THE STABILITY OF A BENTHIC COMMUNITY OF SOFT SEDIMENT

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(Figs. 1–3)

An Oslofjord benthic community showed a range of variability for its constituent populations from small to large fluctuations over a two-year period. The five common species completing at least one turnover of all individuals within the time span studied showed stable equilibria, being persistent within bounds of ±10% of the transformed mean. Although rare species were highly variable in abundance and the dominance patterns of common species changed over time, overall, the community showed a consistent pattern of the distribution of individuals among species. Adjustment occurred within the community so that increases in the abundance of some species were accompanied by decreases in the abundance of others to maintain the overall pattern. It is suggested that this consistency of pattern describes a community at dynamical equilibrium where species are able to fluctuate in abundance but, by means of adjustment of densities, a stable pattern holds.

INTRODUCTION

Recently, Connell & Sousa (1983) have reviewed the disparate terminology applied to the meaning of the stability of ecological systems and the evidence needed to judge whether ecological systems are ever stable. They suggested that two independent concepts which have both been applied to stability should be defined. These are (*a*) resistance, which is the tendency to withstand being perturbed from equilibrium, and (*b*) adjustment stability, which is the ability of a perturbed population or community to return to the same equilibrium point or limit cycle. Connell & Sousa (1983) define the stable equilibrium state as (p. 790) 'the population density at which a population will remain or, if moved away, to which the population will return'. If the system remains at an equilibrium state when perturbed it is resistant, whilst if it returns to an equilibrium state when perturbed it shows adjustment stability.

After a detailed analysis of a wide variety of data, Connell & Sousa concluded that: (1) natural populations, guilds and communities are not stable beyond one complete turnover of individuals, and (2) only rarely (three instances) did populations show adjustment stability. The complete turnover of all individuals in a population was a major facet of Connell and Sousa's definition of stability giving a common scaling factor to compare the stability of short-lived and long-lived organisms.

As evidence that populations, guilds and communities do not show stable equilibria, Connell & Sousa calculated for a variety of local populations the standard deviations of log numbers in censuses separated by at least one turnover of individuals. The populations showed a continuum of variability among populations and taxa ranging from 'remarkable constancy to wild fluctuations'. Connell & Sousa concluded that there was no evidence of equilibrium states and hence multiple equilibrium states. Whilst this evidence is acceptable for the argument that populations picked at random show random fluctuations, it does not necessarily apply to populations within a given community.

Connell & Sousa used, as an example of adjustment stability, the data of McGowan (1977), McGowan & Walker (1979) and Hayward & MacGowan (1979) to show that copepods in the central Pacific gyre exhibited the same dominance patterns in two surveys 10 years apart, despite the fact that between the two surveys a large temporary disturbance occurred which led to an increase in numerical abundance. Hayward & MacGowan's data show that the dominance pattern was constant over time whereas numerical abundance clearly was not. Ir our opinion, this indicates that community stability and population stability are not synonymous (see also Peterson, 1975).

Connell & Sousa also consider a third definition of stability: persistence withi bounds (Lewontin, 1969; Holling, 1973; Chesson, 1978). However, Connell & Sousa claim that 'to see whether this idea applies to real ecological systems on would need to show that there were no trends in population numbers and n upward trend in magnitude of population fluctuations, i.e. extinctions or irrup tions of numbers in populations within communities'. This requirement is, w believe, too severe and will necessarily result in the suggestion that no populatio or communities are stable, as indeed Connell & Sousa conclude. Yet there ma well be compensatory mechanisms operating within communities whereb increases in one or a few species are accompanied by decreases in others.

