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Oligochaeta from the abyssal zone of Lake Baikal (Siberia, Russia)

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Abstract

Lake Baikal is unique because the water circulation carries oxygen to its deepest point (1637 m), which makes it the only freshwater lake in the world with an inhabitable abyssal area. The sampling of the abyssal of the Lake was recently made possible, allowing a study of the bathymetric and vertical distribution in the sediment of Oligochaeta. Samples were taken with a Reineck box corer and subsamples were extracted and subsequently divided into slices. Factors likely to affect oligochaete abundance with depth and in the sediment were then evaluated. Identification to the species-level allowed discussion of the possible role of the abyss of Lake Baikal in the origin of oligochaete taxa and to assess if genuine deep-water taxa exist. Abundance of Oligochaeta generally follows an exponential decline with depth. An exception was one station located near a deep hot vent. In the abyssal area, all families of Oligochaeta are concentrated near the surface of the sediment. While there are generally no Naididae below 50 m, Tubificidae, Lumbriculidae, Propappidae, Enchytraeidae and Haplotaxidae are present at all depths. Evidence suggests, for the first time, that food abundance is a limiting factor of oligochaete distribution. The possibility of a genuine deep-water oligochaete fauna in Lake Baikal cannot be excluded but the low densities and the very small sizes of animals in this environment might have caused biased samples.

Introduction

Lake Baikal, situated in the Great Eastern Siberian Rift, is the deepest (1637 m) of all extant lakes (Kozhov, 1963; Martin, 1994). Its location in an active graben trough has permitted its preservation despite continuous deposition of sediments. Lake Baikal is truly ‘ancient’ or ‘long-lived’ (Gorthner, 1994) (25–30 Ma) and holds a very diverse and largely endemic fauna. A total of 152 oligochaete species was recently reported, 111 of these being endemic (Martin, 1996), today we know of 155 and 114 species, respectively (Martin & Brinkhurst, 1998; Martin et al., 1998a).

The area deeper than 250 m is commonly defined as the abyssal zone of Lake Baikal (Kozhov, 1963). Although a very different depth compared to abyssal or deep sea depths (Gage & Tyler, 1991), the abyssal of Lake Baikal and the deep sea have common characteristics. They are both very stable and homogeneous in physical and chemical parameters (Kozhov, 1963; Falkner et al., 1991; Weiss et al., 1991; Liebezeit, 1992; Hohmann et al., 1997a). Major environmental characteristics of the abyssal of Lake Baikal are low temperatures (3.2–4.0 °C), high concentrations of dissolved oxygen (347 μmol kg^{-1}), elevated hydrostatic pressures and distance from the zone of primary organic production, indicative of a psychrosphere (Martens, 1997).

Due to a deep-water renewal below the dimictic 250 m upper layer (Kozhov, 1963; Weiss et al., 1991; Shimaraev et al., 1993; Killworth et al., 1996; Hohmann et al., 1997a,b), oxygen is carried to the deepest point and makes these depths inhabitable by metazoans. Other ancient and deep lakes, such as Lake Tanganyika (East Africa), are virtually anoxic below the first 100–250 m (Coulter, 1994).

Although Lake Baikal has been an active centre of research for about 100 years, studies of ecology and distribution of oligochaetes in the vast abyssal zone really started only twenty years ago. Tubificidae from depths exceeding 500 m were studied for the first time by Chekanovskaya in 1975. A detailed study of the northern basin by Snimschikova (1982, 1985a, 1987) filled in many taxonomic gaps but mainly focused on shallow areas down to 500 m. Semernoi (1983) was the first to give a comprehensive list of oligochaete species, with their respective distribution ranges, from the abyssal zone of Lake Baikal. Semernoi's list included species from the families Naididae, Tubificidae, Lumbriculidae, Enchytraeidae and Haplotaxidae. Takhteyev et al. (1993) gave a description of the general benthos of the abyssal zone but the distribution of oligochaetes in the deep lake was still imprecise.

