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Structure, diversity and stability of two oligochaete communities according to sedimentary inputs in Lake Geneva (Switzerland)

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ABSTRACT

Two oligochaete communities were sampled monthly during one year in two 35 m deep locations of Lake Geneva (Switzerland). Organic sedimentation was lower and less variable in station 1 than in station 2 (157 versus 214 g C $m^{-2}yr^{-1}$). The oligochaete community in station 1 was more diverse and more stable (persistent over time) than in station 2, as long as the organic sedimentation was low. Diversity and stability decreased in station 1 when the organic sedimentation increased, and during an *Oscillatoria* bloom. The less diverse community in station 2 was more resistent to these changes. Diversity was associated with environmental stability, but resistance to perturbation was greater in the simpler community which is adapted to changing environmental conditions. The value of oligochaete communities as an indicator of the level of eutrophication was reassessed according to our present data. Changes in the structure of oligochaete communities were related to changes in sedimentation processes.

Introduction

In the present study, we have attempted to identify some of the factors which determine the structure of animal benthic communities in lakes. The structure of communities is the result of complicated interactions between several biotic (predation, competition) and abiotic factors [8].

Benthic communities located under the photic layer depend directly or indirectly of sedimentation processes for their food supply [1, 16]. Therefore, we have selected in Lake Geneva (Switzerland) two locations exposed to different inputs of organic matter; these stations have been utilized in a previous study [5]. In both locations, the bulk of the benthic macrofauna consisted of tubificid and lumbriculid worms.

These two oligochaete communities have been used to analyse relationships between: a) diversity and stability in benthic communities [3, 13]; b) structure of oligochaete communities and changes of sedimentary inputs, in order to verify the value of oligochaete communities as indicators of the level of eutrophication [9, 17].

In this paper, we have attempted to study the benthic communities from a practical point of view (their value as an indicator) and from a theoretical point of view (factors explaining their structure). These two points of views are closely related:

benthic communities may be utilized as an indicator of eutrophication level as far as their structure reflects mainly the influence of abiotic factors, such as organic sedimentation.

Stations and methods

From February 1978 to February 1979, 6 sediment cores (22.9 cm^2 each) were taken every 4 weeks by a diver from two 35 m deep sampling stations in Lake Geneva (Switzerland). Station 1 is located 500 m west of the outfall of the sewage treatment plant of Lutry (a town east of Lausanne); station 2 is located 100 m west of the same outfall.

In both locations, sedimentary inputs to the bottom were measured in 3 sediment traps. Sediment traps were constituted by 30 cm long and 5.4 cm wide aluminum cylinders (sampling area 22.9 cm^2); they were situated 160 cm above the sediment on a metal pole and emptied every 2 weeks. Total sedimentation was expressed by the total dry weight of sedimented matter in the 3 traps; organic sedimentation was calculated from the percentage of organic carbon in the sedimented matter [5].

Tubificid and lumbriculid worms, colored with Bengal Rosa, were separated from the sediment with a sieve (0.2 mm mesh size aperture) and counted in every core. A random subsample of 100 worms taken from the 6 cores pooled together was mounted in Hydramount of Gurr and identified. Immature worms were identified according to the shape of pectinate setae. The relative density of every worm species in the subsample was related to the total mean density of worms per core. From that relation, density of every worm species per m^2 was calculated.

Diversity of the oligochaete community was measured with the following formula [8]:

$$\text{diversity} = 1/\sum_{i=1}^{s} p_i^2 .$$

In this formula, p_i represented the relative density of species i, and s the total number of species present in the sample.

In this paper, stability means persistence stability: it is simply a measure of how constant the oligochaete populations, the oligochaete communities or the environmental variables have remained over a period of time. Stability of oligochaete populations and variation of environmental variables was measured by dividing sample variance by sample mean [13]. Increasing value of this ration corresponds to decreasing persistence stability. An index of similarity was also used to measure stability of the oligochaete community [13]. The proportionate similarity between two samples A and B was equal to:

$$I = 1.0 - 0.5 \sum_{i=1}^{s} |a_i - b_i| .$$

In this formula, a_i is the proportion of total individuals in sample A that belongs to species i, and b_i is the proportion of sample B belonging to species i; and there are s different species in the two samples.

