Zoosymposia 9: 024–035 (2014)
www.mapress.com/zoosymposia/

ISSN 1178-9905 (print edition)
ZOOSYMPOSIA
ISSN 1178-9913 (online edition)

http://dx.doi.org/10.11646/zoosymposia.9.1.7
http://zoobank.org/urn:lsid:zoobank.org:pub:87CE37D4-408C-4750-8D7D-B87ADE6FACA9

Profundal oligochaete faunas (Annelida, Clitellata) in Japanese lakes

AKIFUMI OHTAKA
Faculty of Education, Hirosaki University, Hirosaki 036-8560, Japan.
Email: ohtaka@cc.hirosaki-u.ac.jp

Abstract

Thirty-eight species of oligochaetes (Annelida, Clitellata) belonging to five families were recorded from profundal bottoms of 50 freshwater lakes on Japanese islands. They were mostly widely distributed species, and the composition of fauna is basically explained by the scheme of Timm (2012), with parallel replacement of European species. Oxygen, temperature and surrounding fauna could be main factors determining the profundal fauna in the lakes. The lumbriculids (*Styloscolex japonicus, Yamaguchia toyensis* and *Lumbriculus variegatus*), haplotaxids (*Haplotaxis gordioides*) and enchytraeids (*Marionina klaskisharum*) were restricted to several deep and oligotrophic lakes located in Hokkaido and northern Honshu, where *Rhyacodrilus komarovi* often accompanied them. *Limnodrilus hoffmeisteri* was the commonest species, occurring irrespective of the trophic status and bottom temperature of the lake. *Tubifex tubifex* also occurred in wide trophic scale, but it has never been found in shallow eutrophic lakes where the bottom temperature exceeds 15°C, where *L. hoffmeisteri, Branchiura sowerbyi* and several *Aulodrilus* species were the main representatives.

Key words: oligochaetes, fauna, lake profundal, Japan

Introduction

In the lake profundal, which is herein defined as the deepest vegetation-free muddy zone in lacustrine benthal as in Thienemann (1925) and Timm (2012), it has been recognized that oligochaetes have played a dominant role in the saprobic system, and their compositions have been discussed in terms of lake typology and other ecological and zoogeographical aspects (e.g., Brinkhurst 1974).

Timm (2012) recently reviewed the profundal oligochaete fauna in Palaearctic lakes and he showed that the fauna is mostly formed of species present also in shallower water, except for those in ancient rift lakes like Lake Baikal where endemic species living in the profundal have arisen through evolutionary radiation. The faunal composition in the "usual" lakes usually depends on geographical region and trophic state of the lake, the latter regulating the amount of oxygen in the bottoms, and parallel replacement species can be recognized between faraway European and Asian lakes (Timm 2012).

Along with Kurile Islands and the Kamchatka Peninsula, Japanese archipelago is part of the northwestern Pacific Rim and has variable kinds of lakes. In contrast to European and North American lakes, which are mostly glacial origin, there are many volcanic and maritime coastal ones in Japanese islands. In addition, the Japanese islands stretch a long way north to south with a corresponding heterogeneous climate, resulting in presence of both dimictic and monomictic lakes (Yoshimura 1936).

The first study on profundal oligochaetes in Japanese lakes was conducted by Stephenson (1917) in the ancient Lake Biwa, based on Annandale's samples collected in 1915 (cf. Annandale 1922). He originally described *Criodrilus bathybates* (syn. *Biwadrilus bathybates* (Stephenson)) and *Kawamuria japonica* (syn. *Branchiura sowerbyi* Beddard) along with unidentified tubificids and lumbriculids from the deep profundal of the lake.

Miyadi (1931a,b, 1932a–g) and Kitagawa (1973, 1974a,b, 1975a,b, 1978, 1979) intensively studied the structure of bottom fauna in many Japanese lakes from the viewpoint of lake typology. Miyadi (1933) classified them into eight types on the basis of causal-ecological concept. He classified four deep and

Accepted by Adrian Pinder: 31 Oct. 2013; published: 12 Jun. 2014

oligotrophic caldera lakes (Lakes Shikotsu, Toya and Kuttara in Hokkaido, and Lake Ideda in Kyushu) into "Oligochaeta lakes" where the profundal bottom fauna was composed of oligochaetes almost exclusively. Miyadi and Kitagawa recorded many "*Tubifex*" in their lists of zoobenthos, however, their "*Tubifex*" could not denote the taxon *Tubifex* but an oligochaete assemblage (Ohtaka and Iwakuma 1993), thus species composition can not be read in their studies.

Faunal records of lake profundal oligochaetes in Japanese lakes have been accumulated since 1980s in accordance with an increase in faunistic and ecological studies of lake zoobenthos (Ito 1978; Ito and Uno 1980; Ito et al. 2002, 2005; Fukuhara et al. 1987; Yasuda and Okino 1987; Ohtaka 1994, 1995, 2001a, b, 2004, 2006, 2009a, b; Ohtaka and Kikuchi 1997; Ohtaka and Ito 2002; Ohtaka and Iwakuma 1993; Ohtaka and Martin 2011; Ohtaka and Nishino 1995, 1999; Ohtaka et al. 1988, 2006, 2010; Nishino et al. 1999; Fend and Ohtaka 2004; Hirabayashi et al. 2007, 2012; Martin and Ohtaka 2008). Comparing these records, species composition of profundal oligochaetes in Japanese lakes can be basically explained by the scheme of Timm (2012), but faunal differences among respective lakes and the factors determining the species composition have not been well understood yet. Therefore, in the present study, I show the present status of profundal oligochaete composition in 50 Japanese freshwater lakes in relation to lake environments and long-term changes.

Study area and methods

Fifty freshwater lakes in Japanese islands were studied for their profundal oligochaete faunas (Table 1; Fig. 1). They include 4 tectonic, 14 volcanic, 23 dammed and 9 other lakes, with variable area, depth and trophic status. The majority of the specimens were collected by the author during 1982-2010 with the aid of an Ekman–Birge bottom sampler (grasp area 225 cm^2) from the ecological profundal, i.e., bottoms in aphotic zones or, when the lakes were shallower than the compensation depth, from offshore muddy bottoms without vegetation. The bottom samples were passed through a screen with a mesh pore size of 0.25 mm, and the retained worms were immediately fixed in 10% formalin solution, then dehydrated whole in a graded dilution series of ethanol : water, cleared in methyl salicylate, and mounted in Canada balsam on slides for identification. Selected specimens were dissected directly or cut serially for anatomical and histological observations. In addition, oligochaete specimens collected by colleagues from several lakes (Nos 4, 7, 23, 28, 34, 36), and those in voucher specimens of previous studies were examined and incorporated into the present study.

For environmental factors, bottom temperature was measured in 42 lakes when profundal specimens were collected during summer periods, and a modified Carson's trophic state index (mTSI; Aizaki et al. 1981) was calculated for every lake on the basis of Secchi disk transparency presented by NCBEA (1993) or author's observations. Oligotrophic, mesotrophic and eutrophic status of the lake water approximately correspond to lower than 30, from 30 to 50, and higher than 50 for the mTSI values, respectively.

Results

Faunal composition and regional characteristics

Thirty-eight oligochaete species were recorded from profundal bottoms of the 50 Japanese lakes studied (Table 2). Thirty-one species or 82 % of the total fauna belonged to the family Naididae sensu Erséus et al. (2008), which consisted of 11 naidines, 6 rhyacodrilines and 14 tubificines, and they were mostly widely-distributed species. Oligochaetes in other families were composed of three lumbriculid, one haplotaxid, two enchytraeid and one phreodrilid species.

The most frequently recorded species in the list was *Limnodrilus hoffmeisteri*, occurring in 36 lakes. It was followed by *Tubifex tubifex* (31 lakes), *Bothrioneurum vejdovskyanum* (11), *Limnodrilus claparedianus*, *Ilyodrilus templetoni* and *Aulodrilus* sp. (10 each), *Branchiura sowerbyi* and *Teneridrilus mastix* (9 each). The number of oligochaete species occurring in individual lake ranged from one to 14. The sole representatives in the profundal bottom were *Tubifex tubifex* in 5 lakes (Nos 3, 21, 24, 30, 48), *L. hoffmeisteri* in 2 lakes (Nos 31, 50) and *Rhyacodrilus coccineus* in the acidotrophic Lake Inawashiro (No. 20).