Recent fieldwork on Lake Baikal has been possible within the framework of BICER (Baikal International Center for Ecological Research). In 1994, a joint Russian-Belgian expedition focused on sampling the abyssal zone of the lake. Data collected during this expedition enabled us to study the bathymetric and vertical distribution of Oligochaeta in the sediment. This is compared to similar data from shallower zones accumulated during previous cruises. Specimens were identified to species-level, allowing us to discuss the possible role of the abyss of Lake Baikal in the origin of extant oligochaete diversity and to assess whether or not genuine deep-water taxa exist.

Material and methods

Sampling was done at the widest part of the lake, along a transect from Barguzin Gulf to the deepest point (1680 m as measured by the echo sounder). Four sample stations were on the slopes of the underwater feature called 'Akademichesky ridge', which marks the boundary between the central and northern basins (Figure 1). Transects in previous studies were in shallower depths: three in front of Selenga delta (18–84 m, 1991 cruise) and two in the southern basin, on Murinsk bank (135–650 m, 1991) and in the vicinity of Posolskaya Bank (20–400 m, 1990; Martin et al., 1994), including a few isolated stations deeper than 250 m (Figure 1).

All samples were taken with a modified Reineck box corer (0.079 m^2). Subsamples were extracted for faunal analysis with Perspex tubes, the surface area of the cores was modified for each cruise in order to obtain adequate numbers of animals and minimize sample processing (1990: 37.7 cm^2, 1991: 84.9 cm^2; 1994: 62.2 cm^2). Each subsample was mounted on an extruder and subsequently divided into slices. Samples were fixed in 7% buffered formalin, washed in the laboratory through a sieve (250 μm mesh), and preserved in 70% alcohol.

All mature oligochaetes from the 1994 samples were identified. Larger specimens were dissected, smaller ones were mounted whole. Worms were stained with alcoholic carmine and mounted in Canada balsam. These animals are deposited in the Royal Belgian Institute of Natural Sciences (RBINSc; Brussels) under No I.G. 28051.

The bathymetric distribution of oligochaete abundance was studied using all available quantitative data. Data from the 1990 study were excluded from the analyses of vertical distribution within the sediments because of the different slice thickness.

Results

The abundance of Oligochaeta (no. individuals per m^2) follows an exponential decline with depth, although a slightly better curve fit is achieved using a power decay (Figure 2). The latter can be expressed as $Y = ax^{-b}$ where Y is density, x is depth, and a and b are constants. As the b value is very close to 1, this means that for each doubling of depth, densities decrease by a factor of 2. Thus, there is a rapid decrease in oligochaete abundance in the first 200 m but abundance is almost constant in the abyssal zone of the lake. Density decreases 300 times from 20 m to the greatest depth. Stations at 1500–1680 m have densities 3–15 times lower than those at 225 m. One station, at 420 m, stands distinctly out of the data sequence, with a density of 15 956 ind. m^{-2} (open circle, Figure 2). This station is located near the Frolikha Bay vent, a deep lake vent discovered more than 10 years ago (Golubev et al., 1993).

The vertical distribution of Oligochaeta in the sediment was studied by estimating the interaction between:

1. depth zone and sediment depth for each family that was significant in our abyssal samples (Tubificidae, Lumbriculidae and Enchytraeidae) and
2. family and sediment depth for each depth zone (Figures 3 & 4).