Pearson correlation coefficient was utilized to estimate if the variations of the same variable occurred simultaneously in both locations. Calculations and statistic tests were performed according to the SPSS package [10].

Results and discussion

Sedimentary inputs

Annual organic sedimentation arriving on the bottom was equal to 157 g C per m^2 in station 1 versus 214 g C in station 2 [5]. Similarly, total dry weight of sedimented matter and its percentage of organic carbon were higher in station 2 (table 1). This difference was due to the impact of the sewage treatment plant of Lutry town on station 2. Bottom temperature was similar in both locations.

An exceptional *Oscillatoria* bloom was recorded in Lake Geneva from September to December 1978 [14]; *Oscillatoria bourrellyi* was predominant in September and October, then *Oscillatoria rubescens.*

Chlorophyll concentrations were high in the water column (0-20 m) during this bloom [5, 12], and sometimes the 35 m deep sediment was covered by a red layer of *Oscillatoria* threads. Such a bloom seems able to modify considerably benthic communities. As previously shown [5], oxygen uptake by the sediment and by the sedimented matter was very high when the sedimented material consisted mostly of *Oscillatoria* threads.

Sedimentary inputs were less variable in location 1 than in location 2 (table 1). Sedimentary inputs provide food to the oligochaete communities [1] and they also influence the conditions of oxygen, nutrients, etc., of the water sediment interface. Therefore, food supply to the bottom was smaller but more stable in station 1 than in station 2.

Table 1. Mean values and temporal variations of 6 environmental variables in sampling stations 1 and 2. The temporal variation is estimated from the ratio variance on mean. Data from [5].

Tableau 1. Valeurs moyennes et variations temporelles de 6 variables décrivant l'environnement dans les stations 1 et 2. La variation temporelle est estimée à partir du rapport variance sur moyenne. Les résultats sont tirés de [5].

Environmental variables	Units	Mean values		Temporal variation	
		station 1	station 2	station 1	station 2
Total sedimentation expressed as dry weight of sedimented matter (SM)	$g \cdot m^{-2} \cdot 14\ d^{-1}$	154.6	189.3	91.2	127.4
Organic sedimentation expressed as weight of organic carbon in SM	$g \cdot m^{-2} \cdot 14\ d^{-1}$	6.035	8.212	1.902	2.581
Weight of organic nitrogen in SM	$g \cdot m^{-2} \cdot 14\ d^{-1}$	0.902	1.158	0.162	0.260
Percentage of organic carbon in SM	%	3.90	4.34	0.468	0.560
Percentage of organic nitrogen in SM	%	0.58	0.61	0.149	0.193
Temperature of bottom water at time of sampling	°C	8.2	8.2	0.296	0.296

Sedimentary inputs and oligochaete populations

Total and organic sedimentation presented the same general pattern of variation in both locations (fig. 1, 2). Sedimentation peaks occurred at the same time in both stations, but they were higher in station 2. In spite of this, variations of oligochaete population density for the same species were in general not correlated (table 2). For instance, compared with station 2 the peaks of population density occurred two months later in station 1 for *Potamothrix hammoniensis*, one month later for *P. heuscheri* and *P. vejdovskyi*.

In station 1, density of oligochaete species was higher in February 1979 after the exceptional *Oscillatoria* bloom than in February 1978 (fig. 1). This increase suggests that the density of oligochaete populations in station 1 was limited by the food availability during the first part of 1978.

Persistence stability of oligochaete populations was higher in station 1 where organic inputs were less variable: environmental stability seems to favour stability at the level of oligochaete populations (tables 1, 2). According to these data, oligochaete populations seemed to be influenced by sedimentary inputs. Mechanism underlying this influence was not clear, but food supply and oxygen concentrations at the interface level are clearly involved [6].

Structure of oligochaete communities

Correlated with increased organic inputs to the bottom, total oligochaete density was fivefold higher in station 2 and the structure of oligochaete community was modified (table 2). Frequency, absolute and relative density of *Stylodrilus heringianus* and *Peloscolex velutinus* decreased sharply between station 1 and 2. These two species predominate in oligotrophic lakes [9]. Their disappearance in station 2 confirms their sensitivity to increased organic inputs and their value as indicator of oligotrophic conditions.

