

Noriko Takamura · Tomiko Ito · Ryuhei Ueno  
Akifumi Ohtaka · Isamu Wakana · Megumi Nakagawa  
Youichi Ueno · Hirotsugu Nakajima

## Environmental gradients determining the distribution of benthic macroinvertebrates in Lake Takkobu, Kushiro wetland, northern Japan

Received: 10 July 2007 / Accepted: 7 May 2008 / Published online: 20 June 2008  
© The Ecological Society of Japan 2008

**Abstract** Effects of environmental variables on the distribution of benthic macroinvertebrates inhabiting sediments were studied at 25 sites along the shoreline of Lake Takkobu in the Kushiro wetland of northern Japan in summer 2003. During the last decade, the lake's status has undergone a drastic shift from clear water dominated by submerged macrophytes to turbid water dominated by phytoplankton. The canonical correspondence analysis showed that four environmental variables explained the significant variation in the macroinvertebrate species composition: submerged plant biomass, bottom sediment organic matter content (OMC), distance from the mouth of the Takkobu River, and bottom-layer pH. Five species of Chironomidae [*Chironomus* sp. (except *plumosus* group), *Psectrocladius* sp., *Corynoneura* sp., *Parachironomus* sp. *arcuatus* group, and *Zavreliella* sp.] occurred in sites with relatively lower pH and a high submerged plant biomass, whereas three species of Tubificidae (*Tubifex tubifex*,

*Aulodrilus limnobius* and *Aulodrilus* sp.) and two of Chironomidae (*Nanocladius* sp. and *Monodiamesa* sp.) occurred in sites with high pH and little vegetation. The three Tubificidae species also preferred organic-rich sediments. Irrespective of aquatic vegetation, *Sphaerium* sp. (Bivalvia) and *Monodiamesa* sp. (Chironomidae) occurred in low-OMC sites, whereas *Tanytus* sp. (Chironomidae) preferred high-OMC sites. The number of macroinvertebrate taxa showed the highest correlation with the number of submerged plants, suggesting that macroinvertebrate species richness was related mostly to submerged plant species diversity in this lake. The quantity and species richness of submerged plants and OMC are thus important determinants of the community structure of macroinvertebrates inhabiting sediments in Lake Takkobu.

**Keywords** Benthic macroinvertebrates · Environmental gradient · Aquatic macrophytes · Lake eutrophication · Canonical correspondence analysis (CCA)

N. Takamura (✉) · R. Ueno · M. Nakagawa  
National Institute for Environmental Studies,  
16-2 Onogawa, Tsukuba, Ibaraki 305-8506, Japan  
E-mail: noriko-t@nies.go.jp  
Tel.: +81-29-8502471  
Fax: +81-29-8502577

T. Ito  
3-3-5 Hakuyo-cho, Eniwa, Hokkaido 061-1434, Japan

A. Ohtaka  
Faculty of Education, Hirosaki University,  
1 Bunkyo-cho, Hirosaki, Aomori 036-8560, Japan

I. Wakana  
Lake Akan Eco-museum Center,  
1-1-1 Akanko-onsen, Akan, Kushiro, Hokkaido 085-0467, Japan

Y. Ueno  
Hokkaido Institute of Environmental Sciences,  
Kita-19 Nishi-12 Kitaku, Sapporo, Hokkaido 060-0819, Japan

H. Nakajima  
Wildlife Research Institute Co., Ltd., Kita-17 Nishi-4-1-3 Kitaku,  
Sapporo, Hokkaido 001-0017, Japan

### Introduction

The distribution and species composition of benthic macroinvertebrate communities inhabiting lakes are determined by independent or cumulative biotic and abiotic factors at different spatial scales. Recently, Johnson et al. (2004) revealed that in lakes the among-site variance in macroinvertebrate communities is best explained by habitat-scale characteristics. In littoral areas, differences of substrate (e.g., stone, gravel, cobbles, sand, silt, aquatic plants, or woody debris) are considered most important in determining the density, size structure, species composition, and species richness of the macroinvertebrate community (Hanson 1990; Oertli 1995; Dvořák 1996; van den Berg et al. 1997; Gardner et al. 2001; Tolonen et al. 2001; Weatherhead and James 2001).

An aquatic vegetation substrate has been shown to develop a unique macroinvertebrate fauna in littoral areas compared with other substrates such as stone,

sand, or silt (Tolonen et al. 2001). Not only the presence or absence of vegetation but also the life form, species, and biomass of aquatic macrophytes can greatly influence the abundance, taxonomic composition, and size structure of the macroinvertebrate community (Hanson 1990; Rasmussen 1993; Strayer et al. 2003). In addition, submerged, coarse, woody debris in the littoral area (Bowen et al. 1998), wind exposure, presence of filamentous algae, the shore slope (Brodersen 1995), dissolved oxygen (DO) content, high nutrient levels due to the inflow of organic pollutants (Petridis 1993), and water depth (Petridis 1993; Kato et al. 1999) have been shown to affect the habitat-scale community structure of benthic macroinvertebrates.

Fish predation (e.g., Wellborn and Robinson 1991) also clearly affects the community structure of benthic macroinvertebrates. Fish are also known to influence the community structure of benthic macroinvertebrates indirectly to some extent, through their excretion (Matsuzaki et al. 2007), or direct or indirect habitat disturbance or modification by serving as “ecosystem engineers” (Moore 2006). Field manipulations have revealed that the presence of macrophyte vegetation decreases the efficiency of fish predation and provides refuge for benthic macroinvertebrates (Crowder and Cooper 1982; Diehl 1992, 1993, 1995; Hanson and Butler 1994).

