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Contrasting responses of oligochaetes (Annelida) and chironomids (Diptera) to the abatement of eutrophication in Lake Neuchâtel

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ABSTRACT

Lake Neuchâtel (Switzerland) has been recovering from human-induced eutrophication since 1982. Oligochaetes and chironomid larvae were used to monitor the recovery of sediment at a depth of 40 m. In oligochaete communities, the mean proportion of individuals belonging to species indicative of oligotrophic conditions (mostly *Spirosperma velutinus* and *Stylodrilus heringianus*) increased from 16 % in 1984 to 33 % in 1992, but decreased to 11 % in 1997. Based on oligochaetes, benthic conditions deteriorated in 1997 whereas, based on the increase of oligotrophic chironomids (mostly *Micropsectra*), they improved. This difference was attributed to the impact of large planktonic algae whose sedimentation had altered oxygen concentrations at the water-sediment interface. Oligochaetes were more affected than chironomids because they are less mobile and they depend more on the inner sediment for their food and reproduction than the latter. However, based on the combined response of oligochaetes and chironomids, benthic recovery was stalled in 1997 but was not reversed.

Introduction

Following the strict limitation of phosphorus inputs, many European lakes are recovering from man-made eutrophication (Sas, 1989). In general, the recovery is monitored only from the chemical and biological responses within the pelagic water body. Deep sediments are comparatively neglected, even if they are located at the receiving end of all the processes going on within a lake (Levine and Schindler, 1989). Therefore, the restoration of pristine sediment conditions, insofar as this goal is realistic, is the landmark of a successful recovery of the whole lake. Their recolonization by the benthic species which prevailed before the onset of eutrophication can be used to monitor the progress of recovery (Lang, 1990).

Oligochaetes and chironomids are reliable indicators of eutrophication for lakes (Johnson et al., 1993), even if they neither feed nor reproduce in the same way

(Wiederholm, 1980; Brinkhurst, 1974). Firstly, chironomid larvae feed on algae and detritus freshly deposited on the sediment, while oligochaetes feed on bacteria within the sediment. Secondly, chironomids have winged adults which lay eggs on the water surface, whereas oligochaetes reproduce within the sediment. In summary, chironomids are more mobile and they depend less on the inner sediment for their food and reproduction than the oligochaetes. These differences could explain why, in some cases, chironomids react more rapidly than oligochaetes to the improvement of lakes (Dinsmore and Prepas, 1997; Lang and Lods-Crozet, 1997). Due to these differences, both groups were used to monitor the benthic recovery of Lake Neuchâtel.

In Lake Neuchâtel (215 km^2, 13.8 km^3), mean total phosphorus concentrations in the water column (0–150 m) have steadily decreased from 42 mg m^{-3} in 1982 to 13 mg m^{-3} in 1996 (Pokorni, 1997). This is attributed to the elimination of phosphorus by sewage treatment plants and to the ban of phosphorus in detergents since 1986 in Switzerland.

In response to the reduction of phosphorus inputs, the population density of phytoplankton has decreased (Pokorni, 1997). As the water became clearer, algae were able to survive and to assimilate nutrients deeper in the water column than previously. For instance, phosphorus was almost completely depleted from the surface down to a depth of 40 m during the summer of 1996 (Pokorni, 1997). In addition, large filamentous algae (mostly diatoms) tended to prevail in the phytoplankton, at least between 1993 and 1996. As a result, the nets of professional fishermen were often covered by these algae, even to a depth of 60 m (i.e., the mean depth of the lake). These observations suggest that, if the total biomass of algae was reduced, the settlement of large and intact algae on deep sediments was facilitated. This changes the quality of organic sedimentation – i.e., the pelagic-benthic coupling (Johnson and Wiederholm, 1992) – upon which the rate of benthic recovery depends.

The zoobenthic species which prevailed around 1917 during the oligotrophic state of Lake Neuchâtel were used as references for pristine conditions (Monard, 1919). Their decrease after the highest degree of eutrophication (i.e., around 1980) has been documented (Lang, 1989). In contrast, their abundance increased between 1984 and 1992, at least at a depth of 40 m, in response to the decrease of phosphorus (Lang and Reymond, 1993). In this study, the area sampled in 1984 and in 1992 was sampled again in 1997 to monitor the progress of benthic recovery in the presence of large planktonic algae. In addition, the response of Lake Neuchâtel was compared with that of Lake Geneva, located 30 km south (Lang, 1998), to see if the recovery trajectory was the same in both lakes.