Absolute and relative density of *Potamothrix hammoniensis*, *P. heuscheri* and *Tubifex tubifex* increased in station 2. The importance of these species resistant to environmental stress increases in eutrophic lakes [9]. Absolute density of *Potamothrix vejdovskyi* was greater in station 2 whereas its relative density decreased. The contrasted response of this species suggests an intermediate sensitivity to increased organic inputs which corresponds to mesotrophic conditions. This classification fits to Milbrink's views [9] and contrasts with our previous analysis [7] which attributes an oligotrophic value to *Potamothrix vejdovskyi*.

Oligochaete communities as an indicator of trophic level

According to these and to other data [7, 9], we have classified oligochaete species into three categories: a) species highly sensitive to increased organic inputs to the bottom which characterize oligotrophic lakes; b) species very resistant to high organic inputs, which become predominant in eutrophic lakes; c) tolerant species whose sensitivity is intermediate between that of categories a and b; their density increases in mesotrophic lakes (table 2). The total relative density of each species category, in a given oligochaete community, reflects the intensity of organic inputs arriving on the bottom, which depends itself on the trophic level of the lake [7].

In station 1, the relative density of oligotrophic species increased at the beginning of the year; it decreased when the organic inputs increased (fig. 2). The lowest values recorded in station 1 were related to the *Oscillatoria* bloom whose sedimented threads formed a reddish layer on the bottom at 35 m deep. The relative density of oligotrophic species increased after the organic input decreased.

Table 2. Structure of oligochaete communities in sampling stations 1 and 2. The Wilcoxon sign ranks test (W) indicates if the relative or the absolute value of a given variable is significantly different ($p < 0.05$, *) between the two locations. The Pearson correlation coefficient (P) indicates if the variables change synchronously in both locations (NS not significant; * positive correlation; - not calculated, number of values too small).

Tableau 2. Structure des communautés d'oligochètes dans les stations 1 et 2. Le test du signe de Wilcoxon indique si la valeur relative ou absolue d'une variable donnée est significativement différente ($p < 0,05$, *) entre les deux stations. Le coefficient de corrélation de Pearson indique si les variables changent de façon synchrone dans les deux stations (NS pas significatif; * corrélation positive; - pas calculé, nombre de valeurs trop petit).

Variable number	Worm species (authors) and other variables	n = 14 Frequency (%)		Mean absolute density m^{-2} or value				Mean relative density (%)				Persistence stability ($s^2/\bar{x}$)	
		1	2	1	2	W	P	1	2	W	P	1	2
1	*Stylodrilus lemani* (Grube)	7.1	7.1	15	23	-	-	0.2	0.1	-	-	-	-
2	*Stylodrilus heringianus* (Claparède)	85.7	7.1	762	69	-	-	6.5	0.1	-	-	-	-
3	*Peloscolex velutinus* (Grube)	85.7	0	637	0	-	-	6.8	0	-	-	-	-
4	*Potamothrix vejdovskyi* (Hrabe)	100.0	100.0	3622	11482	*	NS	23.7	16.6	*	NS	3410	5257
5	*Psammoryctides barbatus* (Grube)	35.7	57.1	119	316	*	NS	1.3	1.2	NS	*	316	950
6	*Peloscolex ferox* (Eisen)	71.4	35.7	155	271	NS	NS	1.3	0.5	*	*	164	623
7	*Aulodrilus pluriseta* (Piguet)	0	35.7	0	386	-	-	0	0.5	-	-	-	-
8	*Potamothrix bavaricus* (Oeschmann)	0	21.4	0	210	-	-	0	0.4	-	-	-	-
9	*Ilyodrilus templetoni* (Southern)	7.1	7.1	53	45	-	-	0.3	0.2	-	-	-	-
10	*Limnodrilus profundicola* (Verril)	7.1	0	4	0	-	-	0.2	0	-	-	-	-
11	*Limnodrilus hoffmeisteri* (Claparède)	78.6	42.9	411	671	NS	NS	3.7	1.8	NS	NS	706	1147
12	*Tubifex tubifex* (Müller)	100.0	100.0	1195	7665	*	*	9.8	12.8	NS	NS	277	1231
13	*Potamothrix heuscheri* (Bretscher)	100.0	100.0	3357	21007	*	*	24.6	34.2	*	NS	1453	4555
14	*Potamothrix hammoniensis* (Michaelsen)	100.0	100.0	3121	21129	*	NS	21.4	31.6	*	NS	2258	7203
15	Oligotrophic species	100.0	14.3	1414	92	-	-	13.6	0.1	-	-	972	-
16	Mesotrophic species	100.0	100.0	3950	13068	*	NS	26.6	19.4	*	NS	3066	5044
17	Eutrophic species	100.0	100.0	8089	50472	*	NS	59.8	80.4	*	NS	3160	7638
18	Total density	100.0	100.0	13453	63632	*	NS	100.0	100.0	-	-	4979	10674
19	Diversity	100.0	100.0	4.79	3.52	*	NS	-	-	-	-	25	4
20	Stability	100.0	100.0	0.82	0.82	NS	NS	-	-	-	-	0.004	0.002