Lake Takkobu (surface area, 1.33 km<sup>2</sup>; mean depth, 1.0 m) is a lagoon in the east Kushiro wetland, and its catchment area (23.8 km<sup>2</sup>) is mostly covered with natural vegetation. However, a fragmentary summer survey by the Hokkaido Institute of Environmental Sciences and the National Institute for Environmental Studies revealed that the chlorophyll *a* (Chl *a*) concentrations rapidly increased between 1996 and 2000, and water blooms of cyanobacteria were observed in summer 2000 (Takamura et al. 2003). Concurrently, the number of aquatic plant species in the lake clearly decreased (Kadono 2007). According to the Geographic Survey Institute of Japan, most of the lake was occupied by submerged plants in 1992, but submerged vegetation remained only in the southern part of this lake in 2004 (Takamura et al. 2007). Therefore, in the last two decades, the state of Lake Takkobu has shifted from clear water dominated by submerged macrophytes to turbid water dominated by phytoplankton (Scheffer et al. 1993). Presumably, the benthic macroinvertebrate community structure in this lake also changed along with this drastic regime shift. An analysis of subfossil remains in a sediment core in Lake Søbygaard, Denmark, for example, showed distinct changes in chironomid communities reflecting eutrophication and a macrophyte succession through *Chara*, *Ceratophyllum*, and *Potamogeton* dominance to the present state, characterized by a complete loss of submerged vegetation and dominance of phytoplankton (Brodersen et al. 2001).

We aimed to elucidate the environmental factors that regulate the macroinvertebrate community inhabiting sediments in Lake Takkobu. Although this lake has

undergone a rapid loss of submerged vegetation, a clear environmental gradient of water quality from south to north is present (Takamura et al. 2007). This gradient should influence the present macroinvertebrate community structure in the lake. Among environmental factors, we focused on water depth, distance from the main inflowing river, macrophyte biomass and the number of macrophytes species, organic matter content of sediments, bottom-layer DO, bottom-layer pH, Chl *a* content in the water, and abundance of benthivorous fish.

---

## Methods

### Study site

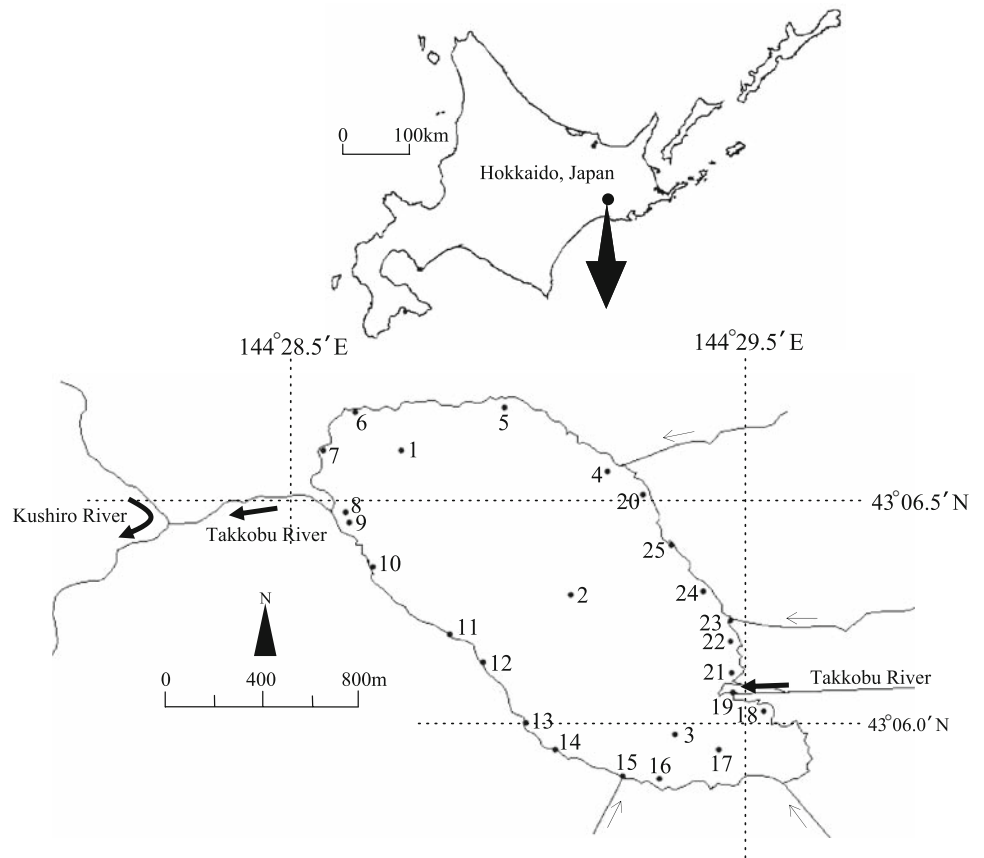
All surveys except for fish sampling were conducted during 23–25 July 2003. Fish were collected between 26 July and 5 August 2003. We selected 25 sampling sites along the lakeshore on the basis of the locations of river mouths and the main type of vegetation present (Fig. 1). The geographical location of each sampling site was recorded by differential global positioning system (DGPS) (Trimble Pro XR, Sunnyvale, CA, USA).

The main stream inflowing into this lake is the Takkobu River, and its catchment area accounts for 64.7% of the total catchment area of the lake. All other inflowing streams are small. In addition, the Kushiro River, which drains the lake, sometimes flows backward into the lake when the river's water level is high. According to Takamura et al. (2007), the lake shows a clear environmental gradient during the summer, from the mouth of the Takkobu River in the south to the Takkobu River outlet in the north. Little vegetation remains in the northern part of the lake, where only small patches of *Trapa* vegetation close to the lakeshore are found, whereas the southern area is mostly covered with *Trapa*, along with a narrow belt of submerged macrophytes and sparse patches of *Nuphar pumilum*. The submerged plants are dominated by *Potamogeton maackianus*. In addition, *Ceratophyllum demersum*, *Hydrilla verticillata*, *Myriophyllum verticillatum*, and *Potamogeton compressus* were observed. Water blooms occur widely in the north, where the water quality tends to be uniform. In the south, however, the water quality is heterogeneous, influenced not only by water inflowing from the Takkobu River but also by water from springs or sediments having a high redox potential.