Stations and methods

In 1997, 30 sampling sites, distributed evenly (500 m apart) along the southern shore of Lake Neuchâtel (between Portalban and Font, areas 11 to 15 in Lang 1989), were visited six times in May, before the emergence of chironomids. At each site, six 16 cm^2 cores (30 cm long) were taken at a depth of 40 m with a gravity corer lowered from the surface. The 6 cores collected in each site were spread randomly 150 m around the central location of each site. The 1992 and the 1997 sampling designs were the same. In 1984, 16 sampling sites were distributed among 4 transects, regularly spaced (4 km apart), between Portalban and Font as in 1997. On each transect, 4 depths were sampled: 40 m, 60 m, 90 m, 120 m. At each depth, 4 cores were collected. As the abundance of the main oligochaete species was not different between the 4 depths (Lang and Reymond, 1993), the 1984 survey can be compared with the 1992 and the 1997 surveys made at a depth of 40 m.

In the laboratory, the sediment was sieved (mesh size 0.2 mm) and the retained material preserved in 5% formalin. The collected macrofauna consisted mainly of tubificids, lumbriculids, and chironomid larvae which were picked and counted against a white background under a low magnification (6×) binocular microscope. Oligochaetes whose diameter (when preserved) was greater than 0.29 mm were mounted (Reymond, 1994) and identified to species. Juveniles (diameter less than 0.3 mm) were excluded because they could have passed through the 0.2 mm mesh as living animals (Lang, unpubl. data). After preservation, these small oligochaetes are retained on the sieve because they are coiled and twisted. Their exclusion decreased the effects of seasonal variability (recruitment of juveniles) on the evaluation of species abundance (Lang, 1998).

Chironomid larvae were identified according to Wiederholm (1983) and the indicative value of taxa was based on the findings of Saether (1979). In 1997, chironomids were counted and identified separately in each core. In 1992, they were counted separately in each core, but they were identified only as a whole sample based on 171 cores. In 1984, chironomids were too scarce to be included in the comparison.

Those species whose numerical dominance in tubificid and lumbriculid communities indicates oligotrophic, mesotrophic or eutrophic conditions were designated oligotrophic, mesotrophic or eutrophic species (Lang, 1990). Species were characterized either by their occurrence or by their abundance: i.e. respectively the number of cores in which a given species was present or the number of individuals per core. The relative abundance of oligotrophic species (OS) was calculated as a percentage of the total number of adult tubificid and lumbriculid individuals present in each core. In addition, the relative abundance of oligotrophic oligochaetes and chironomids was calculated in 1997 as a percentage of the total number of identified oligochaetes and chironomids present in each core. Then the mean value for the 1997 survey was computed from these individual results.

The mean abundance of OS per survey was used to monitor the recovery of sediments: OS is zero if conditions are eutrophic, it varies between 1% and 17% under meso-eutrophic conditions, between 18% and 52% under mesotrophic conditions (mid-point: 35%), between 52% and 69% under oligo-mesotrophic conditions, and OS is above 69% under oligotrophic conditions (Lang, 1990). These values were used as guidelines to classify the surveys.

An empirical relationship between the mean abundance (%) of OS per survey and mean concentrations (mg m^{-3}) of total phosphorus (TP), recorded in the water column (0–100 m), has been previously computed (Lang, 1990):

$$\mathrm{OSP} = 80.29 - 8.35\ \mathrm{TP}^{0.5} \qquad r^2 = 0.81 \qquad n = 15$$

This relationship was based on 15 surveys conducted in 6 European lakes (Geneva, Neuchâtel, Garda, Maggiore, Constance, and Bienne) and 3 American lakes (Superior, Michigan, and Ontario). OSP was computed from TP concentrations averaged over the 5 years preceding the sampling of worms. This was done because oligochaete communities do not react immediately to a change in TP concentrations (Lang, 1990): recovery of the sediment often lags behind that of the water body (Levine and Schindler, 1989).

In this study, the values of OSP predicted from TP were used to evaluate the progress of recovery. If OS and OSP values are close, it indicates that the recovery of sediment follows that of water, with a time lag of 5 years or less (Lang, 1997). If OS is lower than OSP, it indicates that the recovery of sediment is delayed either by an excess of organic deposition or by persistence of low oxygen concentrations (Lang, 1998).

All computations were made with the SPSS software for Windows (Norusis, 1993).