Oligochaete species 1 to 3 are oligotrophic, species 4 to 9 are mesotrophic, species 10 to 14 are eutrophic.

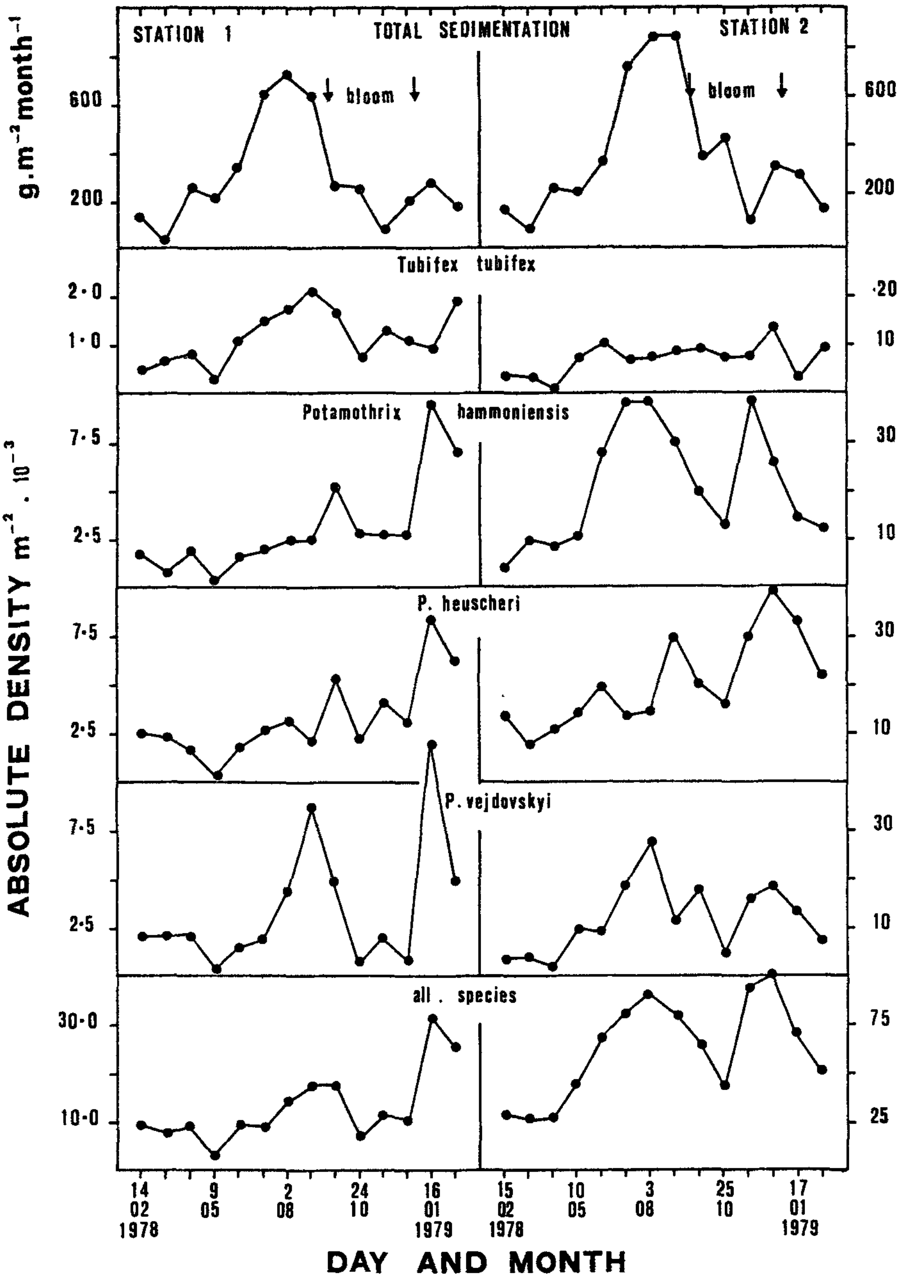

Figure 1. Monthly variations of total sedimentation, of absolute density of 4 oligochaete species, of total density of oligochaete species in stations 1 and 2. The *Oscillatoria* bloom is indicated by the space between the 2 arrows. To improve readability, the scale for absolute density of oligochaete is not the same in stations 1 and 2.

Figure 1. Variations mensuelles de la sédimentation totale, de la densité absolue de 4 espèces d'oligochètes, de la densité totale des oligochètes dans les stations 1 et 2. La floraison d'*Oscillatoria* est indiquée par l'espace entre les 2 flèches. Afin de rendre des résultats plus lisibles, l'échelle pour la densité absolue des oligochètes n'est pas la même dans les stations 1 et 2.

The mesotrophic species increased when the oligotrophic species decreased and the organic inputs increased; they became the most abundant species one month after the summer peak of organic sedimentation. Then, they were supplanted by the eutrophic species which were numerically dominant during the *Oscillatoria* bloom. Mesotrophic species increased a second time after the end of the *Oscillatoria* bloom.

The species succession observed in station 1 was clearly related to changes in sedimentation processes. To increased organic inputs corresponded a succession of oligotrophic, then of mesotrophic, finally of eutrophic species; to decreased organic inputs corresponded the same succession in reverse.

In station 2, the eutrophic species were numerically dominant during the whole year, the oligotrophic species were very scarce. There was no clear species succession and, consequently, no clear pattern relating species succession and sedimentary inputs.

