Zooplankton of Lake Orta after liming: an eleven years study

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ABSTRACT

Lake Orta (N. Italy) was severely polluted from 1927 by an effluent from a rayon factory, which discharged great amounts of ammonium nitrogen and copper into the lake. In the mid nineteen fifties, some plating factories also started dumping chromium and aluminum. As a result of ammonium oxidation, the lake became very acid and the concentration of metals in the waters reached very high values. Phytoplankton, zooplankton and fish disappeared suddenly from the lake which was by 1930 classified as "sterile". Later on, about the fifties, a small population of Cyclops abyssorum re-colonised the lake together with some rotifers, in particular Hexarthra fennica. In mid eighties following the introduction of anti-pollution legislation, ammonium loads were greatly reduced and Daphnia obtusa was recorded. The lake waters however were still very acid, prompting the proposal of the Istituto Italiano di Idrobiologia to lime the lake with calcium carbonate to neutralise the excess acidity and reconstruct the alkaline reserve. This was done successfully from May 1989 to June 1990. pH values began to rise and in the same time the metal concentrations decreased, so that at present the lake waters are almost "normal". In the meantime, due to the increased pH values, D. obtusa was replaced by D. longispina and, as toxic metal concentrations became lower, Megacyclops viridis, Bosmina longirostris, Diaphanosoma brachyurum, Keratella quadrata, Asplanchna priodonta. and other Brachionidae species appeared. Diaptomidae are still absent, except for some specimens of Arctodiaptomus wierzejskii.

Key words: zooplankton, acidification, liming

1. INTRODUCTION

The case history of Lake Orta pollution has been exhaustively discussed in many previous papers (see Bonacina 2001b) and also summarised in this volume (Bonacina 2001a). However, the following is a short account of the zooplankton assemblage before 1987.

After the onset of pollution in 1926, zooplankton disappeared almost completely (Monti 1930). In the years that followed, up to 1950, samples taken from all over the lake in various seasons demonstrated that zooplankton community was still absent, apart from sporadic rotifers blooms (Baldi 1949).

In 1959-1961 (Vollenweider 1963) and in 1968-1969 (Bonacina 1970) sampling was performed monthly at stations 1, 2 and 3, roughly corresponding to the centre of the three sub-basins (Fig. 1). Data obtained from these two researches substantially confirmed the presence of a very poor population made up of one species of copepod (*Cyclops "strenuus"*) and some species of rotifers. Among these, *Hexarthra fennica* sporadically showed a bloom.

From February 1971 to March 1972 samples taken monthly at station 1 (Fig. 1) revealed the presence of the known "*C. strenuus*", *Brachionus calyciflorus*, *H. fennica*, and the new entry of *Daphnia longispina* and *Bosmina coregoni* both of which very poorly represented (Barbanti *et al.* 1972). From 1972 on, samples were taken approximately at monthly intervals, and showed the constant presence of C. *strenuus*, while other species, both cladocerans and rotifers, might appear and disappear in the course of a month (Bonacina & Bonomi 1984; Bonacina, unpublished).

Finally, in September 1986 a small *Daphnia obtusa* population was found (Bonacina *et al.* 1988a) which rapidly increased in number establishing a permanent colony in the lake.

The aim of the present paper is to document changes in the zooplankton population resulting from the environmental modifications which followed the liming (1989-1990, Bonacina 2001a).

2. MATERIALS AND METHODS

2.1. Field and laboratory procedures

Zooplankton from Lake Orta was sampled fortnightly from January 1987 to December 1997, although this paper will deal only with data from monthly samples. The sampling station (Fig. 1) corresponded to the point of maximum depth (-143 m). Samples were taken using a Clarke-Bumpus plankton sampler equipped with a 76 μ m net. A 50 m layer (from the surface to -50 m) was explored, usually filtering a volume of about 2000 l. The animals collected were killed with ethyl alcohol at 90% to prevent egg loss in cladocera due to valve opening, and then preserved in a formaldehyd solution at 10%. Before being counted, samples were reduced to a volume of 75 ml, 10 ml of which were counted. Although all species, as well as all instars within the species, were taken into account, and eggs counted in all ovigerous females, in this paper we have chosen to consider only the total densities of each species. As the main purpose of the paper, as well as of the whole volume, is to demonstrate whatever effectiveness the liming may have had on the lake, we shall ignore population dynamics or species relationships and focus on population changes during 1987-1997.