### Measurements of environmental variables

We measured water depth, water temperature (WT), pH (HM-12P; DKK-TOA, Tokyo, Japan), and DO (YSI model 58; YSI, YellowSpring, Ohio) at the bottom of the water column at each sampling site. Water samples for measurement of the Chl *a* content were collected at 0.5-m depth at each site and were kept cool (4°C) in the field.

**Fig. 1** Location of Lake Takkobu in the southeastern part of Kushiro wetland. Numbers 1–25 indicate the sampling sites, and the *arrows* show the five inflowing rivers and one outflowing river of this lake



The water samples were immediately passed through a filter (Whatman GF/F), and then the filter was frozen at  $-20^{\circ}\text{C}$  for several days. Then, Chl *a* content was measured with a spectrophotometer (model 220A; Hitachi, Tokyo, Japan) after the filter was soaked in 99.9% methanol for 24 h (Marker et al. 1980).

The geographical location of each river mouth was determined on a 1:25,000 topographic map (Geographical Survey Institute, Tokyo, Japan) by using geographical information system (GIS) data (ArcGIS 9.1, Redlands, CA, USA). The distance between each river mouth and each sampling site was calculated from GIS data.

Sediment was collected with an Ekman grab sampler. The organic matter content in 5 g of the surface sediment was determined by combustion at  $600^{\circ}\text{C}$  to a constant weight. All plant bodies within a  $1\text{-m}^2$  randomly established quadrat were collected by scuba divers. The plants were washed to remove attached organisms, separated according to species, and then allowed to dry at  $90^{\circ}\text{C}$  to a constant weight.

We constructed a cubic frame (a  $2\text{-m}^2$  quadrat, 2.1 m high) to estimate fish density at each sampling site and covered the sides of the cube with a 4-mm mesh net, weighting its bottom so that it would sink. The cube was thrown into each sampling site, and all fish in the quadrat were collected with scoop and seine nets. Seventeen species of fish were collected in Lake Takkobu in

2003 (Hariu et al. 2007). The total number of fish of four benthivorous species (*Lefua nikkonis*, *Misgurnus anguillicaudatus*, *Rhinogobius* sp. OR, and *Gymnogobius castaneus*) was used as the variable for predator of benthic macroinvertebrates.

#### Collection of benthic macroinvertebrates

Sediment samples for benthic macroinvertebrates were collected with a stainless core sampler (200 mm in diameter, 300 mm high) by scuba divers and washed through a 0.2-mm mesh sieve within 24 h. The collected organic materials, including plant debris, were preserved in 4% formaldehyde solution. In the laboratory, the samples were sorted, washed through a 0.2-mm mesh net to remove the formaldehyde, and separated, using the unaided eye, into taxonomic groups (T. Ito). Chironomidae were identified to the species level by R. Ueno following Webb et al. (1985) and Wiederholm (1983), and Oligochaeta were identified by A. Ohtaka after Brinkhurst and Jamieson (1971). Gastropoda and Bivalvia were identified by Y. Kuwahara after both Masuda and Uchiyama (2004) and Tsalolikhin (2004), Hirudinoidea by T. Itoh following Yang (1996), Mysidae by S. Hiruta following Murano (1997), Ceratopogonidae by S. Kitaoka following Borkent and Wirth (1997), and Trichoptera and others by T. Ito following Wiggins (1996).

## Data analysis

A canonical correspondence analysis (CCA) was carried out with CANOCO 4.5 software (ter Braak and Šmilauer 2002) to elucidate the relationships between the species composition and their explanatory environmental variables. CCA can be appropriate to find a particular set of observed environmental variables to which the present macroinvertebrate taxa respond (McCune 1997). We identified 43 macroinvertebrate taxa, but seven taxa that occurred at only one site as well as eight taxa that included two or more species (Table 1) were excluded from the analysis, because casual and uncertain taxa might distort the species ordination. Then, we considered 28 taxa and 13 environmental variables (Table 2).

Before performing CCA, we conducted a detrended correspondence analysis (DCA) with our data set, identified environmental variables (10 variables) that significantly correlated with the DCA site scores of the first or second axis by Kendall's rank correlation ( $P < 0.05$ ), and then calculated Pearson correlation coefficients among the 10 environmental variables. On the basis of this information, several CCA ordinations were performed to identify the significant environmental variables explaining the variance of species data in the CCA. We avoided using a combination of environmental variables that were correlated with one another (Table 3;  $|r| \geq 0.5$ ). The DCA was also performed with CANOCO 4.5 software. Statistical significance of eigenvalues and species-environment correlations for the first two axes generated by the CCA were tested by the Monte Carlo method based on 999 permutations. The density values of 28 macroinvertebrate taxa were  $\ln(\chi + 1)$ -transformed to obtain homogeneity of variance. Organic matter content (%) values of the sediments were arcsine-transformed, and biomass values of aquatic plants and abundance of fish were  $\ln(\chi + 1)$ -transformed. Kendall's rank correlation and Pearson correlation were calculated with R software (Dalgaard 2002).

## Results

### Macroinvertebrates and environmental variables

Forty-three macroinvertebrate taxa were identified, including 1 Nematoda, 1 Gastropoda, 2 Bivalvia, 6 Oligochaeta, 2 Hirudinea, 1 Mysidae, 2 Hydroptilidae, 1 Ceratopogonidae, and 27 Chironomidae (Table 1). *Limnodrilus hoffmeisteri* (Tubificidae), *Chironomus* sp. *plumosus* group, *Procladius* sp., and *Glyptotendipes* spp. (Chironomidae) were the most common taxa. Each of these taxon was recorded at more than 17 of the 25 sampling sites. The most abundant taxa were *Glyptotendipes* spp., *Chironomus* sp. *plumosus* group, and *L. hoffmeisteri*, accounting for 28, 15, and 13%,

respectively, of the total number of macroinvertebrate individuals. Mean density (no.  $m^{-2}$ ) of each taxon ranged from 32 to 3,141 when counted only at sites where the taxon was present (Table 1).