Lumbriculids (*Styloscolex japonicus, Yamaguchia toyensis* and *Lumbriculus variegatus*), haplotaxids (*Haplotaxis gordioides*) and enchytraeids (*Marionina klaskisharum*) were restricted to five deep and oligotrophic lakes located in Hokkaido and northern Honshu (Nos 5, 9, 10, 11, 15), where *Rhyacodrilus komarovi* was present, except for Lake Shikaribetsu (No. 5). Species composition of Lake Shikotsu (No. 9) and the neighboring L. Toya (No. 10) closely resemble each other, where all six species in L. Shikotsu were common to L. Toya, and five of them (*S. japonicus, Y. toyensis, H. gordioides, M. klaskisharum, Rhyacodrilus* sp.) were not found from other Japanese lake profundals. In addition, a minute polychaete, *Aeolosoma hemprichi* Ehrenberg was recorded only from the profundal of L. Shikotsu and Toya.

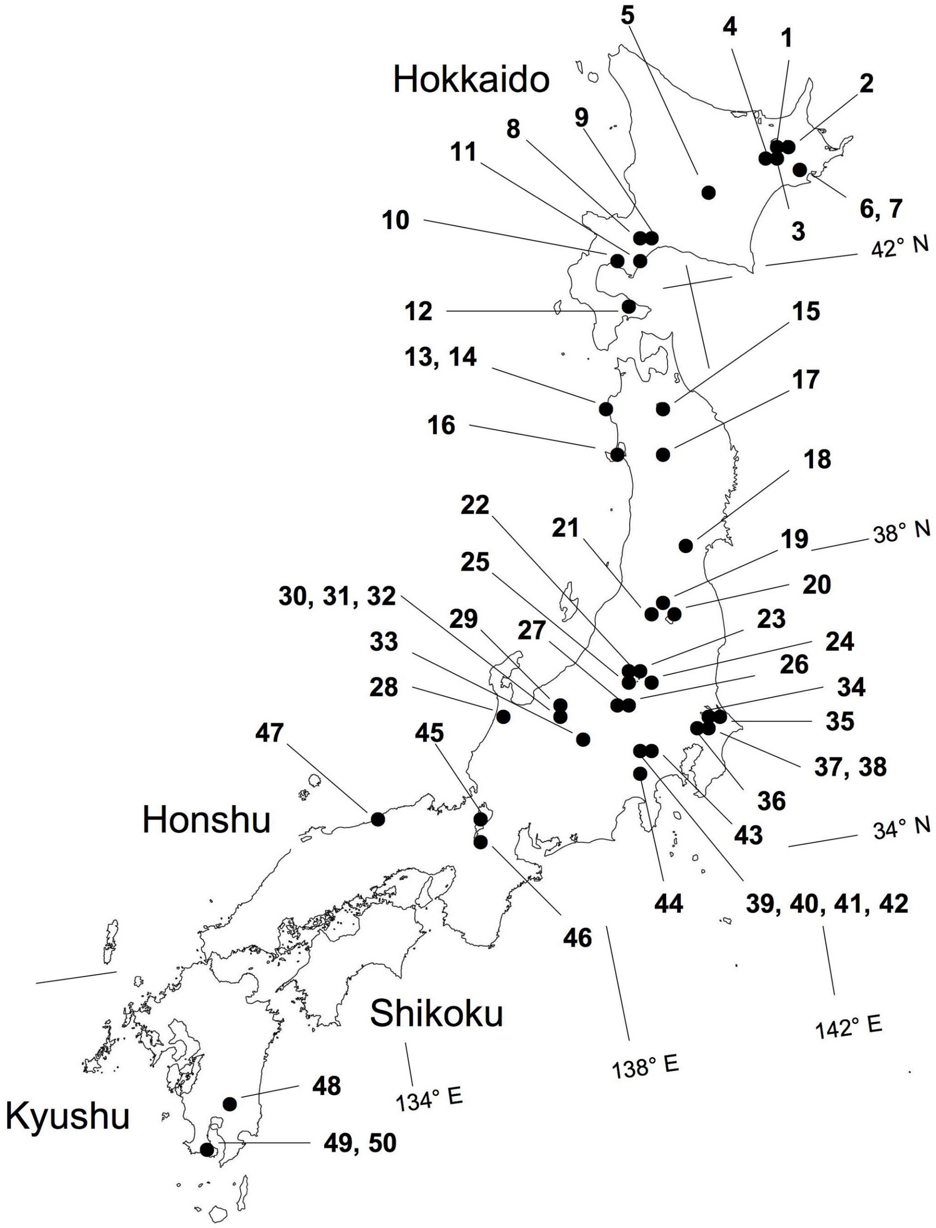

FIGURE 1. Distribution of lakes under study in the Japanese Archipelago. Lake number corresponds to those in Table 1.

Occurrence of oligochaetes in relation to lake environments

Bottom temperature ranged from 3.9 °C to 26.9 °C among 42 lakes in which temperature was measured during the summer season. Although many species occurred at a wide range of bottom temperatures, some were found only in a restricted range of temperatures (Fig. 2). For example, the lumbriculids, haplotaxid, enchytraeids and several naidids (*R. coccineus, R. komarovi, Krenedrilus towadensis, Embolocephalus nikolskyi*) were recorded in the bottoms with temperature lower than 8 °C. On the other hand, occurrences of *Rhyacodrilus hiemalis, L. claparedianus, Limnodrilus grandisetosus, I. templetoni* and *Aulodrilus* sp. were biased toward higher temperatures. They were found in thermally non-stratified shallow lakes where the bottom temperature exceeded 13 °C. *Branchiura sowerbyi* was usually found at the bottoms whose temperature was higher than 20 °C, but the gill-less variant form in the north basin of Lake Biwa (No. 45) inhabited the ever-cool bottom with 7-8 °C. *Limnodrilus hoffmeisteri* occurred at every temperature, while the second commonest tubificine, *T. tubifex* was never found in shallow lakes with bottom temperature higher than 15 °C.

TABLE 1. A list of Japanese freshwater lakes in which profundal oligochaete fauna were studied.