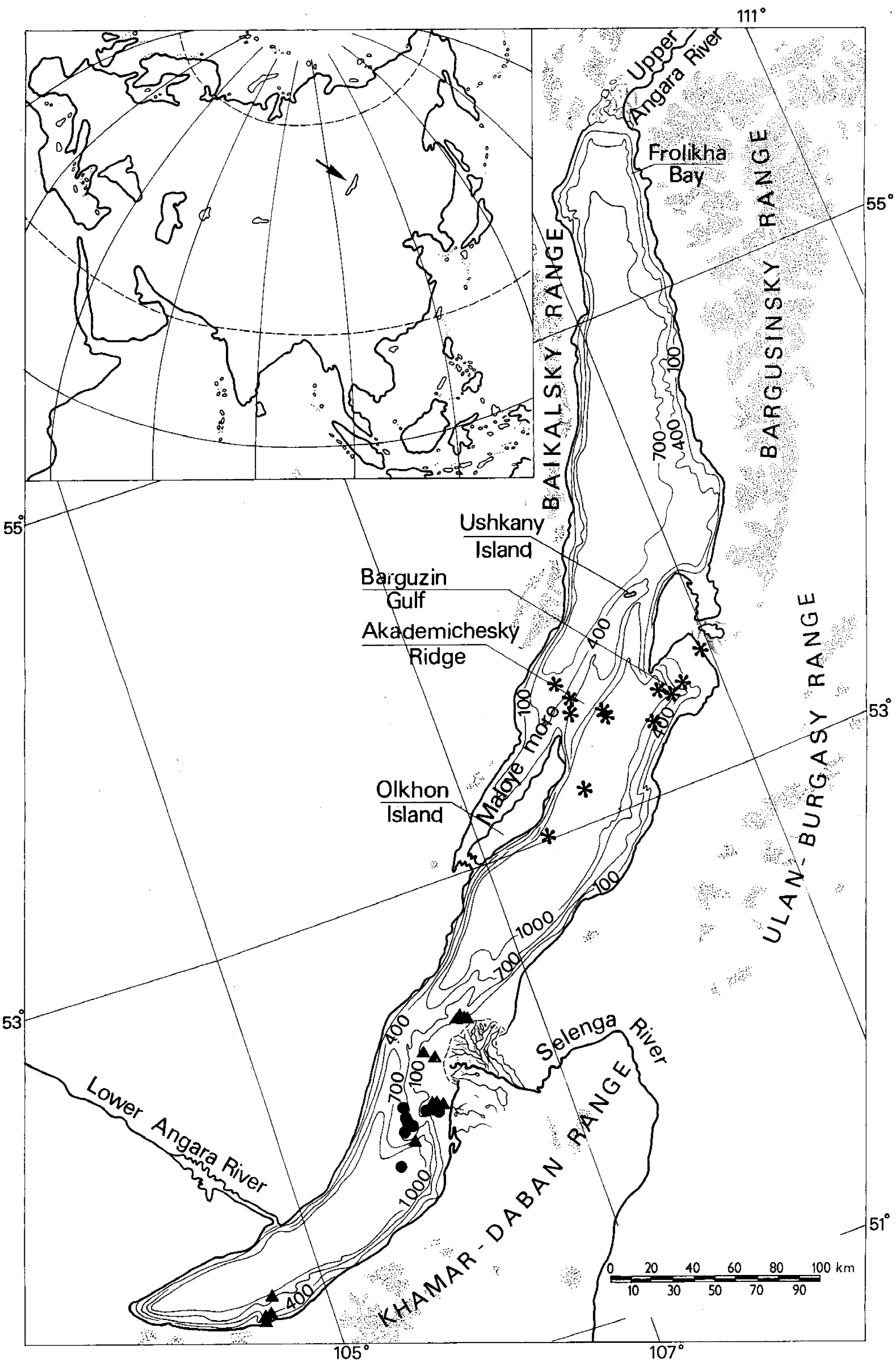

Figure 1. Location of Lake Baikal and the stations sampled in 1990 (dots), 1991 (triangles) and in 1994 (stars).