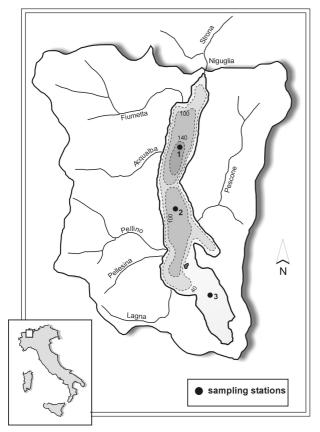


Fig. 1. Map of Lake Orta and location of zooplankton sampling stations.

2.2. Data analysis

A multivariate data analysis was performed following the approach of Clarke (1993) and Clarke & Warwick (1994). The starting point was a species by years data matrix, whose entries are the mean abundances of each species for each year. The dissimilarity between every pair of years was measured using Bray-Curtis coefficient:

$$\delta_{jk} = 100 \frac{\sum_{i=1}^{p} |y_{ij} - y_{ik}|}{\sum_{i=1}^{p} (y_{ij} + y_{ik})}$$
(1)

where: δ_{jk} is the dissimilarity between the *j*th and *k*th year; y_{ij} and y_{ik} are the mean abundances of the *i*th spe-

cies in the *j*th and *k*th year, respectively; *p* is the total number of species. Abundance data were 4th root transformed before applying the formula, to down-weight the importance of the very abundant species so that the less dominant, and even the rare species, play some role in determing dissimilarity values. The dissimilarity values were set in a years by years dissimilarity matrix, which was the basis of hierarchical agglomerative clustering by average linking and ordination by non-metric multidimensional scaling (MDS). This was preferred to other ordination methods because it is conceptually simple, does not make assumptions about the distribution of the original data or the proprieties of the dissimilarity measure and is not negatively affected by the presence of many zeroes in the original data matrix. MDS, like all the ordination methods, produces a map of points, each representing an object (in our case a year). The distances between the points on the map are selected, by an iterative procedure, to match the dissimilarities between the objects: if object 1 has higher dissimilarity to object 2 than to object 3, it should be placed farther on the map to object 2 than to object 3. The final configuration of points is achieved by minimization of the stress value which is a measure of the mismatch between the original dissimilarity values and the distances in the map. Since the match is never perfect, the stress value associated with the selected configuration of points is a measure of the success of the MDS in representing the relationships among the objects.

The contribution of each species to the separation among the groups formed by the clustering was assessed using the SIMPER procedure. The contribution from the ith species to the Bray-Curtis dissimilarity between two years j and k can be defined as:

$$\delta_{jk}(i) = 100 \frac{|y_{ij} - y_{ik}|}{\sum_{i=1}^{p} (y_{ij} + y_{ik})}$$
(2)

When comparing two clusters, δ_{jk} is averaged over all pairs (j, k) of years with *j* in the first and *k* in the second cluster, to give $\overline{\delta}$, the mean dissimilarity between the clusters. The same procedure for $\delta_{jk}(i)$ gives $\overline{\delta}_i$, the average contribution from the *i*th species to the overall dissimilarity between the two years. The values of $\overline{\delta}_i$ reported below are rescaled as percentages of $\overline{\delta}$.

Starting with the same species by years data matrix, the Bray-Curtis dissimilarity between any pair of species was computed, in the same way as that for years. Clustering and MDS of the species were performed on the resulting dissimilarity matrix. Since the focus of the present paper is on the modification of the zooplanktonic community over time and not on the relationships between species, the results of the multivariate analysis on the species are not reported in full here. However, some of the information from this analysis has been used to illustrate the differences among years.

Tab. 1. List of species found in Lake Orta over the period 1987-1997.