No. in Fig. 1	Lake name	Prefecture	Location[1] N	E	Area[2] (km^2)	Maximum depth[2] (m)	Origin[1, 2, 3]	Lake type[2, 3]	mTSI[4]
1	Kussharo	Hokkaido	43° 37'	144° 20'	79.5	117.0	caldera	acidtrophic	35
2	Mashu	Hokkaido	43° 35'	144° 33'	19.1	211.5	caldera	oligotrophic	9
3	Panke-to (Akan)	Hokkaido	43° 29'	144° 11'	2.8	54.0	dammed	oligotrophic	21
4	Akan	Hokkaido	43° 27'	144° 06'	13.3	45.0	caldera	eutrophic	38
5	Shikaribetsu	Hokkaido	43° 17'	143° 07'	3.4	99.0	dammed	oligotrophic	27
6	Toro	Hokkaido	43° 09'	144° 33'	6.4	7.0	lagoon	eutrophic	63
7	Takkobu	Hokkaido	43° 06'	144° 29'	1.4	2.3	lagoon	oligotrophic	55
8	Okotanpe	Hokkaido	42° 48'	141° 16'	0.4	20.5	dammed	oligotrophic	30
9	Shikotsu	Hokkaido	42° 45'	141° 20'	78.8	363.0	caldera	oligotrophic	17
10	Toya	Hokkaido	42° 36'	140° 51'	70.4	180.0	caldera	oligotrophic	26
11	Kuttara	Hokkaido	42° 30'	140° 11'	4.7	148.0	caldera	oligotrophic	13
12	O-numa (Oshima)	Hokkaido	42° 00'	140° 41'	5.5	13.6	dammed	eutrophic	50
13	O-ike	Aomori	40° 34'	139° 58'	0.05	24.0	dammed	mesotrophic	36
14	Ochikuchi-no-ike	Aomori	40° 34'	139° 59'	0.02	20.3	dammed	mesotrophic	47
15	Towada	Aomori/Akita	40° 28'	140° 53'	61.1	327.0	caldera	oligotrophic	28
16	Hachiro-gata	Akita	40° 00'	140° 00'	27.6	12.0	lagoon	eutrophic	60
17	Tazawa	Akita	39° 43'	140° 40'	25.8	423.0	caldera	acidtrophic	42
18	Izu-numa	Miyagi	38° 43'	141° 06'	2.9	1.3	fluvial	eutrophic	65
19	Hibara	Fukushima	37° 41'	140° 03'	10.8	31.0	dammed	mesotrophic	40
20	Inawashiro	Fukushima	37° 28'	140° 06'	104.8	94.6	tectonic	acidtrophic	35
21	Numazawa	Fukushima	37° 27'	139° 35'	2.9	96.0	caldera	oligotrophic	28
22	Oze-numa	Fukushima/Gunma	36° 56'	139° 18'	1.8	9.5	dammed	mesotrophic	36
23	Yu-no-ko	Tochigi	36° 48'	139° 25'	0.3	12.5	dammed	mesotrophic	43
24	Chuzenji	Tochigi	36° 44'	139° 28'	11.6	163.0	dammed	oligotrophic	28
25	Maru-numa	Gunma	36° 49'	139° 21'	0.5	47.0	dammed	mesotrophic	28
26	O-numa (Akagi)	Gunma	36° 33'	139° 11'	0.9	16.5	caldera	mesotrophic	41
27	Haruna	Gunma	36° 28'	138° 52'	1.2	14.0	caldera	mesotrophic	36
28	Kahoku-gata	Ishikawa	36° 40'	136° 41'	4.1	6.5	lagoon	eutrophic	73
29	Nojiri	Nagano	36° 49'	138° 13'	3.9	37.5	dammed	oligotrophic	37
30	Aoki	Nagano	36° 37'	137° 51'	1.9	58.0	dammed	oligotrophic	27
31	Nakatsuna	Nagano	36° 36'	137° 51'	0.1	12.0	dammed	mesotrophic	32
32	Kizaki	Nagano	36° 33'	137° 50'	1.4	29.5	dammed	mesotrophic	41
33	Suwa	Nagano	36° 03'	138° 05'	13.3	6.3	tectonic	eutrophic	76
34	Kasumi-ga-ura	Ibaraki	36° 02'	140° 24'	168.2	7.0	lagoon	eutrophic	73
35	Kita-ura	Ibaraki	36° 01'	140° 34'	34.4	10.0	lagoon	eutrophic	73
36	Naka-numa	Ibaraki	35° 53'	140° 10'	0.01	13.4	fluvial	eutrophic	44
37	Tega-numa	Chiba	35° 51'	140° 05'	6.5	3.8	dammed	eutrophic	80
38	Inba-numa	Chiba	35° 46'	140° 13'	11.6	2.5	dammed	eutrophic	69
39	Kawaguchi	Yamanashi	35° 31'	138° 45'	5.7	14.6	dammed	eutrophic	37
40	Motosu	Yamanashi	35° 28'	138° 35'	4.7	121.6	dammed	oligotrophic	25
41	Sai-ko	Yamanashi	35° 30'	138° 41'	2.1	73.2	dammed	oligotrophic	34
42	Shoji-ko	Yamanashi	35° 29'	138° 37'	0.5	15.2	dammed	eutrophic	37
43	Yamanaka	Yamanashi	35° 25'	138° 52'	6.8	13.3	dammed	mesotrophic	36
44	Ashi-no-ko	Kanagawa	35° 13'	139° 00'	6.9	43.5	dammed	mesotrophic	31
45	Biwa (north basin)	Shiga	35° 15'	136° 05'	614.7	103.6	tectonic	mesotrophic	35
46	Biwa (south basin)	Shiga	35° 03'	135° 54'	54.5[5)]	6	tectonic	eutrophic	60*
47	Koyama-ike	Tottori	35° 30'	134° 09'	7.0	6.3	lagoon	eutrophic	65
48	Mi-ike	Miyazaki	31° 53'	130° 58'	0.7	93.5	crater	oligotrophic	46
49	Ikeda	Kagoshima	31° 14'	130° 34'	10.9	233.0	caldera	mesotrophic	34
50	Unagi-ike	Kagoshima	31° 13'	130° 36'	1.2	56.5	crater	mesotrophic	53

1) after Horie (1962); 2) after NCBEA (1993); 3) after Japanese Society of Limnology (2006); 4) modified Carlson's Trophic State Index (Aizaki et al., 1981) based on Secchi depth in meter in NCBEA (1993) or author's values (*); 5) after Haga (2006)

TABLE 2. Profundal oligochaete fauna in 50 freshwater lakes in Japan.

+, present; ++ dominant

Lake number in Table 1 and Fig. 1	1 Kussharo	2 Mashu	3 Panke-to	4 Akan	5 Shikaribetsu	6 Toro	7 Takkobu	8 Okotanpe	9 Shikotsu	10 Toya	11 Kuttara	12 O-numa (Oshima)	13 O-ike	14 Ochikuchi-no-ike	15 Towada	16 Hachiro-gata	17 Tazawa	18 Izu-numa	19 Hibara	20 Inawashiro	21 Numazawa	22 Oze-numa	23 Yu-no-ko	24 Chuzenji	25 Maru-numa	26 O-numa (Akagi)	27 Haruna	28 Kahoku-gata	29 Nojiri	30 Aoki	31 Nakatsuna	32 Kizaki	33 Suwa	34 Kasumi-ga-ura	35 Kita-ura	36 Naka-numa	37 Tega-numa	38 Inba-numa	39 Kawaguchi	40 Motosu	41 Sai-ko	42 Shoji-ko	43 Yamanaka	44 Ashi-no-ko	45 Biwa (north basin)	46 Biwa (south basin)	47 Koyama-ike	48 Mi-ike	49 Ikeda	50 Unagi-ike	No. of lakes occurred
Lumbriculidae																																																			
Styloscolex japonicus Yamaguchi, 1937									++	+																																									2
Lumbriculus variegatus (Müller, 1774)					+					+					+																																				3
Yamaguchia toyensis Fend and Ohtaka, 2004									+	+																																									2
Haplotaxidae																																																			
Haplotaxis gordioides (Hartmann, 1821)									+	+																																									2
Enchytaeidae																																																			
Marionina klaskisharum Coates, 1983									+	+																																									2
Enchytraeidae non det.											+																																								1
Naididae																																																			
Amphichaeta sp.																																		+																	1
Paranais frici Hrabě, 1941																																		+			+														2
Specaria josinae (Vejdovský,1883)				+																																							+		+	+			+		5
Uncinais uncinata (Ørsted,1842)																																							+						+	+					3
Ophidonais serpentina (Müller, 1773)																							+																							+					2
Nais communis Piguet, 1906											+																																								1
Slavina appendiculata (d'Udekem,1855)																																													+	+					2
Vejdovskyella simplex Liang,1958												+						+																											+						3
Stylaria fossularis Leidy, 1852																		+																																	1
Dero digitata (Müller, 1773)							+					+				+												+					+	+	+														+		8
Stephensoniana trivandrana (Aiyer, 1926)																+												+						+	+										+		+				6
Bothrioneurum vejdovskyanum Štolc, 1886												+				+		+							+								+	+					+				+		+	+	+				11
Branchiura sowerbyi Beddard, 1892																+		+															+	+	+		+								+	+	+				9
Rhyacodrilus coccineus (Vejdovský, 1875)															+					++																															2
Rhyacodrilus komarovi Timm, 1990	+	++							+	+	+				++																																				6
Rhyacodrilus hiemalis Ohtaka, 1995																		+															+	+	+				+							+					6
Rhyacodrilus sp.									+	+																																									2
Krenedrilus towadensis Ohtaka, 2004															+																																				1
Tubifex tubifex (Müller, 1774)	+	+	++	++	++	+	+	+			++	+	+	+	+				++		++	++	++	++	++	++	++		+	++		++				++				++	++			++	++			++	++		31
Limnodrilus hoffmeisteri Claparède, 1862				+		++	++	++			+	++	+	+		++		++	+			+	+		+	+	+	++			++	+	++	++	++	+	++	+	++	+	+	++	++	+	+	++	++		+	++	36
Limnodrilus claparedianus Ratzel, 1868												+	+																				+	+	+	+	+	+								+	+				10
Limnodrilus grandisetosus Nomura, 1932																+		+															+	+	+		+									+	+				8
Limnodrilus profundicola (Verrill, 1871)																													++																+						2
Ilyodrilus templetoni (Southern, 1909)												+				+		+										+					+					+	+			+	+				+				10
Embolocephalus nikolskyi (Lastočkin, 1953)										++					+																																				1
Teneridrilus mastix (Brinkhurst, 1978)																+		+										+					+				+	++							+	+	+				9
Aulodrilus limnobius Bretscher, 1899								+								+																													+						3
Aulodrilus pigueti Kowalewski, 1914												+						+															+	+	+											+	+		+		8
Aulodrilus japonicus Yamaguchi, 1953																							+		+														+						+						4
Aulodrilus pluriseta (Piguet, 1906)																																		+			+	+													3
Aulodrilus sp.						+	+									+		+										+						+	+			+								+	+				10
Phreodrilidae																																																			
Astacopsidrilus ryuteki Martin and Ohtaka, 2008																																													+						1
No. of species occurred	2	2	1	3	2	3	4	3	6	8	5	8	3	2	6	10	0	11	2	1	1	2	4	1	4	2	2	6	2	1	1	2	10	13	9	3	7	6	6	2	2	2	4	2	14	13	10	1	5	1	