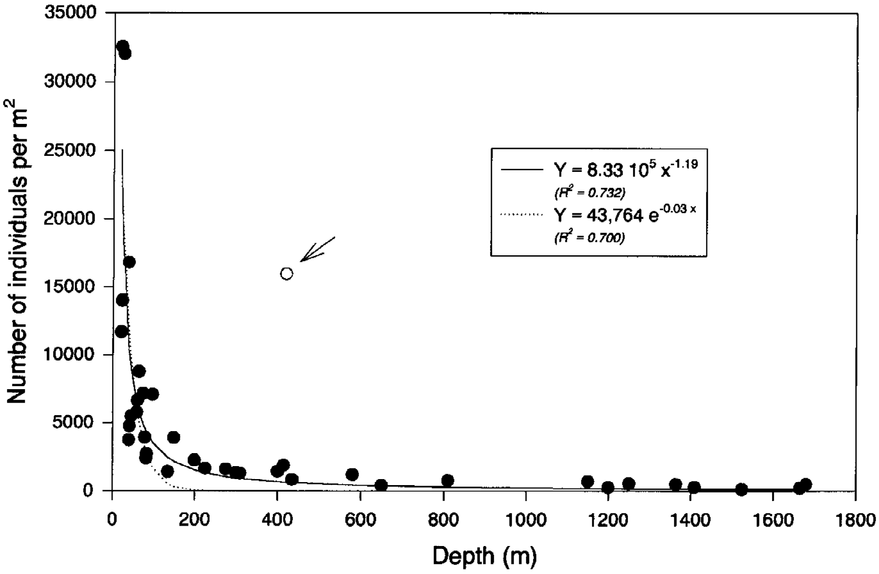

Figure 2. Bathymetric distribution of density of Oligochaeta (dashed line: exponential curve fit; solid line: power decay curve fit). The open circle (arrowed) refers to one station located near the Frolikha Bay vent in the northern basin of the lake, at 420 m depth. This value was excluded from computation of the curve fits. Data are from 1990, 1991 and 1994 collections.

Table 1. Summary of size measurements of selected Oligochaeta from the abyssal zone of Lake Baikal (from Martin & Brinkhurst, 1998)

	Breadth at widest	Length	Depth
Burchanidrilus petitbonum Martin & Brinkhurst, 1998	240 μm	fragment	1250 m
Lymphachaeta pinnigera Snimschikova, 1982	186 μm	4.50 mm	580 m
Rhyacodriloides abyssalis Chekanovskaya, 1975	260 μm	7.30 mm	275 m
Rhyacodriloides gladiiseta Martin & Brinkhurst, 1998	135 μm	3.24 mm	310 and 415 m
Tubifex bazikalovae Chekanovskaya, 1975	310 μm	4.73 mm	415 and 580 m

Tubificids burrow into the sediment of the dimictic area (Figure 3), while they are more concentrated near the surface of abyssal sediments (Figure 4). In contrast, there is no apparent difference in sediment penetration by Lumbriculidae and Enchytraeidae in either depth zone. This is fully confirmed by a two-way ANOVA test which reveals a statistically significant interaction between water depth zonation and sediment depth for Tubificidae ($F_{(7,160)}$ = 4.57; $p <$ 0.0001) (Figures 3 & 4), but none for Lumbriculidae and Enchytraeidae.

There is a statistically significant interaction between family and sediment depth in the dimictic zone ($F_{(14,240)}$ = 1.89; p = 0.0281) and none in the abyssal zone (Figures 3 & 4). While the test isolates Tubificidae as being responsible for this significant interaction, an examination of median values suggests a different pattern of vertical distribution in the sediment between Enchytraeidae, Lumbriculidae and Tubificidae. In the abyssal zone, all families follow a similar pattern and are concentrated near the sediment surface.

Twenty-three species of oligochaetes were identified in all samples (1990, 1991 and 1994 cruises), of a total of 155 reported species from the Lake (Figure 5). The distribution of oligochaete species (Figure 5) is eurybathic for the families Haplotaxidae, Enchytraeidae, Propappidae and Lumbriculidae. All these species were already mentioned in the deep-lake studies (refs in Figure 5) and their distributions are only extended a few hundred metres deeper or even to the greatest depth (1680 m; *Haplotaxis* sp.) with data from our study. Naididae are generally restricted to the first 50 m, with a notable exception at 700 m deep (*Nais abissalis*, Semernoi 1988). One immature specimen of *Nais* ?sp. n. was found at 200 m, extending the distribution range of the family close to the dimictic-abyssal boundary. In Tubificidae, most