CYCLOPIDA Cyclopidae Lepadella ovalis Cyclops abyssorum Squatinella mutica Eucyclops sp. Colurella sp. Megacyclops viridis Lecanidae Thermocyclops sp. Lecane luna Diaptomidae Lecane gr. lunaris Arctodiaptomus wierzejskii Lecane flexilis Lecane subtilis **CLADOCERA** Lecane closterocerca Daphniidae Lecane tenuiseta Daphnia obtusa Lecane stokesi Daphnia longispina Proalidae Daphnia cucullata Proales sp. Ceriodaphnia pulchella Notommatidae Ceriodaphnia setosa Cephalodella sp. Trichocercidae Sididae Diaphanosoma brachyurum Trichocerca capucina Bosminidae Trichocerca cylindrica Bosmina longirostris Trichocerca ruttneri Chydoridae Trichocerca myersi Chydorus sphaericus Trichocerca sp. Alona rectangula Gastropodidae Alona guttata Ascomorpha saltans Alona guttata var. tubercolata Gastropus stylifer Pleuroxus striatus Synchaetidae Macrothricidae Synchaeta sp. Polyarthra gr. dolichoptera-vulgaris Ilyocryptus sordidus Asplanchnidae ROTIFERA Asplanchna brightwelli Asplanchna priodonta Brachionidae Testudinellidae Brachionus calyciflorus Brachionus calvciflorus f. amphiceros Testudinella patina Brachionus calyciflorus f. anuraeiformis Pompholyx sulcata Filinia terminalis Brachionus urceolaris Epiphanes brachionus Hexarthridae Keratella quadrata Hexarthra fennica Keratella cochlearis Conochilidae Kellicottia longispina Conochilus sp. Anuraeopsis fissa Collothecidae Notholca squamula Collotheca mutabilis Notholca acuminata Habrotrochidae Notholca foliacea Habrotrocha sp. Euchlanis sp. Trichotria tetractis MOLLUSCA Trichotria pocillum Dreissena polymorpha (larval instars)

3. POPULATION STRUCTURE

A list of all species found is given in table 1, while data referring to population densities are presented in figure 5 (see over), where only the most important species are taken into account. Copepods, cladocerans and rotifers are now present in the zooplankton of Lake Orta, although it must be stressed that *Daphnia obtusa* was sampled for the very first time in 1986 (see above). However, the total number of species is low. For instance, diaptomids, as well as raptorian cladocerans, have not yet recovered from the crisis of 1927 (Bonacina 2001b). But a trend towards increasing population complexity during the period under study is undoubtedly present, as is evident from figure 2 and from Bonacina *et al.* (1994).

3.1. Copepods

Three Cyclopoid species and one diaptomid species are present in the lake, although it is clear that only *C. abyssorum* (formerly called *C. strenuus*) and, from 1994 on, *M. viridis* truly belong to the pelagic zooplankton community. *Arctodiaptomus vierzejwskii* was found in a sample (April 17th 1997) taken after some days of strong

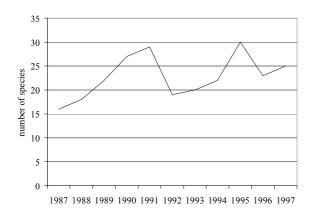


Fig. 2. Variation of the number of zooplanktonic species over the period 1987-97.

C. abyssorum of Lake Orta seems to be a polyciclical species with mating activity showing a maximum during spring and early summer (April to August, Bonacina & Pasteris, in preparation).

3.2. Cladocerans

Up to 1986 cladocerans were represented by a few scattered specimens (Chydorus, Sida, Bonacina, unpublished) most probably coming from the littoral zone. Then, the lake was colonised by Daphnia obtusa. The population was made up of individuals with high genetic similarity (Bachiorri et al. 1991), so supporting the hypothesis that environmental conditions favoured the selection of a particularly resistant clone, and was notable for the presence of an unusually high number of males but not of ephyppial females (Bachiorri et al. 1991; Bonacina et al. 1994; Bonacina, unpublished). Densities fluctuate in the course of the year (and from year to year) till 1996, when D. obtusa disappeared from the pelagic community, being replaced by Daphnia longispina, which started in 1989 with very low densities. In the last three years, 1995, 1966, 1997, Bosmina longirostris and Diaphanosoma brachyurum became established in the community, even though some individuals had also been found in the previous years.

3.3. Rotifers

Rotifers as a whole are without doubt the quickest group to react to changing environmental conditions. This is obviously due to their short life-span and their fast reproduction, two characteristics that allow opportunistic species to rapidly exploit a favourable environment. As a matter of fact, we recorded 5 species of copepods, 13 species of cladocerans but 45 species of rotifers (Tab. 1).