We believe that Connell & Sousa's analysis has not considered adequate whether or not communities show stability. First, consider the concept of stabili related to a community. Connell & Sousa insist that all constituent populatio of species comprising the community should be stable in order for the communi to be regarded as stable. This requirement can be related to the dynamical syste theory where stability is defined as the return to an equilibrium state after so perturbation. From this argument one can regard each population separately a study the effect of different perturbations on each population. This approach legitimate only if one can assume that there are no interactions between speci which is clearly an unrealistic assumption for most natural communiti Secondly, this approach does not allow the community to have properties defined in single populations. From population dynamics we accept that popu tions can have properties that are undefined in individuals, such as densi life-table data etc. Analogously, it is likely that communities have properties t are undefined in populations. One such property may be the tendency for distribution of individuals among species to show similar patterns over time. J as life-table data reflect the structure among the individuals making u population so the consistent pattern probably reflects the sum of interacti between the populations and with the environment. The interactions are explicit but include all of the relevant biological factors, such as environmental responses, competition, predation, mutualism, commensalism etc. which we refer to as structuring forces in the community. If communities were, in fact, unstructured, the curves of the distribution of individuals among species would not be consistent and could be any shape, whereas the curves in fact are usually similar (Ugland & Gray, 1982). The fact that a distinct pattern exists suggests to us that communities of relatively unperturbed environments have a common structure. Thus, in our terminology, Connell & Sousa have only demonstrated that the concepts of dynamical systems theory (and Lyapunov stability) cannot be applied to community stability.

This paper attempts to apply Connell & Sousa's criteria of stability to species within one single community and in particular to address the question of whether or not a stable equilibrium state (persistence within bounds) occurs for some species. Further, a dynamical concept of stability is considered whereby species can fluctuate in abundance but the overall structure is maintained.

THE STUDY AREA AND METHODS

The community studied is one found in a silt–clay deposit at 32 m depth at Bjørnehodebukt in the inner Oslofjord. The community has been fully described elsewhere (Valderhaug & Gray, 1984). The sample site is below the thermocline and has stable temperature (8 ± 2 °C) and salinity (28 ± 2‰) conditions. Although food input as measured by changing C/N ratios and number of bacteria in the sediment varied, the community remained remarkably stable over the two-year period sampled. Species number had a mean of 76·3 (S.D. ± 6·1) with a total of 155 species recorded; the number of individuals had a mean of 1965 (S.D. ± 354). Five 0·1 m^{-2} Day grab samples were taken on each of ten dates between July 1981 and June 1982 and on four dates between June 1982 and June 1983. The sampling period was, therefore, two years. The samples were sieved through 1 mm screens: some juvenile individuals were undoubtedly lost. Despite this underestimation of recruitment, the results show that the dynamics of the community are remarkably stable. This prompted us to apply Connell & Sousa's criteria of stability to these data.

RESULTS

Connell & Sousa used, as their main evidence that populations, guilds and communities are not stable beyond one complete turn-over of all individuals, a plot of variability defined as S.D. ($\log_{10}$) for all species considered. Fig. 1 shows the same plot of the data for the Oslofjord community. Overall, some species show almost no variability (S.D. 0–0·1) whereas others show wild fluctuations (S.D. 0·5–0·6). Yet, if one considers only abundance groupings, a different pattern emerges. Common species, defined as abundances > 100 0·5 m^{-2} show remarkable stability, whilst moderately common species range from stable to highly variable and rare species show the largest variability. Taking only the common and moderately common species (mean 23, total species number 155), there is a significant negative correlation between transformed ($\log_{10}$) S.D. and mean $r = -0·56$ (Fig. 2). Species with high abundance show low variability and species with low abundance show high variability. Throughout the sampling period the proportion of common, moderately common and rare species was very similar

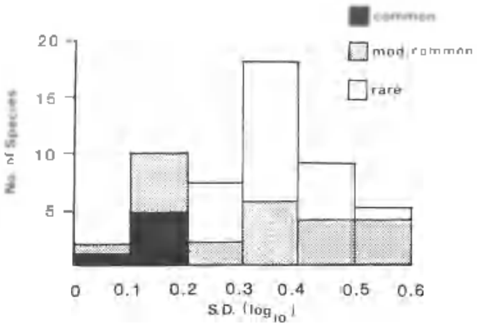

Fig. 1. Variability (S.D. $\log_{10}$) of the benthic community in Oslofjord. Species groups: rare, 0–10 individuals 0·5 m^{-2} 2; moderately common, 10–100 individuals 0·5 m^{-2}; common, > 100 individuals 0·5 m^{-2}.