We hypothesized that the 13 selected environmental variables regulated the benthic macroinvertebrate community structure in Lake Takkobu (Table 2). The values of these variables show that there was considerable heterogeneity among sites. Among them, water depth, abundance of benthivorous fish, and Chl *a* content were excluded because they showed no significant correlations ( $P > 0.05$ ) with the DCA site scores of the first or second axis by Kendall's rank correlation. The Pearson correlation matrix among the 10 included environmental variables is shown in Table 3. The variables relating to aquatic plants, except between the biomasses of *Trapa* and *Potamogeton*, were significantly correlated with one another.

### Relationship of species composition to environmental gradients

In the CCA, distance from the mouth of the Takkobu River (DISTANCE), biomass of submerged plants (BIO-SUB), organic matter content of the bottom sediments (OMC), and bottom-layer pH (BpH) explained the significant variation in the macroinvertebrate species composition (Fig. 2). The first and second canonical axes explained 10.3% (eigenvalue 0.232) and 9.5% (eigenvalue 0.214), respectively, of the variance in the species data, and 39.9 and 36.7%, respectively, of the variance in species-environment relationships (Table 4). Intrasite correlations showed that the first axis was a gradient of both decreasing BIO-SUB and increasing BpH and that the second axis was a gradient of decreasing OMC (Table 4). The species-environment correlation of the first axis became significant in the Monte Carlo permutation test ( $P < 0.05$ ) only when we selected BIO-SUB among the six variables relating to aquatic plants as the environmental variable.

### Species responses to environmental gradients

Five species belonging to Chironomidae (*Chironomus* sp. except *plumosus* group, *Psectrocladius* sp., *Corynoneura* sp., *Parachironomus* sp. *arcuatus* group, and *Zavreliella* sp.) occurred at sites with relatively lower pH and a high biomass of submerged plants (Fig. 2). Three Tubificidae species (*T. tubifex*, *A. limnobius* and *Aulodrilus* sp.) and two Chironomidae species (*Nanocladius* sp. and *Monodiamesa* sp.) occurred at sites with high pH and little vegetation. In addition, the three Tubificidae species preferred organic-rich sediments (Fig. 2). *Sphaerium* sp. (Bivalvia) as well as *Monodiamesa* sp. (Chironomidae) occurred at sites with low OMC, whereas *Tanyppus* sp. (Chironomidae) was found at sites with high OMC.

Table 1 List of benthic macroinvertebrate taxa collected from Lake Takkobu in July 2003

Identifier	Taxon	Abbr.	No. of sites present	% of total number	Mean	Median	Maximum	Mean when present	Median when present
1 <sup>a</sup>	Nematoda Mollusca Gastropoda Heterobranchia, Heterostrophia Valvatidae		9	0.66	53	0	382	147	159
2	<i>Cincinna japonica</i> (Martens) Bivalvia Unionoidea Unionidae	Cin Ano	2 2	0.03 0.23	3 19	0 0	32 325	32 232	32 232
3	<i>Anodonta woodiana</i> (Lea) Veneroidea Pisidiidae		2	0.03	3	0	32	32	32
4	<i>Sphaerium</i> sp. Annelida Oligochaeta Haplotaaxida Tubificidae	Sph	2	0.03	3	0	32	32	32
5	<i>Tubifex tubifex</i> (Müller)	Tub	2	0.14	11	0	159	143	143
6	<i>Limnodrilus hoffmeisteri</i> Claparède	Lim.h	22	13.16	1,049	573	5,000	1,192	605
7	<i>Limnodrilus udekemianus</i> Claparède	Lim.u	7	0.46	37	0	279	132	107
8	<i>Aulodrilus limmobius</i> Bretscher	Aul.l	2	0.11	9	0	191	111	111
9	<i>Aulodrilus</i> sp.	Aul.sp	4	0.78	62	0	159	390	271
10	<i>Botrioneurum vejdoskyanum</i> Stolc Hirudinoidea, Hirudinea Rhynehobdellida	Bot	3	0.11	9	0	96	74	64
11 <sup>b</sup>	Glossiphoniidae								
12 <sup>b</sup>	<i>Hemiclepsis marginata</i> (Müller) <i>Hemiclepsis</i> sp., juvenile		1 1	0.02 0.02	1 1	0 0	32 32	32 32	32 32
13	Arthropoda Crustacea Malacostraca Mysidae <i>Neomysis intermedia</i> (Czerniavsky)	Neo	12	2.83	226	0	1,068	470	451
14 <sup>b</sup>	Insecta Trichoptera Hydroptilidae								
15 <sup>a</sup>	<i>Hydropygia</i> sp. <i>Orthotrichia</i> spp. Diptera		1 8	0.03 1.29	3 103	0 0	64 925	64 323	64 170
16	Ceratopogonidae <i>Pulponia</i> sp. Chironomidae	Pal	15	1.54	123	32	751	205	159
17 <sup>b</sup>	<i>Natarsia</i> sp.		1	0.02	1	0	32	32	32
18	<i>Procladius</i> sp.	Pro	19	3.85	307	186	1,823	404	255
19	<i>Tanyptus</i> sp.	Tan	3	0.57	46	0	1,006	382	107
20 <sup>b</sup>	Tanyptodinae Gen. sp.		1	0.32	25	0	637	637	637
21	<i>Monodiamesa</i> sp.	Mon	2	0.21	17	0	255	207	207
22	<i>Corynoneura</i> sp.	Cor	2	0.17	14	0	315	174	174

Table 1 (Contd.)