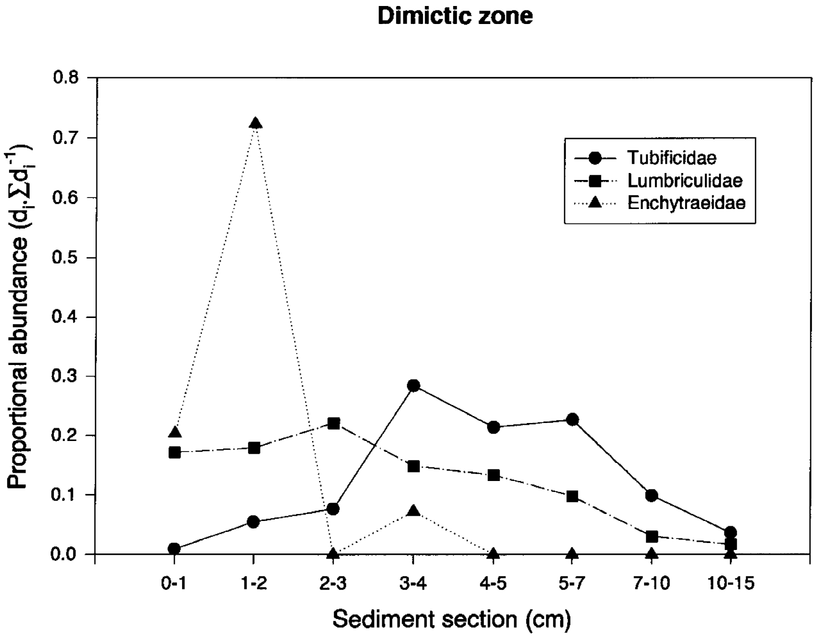

Figure 3. Vertical distribution in the sediment of Oligochaeta in the dimictic zone of Lake Baikal. Proportional abundance calculated as $d_i.\Sigma d_i{}^{-1}$, in which d_i = density of oligochaetes in sediment core segment *i*, expressed as the number of individuals per m^2. Data are from 1991 and 1994 collections.

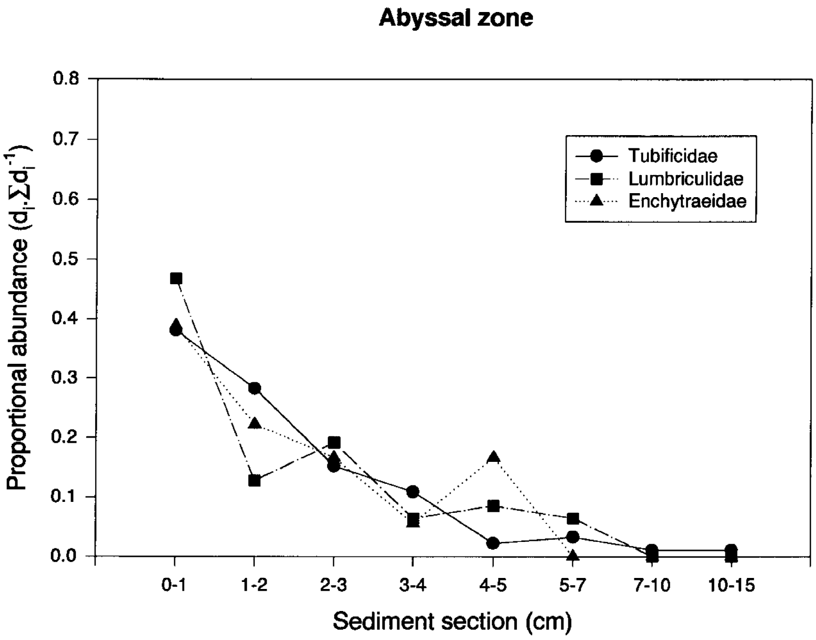

Figure 4. Vertical distribution in the sediment of Oligochaeta in the abyssal zone of Lake Baikal. Proportional abundance calculated as $d_i.\Sigma d_i{}^{-1}$, in which d_i = density of oligochaetes in sediment core segment *i*, expressed as the number of individuals per m^2. Data are from 1991 and 1994.