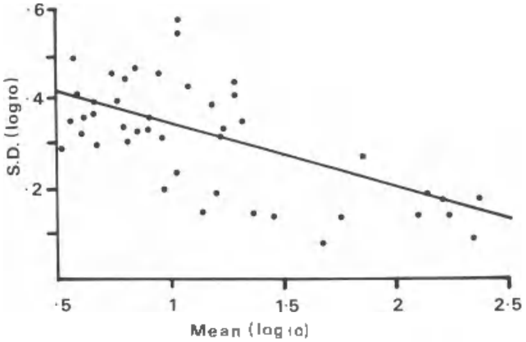

Fig. 2. Regression of transformed ($\log_{10}$) mean against standard deviation (S.D.) of common and moderately common species in the benthic community in Oslofjord. S.D. $Y = 0{\cdot}4758 - 0{\cdot}1312X$; r, −0·5593.

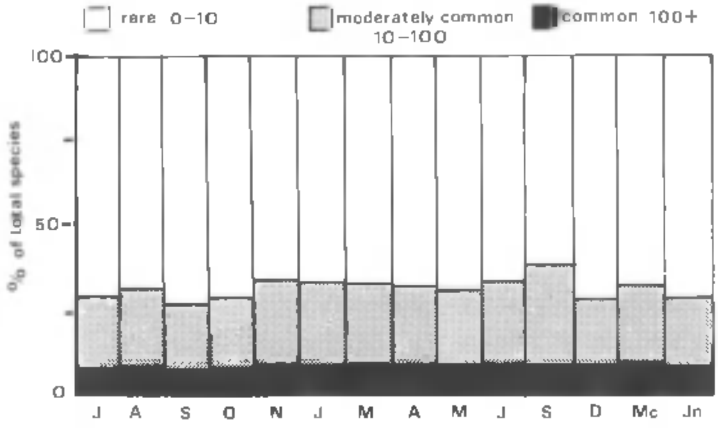

Fig. 3. Composition of the benthic community in Oslofjord by abundance groups.

(Fig. 3). The question then arises: do the common species show stable equilibria (persistence within bounds)?

Using $\log_{10}$ transformed data, bounds were set as $\pm 10\%$ of the mean. If species were persistent within bounds one would expect that the abundance at each sampling time would fall within these limits, whereas if the species were unstable the abundance patterns would vary randomly. Table 1 shows the results for the common and moderately common species. Clearly, there is a remarkable degree of persistence within bounds even though *Nuculoma tenuis* must strictly be excluded as it did not complete a complete turnover of all individuals within the time interval, since it has a life-span of about 9 years at the study site.

Table 1. *Persistence within bounds of a benthic community of Oslofjord, Norway*

The number of sampling times during the period July 1981 to June 1983 that the population abundance fell within, or was above/below, the boundaries of $\pm 10\%$ of the transformed ($\log_{10}$) mean. Common species, > 100 individuals 0·5 m^{-2}; moderately common species, 10–100 0·5 m^{-2}

Species	Number of times		
	Below	Within	Above
Common			
Nuculoma tenuis Montagu*	0	14	0
Ampelisca tenuicornis Lilljeborg	0	13	1
Philomedes brenda (Baird)	1	12	1
Haploops tubicola Lilljeborg	2	12	0
Sosane gracilis (Malmgren)	1	11	2
Heteromastus filiformis (Claparède)	2	10	1
Moderately common			
Lumbrineris fragilis (Müller)*	0	14	0
Pholoe minuta (Fabricius)	2	11	1
Goniada maculata Oersted	3	9	2
Diplocirrus glaucus (Malmgren)	2	9	3
Melinna cristata (M. Sars)	3	8	3
Mediomastus fragilis Rasmussen	3	8	3
Glycera alba (Müller)*	3	8	3
Typocirrus variegata (Grube)	4	8	2
Pseudopolydora paucibranchiata (Okuda)	3	7	3
Streblosoma bairdi (Malmgren)	2	6	6
Prionospio cirrifera Wirén	2	6	6
Spiochaetopterus typicus M. Sars	3	5	6
Trichobranchus roseus (Malm)	3	5	6
Chaetozone setosa Malmgren	5	4	5
Thyasira sp. indet*	5	4	5
Lanassa sp. indet.	6	3	5
Maldane sarsi Malmgren	6	2	6
Ampelisca aequicornis Bruzelius	7	0	7
Prionospio malmgreni Claparède	6	0	8

* Species not undergoing one turnover of all individuals within time span of study.