Identifier	Taxon	Abbr.	No. of sites present	% of total number	Mean	Median	Maximum	Mean when present	Median when present
23 <sup>a</sup>	<i>Cricotopus</i> spp.		9	4.35	347	0	4,013	963	318
24 <sup>b</sup>	<i>Heterotrissocladius</i> sp.		1	0.48	38	0	955	955	955
25	<i>Nanocladius</i> sp.	Nan	2	0.50	39	0	955	494	494
26	? <i>Paratrichocladius</i> sp.	?Par	2	0.14	11	0	255	143	143
27	<i>Psectrocladius</i> sp.	Pse	8	0.56	44	0	318	139	111
28	<i>Chironomus</i> sp. <i>plumosus</i> group	Chi.p	21	15.08	1,203	764	3,468	1,432	1,462
29	<i>Chironomus</i> sp. (except <i>plumosus</i> group)	Chi.sp	4	0.28	22	0	318	138	101
30	<i>Cladopelma</i> sp.	Cla	7	0.83	66	0	559	235	159
31	<i>Dicerotendipes</i> sp.	Dic	7	0.74	59	0	559	212	159
32	<i>Endochironomus tendens</i> (Fabricius)	End	5	2.10	168	0	3,153	838	318
33 <sup>b</sup>	<i>Endochironomus</i> sp.		1	0.09	7	0	178	178	178
34 <sup>a</sup>	<i>Glyptotendipes</i> spp.		18	28.36	2,261	318	20,617	3,141	430
35	<i>Microchironomus</i> sp.	Mic	2	0.17	14	0	315	174	174
36	<i>Parachironomus</i> sp. <i>arcuatus</i> group	Par	11	1.66	133	0	1,261	301	178
37	<i>Polypedilum sordens</i> (van der Wulp)	Pol.s	14	2.59	207	116	1,210	369	182
38	<i>Polypedilum</i> sp.	Pol.sp	8	0.68	54	0	669	169	118
39	<i>Zavrelia</i> sp.	Zav	5	0.49	39	0	315	196	177
40 <sup>a</sup>	<i>Chironomini</i> Gen. spp.		10	1.57	125	0	946	314	239
41 <sup>a</sup>	<i>Paratanytarsus</i> spp.		15	8.84	705	107	4,099	1,175	559
42 <sup>a</sup>	<i>Tanytarsus</i> spp.		15	3.69	294	127	2,037	490	318
43 <sup>a</sup>	<i>Tanytarsini</i> Gen. spp.		2	0.19	15	0	223	191	191

For each taxon, the number of sites where present; percentage of total individuals; mean, median, and maximum density (number per square meter) at 25 sites; and mean and median density (number per square meter) at sites where present are shown

<sup>a</sup> Taxa not included in the CCA because they include two or more species

<sup>b</sup> Taxa not included in the CCA because they were collected at only one site

**Table 2** Summary of statistics of 13 environmental variables at 25 sites

Variable	Units	Mean	Median	Min.	Max.	Mean when present	Median when present	No. of sites present
1 Water depth	m	1.0	0.9	0.4	1.9			
2 Distance from the mouth of the Takkobu River	m	744	642	33	1,641			
3 Benthivorous fish (abundance)	No. m <sup>-2</sup>	30	10	1	426			
4 Floating-leaved plants (biomass)	gDW m <sup>-2</sup>	45.4	0.1	0	296.9	87.2	58.8	13
5 <i>Trapa japonica</i> (biomass)	gDW m <sup>-2</sup>	37.5	0.1	0	296.9	72.2	34.1	13
6 Species richness of floating-leaved plants		0.68	1	0	2	1.3	1	13
7 Submerged plants (biomass)	gDW m <sup>-2</sup>	17.1	2.1	0	91.4	26.8	14.8	16
8 <i>Potamogeton maackianus</i> (biomass)	gDW m <sup>-2</sup>	14.2	0.7	0	85	27.2	22.2	13
9 Species richness of submerged plants		2.4	3	0	5	3.8	4	16
10 Organic content of bottom sediments	%	5.1	5.4	1.8	6.7			
11 Chlorophyll a in the water	µg l <sup>-1</sup>	59.8	60.2	1.3	130.9			
12 Bottom pH		6.9 <sup>a</sup>	6.9	6.3	7.3			
13 Bottom DO	mg l <sup>-1</sup>	4.6	4.1	0.5	11.1			

<sup>a</sup> Calculated geometrically

**Table 3** Pearson's correlation coefficients among the 10 environmental variables that were significantly correlated with the first or second DCA site scores

	(2)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(12)
(2) Distance from the mouth of the Takkobu River									
(4) Floating-leaved plants (biomass)	-0.33								
(5) <i>Trapa japonica</i> (biomass)	-0.33	0.93**							
(6) Species richness of floating-leaved plants	-0.31	0.79**	0.64**						
(7) Submerged plants (biomass)	-0.30	0.52**	0.46*	0.69**					
(8) <i>Potamogeton maackianus</i> (biomass)	-0.17	0.44*	0.37	0.66**	0.97**				
(9) Species richness of submerged plants	-0.55**	0.72**	0.68**	0.76**	0.83**	0.73**			
(10) Organic content of bottom sediments	0.19	-0.15	-0.21	0.04	0.24	0.29	0.05		
(12) Bottom pH	0.49*	-0.55**	-0.61**	-0.38	-0.38	-0.27*	-0.48*	-0.08	
(13) Bottom DO	-0.07	-0.34	-0.28	-0.41*	-0.41*	-0.44*	-0.21	-0.47*	0.61**

\* $P < 0.05$ , \*\* $P < 0.01$

These three species showed little relation to aquatic plants.