The mTSI values calculated from Secchi depth ranged from 9 (No. 2) to 80 (No. 37). Three lumbriculids (*S. japonicus, Y. toyensis* and *L. variegatus*), a haplotaxid (*H. gordioides*), an enchytraeid (*M. klaskisharum*) and a tubificine (*E. nikolskyi*) were restricted to oligotrophic lakes with mTSI values lower than 30 (Fig. 3). Occurrence of *R. komarovi* was also biased to oligotrophic lakes. On the other hand, *Aulodrilus* sp., *L. grandisetosus*, *B. sowerbyi* and *A. pluriseta* were invariably found in eutrophic lakes with mTSI values higher than 50. Many other species were found from meso- to eutrophic lakes. As an exception, *L. hoffmeisteri* occurred in lakes of every trophic state. *T. tubifex* was also found from wide trophic range, but it has been never found from the lakes with mTSI values higher than 60, all of which were shallow and with bottom temperature exceeding 15 °C in summer.

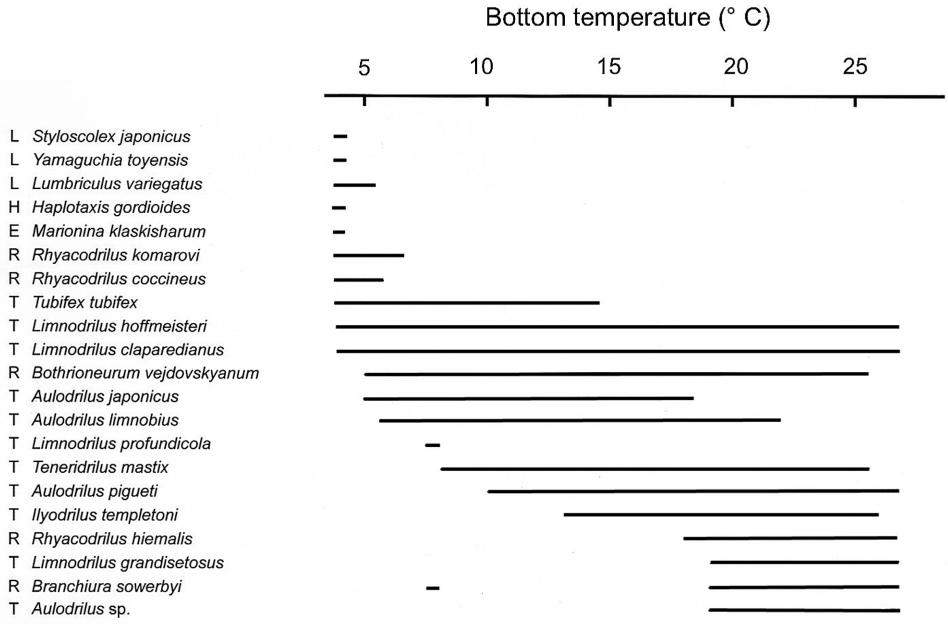

FIGURE 2. Range in summer temperatures in the profundal bottoms where respective oligochaete species were collected. Rare species, including all naidines, were excluded. L, Lumbriculidae; H, Haplotaxidae; E, Enchytraeidae; R, Rhyacodrilinae; T, Tubificinae.

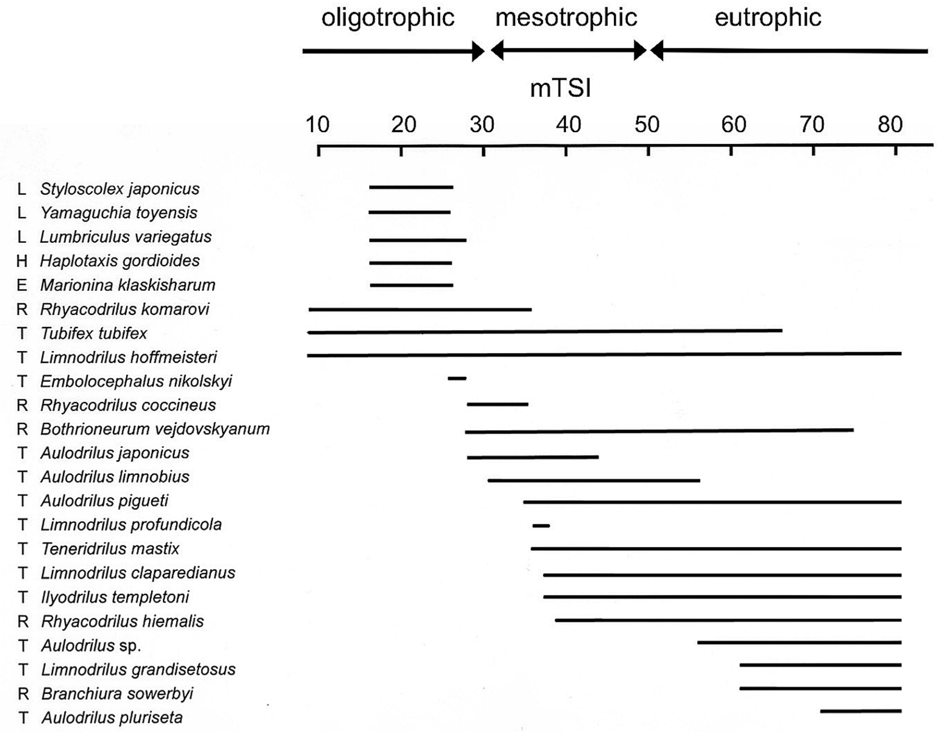

FIGURE 3. Range in the occurrence of oligochaete species in Japanese lakes on the trophic axis. Rare species, including all naidines, were excluded. L, Lumbriculidae; H, Haplotaxidae; E, Enchytraeidae; R, Rhyacodrilinae; T, Tubificinae.

Azoic zone

Practical surveys in the present study found that six lakes (Nos 4, 13, 14, 21, 49, 50) have azoic zones in their deepest profundal, where no zoobenthos was found. The bottom sediments of these lakes were deep black with a smell of H_2S, suggesting anoxic conditions. In addition, no macrozoobenthos including any oligochaetes was found in the profundal of Lake Tazawa (No. 17) as noted by Ohtaka and Martin (2011) although the bottoms were highly aerobic and harbored a small number of nematodes.