Results

In Lake Neuchâtel, the occurrence and the abundance of oligotrophic oligochaete species increased from 1984 to 1992, but decreased in 1997 (Tables 1, 2). This decrease of occurrence and abundance was especially marked for *Stylodrilus*

Table 1. Changes recorded between 1984 and 1997 in the occurrence of lumbriculid and tubificid species in Lake Neuchâtel at a depth of 40 m

Variable	Species	Occurrence (%) per year			Chi2 P
		1984 (n = 64)[a]	1992 (n = 171)	1997 (n = 175)	
1	*Bichaeta sanguinea* (Bretscher)	–[b]	20.5	12.6	0.048
2	*Stylodrilus heringianus* (Claparède)	37.5[c]	46.8	16.6	0.000
3	*Spirosperma velutinus* (Grube)	17.2	19.3	11.4	0.122
4	*Potamothrix vejdovskyi* (Hrabe)	0	23.4	42.9	0.000
5	*Spirosperma ferox* (Eisen)	1.6	13.5	19.4	0.000
6	*Potamothrix moldaviensis* (Vejdovsky, Mrazek)	0[d]	9.3	1.1	–
7	*Limnodrilus hoffmeisteri* (Claparède)	6.2	4.1	13.7	0.000
8	*Limnodrilus profundicola* (Verrill)	7.8	0	0.6	–
9	*Potamothrix hammoniensis* (Michaelsen)	10.9	15.2	15.4	0.659
10	*Tubifex tubifex* (Müller)	25.0	7.6	6.9	0.000
11	Species 7–8	40.6[e]	28.1	49.1	0.000
12	Species 9–10	100.0	67.3	62.0	0.000
13	Oligotrophic species 1–3	43.8	59.1	28.0	0.000
14	Mesotrophic species 4–6	1.6	32.7	52.6	0.000
15	Eutrophic species 7–10	100.0	77.2	82.9	0.000

[a] No. of 16 cm^2 cores.
[b] Missing data.
[c] Results for species 1 pooled with those of species 2.
[d] Results for species 6 to 10 based only on mature individuals.
[e] Results for variables 11 to 15 based on all individuals.

Table 2. Mean abundance (standard error below the mean) of selected groups (Table 1) of oligochaete species in Lake Neuchâtel (1984, 1992, 1997) and in Lake Geneva (1982, 1991, 1996) at a depth of 40 m. Means within the same row that share the same majuscule letter are not significantly different by multiple comparison technique of Scheffé (Norusis, 1993; p. 278)

Species	Unit	Abundance per year					
		Lake Neuchâtel			Lake Geneva		
		1984 (n = 64)	1992 (n = 171)	1997 (n = 175)	1982 (n = 61)	1991 (n = 192)	1996 (n = 170)
Oligotrophic	No. per core	1.01A	1.15A	0.30B	2.10C	2.85D	2.81D
		(0.19)	(0.10)	(0.04)	(0.35)	(0.20)	(0.19)
Mesotrophic		0.01A	0.58B	1.32C	6.55D	2.22C	1.55C
		(0.02)	(0.08)	(0.14)	(0.48)	(0.15)	(0.11)
Eutrophic		4.97A	1.89C	2.37C	4.64A	3.11C	1.99C
		(0.39)	(0.15)	(0.18)	(0.65)	(0.33)	(0.15)
All		6.00A	3.62B	3.99B	13.29C	8.19A	6.35A
		(0.42)	(0.18)	(0.22)	(0.80)	(0.40)	(0.28)
Oligotrophic	%	15.8A	33.0B	11.4A	16.9A	41.3B	44.6B
		(2.8)	(2.7)	(1.7)	(2.7)	(2.5)	(2.3)
OSP[a]		20.3	35.0	44.1	8.8	19.3	32.2
Phosphorus[b]	mg m^{-3}	51.5	29.4	18.8	73.3	53.4	33.2

[a] Abundance of oligotrophic species predicted from phosphorus concentrations (see Stations and methods).

[b] Mean phosphorus concentrations recorded during the 5 years preceding the sampling of worms.

heringianus and *Bichaeta sanguinea*. In contrast, mesotrophic species, especially *Potamothrix vejdovskyi*, increased steadily in occurrence and abundance from 1984 to 1997. This species which was recorded in Lake Neuchâtel for the first time in 1986 (Lang, 1989), was a successful invader, probably coming from Lake Geneva. The abundance of eutrophic species which decreased from 1984 to 1992, was unchanged between 1992 and 1997. Mean relative abundances of oligotrophic species observed in 1984 and in 1992 were close to the values predicted from total phosphorus concentrations in the water column (Table 2). This suggests that the recovery of sediment closely follows that of water (Lang, 1997). In contrast, the difference between the observed and predicted (OS and OSP) values was large in 1997, indicating that the benthic recovery was delayed.