Some observations can be made: first of all, *Hexarthra fennica*, the only rotifer species which formerly inhabited the lake, and which also gave rise to blooms (Baldi 1949; Bonacina 1970) is now represented by very few individuals; second, most of the species belong to the Brachionidae family; third, the overall densities are always low or very low but some species occasionally reach very high densities (namely *Keratella quadrata*, 180,000 individual m⁻³ in April 1994); last, but not least, two raptorian species are now part of the community: *Asplanchna brightwelli* in 1989-1990 and *A. priodonta* since 1994.

4. RESULTS OF DATA ANALYSIS

Figures 3 and 4 show, respectively, the dendrogram resulting from the clustering procedure and the MDS plot of the eleven years. The groups formed by the clustering procedure are also superimposed on the ordination.

The stress value for the MDS is 0.07 which, according to Clarke (1993) and Clarke & Warwick (1994), corresponds to a good ordination with little risk of a misleading interpretation.

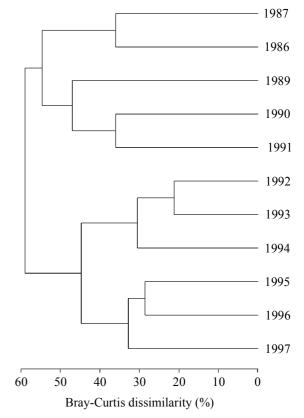


Fig. 3. Dendrogram of the 11 years, using group average clustering from Bray-Curtis dissimilarities on the 4th root transformed mean annual abundances of zooplanktonic species.

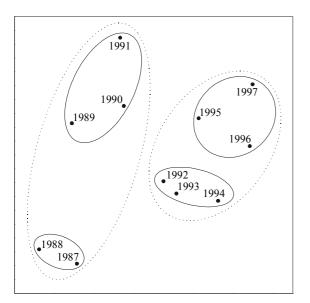


Fig. 4. MDS plot of the 11 years with superimposed clusters from figure 3.

At a 50% dissimilarity level, the clustering procedure forms three groups (years 1987-88, years 1989-91, years 1992-97). These clusters are also fairly evident in the MDS plot. The groups formed at lower dissimilarity levels are less evident, but the results of the clustering and the ordination are still consistent: years placed in the same group never appear distant and groups never overlap in the ordination plot. The consistency between the two methods is an indication that both give an accurate representation of the relationship between years.

Figure 5 shows the mean abundance of the 27 most important species for the years under study, arranged in seven classes. The species included are those that altogether account for 75% of the dissimilarity between clusters, as identified by the SIMPER procedure. The 27 species are arranged according to the results of the clustering and MDS applied to the similarity matrix among them. The brackets on the top and on the left of the figure, indicate clusters of years and species respectively.

							<u> </u>						
		1987	1988	1989	9 1990	1991	1992	1993	1994	1995	1996	1997	
Γ	Cephalodella sp.		•	170		.,,,,	.,,,_	1775	.,,,,	1770	1770	.,,,,	
	Habrotrocha sp.	•	•	•	•	•				•	•		
	Daphnia obtusa	•	•	٠	•	•	٠	٠	•	•			
	Brachionus urceolaris	•	•									•	
	Anuraeopsis fissa	٠	•	•	•	•	٠	•	•	•			
	Lecane flexilis				•	•							
	Hexarthra fennica			•	•	•	•	•	•	•	•	•	
	Trichocerca ruttneri					•							
	Brachionus calyciflorus			•	•	•		•		•			
	B. calyciflorus amphiceros			•									
	B. calyciflorus anuraeiformis			٠		•							
	Chydorus sphaericus	•			•	•				•			
	Asplanchna brightwelli			•	•								
Ē	Proales sp.							•					
	Polyarthra dolichoptera-vulgaris				•			•	•	•	•	•	
	Keratella quadrata						\bullet	\bullet	\bullet	•	٠	•	
Γ	Trichocerca capucina	•		•	•			•	•	•	•		
	Cyclops abyssorum	•	•	٠	•	•	•	•	•	•	•	•	
	Daphnia longispina			•	•		٠	•	•	٠	•	٠	
	Collotheca mutabilis						•	•	•	•	•	•	
	Keratella cochlearis	•	•	•		•		•	•	•	٠	•	
	Bosmina longirostris				•	•				•	•	•	
	Ascomorpha saltans								•		•	•	
	Conochilus sp.			•	•							•	
	Megacyclops viridis viridis					•				•	•	•	
	Diaphanosoma brachyurum				•	•				•	٠	•	
L	Asplanchna priodonta								•	•	•	•	
		•	•		•	(•	•					
	0 <1 <	<10	<10	0	<1,000	<10	,000 <	<100,0	00	ind m ⁻³			

Fig. 5. Presence-absence of the most important zooplanktonic species. The original mean annual abundances have been categorised and represented by symbols of increasing size.