These data demonstrated that the structure of oligochaete community expressed in terms of these three species categories was a reliable indicator of modified organic inputs to the sediment, i.e. of eutrophication level. The oligochaete communities sampled to the end of August in station 1 were representative of meso-oligotrophic conditions; the other communities sampled in stations 1 and 2 were representative of meso-eutrophic conditions. Data of station 1 demonstrated also that the oligochaete communities were able to reflect rapidly changes of sedimentary inputs; provided that these changes were not extreme to wipe out sensitive species as in station 2.

Diversity and stability of oligochaete communities

Diversity and stability of oligochaete communities were positively correlated in station 1 ($r = 0.55$, $n = 13$, $p = 0.04$) whereas no significant correlation appeared in station 2. To the end of the 1978 summer, diversity and stability were very high in station 1 (fig. 2). Then. they decreased strongly, they increased anew, and a new decrease at the beginning of the 1979 year was followed by a new increase. The two sharp decreases of diversity in station 1 were due to the increasing relative density of the mesotrophic species *Potamothrix vejdovskyi* in the community (fig. 1, 2). These low values of the diversity were related with a time lag of one month to peaks of organic sedimentation.

The low value of the stability, which was registered one month after the diversity drop, was attributed to the declining relative density of *Potamothrix vejdovskyi* and to the increasing relative density of the eutrophic species *Potamothrix hammoniensis* and *P. heuscheri* (fig. 1, 2). This change in the community structure reflected the more eutrophic conditions prevailing in station 1 because of an *Oscillatoria* bloom. The second drop of community stability at the beginning of January 1979 was mainly due to the increasing relative density of *Potamothrix vejdovskyi* (fig. 1, 2).