Discussion

Environmental factors determining oligochaete composition

All Japanese lakes except Lake Biwa are young and originated during or subsequent to the most recent glacial maximum (Saijo and Sakaguchi 1978), thus it is expected that their profundal bottom fauna is represented by a part of that distributed in the surrounding area. Most species recorded from profundal bottoms in the present study are certainly widely distributed species and they could be derived from surrounding waters. *Yamaguchia toyensis* and *K. towadensis* have been recorded only from L. Shikotsu and Toya (Fend and Ohtaka 2004), and L. Towada (Ohtaka 2004), respectively. However, these two stenotherm and oxyphilic species have been thought to be primarily subterranean (Fend and Ohtaka 2004; Ohtaka 2004), and they could occur in surrounding underground waters, too. Although enchytraeids are diverse and primarily inhabit terrestrial or marine littoral environments, a series of species have been recorded from profundal habitats of many lakes of the world, mainly in high latitudes (Timm, 1996). *Marionina klaskisharum*, recorded from Lakes Shikotsu and Toya in the present study, is one such species. It was originally described from the Pacific northeastern coast in Canada (Coates 1983) and subsequently recorded from the littoral of Lake Kurilskoe in Kamchatka Peninsula, Russia (Timm and Vvedenskaya 2006). Occurrence of a Gondwanan-originated phreodrilid, *Astacopsidrilus ryuteki*, from profundal Lake Biwa (Martin and Ohtaka 2009) is mysterious. But because there is no sign of former zoogeographical connection between Japan and Gondwanan landmasses, the Japanese record could be based on an introduction (Martin and Ohtaka 2009).

There has been wide recognition that trophic level as well as geographical region regulate oligochaete composition of lakes, and that profundal oligochaetes have been used for assessment of the lake trophic status (Aston 1973; Brinkhurst 1974; Brinkhurst and Kennedy 1965; Milbrink 1978, 1980, 1983; Milbrink et al. 2002; Lang 1985, 1998; Rodriguez and Reynoldson 2011). As in European lakes, two tubificines with high tolerance for oxygen deficiency, *Tubifex tubifex* and *Limnodrilus hoffmeisteri,* were widely distributed in trophic scale in Japan. Five lakes in which *T. tubifex* occurred as a single oligochaete were relatively small but deep and oligotrophic or mesotrophic like similar European lakes (Timm 2012). On the other hand, in Japan, *T. tubifex* has never been found from the hypertrophic lakes with the mTSI values exceeded 60, where *L. hoffmeisteri* was invariably dominating, accompanied by *B. sowerbyi* and *Aulodrilus* species. *Tubifex tubifex*, like most other tubificines, has been regarded to need at least periodically low temperatures for spermatogenesis, and it was absent in tropical regions (Timm 2012). Therefore, absence of *T. tubifex* in hypertrophic lakes in the present study could be due to high temperature, because these hypertrophic lakes are shallow and easily mixed and the bottom temperature exceeded 15 °C in summer, although the bottoms become as cool as in deep lakes in other seasons. The absence of *T. tubifex* and dominant occurrence of *L. hoffmeisteri* followed by *Aulodrilus* species and *B. sowerbyi* found in shallow hypertrophic lakes are also widely encountered in rice paddies in Japan, where the water is very shallow and the bottom temperature exceed 30 °C in summer and close to freezing in winter (Ohtaka unpublished). The present observation for the absence of *T. tubifex* in the lake bottoms with the temperature higher than 15 °C in summer appears to contradict the rearing temperature of higher than 15 °C in many laboratory studies (e.g. Timm 1984; Poddubnaya 1984; Anlauf 1994; Reynoldson et al. 1996; Arrate et al. 2004). This discrepancy might depend on genotypic variants in *T. tubifex* (Anlauf 1994; Beauchamp et al. 2001). It is also probable that other environmental parameters, for example oxygen or diet deficiency, can reduce tolerance to high temperature.

Similar to *L. hoffmeisteri*, adaptation to relatively higher temperatures is also suggested for *L. grandisetosus*, *Aulodrilus* spp. and *Branchiura sowerbyi*. Some *Branchiura sowerbyi* were found in an exceptionally ever-cool (7-8 °C) habitat in the profundal Lake Biwa, where the temperatures are lower than the threshold value for cocoon production (Aston 1968) or embryonic development (Bonacina et al. 1994) of usual *B. sowerbyi* (estimated at 10°C). The profundal L. Biwa population of *B. sowerbyi*, once described as

Kawamuria japonica by Stephenson (1917), reveals only weakly developed gills or is completely devoid of them, and differs from other *B. sowerbyi* populations in the chaetal morphologies too (Ohtaka and Nishino, 1999). A recent study using molecular characters showed that the profundal Lake Biwa *B. sowerbyi* can be regarded as a distinct lineage (Lindström et al. unpublished). It is highly probable that the profundal population of *B. sowerbyi* has adapted to life in the constantly cool lake profundal environment. This is the only oligochaete endemic to the present Lake Biwa as well as the only authentic oligochaete specialized to profundal environment in Japan.

Acidity of lake water can also be an important factor regulating composition of the oligochaete fauna. Roff and Kwiatkowski (1977) studied acid tolerance of several oligochaetes in six lakes in Northern Ontario, and they found that *L. hoffmeisteri* was missing from lakes with pH lower than 5.5-6.6, being more sensitive than *Stylodrilus heringianus* and *Rhyacodrilus montana* whose tolerance reached as low as pH 4. Occurrence of *R. coccineus* as a single oligochaete representative in Lake Inawashiro (No. 20) could be related to the acidic condition of the lake water (pH 4.4-5.5; Tanaka 1992). Another acidic Lake Tazawa (No. 17) used be neutral and harbored oligochaetes throughout the depths (Miyadi 1932f; Uéno 1940), but since 1940 the lake water has become acidic, with pH 4.4-5.3, due to the artificial inflow of very acidic water from Tama-gawa River into the lake for irrigation and power generation (Tanaka 1992). Accordingly, the benthic macroinvertebrates, including oligochaetes, have disappeared since that time (Kitagawa 1978). *Tubifex* (*Peloscolex*) *nomurai* Yamamoto and Okada, 1940, was originally described from the deep profundal of L. Tazawa, but it had gone extinct there and the taxonomic status remain unknown (Ohtaka and Martin 2011).

Rhyacodrilus hiemalis has been recorded from six shallow lakes in central Japan with high productivity (Table 1), and summer aestivation in the deep layer of bottom sediments has been known in at least four lakes: Lakes Suwa (No. 33), Kasumi-ga-ura (No. 34), Kita-ura (No. 35) and south basin of Lake Biwa (No. 46) (Takada et al. 1992 under the name of *Rhyacodrilus* sp; Ohtaka 1995; Narita 2006). *Rhyacodrilus hiemalis* needs aerobic and cool bottoms with a temperature lower than 15 °C for growth and reproduction as well as abundant food for rapid growth (Ohtaka and Kikuchi 1997; Narita 2006) and such environments can be found only in shallow eutrophic lakes where stratification does not last long.

Naidines are generally diverse and prosper in lake littoral with aquatic vegetation, and not common in lake profundals. Among 11 naidine species recorded from profundal in Japanese lakes, seven species (*Specaria josinae, Uncinais uncinata, Nais communis, Slavina appendiculata, Vejdovskyella simplex, Stephensoniana trivandrana, Dero digitata*) were collected from the depth exceeding 50 m. These records were concentrated on the most frequently studied north basin of Lake Biwa (No. 45) where oxygen never disappears from the bottom. Diverse and abundant naidines have been recorded from profundal bottoms in the Finnish Lake Päijänne (Särkkä 1989). Among 8 naidines listed by Särkkä (1989), three species (*S. appendiculata, U. uncinata, D. digitata*) are common with the Japanese deep profundal naidines listed above.