In Lake Neuchâtel, chironomid larvae were present in the same proportion of cores in 1992 and in 1997: 80 % and 84 % respectively (test of Chi^2, P = 0.346). In contrast, their mean abundance increased between 1992 and 1997: 1.58 and 2.71 individuals per core respectively (t test, P = 0.000). The oligotrophic genus *Paracladopelma* which was the most abundant in 1992 (Table 3), was replaced in this position by the oligotrophic genus *Micropsectra*, which was present in 71 % of cores in 1997.

The relative abundance of oligotrophic chironomids increased between 1992 and 1997 whereas that of oligotrophic oligochaetes decreased (Table 3). Based on oligochaetes, benthic conditions deteriorated in 1997, whereas based on chironomids they improved. However, the relative abundance of oligotrophic taxa (oligochaetes and chironomids combined) decreased only slightly between 1992

Table 3. Relative abundance of oligochaete and chironomid taxa in Lake Neuchâtel in 1992 and 1997 at a depth of 40 m

Variable	Taxa	Abundance (%) per year	
		1992 (n = 865)[a]	1997 (n = 1115)
1	*Bichaeta sanguinea*	5.0	2.1
2	*Stylodrilus heringianus*	12.6	0.6
3	*Spirosperma velutinus*	5.2	2.1
4	*Potamothrix vejdovskyi*	8.2	17.5
5	*Spirosperma ferox*	3.2	3.2
6	*Limnodrilus* sp.	9.1	16.6
7	*Tubifex tubifex* and *Potamothrix hammoniensis*	28.3	20.6
8	All species of oligochaetes	71.9	62.7[b]
9	*Paracladopelma* (group *nigritula*)	12.5	1.2
10	*Macropelopia* (group *nebulosa*)	2.0	0.2
11	*Micropsectra* (group *notescens*)	4.3	29.0
12	*Sergentia coracina*	0.6	0
13	*Polypedilum*	0.1	0
14	*Chaetocladius*	0	0.1
15	*Dicrotendipes*	0	0.4
16	*Endochironomus*	0	1.0
17	*Tanytarsus*	0	1.0
18	*Procladius*	8.9	4.4
19	All species of chironomids	28.3	37.3
20	Oligotrophic oligochaetes (1–3)	22.8	4.7[c]
21	Oligotrophic chironomids (9–11)	18.7	30.4
22	Oligotrophic taxa (20 and 21)	41.5	35.2[d]

[a] No. of identified oligochaetes and chironomids in 171 cores (1992) and in 175 (1997) cores respectively.

[b] Test of Chi^2, P = 0.000, based on numbers of oligochaetes and chironomids in 1992 and 1997 (variables 8 and 19).

[c] Test of Chi^2, P = 0.000, based on numbers of oligotrophic oligochaetes and chironomids in 1992 and 1997 (variables 20 and 21).

[d] Test of Chi^2, P = 0.000, based on numbers of individuals belonging to oligotrophic taxa (variable 22) and on numbers of individuals belonging to the other taxa in 1992 and 1997.

and 1997 (Table 3), indicating that the benthic recovery paused in 1997, but was not reversed. In 1997 for instance, the mean relative abundance of oligotrophic oligochaetes and chironomids combined was 35% per core (SD = 28.2, n = 175), indicating mesotrophic conditions as in 1992 .This value was not too far from 44%, the value predicted from phosphorus concentrations in the water column (Table 2).

Discussion

In lakes, the limitation of phosphorus inputs brings about a decrease of phytoplanktonic production (Sas, 1989). This induces a decrease of organic sedimentation (Baines and Pace, 1994) which modifies the oxygen uptake by the sediment (Hargrave, 1973). For the zoobenthos, it means less food but a higher oxygen availability at the water-sediment interface (Dinsmore and Prepas, 1997). As a result, species indicative of oligotrophic conditions will gradually recolonize the profundal zone, indicating its restoration.

In Lake Neuchâtel, this trend was evident for oligochaetes between 1984 and 1992, but not in 1997 (Table 2). The response of zoobenthos to the abatement of eutrophication had changed in 1997 because, between 1993 and 1996, some unknown factor had advantaged chironomids but not oligochaetes (Table 3). This change could denote either an increase of organic sedimentation and/or the decrease of oxygen concentrations at the water-sediment interface (Lang, 1998). As organic sedimentation was not measured in Lake Neuchâtel, the changing composition of oligochaete communities was used as a substitute to evaluate the trend. If organic sedimentation increases strongly, the total abundance of tubificids and the abundance of eutrophic species (especially that of *Potamothrix hammoniensis* and *Tubifex tubifex*) increase rapidly (Lang and Hutter, 1981; Robbins et al., 1989). This trend was not observed in 1997 (Table 2), suggesting that a large increase of organic sedimentation was unlikely.