At the highest level of dissimilarity (=59%), years 1987-1991 are separated from years 1992-1997. *Keratella quadrata* is the species that gives the highest contribution to the dissimilarity between the two groups (=15%). Individuals of this species were found only sporadically in the samples of years 1987-1991 and the average abundance over this period was 0.5 individuals m^{-3} (Fig. 6). Over the period 1992-1997, abundance of *K. quadrata* varied widely among and within years; however it was almost always present in the samples and was often the most abundant species, with a maximum of 357,000 ind. m^{-3} in April 1993. The mean annual abundance never dropped below 1810 ind. m^{-3} and the average over the whole period was 27,600 ind. m^{-3} .

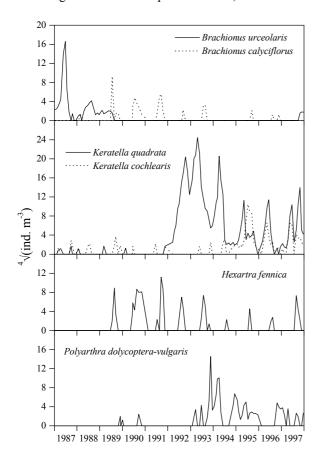


Fig. 6. Population densities of main rotifer species.

Daphnia longispina is the species that gives the second highest contribution to the dissimilarity between the years 1987-1991 and the years 1992-1997 (=5.7%). This cladoceran was absent or scarce in the samples collected over the period 1987-1991, with the exception of autumn 1989, and abundant in most of the samples of 1992-1997 (Fig. 7). As a consequence, the average abundance is 21.5 ind. m⁻³ for 1987-1991, 870 ind. m⁻³ for 1992-1997.

Third, in order of contribution to the dissimilarity between the two clusters of years, is *Polyarthra doly*- *choptera-vulgaris.* (=5.3%) The abundance of this species is null or very low from year 1987 to year 1992 inclusive, and increases beginning from year 1993 (Fig. 6). Thus *P. dolychoptera-vulgaris* has a delay in comparison to *K. quadrata* and *D. longispina* and is not as good as a discriminant species between the two clusters of years. However, the average abundance over 1987-1991 (0.9 ind. m⁻³) is much lower than over 1992-1993 (1030 ind. m⁻³).

Within the period 1987-1991, at a dissimilarity level =55%, years 1987-1988 are distinguished from years 1989-1991. *Hexarthra fennica* (=11.2%), *Brachionus urceolaris* (=10.6%), *Bosmina longirostris* (=6.7%) and *Brachionus calyciflorus* (=6.6%), are the species that give the highest contributions to the distinction between the two clusters.

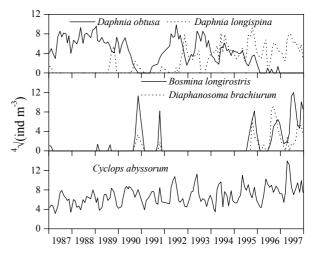


Fig. 7. Population densities of main cladoceran species and *Cyclops abyssorum*.

Over the period 1989-1991, abundances of *H. fennica*, *B. calyciflorus* and *B. longirostris* (Figs 6 and 7) show marked seasonal variations, ranging from 0 to several thousands of ind. m^{-3} in a few months. These species are found only sporadically in the samples of 1987-88.

The mean annual abundance of *B. urceolaris* (Fig. 6) shows a different pattern, decreasing from 1987 to 1990; this species then disappears from the samples until the autumn of 1997, when some individuals were found.

At a dissimilarity level =45%, years 1992-1994 are distinguished from years 1995-1998. The most discriminating species are *Keratella quadrata* (=11.9%), *Bosmina longirostris* (=9.5%), *Daphnia obtusa* (=7.6%) *Diaphanosoma brachyurum* (=7.5%) and *Keratella cochlearis* (=6.4%).