Comparison with other regions

Timm (2012) demonstrated that the profundal oligochaete assemblage in the oligotrophic L. Kurilskoe in Kamchatka displays a remarkable parallel to those in European lakes. Oligochaete composition in Japanese oligotrophic lakes is different from those in the Western Palaearctic and Kamchatkan lakes, although counterpart species are also recognized. In the Scandianvian lakes, *S. heringianus, Rhynchelmis limosella, Spirosperma ferox*, *T. tubifex*, *Lamprodrilus isoporus* etc. are typical of oligotrophic lake profundals, *Psammoryctides barbatus*, *Limnodrilus profundicola, R. coccineus, B. vejdovskyanum* etc. are typical of mesotrophic lakes, and *Potamothrix hammoniensis, L. claparedianus, I. templetoni* and *Aulodrilus pluriseta* etc. are typical of eutrophic lakes (Milbrink 1978, 1983). Among them, occurrences of *Tubifex tubifex* in oligotrophic lakes, *L. profundicola* and *R. coccineus* in mesotrphic ones, *I. templetoni* and *A. pluriseta* in eutrophic ones are common with the Japanese lakes. On the other hand, several lumbriculids in European oligotrophic lakes such as *S. heringianus* are replaced by *S. japonicus* and *Y. toyensis,* and the papillate tubificine *S. ferox* is replaced by *E. nikolskyi* in Japanese oligotrophic lakes. No *Potamothrix* species have been recorded in Japan, whereas, in Japanese eutrophic or hypertrophic lakes *R. hiemalis, Aulodrilus* sp. and *Branchiura sowerbyi* occurred in place of *Potamothrix* in addition to great abundance of *L. hoffmeisteri.*

Long-term changes in profundal oligochaete assemblages

During these several decades, many Japanese lakes have been polluted and a part of them have been recovering. However, long-term succession in species composition of the profundal oligochaete communities is mostly unclear due to absence of past studies, except for a few cases. Lake Biwa used to be oligotrophic, but it has suffered from anthropogenic eutrophication in past 40 years and a steady decrease in dissolved oxygen has been observed in the hypolimnion (Nishino and Ohtaka unpublished). As well as in Yamaguchi (1964), repeated surveys in Lake Biwa in recent decades could not find any lumbriculids and criodrilids (*Biwadrilus bathybates*) from the profundal bottoms, both of which were recorded in the earliest oligochaete research in 1915 (Stephenson 1917). This could have resulted from the environmental changes (Ohtaka and Nishino 2012). It has been widely recognized that as the trophic level rises, profundal oligochaete assemblages become simpler with some oxygen-tolerant species, while the density increases, and acceleration of eutrophication induces an anoxic bottom harboring no zoobenthos in the profundal. Increase in the profundal oligochaete density was recorded in many Japanese lakes such as the eutrophic Lake Yunoko (Ohtaka and Iwakuma 1993) and meso-eutrophic L. Kawaguchi (Hirabayashi et al. 2012), and this can be related to ongoing eutrophication. Among the Japanese lakes harboring oligochaetes throughout the depths in the past, azoic zones have been recorded in Lake Akan since 1970s (Kitagawa 1975; Ito and Uno 1980), L. Numazawa (present study), L. Ikeda since 1990s (Ohtaka et al. 2006) and L. Unagi (present study). In these lakes the last oligochaetes just before disappearing were *T. tubifex* and/or *L. hoffmeisteri*. In some lakes, for example L. Tazawa and L. Biwa, the water quality has been recovered recently, however oligochaete assemblages have not recovered accordingly, as reported in Lake Geneva (Lang 1985, 1998).

Acknowledgments

I would like to thank R. M. Schmelz for identification of *Marionina klaskisharum.* I am also indebted to T. Ueda, T. Ito, K. Hirabayashi, and T. Iwakuma for providing specimens used in the present study. Thanks are also due to M. Nishino, H. Abe, T. Kawai, T. Torii, M. Kawase, C. Yamazaki, T. Ogasawara, K. Naito, M. Kaneko, N. Anno, E. Kikuchi, T. Hanazato, R.B. Kuranishi, E. Inoue, T. Ishida, T. Kikuchi and D. Shirakawa, for their support in collecting the specimens. I am grateful to T. Timm for his useful suggestions in the present study. The present study was partly supported by the Grant-in-Aid from Japan Society for the Promotion of Science (No. 19570079).

References

Aizaki, M., Otsuki, A., Fukushima, T., Kawai, T., Hosomi, M. & Muraoka, K. (1981) Application of Carlson's trophic state index to Japanese lakes and relationships between the index and other parameters. *Verhandlungen der Internationalen Vereinigung für Limnologie*, 21, 643–649.

Anlauf, A. (1994) Some characteristics of genetic variants of *Tubifex tubifex* (Müller, 1774) (Oligochaeta: Tubificidae) in laboratory cultures. *Hydrobiologia*, 278, 1–6.
http://dx.doi.org/10.1007/bf00142306

Annandale, N. (1922) The macroscopic fauna of Lake Biwa. *Annotationes Zoologicae Japonenese,* 10, 127–153.

Arrate, J.A., Rodriguez, P. & Martinez-Madrid, M. (2004) *Tubifex tubifex* chronic toxicity test using artificial sediment: methodological issues. *Limnética*, 23, 25–36.

Aston, R.J. (1968) The effect of temperature on the life cycle, growth and fecundity of *Branchiura sowerbyi* (Oligochaeta: Tubificidae). *Journal of Zoology, London,* 154, 29–40.

Aston, R.J. (1973) Tubificids and water quality: a review. *Environmental Pollution*, 5, 1–10.

Beauchamp, K.A., Kathman, R.D., McDowell, T.S. & Hedrick, R.P. (2001) Molecular phylogeny of tubificid oligochaetes with special emphasis on *Tubifex tubifex* (Tubificidae). *Molecular Phylogenetics and Evolution*, 19, 216–24.

Bonacina, C., Pasteris, A., Bonomi, G. & Marzuoli, G. (1994) Quantitative observations on the population ecology of *Branchiura sowerbyi* (Oligochaeta, Tubificidae). *Hydrobiologia*, 278, 267–274.
http://dx.doi.org/10.1007/bf00142334

Brinkhurst, R.O. (1974) *The Benthos of Lakes.* Macmillan Press, London, 190pp.

Brinkhurst, R.O. & Kennedy, C.R. (1965) Studies on the biology of the Tubificidae (Annelida, Oligochaeta) in a polluted stream. *Journal of Animal Ecology*, 34, 429–443

Coates, K.A. (1983) New records of marine *Marionina* (Oligochaeta, Enchytraeidae) from the Pacific Northeast, with a description of *Marionina klaskisharum* sp. nov. *Canadian Journal of Zoology,* 61, 822–831.
http://dx.doi.org/10.1139/z83-108

Erséus, C., Wetzel, M.J. & Gustavsson, L. (2008) ICZN rules–a farewell to Tubificidae (Annelida, Clitellata). *Zootaxa,*1744, 66–68.

Fend, S.V. & Ohtaka, A. (2004) *Yamaguchia toyensis* n. sp., n. gen. (Annelida, Citellata, Lumbriculidae) from profundal lake habitat in Japan. *Zoological Science,* 21, 677-683.

Fukuhara, H., Ohtaka, A., Isobe, Y. & Sakamoto, M. (1987) Seasonal changes in vertical distribution, standing crop and fecal production of tubificids in the profundal region of a shallow Japanese lake. *Holarctic Ecology,* 10, 8–13.

Haga, H. (2006) Confirmation of surface area of the southern basin of Lake Biwa, Japan. *Japanese Journal of Limnology,* 67, 123–126. (In Japanese with English abstract)

Hirabayashi, K., Oga, K. & Yamamoto, M. (2007) Seasonal change in depth distribution of aquatic oligochaeta in southern Lake Kizaki, central Japan. *Acta Hydrobiologica Sinica,* 31, 109–115.

Hirabayashi, K., Oga, K., Yoshizawa, K., Yoshida, N. & Kazama, F. (2012) A long-term eutrophication process observed from the changes in the horizontal distribution of profundal oligochaete fauna in mesotrophic-eutrophic Lake Kawaguchi, Japan. *Turkish Journal of Zoology,* 36, 39–46.

Horie, S. (1962) Morphometric features and the classification of all the lakes in Japan. *Memories of the College of Science, University of Kyoto, Series B,* 29, 191–262.