The moderately common species *Lumbrineris fragilis* and *Pholoe minuta* were highly persistent, but the first-named species did not undergo a complete turnover of all individuals (life-span > 2 years). Some species (*Goniada maculata* to *Pseudopolydora paucibranchiata*) show a moderate degree of persistence within bounds, whereas the remaining species show random variability.

The rare species with mean abundances < 10 0·5 m^{-2} could not be similarly assessed since most had many zero abundances and became locally extinct (or emigrated) and recruited (or immigrated) into the community at random, resulting in a very high variability. Despite the high variability in the rare and in many moderately common species, using the plotting method of Ugland & Gray (1982), the community showed a consistent pattern of individuals among species at each sampling time (see Valderhaug & Gray, 1984). The species dominating the community also varied from time interval to time interval (Table 2). The data suggest that adjustment is made within the community and increases in abundance of some species are accompanied by decreases in others so that the overall pattern remains the same.

Table 2. *Rank dominance patterns over time of a benthic community of Oslofjord*

	Months													
Species	J	A	S	O	N	J	M	A	M	J	S	D	M	J
Ampelisca tenuicornis	1	4	5	4	6	6	6	6	5	5	3	5	—	5
Nuculoma tenuis	2	1	3	2	2	1	2	2	3	1·5	1	1	2	2·5
Haploops tubicola	3	—	4	5	3	3	4	5	2	4	2	—	4	—
Sosane gracilis	4	5	—	—	4	4	3	—	—	1·5	5	1	3	1
Philomedes brenda	5	2	1	1	1	2	1	1	4	—	4	2	1	2·5
Heteromastus filiformis	—	3	2	3	5	5	5	3	1	3	—	—	5	—
Mediomastus fragilis	—	—	—	—	—	—	—	4	—	—	—	—	—	—
Prionospio malmgreni	—	—	—	—	—	—	—	—	—	—	—	4	—	4

DISCUSSION

The benthic community studied here is unusually stable, as measured by changes in the total number of individuals and the total number of species, both of which fluctuate much less than comparable marine communities from similar depths. However, most other studies have been in areas where environmental variables strongly influence the community, such as Rachor's long-term study of the fauna of the German Bight (Rachor, 1979). The Oslofjord is unusual in that it has small lunar tides (< 20 cm) and, even at 30 m depth, temperature and salinity show little seasonal variation (see Valderhaug & Gray, 1984, for a full description). The community is not, however, unique. Josefson (1981) records a similarly stable community in the soft sediments in the Skagerrak but at much greater depths (100 and 300 m) where environmental conditions are even more stable than those studied here.

One of the criteria established by Connell & Sousa as necessary to study the existence of stable equilibria in biological systems, namely a complete turnover of all individuals, has been applied to most, but not all, species in this community. Even though the total number of species and individuals remained fairly constant over the two-year study period, the pattern of individual species variation was much more variable. The plot of S.D. of $\log_{10}$ abundances for all species gave results (Fig. 1) which, at first sight, appear similar to those found by Connell & Sousa, with populations varying from highly stable to wildly fluctuating. Yet analysis of abundance groups (common, moderately common and rare) gave a different pattern with the common and moderately common groups taken together showing a significant negative correlation between mean abundance and variability (Fig. 2). This finding is unusual in that the commonest pattern is for the S.D. to increase with the mean as found by Taylor & Woiwood (1980) although their data were not concerned with species within a community. The six common species in the Oslofjord all showed stable equilibria over the two-year study period and of these five completed at least one turnover of all individuals within the time period. There were, however, no known large perturbations within this time period and thus it is not known whether the common species are resistant.