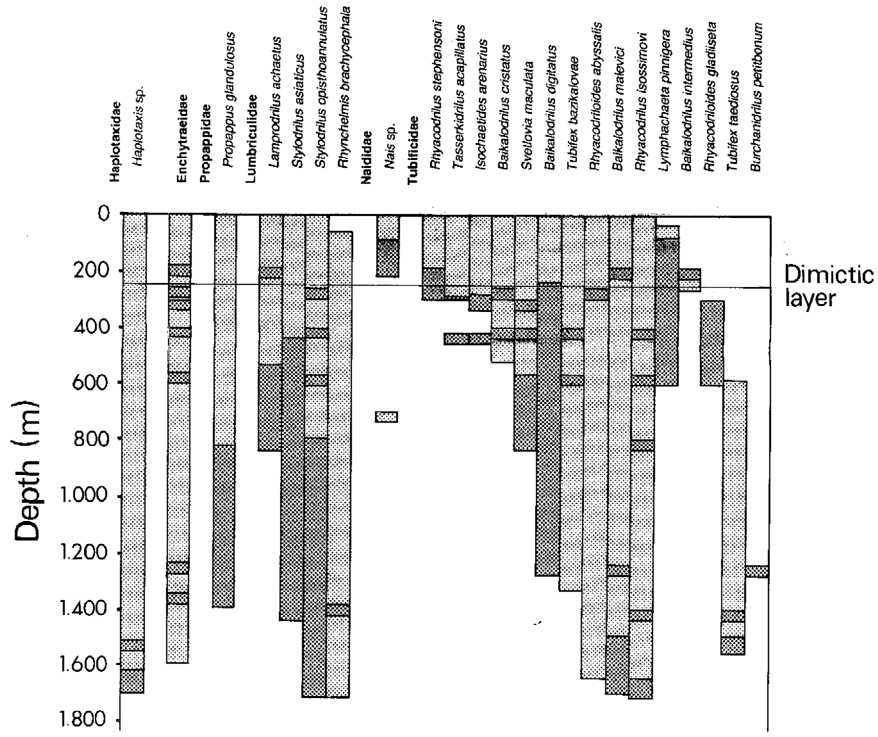

Figure 5. Bathymetric distribution of oligochaetes. Lightly shaded: range of bathymetric distribution as known from literature; darkly shade: ranges from data of the present study. When the present data fall into the former bars, only the depth of the station is indicated as a narrow band; when the data enlarge the previously known distribution, the bar extends as far as the deepest station where the species was found. Isolated stations indicate a possible artefact in Naididae distribution (at 700 m) or correspond to the deep vent station in Frolikha Bay (*T. acapillatus* and *I. arenarius*). Literature data are from Chekanovskaya (1975), Semernoi (1983, 1987), Snimschikova (1985a,b, 1987), Snimschikova & Timm (1992) and Snimschikova & Akinshina (1994).

species are found in both the dimictic and the abyssal zone of the lake, but some seem to be restricted to the shallower zone and others to the abyss.

Discussion

Distribution of abundance

Abundance of food controls density and biomass of both pelagic and benthic deep-sea animals (Sanders & Hessler, 1969; Rowe et al., 1974; Gage & Tyler, 1991; Childress, 1995). During its slow descent from the surface waters to the benthos, organic matter is progressively utilised by mid-water organisms and degraded by autolysis and bacterial decay. The refractory or non-usable proportion of the organic matter increases with depth. Other factors (oxygen concentration, sediment type, temperature) either do not show correlated changes or never reach levels regarded as limiting (Sanders & Hessler, 1969; Khripounoff et al., 1980). There is no reason to believe that such a pattern cannot also apply to Lake Baikal.

In addition to food, other factors could explain variation with depth in oligochaete abundance in Lake Baikal and their possible effects are worthy of being evaluated.