If the amount of organic sedimentation remained unchanged between 1992 and 1997, its quality was certainly altered (Johnson and Wiederholm, 1992) by the presence of large planktonic algae (see introduction). Indeed the changes recorded in the composition of zoobenthic communities could be explained by the settlement of large and intact algae on the sediment. For instance, the abundance of chironomid larvae which feed on the algae deposited at the surface of sediment (Wiederholm, 1980), was doubled between 1992 and 1997. In contrast, the abundance of oligochaetes which feed on bacteria within the sediment did not change (Table 2).

The settlement of large and intact algae, as it occurs in Lake Neuchâtel, is known to increase the oxygen uptake by the sediment and to affect oxygen concentrations at the water-sediment interface (Hargrave, 1978). The decrease of oligotrophic oligochaete species and the increase of *Potamothrix vejdovskyi* which is favored by a mild enrichment (Lang, 1990), support this interpretation (Table 3). The contrasting response of oligotrophic chironomids to this impact could be explained in two ways. Firstly, chironomids are able to recolonize abiotic sediments more rapidly than oligochaetes because their winged adults spread eggs over large areas (Brinkhurst, 1974). This could explain why the oligotrophic chironomids were present in 71 % of cores as opposed to 28 % for oligotrophic oligochaetes in 1997. Secondly, eggs of chironomids hatch at the surface of the sediment whereas those of oligochaetes hatch within the sediment (Wiesniewski, 1979): hence the former are less likely to be affected by a decrease of oxygen.

Oxygen concentrations were not measured at the water-sediment interface, but rather 1 m above the sediment in the deepest area (153 m) of Lake Neuchâtel (Pokorni, 1997). In general, the values recorded between 1982 and 1996 were always higher than 7 mg l^{-1}. However a slight downward trend was observed between 1992 and 1996, following several mild winters. In addition, oxygen concentrations measured at the interface which are relevant for the zoobenthos are often much lower than those measured one meter above the bottom. For instance, in Lake Hallwil which is recovering from eutrophication (Müller, 1992), a thin (5–10 mm) but almost anoxic layer, was present at the interface, even if oxygen concentrations measured one meter above the bottom were always higher than 7 mg l^{-1}. This layer inhibits the embryogenesis of Coregonus lavaretus (Müller, 1992), a fish species typical of oligotrophic lakes. In Lake Neuchâtel, even if the presence of a hypoxic layer at the interface which could have affected the zoobenthos was not documented, its existence seems plausible. The effect of this layer is not the same as the long-term anoxia observed in the profundal zone of eutrophic lakes, which modifies the zoobenthos composition completely (Dinsmore and Prepas, 1997), but rather it is a short-term event which could selectively decrease the reproduction of the most sensitive species.

The path of benthic recovery is not the same in all lakes. In Lake Geneva (582 km^2, 89 km^3), contrary to Lake Neuchâtel, chironomids were relatively scarce and the mean relative abundance of oligotrophic oligochaete species (OS) increased regularly between 1982 and 1996 in response to the decrease of phosphorus concentrations in the water (Table 2). The observed abundances of OS were higher than the predicted ones, indicating that the benthic recovery proceeded rapidly, at least at a depth of 40 m (Lang, 1998). As a general rule, all categories of oligochaete species were more abundant in Lake Geneva than in Lake Neuchâtel. This difference suggests that Lake Geneva is more productive than Lake Neuchâtel: the higher phosphorus concentrations recorded in Lake Geneva support this interpretation (Table 2). In this lake, oligochaetes were good indicators of recovery even in 1996, whereas in Lake Neuchâtel, chironomids were better indicators, at least in 1997 (Table 3). This difference could either be attributed to the impact of large planktonic algae on the sediment of Lake Neuchâtel or to the fact that chironomids are able to outcompete oligochaetes in less productive lakes.

In conclusion, the composition of zoobenthos (oligochaetes and chironomids combined) indicated that the benthic recovery of Lake Neuchâtel paused in 1997, but was not reversed (Table 3). The impact of large algae on the oxygen conditions at the water-sediment interface seemed the most plausible explanation for this pause. Oligochaetes were more affected than chironomids because they are less mobile and they depend more on the inner sediment for their food and reproduction than the latter. The contrasting responses of these two taxonomic groups were useful to analyse what was going on during the recovery of Lake Neuchâtel from eutrophication. Hence, both indicators must be included in the biomonitoring of lakes.

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