The stability of the oligochaete community in February 1978 compared to February 1979 was equal to 0.81 in station 1, to 0.93 in station 2. This difference may be attributed to the influence of the *Oscillatoria rubescens* bloom which has modified more deeply the sensitive oligochaete community of station 1 than the resistant community of station 2. The oligochaete community of station 2 was more apt to resist environmental stress than the community of station 1; its adjustment stability was higher [13]. The more diverse oligochaete community was established in the more stable environment of station 1. However, persistence stability of community 1

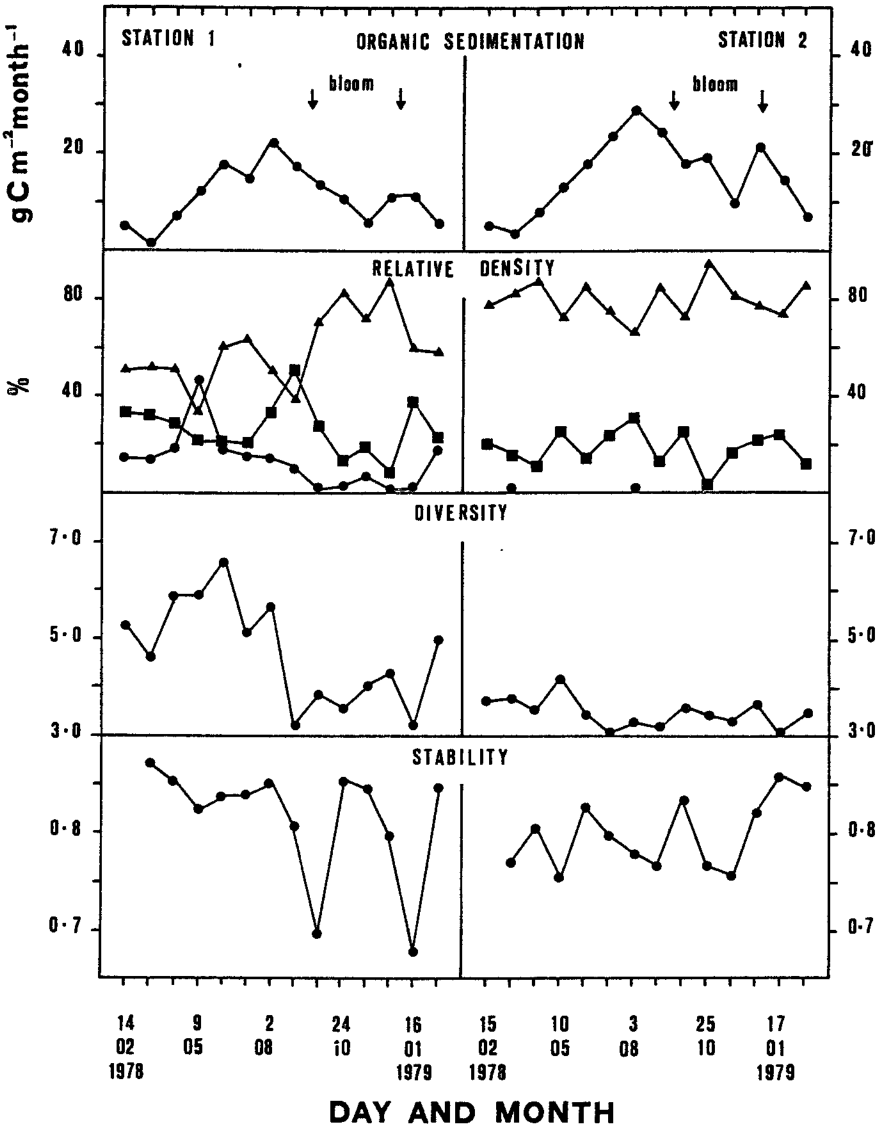

Figure 2. Monthly variations of organic sedimentation, of relative density of oligochaete species typical of oligotrophic conditions (●), of mesotrophic conditions (■), of eutrophic conditions (▲), of diversity and stability of oligochaete communities in stations 1 and 2.