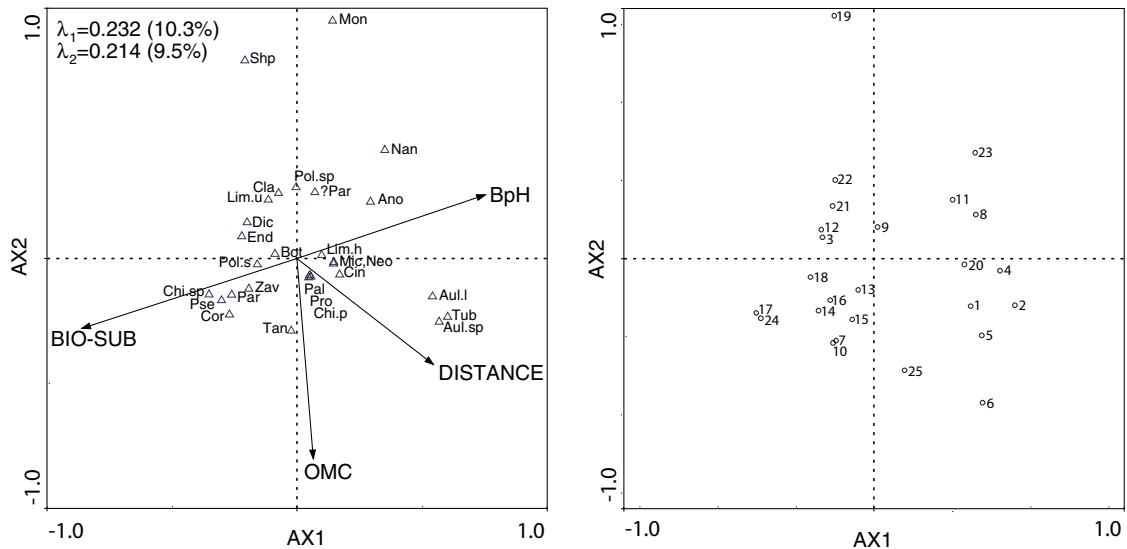
#### Relationships between number of taxa and environmental variables

The number of macroinvertebrate taxa was significantly and positively correlated with the number of species of submerged macrophytes ( $n = 25$ ,  $r = 0.490$ ,  $P = 0.012$ ), the biomass of floating-leaved macrophytes ( $n = 25$ ,  $r = 0.443$ ,  $P = 0.027$ ), and the biomass of *Trapa* ( $n = 25$ ,  $r = 0.453$ ,  $P = 0.023$ ) among the 13 environmental variables.

#### Discussion

The variance in the distribution of the benthic macroinvertebrate community in this lake was well explained by environmental gradients related to BIO-SUB and OMC. The six variables relating to aquatic plants were

closely related to one another (Table 3). Although *Trapa* is the most conspicuous vegetation in the lake, it was not the *Trapa* biomass but BIO-SUB that was selected as the best explanatory variable among them. The life form of aquatic plants seems to influence macroinvertebrate community structure. For example, the total biomass of macroinvertebrates was found to be higher, and the peak of their biomass size spectrum smaller, in *Chara* beds than in rooted-plant (mostly *Isoetes* sp.) weed beds (Hanson 1990; Rasmussen 1993). Chironomids, anisopteran, gastropods, and sphaerid clams dominated the macroinvertebrate community in *Chara* beds, whereas amphipods dominated the community in rooted-plant (mostly *Isoetes* sp.) weed beds (Hanson 1990). Benthic macroinvertebrates were found to dominate in *Vallisneria americana* beds, whereas epiphytic species not only dominated in *Trapa natans* vegetation but also increased the total density of macroinvertebrates, because of the high plant biomass of *Trapa* (Strayer et al. 2003). Although how *Trapa* or submerged vegetation differently influenced the macroinvertebrate community structure was not clear in our study, the presence of



**Fig. 2** Distribution of 28 macroinvertebrate taxa in relation to environmental variables: CCA ordination diagrams showing species (left, open triangles), sites (right, open circles), and environmental variables (left, arrows); the first axis is horizontal, the second

vertical. The abbreviations of 28 species are defined in Table 1. The environmental variables are *DISTANCE* distance from the mouth of the Takkobu River, *BIO-SUB* biomass of submerged plants, *OMC* organic contents of the sediments, and *BpH* bottom-layer pH

**Table 4** Summary statistics for the first two CCA axes

	Axis 1	Axis 2
Eigenvalues	0.232	0.214
Monte Carlo test, <i>P</i> value	0.001	0.001
Species-environment correlations	0.893	0.888
Monte Carlo test, <i>P</i> value	0.036	0.007
Cumulative variance (%)		
Explained by species data	10.3	19.8
Explained by species-environmental relation	39.9	76.6
Intrasect correlations of variables with axes		
Distance from the mouth of the river	0.546	-0.425
Submerged plants (biomass)	-0.861	-0.280
Organic content of bottom sediments	0.065	-0.801
Bottom pH	0.753	0.254

Significance was determined with Monte Carlo tests (999 permutations)

aquatic vegetation was shown to be the most important determinant of the macroinvertebrate community in this lake.

Generally, most studies seem to evaluate the macroinvertebrate community in aquatic vegetation by including both epiphytic and benthic communities. The present study, however, showed that the influence of aquatic vegetation was prominent even when the target was restricted to the benthic community inhabiting sediments. Presumably, vegetation is important to the benthic community because it provides refuge from predators, physically stable habitats, better food conditions, and DO. Among these, the roots of some macrophytes have been shown previously to provide benthic macroinvertebrates with DO (Ságová-Marecková and Kvet 2002).

OMC was shown to be an important environmental variable, followed by BIO-SUB. Beaty et al. (2006) experimentally showed that higher OMC enhances the growth of *Chironomus*, but few studies have suggested that OMC determines the community structure of

benthic macroinvertebrates in lake littoral areas. Irrespective of aquatic vegetation, in this lake, *Tanytus* sp. was shown to prefer organic-rich sediments, whereas *Monodiamesa* sp. and *Sphaerium* sp. preferred environments with the least OMC. *Monodiamesa bathyphila* has been reported to inhabit sandy sediments beneath oligotrophic waters (Sæther 1983), in accordance with our result.

Although bottom DO was not retained as a variable in the CCA, low concentrations of bottom DO might be one important factor (although associated with other factors) affecting species composition at lake littoral sites around the mouth of an organically polluted river (e.g., Petridis 1993). In our study, bottom DO (with a range of 5.6–11.1 mg l<sup>-1</sup>) did not decrease near the mouth of any river. DO often decreases to below the critical threshold for aquatic life below dense *Trapa* vegetation (Caraco and Cole 2002) or submerged macrophytes (Takamura et al. 2003). In this lake, however, concentrations of bottom DO did not correlate with the *Trapa* biomass, probably because some sites with dense



vegetation also had high bottom DO owing to the presence of springs (Takamura et al. 2007).