The mean annual abundance of *K. quadrata* (Fig. 6) is high throughout 1992-1998, as opposed to the previous years, however both maximum values and annual means differ by one order of magnitude between 1992-

1994 (average: 51,900 ind. m^{-3}) and 1995-1997 (average: 3310 ind. m^{-3}). *B. longirostris* (Fig. 7) disappeared from the samples in 1992 to reappear in 1995.

The population of *D. obtusa* (Fig. 7), after recovering from a first collapse in 1991, shows a consistently decreasing trend from 1992 to 1997, despite the obvious seasonal variation. Average abundance was 1710 ind. m^{-3} over 1992-1994, 57.9 ind. m^{-3} over 1995-1997.

D. brachyurum (Fig. 7) was not found in the samples collected over 1992-1994; in contrast, it was generally present after October 1995, the average abundance over 1995-1997 being 599 ind. m⁻³.

K. cochlearis (Fig. 6) was irregularly present until 1994, with an average abundance of 5.26 ind. m^{-3} over 1992-1994, while it was much more abundant over 1995-1996 (average: 621 ind. m^{-3}).

5. DISCUSSION

In acidic lakes both in Scandinavia and Canada there is a dominance of bosminids and a scarcity of daphnids and rotifers (Haines 1981). But unlike these lakelets, Lake Orta has a large volume $(1.3 \ 10^9 \ m^3)$ and at least five major tributaries, which mean annual discharges range from 0.2 to 1.3 m³ s⁻¹; some localised environments could therefore have been formed, in which many more species than those collected in the open lake could have survived. This is the reason why Arctodiaptomus wierzejskii or Sida crystallina or larval instars of Dreissena polymorpha appear and disappear from our collections. On the other hand, these limited environments are most probably a sort of reserve from which opportunistic species start to colonise the whole lake once it has reached favourable environmental conditions, as has happened at various times for Daphnia obtusa, D. longispina, Diaphanosoma brachyurum and so on.

A very concise summary of zooplankton recolonization in Lake Orta is as follows: first came *Cyclops abyssorum* (first report in 1959, Vollenweider 1963, surely absent till 1948, Baldi 1949) which seems to tolerate a wide range of variations in environmental parameters: as a matter of fact, it is the only species always present in the lake with nearly constant, though often low, densities. Like *D. obtusa* it can withstand low pH values but, unlike it, also a high ammonia and copper content.

In September 1986, when environmental conditions were still seriously affected by low pH, which enhanced heavy metals toxicity, but when the ammonium nitrogen concentration was decreasing due to the adoption of recovering plants for the main industrial discharge (Bonacina 2001a) there appeared *Daphnia obtusa*, a species that can tolerate acidic conditions (Fryer 1985; Stenson 1985).

From October 1992, i.e. two years after the liming was performed, with mean epilimnic pH values of 6.8, mean epilimnic ammonium nitrogen concentration of less than 0.1 mg Γ^1 , mean epilimnic Cu concentration of about 8 µg Γ^1 (Calderoni *et al.* 1997), a stable popula-

tion of *D. longispina* settled in the lake (a few specimens were caught sporadically from 1989 on). In the meantime, *D. obtusa* started to decline and disappeared in 1996, but from January on, *Keratella quadrata* became established in the lake, at times reaching tremendous densities (maximum value: 356,884 individuals m^{-3} in April 1993).

In August 1995 with mean epilimnic pH values of 7, mean epilimnic ammonium nitrogen concentration of about 0 mg I^{-1} , mean epilimnic Cu concentration of less than 5 µg I^{-1} (Calderoni *et al.* 1997) there appeared *B. longirostris*, after isolated bursts in November 1990 and October 1991. In October of the same year, a population of *Diaphanosoma brachyurum* was also recorded (some specimens were collected in December 1990 and October 1991).

Many other rotifer species are now present in the lake, either occasionally or permanently (Tab.1).

The succession from *D. obtusa* to *D. longispina* can definitely be attributed to variations in pH, the mean epilimnic values of which increased from about 5.2 in 1988 to 6.7 in 1998 due to the liming and to consequent precipitation of heavy metals (Calderoni & Tartari 2001): it was demonstrated (Hamza *et al.* 1998a, 1998b) that *D. obtusa* living in Lake Orta shows its highest new-born production at pH 6, as it is unable to live in neutralized conditions; the same study showed that, on the other hand, *D. longispina* is very sensitive to the toxic effect of copper ions, the concentration of which is higher at lower pH levels.