Ito, T. (1978) Benthic macroinvertebrates and bottom sediments in Lake Onuma Group (Onuma, Konuma and Junsainuma), Hokkaido. *Scientific Reports of the Hokkaido Fish Hatchery,* 33, 1–19. (In Japanese with English abstract)

Ito, T., Ohtaka, A., Fukuhara, H., Ito, T., Wu, J., Mikami, H., Ishikawa, Y., Igarashi, S., Nagahora, S., Takano, K. & Yasutomi, R. (2002) Benthic macroinvertebrates in Lakes Toro and Shirarutoro, Kushiro Mire, Hokkaido, northern Japan. *Biology of Inland Waters,* 17, 17–24. (In Japanese with English abstract)

Ito, T., Ohtaka, A., Ueno, R., Kuwahara, Y., Ubukata, H., Hori, S., Ito, T., Hiruta, S., Tomikawa, K., Matsumoto, N., Kitaoka, S., Togashi, S., Wakana, I. & Ohkawa, A. (2005) Aquatic macroinvertebrate fauna in Lake Takkobu, Kushiro Marsh, norhtern Japan. *Japanese Journal of Limnology*, 66, 117–128. (In Japanese with English abstract)

Ito, T. & Uno, T. (1980) Long-term change of benthic macroinvertebrates and high content of organic matter in bottom sediments in Lake Akan, Hokkaido. *Scientific Reports of the Hokkaido Fish Hatchery,* 35, 11–19. (In Japanese with English abstract

Japanese Society of Limnology (2006) *Encyclopedia of Limnology*. Kodansha Publishing, Tokyo, 578 pp. (In Japanese)

Kitagawa, N. (1973) Studies on the bottom fauna of Lakes Kizaki-ko, Aoki-ko, Nakatsuna-ko, Nojiri-ko and Suwa-ko. *Japanese Journal of Limnology,* 34, 12–23. (In Japanese with English abstract)

Kitagawa, N. (1974a) Studies on the bottom fauna of Lakes Tyuzenji-ko, Yuno-ko, Suge-numa and Maru-numa. *Japanese Journal of Limnology,* 35, 32–41. (In Japanese with English abstract)

Kitagawa, N. (1974b) Studies on the bottom fauna of seven lakes of North Japan. *Japanese Journal of Limnology,* 35, 162–172. (In Japanese with English abstract)

Kitagawa, N. (1975a) Studies on the bottom fauna of five lakes in southern Hokkaido (Lakes Shikotsu-ko, Kuttara-ko, Toya-ko, Hangetsu-ko and Oshima O-numa). *Japanese Journal of Limnology,* 36, 48–54. (In Japanese with English abstract)

Kitagawa, N. (1975b) Studies on the bottom fauna of lakes Mashu-ko, Akan-Panke-ko and Toyoni-ko, Hokkaido, Japan. *Japanese Journal of Ecology,* 25, 155–159. (In Japanese with English abstract)

Kitagawa, N. (1978) A classification of Japanese lakes based on hypolimnetic oxygen and benthonic fauna. *Japanese Journal of Limnology,* 39, 1–8. (In Japanese with English abstract)

Kitagawa, N. (1979) Studies on the bottom fauna of four lakes in southern Kyushu, L. Ikeda-ko, Unagi-ike, Sumiyoshi-ike and Kirishimamiike. *Tansui-Seibutsu,* 30, 103–113. (In Japanese with English abstract)

Lang, C. (1985) Eutrophication of Lake Geneva indicated by the oligochaete communities of the profundal. *Hydrobiologia*, 126, 237–243.

Lang, C. (1998) Using oligochaetes to monitor the decrease of eutrophication: the 1982-1996 trend in Lake Geneva. *Archiv für Hydrobiologie*, 141, 447–458.

Martin, P. & Ohtaka, A. (2008) A new phreodrilid species (Annelida; Clitellata; Phreodrilidae) from Lake Biwa, Japan. *Species Diversity,* 13, 221–230.

Milbrink, G. (1978) Indicator communities of oligochaetes in Scandinavian lakes. *Verhandlungen der Internationalen Vereinigung für Limnologie,* 20, 2406–2411.

Milbrink, G. (1980) Oligochaete communities in pollution biology: the European situation with special reference to lakes in Scandinavia. *In*: Brinkhurst, R.O. & Cook, D.G. (Eds.) *Aquatic Oligochaete Biology*. Plenum Press, New York, pp. 433–455.

Milbrink, G. (1983) An improved environmental index based on the relative abundance of oligochaete species. *Hydrobiologia,* 102, 89–97.

Milbrink, G., Timm, T. & Lundberg, S. (2002) Indicative profundal oligochaete assemblages in selected small Swedish lakes. *Hydrobiologia,* 468, 53–61.

Miyadi, D. (1931a) Studies on the bottom fauna of Japanese lakes. I. Lakes of Sinano province. *Japanese Journal of Zoology,* 3, 201–257.

Miyadi, D. (1931b) Studies on the bottom fauna of Japanese lakes. II. Mountain lakes of the tributaries of the River Tone, with special reference to azoic zone. *Japanese Journal of Zoology,* 3, 259-297.

Miyadi, D. (1932a). Studies on the bottom fauna of Japanese lakes. III. Lakes of the Kwanto plain. *Japanese Journal of Zoology,* 4, 1–39.

Miyadi, D. (1932b). Studies on the bottom fauna of Japanese lakes. IV. Lakes of the Japan sea coast of southern Honsyû. *Japanese Journal of Zoology,* 4, 41–79.

Miyadi, D. (1932c). Studies on the bottom fauna of Japanese lakes. V. Five lakes at the north foot of Mt. Hudi and Lake Asi. *Japanese Journal of Zoology,* 4, 81–125.

Miyadi, D. (1932d): Studies on the bottom fauna of Japanese lakes. VI. Lakes of southern Kyûsyû. *Japanese Journal of Zoology,* 4, 127–149.

Miyadi, D. (1932e). Studies on the bottom fauna of Japanese lakes. VII. Lakes of Hokkaidô. *Japanese Journal of Zoology,* 4, 223–255.

Miyadi, D. (1932f). Studies on the bottom fauna of Japanese lakes. VIII. Lakes of North Japan. *Japanese Journal of Zoology,* 4, 253–287.

Miyadi, D. (1932g). Studies on the bottom fauna of Japanese lakes. IX. Lakes of the Yodo-gawa basin. *Japanese Journal of Zoology,* 4, 289–313.

Miyadi, D. (1933) Studies on the bottom fauna of Japanese lakes. X. Regional characteristics and a system of Japanese lakes based on the bottom fauna. *Japanese Journal of Zoology,* 4, 417–438.

Narita, T. (2006) Seasonal vertical migration and aestivation of *Rhyacodrilus hiemalis* (Tubificidae, Clitellata) in the sediment of Lake Biwa, Japan. *Hydrobiologia,* 564, 87–93.
http://dx.doi.org/10.1007/s10750-005-1710-3

NCBEA (Nature Conservation Bureau of the Environment Agency, Japan) (1993) *Report on the Environmental Researches in Japanese Lakes*. Japan Environment Agency, Tokyo, 188 pp. (text) and 238 pp. (data). (In Japanese)

Nishino, M., Ohtaka, A. & Narita, T. (1999) Studies on the aquatic oligochaete fauna in Lake Biwa, Central Japan. III. Distributions of respective species. *Japanese Journal of Limnology*, 60, 539–558.

Ohtaka, A. (1994) Redescription of *Embolocephalus yamaguchii* (Brinkhurst, 1971) comb. nov. (Oligochaeta, Tubificidae). *Proceedings of the Japanese Society of Systematic Zoology,* 52, 34–42.

Ohtaka, A. (1995) A new species of the genus *Rhyacodrilus* Bretscher (Oligochaeta, Tubificidae) from Japanese lakes. *Zoological Science,* 12, 491–498.
http://dx.doi.org/10.2108/zsj.12.491

Ohtaka, A. (2001a) Aquatic oligochaete fauna in the profundal zone of oligotrophic caldera lakes in northern Japan. *Research Report from the National Institute for Environmental Studies, Japan,* 167, 106–114. (In Japanese)

Ohtaka, A. (2001b) Oligochaetes in Lake Towada, Japan, an oligotrophic caldera. *Hydrobiologia,* 436, 83–92.