The second criterion of Connell & Sousa (p. 793) was the minimum area to study, defined as 'the minimum area in which a population or community is stable and/or persistent' and in which environmental conditions allow "the development, growth and survival of offspring for the replacement of existing adults". In the present study, 60–70% of the species were rare, that is, represented by 1 or 2 individuals 0·5 m^{-2} at every sampling time (Fig. 3): this is in keeping with Ugland & Gray's (1982) suggestion. Yet species area curves (unpublished) indicate that five 0·1 m^2 samples give a reasonable estimate of total species number, although the mean species number taken was only 76 compared with a total number of species recorded of 155. However, species may be present, but not sampled, at each sampling time so that it is impossible to distinguish between emigration, extinction and sampling error. We suggest that in most natural communities, be they terrestrial, fresh-water or marine, most species are rare, represented by 1 or 2 individuals whatever the sampling unit: in the Oslofjord, rare species constituted 60–70% of the total species number of any sampling occasion. Most rare species are never found in high densities and their dynamics may be regarded as chaotic and thus there is no simple explanation for rareness (Vandermeer, 1983). If the area is increased in size then, rather than finding a stable state, more rare species will be encountered. Both Connell & Sousa's data and that shown here refer to local populations *sensu* Taylor & Woiwood (1980). The latter authors claim that local populations cannot be expected to be stable and only when the total species' population is examined can stability be considered. Yet in this study a few species do show stability of local populations.

Connell & Sousa's requirements for persistence within bounds (that there are no trends in population numbers and no upward trend in magnitude of fluctuations) are met by the five common species that show a turnover of individuals, namely *Ampelisca tenuicornis*, *Philomedes brenda*, *Haploops tubicola*, *Sosane gracilis* and *Heteromastus filiformis*, plus *Pholoe minuta* from the moderately common group. Thus, only 6 of 155 species in the Oslofjord community can be regarded as showing stable equilibria (persistence within bounds). The surprising result of this study is therefore that, despite highly stable environmental conditions, most species are not stable under Connell & Sousa's definition.

In this study, rare species were found to fluctuate more than moderately common or common species. This is partly due to the method of analysis using logarithms, which emphasise small arithmetic scale changes, but the negative correlation between abundance and variability (Fig. 2) shows that common species were less variable. The rare species did not, however, fluctuate at random. If this were the case then one would expect large influxes at irregular intervals and large local extinctions and/or absences. This did not occur, a consistent overall pattern of the distribution of individuals among species typical of undisturbed communities was found (Valderhaug & Gray, 1984). Gray (1981), Ugland & Gray (1982) and Pearson, Gray & Johannessen (1983) have shown that the pattern of individuals among species for communities disturbed by larval recruitment, storms, organic enrichment, oil and other forms of pollutants, is very different to that for undisturbed communities.

We believe that this consistent pattern is typical for most natural assemblages in undisturbed environments and this consistency of pattern can be regarded as stable. In the Oslofjord community, increases in abundance in some species (e.g. the changing dominance patterns: Table 2) are compensated by decreases in others to maintain the overall pattern. This adjustment occurs within the community although the populations may not return to exactly the same numerical abundance after one turnover of individuals. Connell & Sousa's requirement of a return to exactly the same abundance is too parsimonious and would reject patterns that we regard as stable. By allowing fluctuations within bounds, a more dynamic definition of stability is derived, in keeping, we believe, with the definition that most ecologists would apply to a stable state.

The stability found in the Oslofjord community is comparable to that found by Pearson (1975) in two Scottish sea lochs where the benthic communities at two stations between 1963 and 1966 sampled at similar times showed consistent patterns of individuals among species yet dominance varied markedly from year to year. Again, adjustment is being made within the community. Similarly, Josefson's (1981) study of the soft-bottom benthos at two stations at 100 m and 300 m depth over a 5-year period in the Skagerrak showed stable equilibria for the common species over the time period studied. In both of these studies only a few long-lived bivalves and echinoderms did not show complete turnover of all individuals in the time period covered. Buchanan, Sheader & Kingston (1978), in a study of a community off the coast of Northumberland, found that although there was a long-term increase in abundance of the top 17 ranked species over a 7-year period, increases in some were accompanied by decreases in others, a feature demonstrating dynamic adjustment within the community. During the period studied there was a dramatic rise in the long-term mean temperature off Northumberland which led to a change in the species composition. Connell & Sousa would dismiss this as evidence of adjustment stability but the pattern found is consistent with a dynamical equilibrium state for communities that cannot be defined at the population level. The idea of a community in dynamical equilibrium is supported by the data of McGowan (1977), McGowan & Walker (1979) and Hayward & McGowan (1979).

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