Chironomidae is the most numerous taxonomic group inhabiting the sediments in this lake. Their densities were similar to or higher than those reported in *Trapa* and *Vallisneria* vegetation of the freshwater tidal Hudson River (Strayer et al. 2003). The CCA revealed that the occurrence of several chironomid species largely depended on biomass of submerged plants in this lake. Among them, five species, *Chironomus* sp. except *plumosus* group, *Psectrocladius* sp., *Corynoneura* sp., *Parachironomus* sp. *arcuatus* group, and *Zavreliella* sp., preferred more organic-rich sediments than *Endochironomus tendens*, *Dicrotendipes* sp. and *Polypedilum sordens*. According to Brodersen et al. (2001), *E. tendens*, *Parachironomus arcuatus*, and several species of *Psectrocladius* and *Polypedilum* show high levels of dependence on aquatic macrophytes. Many species of *Dicrotendipes* and *Psectrocladius* inhabit aquatic plants (Epler 1988; Kornijów 1989a, b). *Chironomus* sp. *plumosus* group and *Procladius* sp. occurred at 21 and 19 sites, respectively; therefore, these taxa are widely distributed in Lake Takkobu and as a result might not show specific demands in relation to the environmental gradient in this lake. *Chironomus* sp. *plumosus* group and species of *Procladius* and *Tanytus* have been shown to prefer pelagic or profundal waters to the littoral area (Serruya 1978; Ueno et al. 1993; Tolonen et al. 2001).

Among the six oligochaete species, the CCA (Fig. 2) revealed that the three species of *T. tubifex*, *A. limnobiis*, and *Aulodrilus* sp. occurred in relatively organic-rich sediments with less vegetation, farther from the mouth of the Takkobu River, than *L. hoffmeisteri*, *Limnodrilus udekemianus*, and *Bothrioneurum vej dovskyanum*. Generally, all six oligochaete species are reported to be able to tolerate extremely oxygen-deficient environments (Brinkhurst 1974; Ohtaka and Kikuchi 1997). However, the present study showed that the former three species seem to have different habitat preferences from the latter three species. *L. hoffmeisteri* has been reported to occur abundantly in lake littorals with low bottom DO and high ammonium concentrations around the mouth of an organically polluted river (Petridis 1993). However, in our study, this species appeared at 22 sites regardless of bottom DO concentrations and was widely distributed in Lake Takkobu.

The species richness of benthic macroinvertebrates (Table 1) was correlated with three variables relating to aquatic vegetation: the species number of submerged macrophytes and the biomasses of *Trapa* and floating-leaved macrophytes. The abundance and richness of the macroinvertebrate community seem to increase as the density or biomass of freshwater macrophytes increases (e.g., Crowder and Cooper 1982; Lodge 1991). One reason why aquatic plants, particularly submerged macrophytes, support an abundant and diverse macroinvertebrate community is that they increase the available substrate area. More surface area provides the macroinvertebrate community with more habitat and

more food (e.g., epiphytic algae) (Warfe and Barmuta 2006). Independently of habitat area, architectural complexity increased the abundance and richness of epiphytic invertebrates in an artificial plant experiment (Taniguchi et al. 2003). Complex macrophyte architecture might result in the trapping of more organic matter, which means more food for the macroinvertebrates. It might also provide more interstitial space, which functions as a refuge from predation (Crowder et al. 1998; Diehl and Kornijów 1998). In general, macrophyte vegetation decreases the efficiency of fish predation and provides a refuge for benthic macroinvertebrates (Crowder and Cooper 1982; Diehl 1992, 1993, 1995; Hanson and Butler 1994), although a complex macrophyte architecture per se does not necessarily help the macroinvertebrate community to escape from their predators (Warfe and Barmuta 2006).

We investigated only the benthic macroinvertebrate community in the sediments. Ito et al. (2005) collected 46 additional macroinvertebrate taxa from macrophyte vegetation in Lake Takkobu, including several species highly dependent on macrophytes. Thus, aquatic vegetation is surely important for supporting a diverse macroinvertebrate community in Lake Takkobu. The present study not only showed that the rapid loss of submerged vegetation has altered the macroinvertebrate community structure but also that the decrease in species richness of submerged plants has decreased the number of macroinvertebrate species. Therefore, the restoration of the species diversity of the submerged macrophytes as well as the quantity of the submerged vegetation, the levels of both of which have decreased in the past decade (Kadono 2007), is desirable for maintaining a diverse and unique macroinvertebrate community in this lake.

**Acknowledgements** We are grateful to Dr. Tetsuya Itoh of the School of Science, Hokkaido University, and Dr. Shigeo Kitaoka of Kashiwazaki City, Dr. Shin-ichi Hiruta of Hokkaido University of Education at Kushiro, and Dr. Yasuhiro Kuwahara of Hokkaido Abashiri Fisheries Experimental Station for the identification of Hirudinea, Ceratopogonidae, Mysidae, and Gastropoda and Bivalvia, respectively. Our thanks are also extended to Dr. Naotoshi Kuhara of the Chitose Board of Education, Dr. Hidenori Ubukata of Hokkaido University of Education at Kushiro, Dr. Tsutomu Hariu of Kushiro City Museum, Dr. Masaki Kyono of Sapporo Technical College, and Dr. Munemitsu Akasaka of the National Institute for Environmental Studies for their help throughout this study. This study was supported by the Kushiro nature restoration project of the Ministry of the Environment, Japan.