Ohtaka, A. (2004) A new species of the subterranean genus *Krenedrilus* Dumnicka (Oligochaeta, Tubificidae) from the deep bottom of an oligotrophic caldera lake in Japan. *Zoological Science,* 21, 465–471.
http://dx.doi.org/10.2108/zsj.21.465

Ohtaka, A. (2006) Aquatic oligochaete fauna in offshore Lake Hachiro-gata, Akita Prefecture, northern Japan. *Biology of Indand Waters,* 21, 11–19. (In Japanese with English abstract)

Ohtaka, A. (2009a) Records of aquatic oligochaetes (Annelida, Clitellata) from Lake Izunuma and Kabukurinuma Marsh, Miyagi Prefecture, northern Japan. *Izunuma-Uchinuma Wetland Researches*, 3, 1–11. (In Japanese with English abstract)

Ohtaka, A. (2009b) Profundal oligochaete fauna (Annelida, Clitellata) in three deep lakes, L. Tazawa, Inawashiro and Numazawa in Tohoku District, northern Japan. *Biology of Inland Waters*, 24, 25–32. (In Japanese with English abstract)

Ohtaka, A. & Ito, T. (2002) Outline of profundal zoobenthos in oligotrophic caldera Lakes Shikotsu and Toya in Hokkaido, northern Japan, with special reference to oligochaetes. *Biology of Inland Waters,* 17, 9–16. (In Japanese with English abstract)

Ohtaka, A. & Iwakuma, T. (1993) Redescription of *Ophidonais serpentina* (Müller, 1773) (Naididae, Oligochaeta) from Lake Yunoko, Central Japan, with record of the oligochaete composition in the lake. *Japanese Journal of Limnology*, 54, 251–259.
http://dx.doi.org/10.3739/rikusui.54.251

Ohtaka, A. & Kikuchi, H. (1997) Composition and abundance of zoobenthos in the profundal region of Lake Kitaura, Central Japan during 1980-1985, with special reference to oligochaetes. *Publications of Itako Hydrobiological Station, Faculty of Science, Ibaraki University,* 9, 1–14

Ohtaka, A., Kuranishi, R.B. & Kobyashi, T. (2010) Offshore benthic invertebrate fauna of Lakes Inba-numa and Tega-numa, Chiba Prefecture, Central Japan. *Journal of the Natural History Museum and Institute, Chiba,* 11, 1–9. (In Japanese with

English abstract)

Ohtaka, A. & Martin, P. (2011) Redescriptions of *Spirosperma apapillatus* and *Embolocephalus nikolskyi* (Annelida, Clitellata, Tubificinae) from Japan, with reference to distribution of papillate tubificines in Japanese freshwaters. *Zoological Science,* 28, 368–379.
http://dx.doi.org/10.2108/zsj.28.368

Ohtaka, A. & Nishino, M. (1995) Studies on the aquatic oligochaete fauna in Lake Biwa, Central Japan. I. Checklist with taxonomic remarks. *Japanese Journal of Limnology,* 56, 167–182.

Ohtaka, A. & Nishino, M. (1999) Studies on the aquatic oligochaete fauna in Lake Biwa, Central Japan. II. Records and taxonomic remarks on nine species. *Hydrobiologia*, 406, 33–47.

Ohtaka, A. & Nishino, M. (2012) Diversity and distribution of aquatic oligochaetes (Annelida, Clitellata) in Lake Biwa. *In*: Kawanabe, H., Nishino, M. & Maehata, M. (Eds.) *Lake Biwa: Interactions Between Nature and People*. Springer, Berlin, pp. 79–83.

Ohtaka , A., Nishino, M. & Kobayashi, T. (2006) Disappearance of deep profundal zoobenthos in Lake Ikeda, southern Kyushu, Japan, with relation to recent environmental changes in the lake. *Limnology*, 7, 237–242.
http://dx.doi.org/10.1007/s10201-006-0180-2

Ohtaka, A., Ujiiye, A. & Mawatari, S.F. (1988) Composition and abundance of zoobenthos in the profundal zone of Lake Ozenuma, Central Japan. *Japanese Journal of Limnology,* 49, 109–117.
http://dx.doi.org/10.3739/rikusui.49.109

Poddubnaya, T.L. (1984) Life cycles of mass species of Tubificidae, *In*: Brinkhurst, R.O. & Cook, D.G. (Eds.) *Aquatic Oligochaete Biology*. Plenum Press, New York, pp. 175–184.

Reynoldson, T.B., Rodriguez, P. & Madrid, M.M. (1996) A comparison of reproduction, growth and acute toxicity in two populations of *Tubifex tubifex* (Müller,1774) from the North American Great Lakes and Northern Spain. *Hydrobiologia*, 334, 199–206.

Roff, J.V. & Kwiatkowski, R.E. (1977) Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. *Canadian Journal of Zoology*, 55, 899–911.

Rodriguez, P. & Reynoldson, T.B. (2011) *The Pollution Biology of Aquatic Oligochaetes*. Springer, Dordrecht, 265 pp.

Saijo, Y. & Sakaguchi, Y. (1978) Lakes in Japan. *Kagaku,* 48, 352–362 (In Japanese).

Särkkä, J. (1989) Meiobenthic naidid and aeolosomatid oligochaetes from the profundal zone, and relations of species to eutrophication. *Hydrobiologia,* 180, 185–190.
http://dx.doi.org/10.1007/bf00027551

Stephenson, J. (1917) Zoological results of a tour in the Far East. Aquatic Oligochaeta from Japan and China. *Memoirs of the Asiatic Society of Bengal,* 6, 85–99.

Takada, K., Kato, K. & Okino, T. (1992) Environmental parameters and estivation of *Rhyacodrilus* (Tubificidae, Oligochaeta) in Lake Suwa, Japan. *Ecography,* 15, 328–333.
http://dx.doi.org/10.1111/j.1600-0587.1992.tb00043.x

Tanaka, M. (1992) *The Lakes in Japan*. Nagoya University Press, Nagoya, 530 pp. (In Japanese)

Thienemann, A. (1925) Die Binnengewässer Mitteleuropas. Eine limnologiche Einführung. *Binnengewässer*, 1. Stuttgart.

Timm, T. (1984) Potential age of aquatic Oligochaeta. *Hydrobiologia,* 115, 101–104.
http://dx.doi.org/10.1007/bf00027901

Timm, T. (1996) Enchytraeids (Oligochaeta, Enchytraeidae) as lake-dwellers. *Newesletter on Enchytraeidae,* 5, 47–55.

Timm, T. (2012) Profundal oligochaete assemblages in Palaearctic lakes. *Turkish Journal of Zoology,* 36, 121–131.

Timm, T. & Vvedenskaya, T.L. (2006) Oligochaeta (Annelida) of Lake Kurilskoe, Kamchatka Peninsula. *Species Diversity,* 11, 225–244.

Uéno, M. (1940) The life in Lake Tazawa before the introduction of acid water from the stream "Tama-gawa". *Japanese Journal of Limnology,* 10, 106–113. (in Japanese)

Yamaguchi, H. (1964) Aquatic Oligochaeta of Lake Biwa. *Tansui Seibutsu,* 9, 45. (In Japanese)

Yamamoto G, & Okada, K. (1940) An anatomical study of *Tubifex* (*Peloscolex*) *nomurai* n. sp., obtained at the bottom of Lake Tazawa, the deepest lake of Japan. *Science Reports of the Tôhoku Imperial University, Fourth series (Biology)*, 15, 427–455.

Yasuda, K. & Okino, T. (1987) Distribution and seasonal changes of aquatic Oligochaeta in Lake Suwa. *Japanese Journal of Limnology,* 48, 1–8.

Yoshimura, S. (1936) A contribution to the knowledge of deep water temperatures of Japanese lakes. Part 1. Summer temperature. *Japanese Journal of Astronomy and Geophysics,* 13, 61–120.