Three factors which co-vary with depth are:

1. hydrostatic pressure,
2. ambient light, and
3. temperature.

Oxygen is neglected here because the range of dissolved O_2 in the water column (0–1637 m) is very narrow in Lake Baikal (347–383 μmol; Martin, 1994) and the sediment is well-oxygenated at all depths (Martin et al., 1998b).

Although hydrostatic pressure could limit the species present, there is no apparent way in which it can regulate abundance. Suggestions that pressure might, in some way, act so as to limit metabolic rates were recently rejected (Childress, 1995).

Ambient light has an indirect influence on abundance because it determines the thickness of the euphotic zone which, in turn, affects phytoplankton production and, hence, food availability to benthic organisms. However, this effect is mainly restricted to the first 100 m, as attested by the concentration of phytoplankton in this upper layer, with subsurface maxima (Bondarenko et al., 1996).

An intuitively attractive variable that could be responsible for lower abundances at depth is temperature. This suggestion can, however, be rejected. In situations with deep-sea water mass being much warmer than elsewhere, benthic standing crop is always lower (Gage & Tyler, 1991). This is so, because pelagic consumption is enhanced, due to a high energy demand of temperature-related metabolism and much of the organic matter available at the bottom is lost for benthic production. In Lake Baikal, while temperatures can be considered to be constant from 100 m down, in August, the pattern of distribution still follows a power decay (R^2 = 0.797) along this depth range.

Another test of the potential importance of temperature on abundance comes from the hydrothermal vent oligochaetes. Increased temperature in the vent is not higher than 0.06 °C due to rapid dilution of vent water by ambient water. At 10 cm into the sediment, temperature is less than 5 °C, compared with 3.2 °C for bottom water at 420 m (Golubev et al., 1993). The independence of abundance at the vent from temperature indicates that much higher densities cannot be attributed to this variable. Hot vent communities apparently have much higher densities than other abyssal oligochaetes communities (15 956 *vs*. 807 ind. m^{-2} on average, respectively) because they do not depend on energy coming from the lake surface but from an *in situ* chemosynthetic primary production (Grachev et al., 1995).

Vertical distribution in the sediment

Lower food availability at depth is the most likely explanation for the limited vertical distribution of oligochaetes in the sediment of the abyssal zone. In the dimictic zone, the vertical distribution in the sediments confirms the preference of Enchytraeidae for the sediment surface and of Tubificidae for deeper sediment, while Lumbriculidae usually penetrate into intermediate depths (Healy, 1987). In the abyssal zone, the impressive concentration of all families near the sediment surface suggests that food is restrictive at such depths. In the dimictic zone, where food scarcity is probably less stressing, oligochaetes are not impeded from fully expressing their burrowing behaviour.

Many attempts were made to estimate available food. Total organic carbon in the sediment has been used but there are numerous examples showing that it is not a good index (Sanders & Hessler, 1969; Bekman & Mizandrontzev, 1971; Rowe et al., 1974; Khripounoff et al., 1980). In Lake Baikal, an increase in organic carbon content of the sediments with depth was noted, parallel to a decrease in benthic biomass (Bekman & Mizandrontzev, 1971). Estimation of available food cannot be carried out in a simple way. It requires either a careful biochemical analysis of organic matter in the laboratory (Khripounoff & Rowe, 1985) or the use of sediment traps (estimation of the flux of organic matter; Hinga et al., 1979; Khripounoff & Rowe, 1985), which are beyond the scope of the present paper. Such a work in Lake Baikal is clearly needed in the future, however, in order to bring a confirmation of the above assumptions.

Bathymetric distribution of species

The bathymetric distribution of species is one of the oldest problems in the study of lakes and is related to presence or absence of a specially evolved deepwater fauna. Due to its age and habitable abyssal zone, Lake Baikal offers a unique opportunity to study this issue. It should be noted, however, that the Baikal abyss, as a biosphere, is rather recent, relative to the age of the lake itself. Siberia had a warm subtropical climate in the late Oligocene-Miocene periods (30–6 Mya) and the palaeothermohaline regime of Lake Baikal was similar to that of the modern Tanganyika (Sherstyankin et al., 1995), resulting in an anoxic abyssal zone.