Changes in copper concentrations rather than directly in pH values are probably responsible for subsequent modifications in species composition. As a matter of fact, from mid 1995 epilimnetic copper concentration dropped to 5 μ g l⁻¹ (Calderoni & Tartari 2001).

The behaviour of Bosmina longirostris, which appeared in 1989-1991, declined in 1992-1994, recovered in 1995-1997 and flourished in 1998 (Bonacina, unpublished) cannot yet be explained with our data. It is probably not a question of competition for food, because other micro filter-feeders (rotifers as well as D. brachyurum) are present both at the same time as Bosmina and in its absence. It is known from the literature that bosminids are the dominant species in acidic lakes (Haines 1981, see above) but the high concentrations of dissolved copper in Lake Orta masked this effect. After the liming, B. longirostris appeared for the first time with high densities $(16,354 \text{ ind. m}^{-3})$ in November 1990 with copper concentrations of about 30 μ g l⁻¹ and mean epilimnetic pH value of about 6.5 (Calderoni et al. 1997) and for the second time in October 1991 (4467 ind. m^{-3} , with copper concentrations of 22 µg l⁻¹ and mean epilimnetic pH value of 6.8). Then, no Bosmina was found for three years. In 1995 and 1996 a small population appeared. We can only suppose that the sudden increase in pH values put the population in a condition of stress from which it recovered only slowly.

6. CONCLUSIONS

Three major events mark the history of Lake Orta over the last fifty years: the copper recovery of the mid fifties (Bonacina & Bonomi 1984), the ammonia recovery of the early eighties (Bonacina *et al.* 1986; Mosello *et al.* 1986a, 1986b; Bonacina *et al.* 1988a, 1988b), both on behalf of the Bemberg factory, and the liming of 1989-1990, proposed by CNR-Istituto Italiano di Idrobiologia (Bonacina *et al.* 1987) and funded by Ministry of Environment and regional Authorities.

The bibliographical evidence is unhelpful in an evaluation of the effects of liming on the structure of biological community as a whole, mainly because almost all the literature refers to small lakes continuously re-acidified by acid rain, so that the problems involved are very different from those which arose in Lake Orta (the biggest acidified lake in the world). In bogs and small lakes in Scandinavia and Canada, for example, fish play a very important role: absent in acidified condition, fish fry hatch very quickly after liming, and as they are size selective planktivorous, their presence influences the zooplankton community in many direct and indirect ways. (Henrikson et al. 1985). Because of its great volume, and thus the resilience of its ecosystem, we cannot expect a similar rapid reaction in Lake Orta. Fish are certainly present, but with densities that may not affect zooplankton significantly. Consequently, all changes in zooplankton community must be attributed almost exclusively to changes in the chemical parameters.

As a matter of fact, when ammonia concentration dropped to about 1.5 mg N l⁻¹ (mean for the whole lake, Calderoni *et al.* 1997), *Daphnia obtusa* appeared, although pH was still low and copper content still high (pH about 4 and 40 μ g Cu l⁻¹, mean values for the whole lake, Calderoni *et al.* 1997).

But it was only after the liming, when the whole lake was neutralized and toxic metals precipitated, that the zooplankton community began to show a more complex structure. The two main clusters (years 1987-1991 and years 1992-1997) in figure 5 are different, in that in the former period copper concentrations were always above 20 μ g l⁻¹ and pH values always under 5 (Calderoni *et al.* 1997). Once the toxic effect of both copper and low pH had been reduced or stopped, other species could survive in the pelagic waters, namely *Keratella quadrata*, *D. longispina* and *Diaphanosoma brachyurum*.

There is one more consideration to be made. The waters of Lake Orta are now almost "normal"; ion content, pH values, and the alkaline reserve are similar to those existing in nearby lakes with similar drainage basins, but the biological community is far from being settled, mainly because there is still a lack of predators, apart from *Asplanchna* spp. and *Cyclops abyssorum*. In this situation, opportunistic species may be expected to be very successful for a limited period of time, and then

be rapidly replaced by others, as happened with the pair *Daphnia obtusa-Daphnia longispina*. We know now, however, that recovering a heavily polluted lake may be a difficult task, but not an impossible one.

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