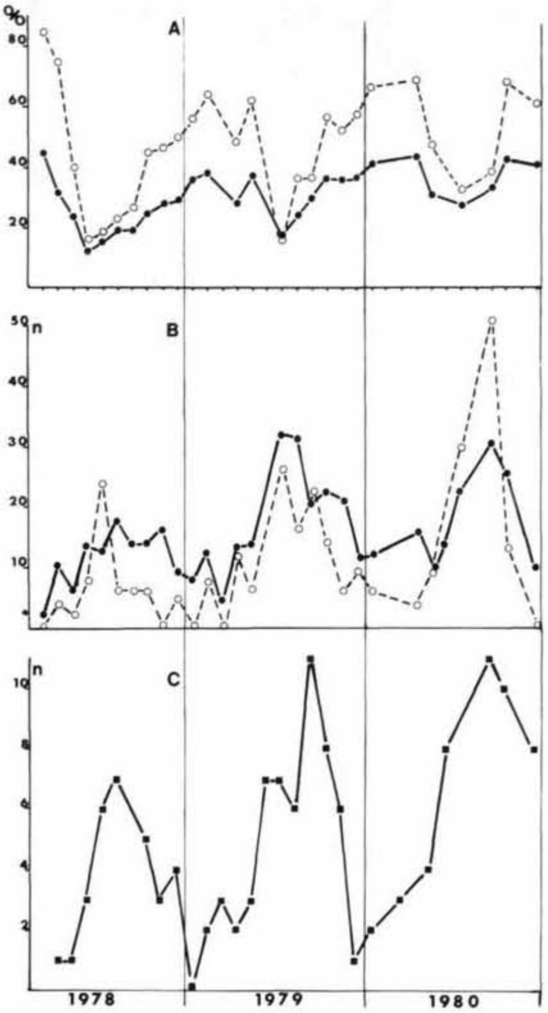

Figure 4

Comparison of percent cover of free space (A) and Asterias rubens *(B) on control area (●—●) and on scraped area (○- - -○). (C) Numbers of species settled on settlingplates.*

a dense (ca. 90 %) cover of organisms, first the hydroids settled, but the panel was later totally dominated by *Mytilus edulis*. The control panel followed the same pattern as the scraped area (Fig. 4 *A*), a dense settlement through the summer and a subsequent disappearance of organisms (due to predation).

DISCUSSION

Of the few species important for structuring the community, two occur continuously (Fig. 3), whilst the rest show seasonal oscillations (Fig. 1, 2). The annual patterns are predictable (Fig. 1), but maximum abundance varies from year to year. These longer-term changes were not random variations, but followed increasing or decreasing trends during the 3-4 years of study, and are probably an example of one of the long term cycles described by Gray and Christie (1983).

The community is dominated by a summer recruitment (Fig. 4 *C*) followed by removal of settled organisms by predators and grazers. The most important predator, *Asterias rubens*, kept the bivalve populations down to almost zero abundance (also found by *e.g.* Dare, 1982).

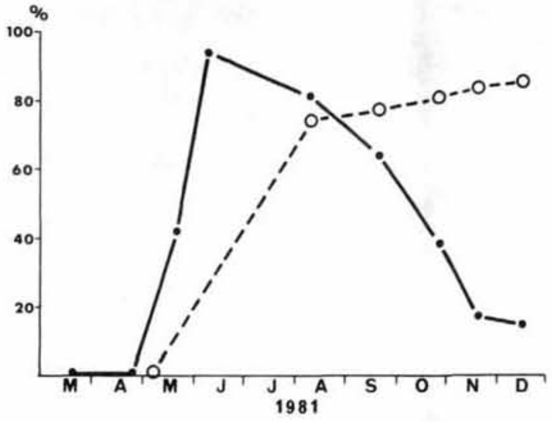

Figure 5

Total percent cover of organisms on settling panels (●—●), control panels (○---○), predator exclusion panels.

Exclusion of *Asterias* resulted in total dominance by *Mytilus edulis* (Fig. 5), as also found by *e.g.* Paine (1966) with *M. californianas* on the US West coast. Hydroid population also exhibited annual rapid increases (Fig. 1, 2, *A* and *B*), the latter mainly due to cropping by *Coryphella* sp. (Christie, 1980). Important is also the grazing by *Psamechinus miliaris* and *Acmaea* sp. on other settled organisms. This pattern demonstrates that predators and grazers are the key structuring species. The trend of increased abundance of predators was inversely related to the decreased dominance of sessile organisms (Fig. 2 *C*), and long term trends in these species must influence community structure and stability. Rocky communities have often been found to be controlled by predator activity (*e.g.* Paine, 1966; Dayton, 1971; Karlson, 1978).

Predators are dependent on new recruits for food source and recruitment is only possible where space is provided by predators. These factors seem to be in a seasonal equilibrium. If sampled once a year and at the same time (season), the community would appear to be constantly at the same point. However, with monthly sampling the community was found to be governed by continuous perturbations providing spatial and temporal changes in species composition. As the influence of the species (and factors) occurs more or less at the same time each year, the community is suggested as being in an " annual stability " or an " annual pattern of stability ". Dramatic changes in the populations of key species which produce this pattern might change this annual stability and the community might develop toward a stable point (Sutherland, 1974) as shown by the predator exclusion experiment, which resulted in mussel domination. Similar mussel-dominated communities studied by Dayton (1971), Paine (1966; 1974) and Menge (1976) are described by Sutherland (1981) to be stable over many years.

When predation is the main perturbation, following a disaster event (studied by the scraping experiment) the community must be taking longer than three years to return to normal conditions.

In a monitoring context, non destructive stereophotographic sampling of rocky surface communities has been shown to be a good method for following dynamical changes in community structure. Knowledge of natural fluctuations, change in community structure and stability must be determined before it is possible to distinguish changes induced by anthropogenic activity from the natural ones.

Curve fitting models (Fourier series) of fluctuations are a useful tool in making predictions and in selecting the best times for sampling.

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