Figure 2. Variations mensuelles de la sédimentation organique, de la densité relative des espèces d'oligochètes typiques des conditions oligotrophes (●), des conditions mésotrophes (■), des conditions eutrophes (▲), de la diversité et de la stabilité des communautés d'oligochètes dans les stations 1 et 2.

was greater only during the first part of the year. Persistence stability of community 1 dwindled under the impact of the *Oscillatoria* bloom; its resistance to changing conditions was less than that of community 2.

These results support Pielou's view [11] that a stable environment results in a stable (persistent over time) community. This stability of the community leads to a high diversity. However, a more diverse community is not more stable, i.e. resistant to changing conditions.

As in Peterson's study [13], the community of station 2 with the lower diversity was constituted by oligochaete species whose density variations were greater. However, persistence stability of both communities was equivalent. Our data, as, those of Peterson [13], demonstrate that stability at the species and stability at the community level are not equivalent.

Our data support the view that more diverse communities are less stable. As in most empirical data reviewed by Goodman [3], increased diversity does not yield increased stability to the community. On the contrary, the more diverse community was more sensitive to environmental stress.

General discussion and conclusion

Major changes in the structure of the two studied oligochaete communities seemed to be related, with a variable time lag, to changes of the organic input to the bottom. For instance, the change from an oligo-mesotrophic oligochaete community to a meso-eutrophic community in station 1 corresponded to a decrease of diversity and of stability in the oligochaete community; these changes were concomitant with increasing organic inputs (fig. 2). These increased inputs influenced benthic communities by increasing their food supply and by decreasing oxygen concentrations at the sediment level [1, 6]. In the present study, these two factors contributed to explain the changing structure of oligochaete communities. However, other factors such as, for instance, predation and/or competition might be involved.

Predation

Macroinvertebrates other than oligochaete were few in both locations (mostly chironomid larvae). Invertebrate predators such as leeches or triclads were not found. Roughly same numbers of benthic fishes such as burbot (*Lota lota* L.) were observed in both locations. Holes in the sediment, due to predation by the bream (*Abramis brama* L.), were not seen at a depth of 35 m. Moreover, predation by fish on inconspicuous animals, of the same size, as oligochaete is unlikely to select some species rather than others, thus altering the structure of the community. Furthermore, field experiments of Thorp and Bergey and other data reviewed by these authors [15] demonstrate that, in freshwater benthic communities, contrary to some marine benthic communities, predation is not a key factor structuring the community.

Competition

There is some field evidence of competition between species in oligochaete communities but experimental data indicate rather a kind a positive interaction between some species [1, 7, 9].

Huston [4] hypothesizes that 'most communities exist in a state of nonequilibrium where competitive equilibrium (reduction or exclusion of some species) is prevented by periodic populations reductions and environmental fluctuations'. According to the predictions of this hypothesis, increasing the nutrient availability should increase the population growth rate of competing species and should decrease the diversity.

In station 1, the increasing organic inputs correspond to the increasing density of more resistant oligochaete species whereas the diversity dwindles. The diversity is low during the whole year in station 2 where the nutrient availability and the density of resistant species is high. During the first part of the 1978 year, low availability of food reduces population growth rates in oligochaete communities of station 1 and prevents the approach to competitive equilibrium, thus maintaining a high diversity. As pointed out by Huston [4], 'diversity is determined not so much by the relative competitive abilities of the competing species as by the influence of the environment on the net outcome of their interactions'.

This hypothesis is consistent with our observations, stressing so the combined influence of competition and of environment on oligochaete communities. The combination of these two factors might also explain the regular pattern of species succession observed in many pollution gradients around the northern hemisphere as well as some puzzling irregularities [1, 7, 9]. Further investigations are badly needed at the level of oligochaete population growth (mainly reproductive processes) in response to environmental perturbations. However, in spite of these difficulties, oligochaete communities seem to be an heuristic tool to indicate the impact of pollution and/or eutrophication in lakes, as demonstrated by many field surveys [1, 7, 9].