In spite of this, the presence of genuine deep-water species in Lake Baikal have been documented in major benthic groups such as Gammaridae (Takhteyev, 1996; Takhteyev & Mekhanikova, 1996), Ostracoda (Mazepova, 1994), and Turbellaria (Timoshkin, 1994). In Oligochaeta, only two apparently ‘truly’ abyssal species are known to exist, *Lamprodrilus inflatus* Michaelsen, 1905 and *Lamprodrilus bythius* Michaelsen, 1905. These species are assumed to have specific morphological adaptations to deep-lake conditions (thinning down of tegument, extension of ventral setae, transparency of the body), although their bathymetric distribution includes depths shallower than 90 m (Isossimov, 1962).

As a rule, Naididae mainly feed on algae and higher plants (Brinkhurst & Gelder, 1991). As the biomass of phytoplankton is not significant below the first 100 m (Bondarenko et al., 1996), their restriction to this depth range is expected. The presence of *Nais abissalis*, described from one immature specimen found at 700 m (Semernoi, 1988) and one immature specimen of *Nais* ?n. sp. found at 200 m in our study, are therefore enigmatic and probably artefacts linked to sinking of plant debris or transport by water circulation. Transport of metazoans via sinking of large aggregates to the deep-sea floor is not uncommon (Shanks & Edmondson, 1990; Bochdansky & Herndl, 1992) and during deep-water renewal in Lake Baikal, considerable water masses can suddenly sink to a greater depth as a result of 'thermobaric instability' (Weiss et al., 1991).

All species of Haplotaxidae, Enchytraeidae, Propappidae or Lumbriculidae found are eurybathic and give no indications of potential deep-water speciation. The family Tubificidae is currently considered to be eurybathic (Snimschikova & Akinshina, 1994). Here we report the presence of *Tubifex taediosus* Chekanovskaya, 1975, *Rhyacodriloides gladiiseta* Martin & Brinkhurst, 1998 and *Burchanidrilus petitbonum* Martin & Brinkhurst, 1998 exclusively below the dimictic layer of the lake, suggesting the existence of genuine abyssal species in this family. However, two of these species (*R. gladiiseta* and *B. petitbonum*) were recently described for the first time and their presumed restricted depth range could result from a biased sampling effort.

Some tubificid species are only found in the dimictic zone: *Baikalodrilus intermedius* Snimschikova, 1991, *Rhyacodrilus stephensoni*, Cernosvitov 1941, *Isochaetides arenarius* (Michaelsen, 1926) and *Tasserkidrilus acapillatus* (Finogenova, 1972). A restricted depth distribution due to food shortage is suggested by the latter two species, as the only place they are found deeper than 250 m is at 420 m near the Frolikha hot vent.

In the abyssal zone, oligochaetes are not only rare but also very small, probably a consequence of food shortage at depth. As a result, classical sorting-out methods, based on the use of a sieve of 250 μm mesh, are perhaps unsuitable for organisms coming from this environment. A summary of some species measurements suggests that mesh size lower than 250 μm should be used in future studies (Table 1). Sampling the abyssal region of Lake Baikal is thus hampered, not only by low densities, but also by the small sizes of organisms. As this problem is underscored here for the first time, it is impossible to evaluate its importance on estimates of abundance distributions of Baikalian oligochaetes in our samples.

In conclusion, our evidence suggests that food restricts oligochaete distribution in Lake Baikal. As such, it is an excellent candidate for being a factor at the origin of segregation in populations, a necessary prerequisite for speciation. Clinal preferences along an ecological gradient are indeed deemed to create so-called 'dumb-bell' population structures, with limited gene-flow in intermediate environments, leading to parapatric speciation as a result of ecological segregation (Martens et al., 1994).

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