Structure of oligochaete communities

In both locations, major changes of community structure described by the indices of diversity or stability were related to the changing relative density of three abundant oligochaete species *(Potamothrix vejdovskyi, P. heuscheri* and *P. hammoniensis).*

However, the most striking difference between communities 1 and 2 was the relative density of sensitive oligochaete species *(Stylodrilus heringianus, Peloscolex velutinus);* this density was relatively high in station 1, very low in station 2. Relative density of well choosen species, however not very abundant, appears as the best tool to indicate a difference in sedimentary inputs between the two locations. Global properties of the community, such as diversity and stability, were less effective to track these changes. As pointed out by Coull and Fleeger [2], diversity per se leaves us with generalities and does not provide insight into the species responsible for the community dynamics. As advocated by Goodman [3], we must ask more specific questions about the changing structure of communities such as: what kind of perturbation and which species?

Summary

1. Two oligochaete communities were sampled monthly during one year in two 35 m deep locations of Lake Geneva (Switzerland).
2. The more diverse oligochaete community was established in station 1 where the organic input to the bottom was less heavy and less variable than in station 2 (tables 1, 2).
3. Diversity and stability of the oligochaete community were high at the beginning of the year in station 1. They decreased and fluctuated strongly when the organic sedimentation increased, and during an exceptional *Oscillatoria* bloom (fig. 2).
4. The decrease of diversity and stability in station 1 was due, first to the decreasing relative density of oligochaete species typical of oligotrophic lakes, then to the increase of mesotrophic species, finally to the strong increase of eutrophic species (fig. 1, 2).
5. Diversity of the community in station 2 was low because heavy organic inputs had wiped out oligotrophic species and increased the dominance of some eutrophic species. However, this community 2 was more resistant to increased organic inputs than community 1.

ZUSAMMENFASSUNG

1. Die Oligochaetengemeinschaften zweier in 35 m Tiefe des Genfersees (Schweiz) gelegenen Stellen wurden während eines Jahres monatlich untersucht.
2. Die Oligochaetengemeinschaft mit der grösseren Diversität befand sich an der Stelle 1, die einem kleineren und weniger variablen Input an organischem Material ausgesetzt war als die Stelle 2 (Tab. 1, 2).
3. Diversität und Stabilität der Gemeinschaft der Stelle 1 waren hoch in der ersten Jahreshälfte. Bei steigendem organischem Input und während einer aussergewöhnlichen *Oscillatoria*blüte (Abb. 2) nahmen sie ab und fluktuierten.
4. Die Abnahme von Diversität und Stabilität an der Stelle 1 war zunächst die Folge der Abnahme der relativen Dichte der für oligotrophe Seen typischen Oligochaetenarten, dann der Zunahme der mesotrophen Arten und schliesslich des starken Vorherrschens der eutrophen Arten (Abb. 1, 2).
5. Die Diversität der Gemeinschaft der Stelle 2 war niedrig, da ein starker Input an organischem Material die oligotrophen Arten eliminierte und die Dominanz einiger eutropher Arten begünstigte. Diese wenig diverse Gemeinschaft war hingegen einem erhöhten organischen Input gegenüber resistenter als die diversere Gemeinschaft der Stelle 1.

RÉSUMÉ

1. Deux communautés d'oligochètes ont été étudiées chaque mois pendant une année dans deux stations du lac Léman (Suisse), situées à 35 m de profondeur.
2. La communauté d'oligochètes la plus diverse est établie dans la station 1 où l'apport organique annuel au niveau du sédiment est moins important et moins variable que dans la station 2 (tabl. 1, 2).
3. La diversité et la stabilité de la communauté dans la station 1 sont élevées pendant la première moitié de l'année. Elles diminuent, puis elles fluctuent fortement lorsque la sédimentation organique augmente et lors d'une fleur d'eau exceptionnelle à *Oscillatoria* (fig. 2).
4. La baisse de la diversité et de la stabilité dans la station 1 est la conséquence de la diminution de la densité relative des espèces d'oligochètes typiques des lacs oligotrophes, puis de l'accroissement des espèces mésotrophes, enfin de la prépondérance accrue des espèces eutrophes (fig. 1, 2).
5. La diversité de la communauté dans la station 2 est faible parce que des apports organiques importants ont éliminé les espèces oligotrophes et accru la dominance de quelques espèces eutrophes. Par contre, la résistance de cette communauté à des apports organiques accrus est plus grande que celle de la communauté 1.

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