## References

- Beaty SR, Fortino K, Hershey AE (2006) Distribution and growth of benthic macroinvertebrates among different patch types of the littoral zones of two arctic lakes. *Freshw Biol* 51:2347–2361
- Borkent A, Wirth WW (1997) World species of biting midges (Diptera: Ceratopogonidae). *Bull Am Mus Nat Hist* 233:1–257
- Bowen KL, Kaushik NK, Gordon AM (1998) Macroinvertebrate communities and biofilm chlorophyll on woody debris in two Canadian oligotrophic lakes. *Arch Hydrobiol* 141:257–281

- Brinkhurst RO (1974) The benthos of lakes. Macmillan, London
- Brinkhurst RO, Jamieson BGM (1971) Aquatic Oligochaeta of the world. Oliver and Boyd, Edinburgh
- Brodersen KP (1995) The effect of wind exposure and filamentous algae on the distribution of surf zone macroinvertebrates in Lake Esrom, Denmark. *Hydrobiologia* 297:131–148
- Brodersen KP, Odgaard BV, Vestergaard O, Anderson NJ (2001) Chironomid stratigraphy in the shallow and eutrophic Lake Søbygaard, Denmark: chironomids-macrophyte co-occurrence. *Freshw Biol* 46:253–267
- Caraco NF, Cole JJ (2002) Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. *Ecol Appl* 12:1496–1509
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813
- Crowder LB, McCollum EW, Martin TH (1998) Changing perspectives on food web interaction in lake littoral zones. In: Jeppesen E, Søndergaard M, Søndergaard M, Christoffersen K (eds) The structuring role of submerged macrophytes in lakes. Springer-Verlag, New York, pp 240–249
- Dalgaard P (2002) Introductory statistics with R. Springer, Tokyo
- Diehl S (1992) Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology* 73:1646–1661
- Diehl S (1993) Effects of habitat structure on resource availability, diet and growth of benthivorous perch, *Perca fluviatilis*. *Oikos* 67:403–414
- Diehl S (1995) Direct and indirect effects of omnivory in a littoral lake community. *Ecology* 76:1727–1740
- Diehl S, Kornijów R (1998) Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. In: Jeppesen E, Søndergaard M, Søndergaard M, Christoffersen K (eds) The structuring role of submerged macrophytes in lakes. Springer-Verlag, New York, pp 24–46
- Dvořák J (1996) An example of relationships between macrophytes, macroinvertebrates and their food resources in a shallow eutrophic lake. *Hydrobiologia* 339:27–36
- Epler JH (1988) Biosystematics of the genus *Dicrotendipes* Kieffer, 1913 (Diptera: Chironomidae: Chironominae) of the world. *Mem Am Entomol Soc* 36:1–214
- Gardner SC, Grue CE, Major WW III, Conquest LL (2001) Aquatic invertebrate communities associated with purple loosestrife (*Lythrum salicaria*), cattail (*Typha latifolia*) and bulrush (*Scirpus acutus*) in central Washington, USA. *Wetlands* 21:593–601
- Hanson JM (1990) Macroinvertebrate size-distributions of two contrasting freshwater macrophyte communities. *Freshw Biol* 24:481–491
- Hanson MA, Butler MG (1994) Responses to food web manipulation in a shallow waterfowl lake. *Hydrobiologia* 279/280:457–466
- Hariu T, Nakajima H, Takamura N (2007) Distribution and present status of fishes in Lake Takkobu and adjacent rivers (in Japanese with English abstract). *Jpn J Limnol* 68:157–167
- Ito T, Ohtaka A, Ueno R, Kuwahara Y, Ubukata H, Hori S, Itoh T, Hiruta S, Tomikawa K, Matsumoto N, Kitaoka S, Togashi S, Wakana I, Ohkawa A (2005) Aquatic macroinvertebrate fauna in Lake Takkobu, Kushiro Marsh, northern Japan (in Japanese with English abstract). *Jpn J Limnol* 66:117–128
- Johnson RK, Goedkoop W, Sandin L (2004) Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. *Freshw Biol* 49:1179–1194
- Kadono Y (2007) Changes in macrophytic flora of Lake Takkobu, Kushiro, Japan, in past 30 years (in Japanese with English abstract). *Jpn J Limnol* 68:105–108
- Kato H, Takamura N, Mikami H (1999) Distribution of macroinvertebrates in deep and oligotrophic Lake Towada, Japan. *Acta Hydrobiol Sinica* 23:96–105
- Kornijów R (1989a) Macrofauna of elodeids of two lakes of different trophy. I. Relationships between plants and structure of fauna colonizing them. *Ekol Pol* 37:31–48
- Kornijów R (1989b) Macrofauna of elodeids of two lakes of different trophy. II. Distribution of fauna living on plants in the littoral of lakes. *Ekol Pol* 37:49–57
- Lodge DM (1991) Herbivory on freshwater macrophytes. *Aquat Bot* 41:195–224
- Marker AFH, Nusch EA, Rai H, Riemann B (1980) The measurement of photosynthetic pigments in freshwaters and standardization of methods: conclusions and recommendations. *Arch Hydrobiol Beih Erg Limnol* 14:91–106
- Masuda O, Uchiyama R (2004) Freshwater molluscs of Japan, including brackish water species. *Pisces*, Tokyo
- Matsuzaki SS, Usio N, Takamura N, Washitani I (2007) Effects of common carp on nutrient dynamics and littoral community composition: roles of excretion and bioturbation. *Fundam Appl Limnol* 168:27–38
- McCune B (1997) Influence of noisy environmental data on canonical correspondence analysis. *Ecology* 78:2617–2623
- Moore JW (2006) Animal ecosystem engineers in streams. *Bioscience* 56:237–246
- Murano M (1997) Order Mysidacea. In: Chihara M, Murano M (eds) An illustrated guide to marine plankton in Japan (in Japanese). Tokai University Press, Tokyo, pp 1010–1084
- Oertli B (1995) Spatial and temporal distribution of the zoobenthos community in a woodland pond (Switzerland). *Hydrobiologia* 300/301:195–204
- 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. *Pub Itako Hydrobiol Stn* 9:1–14
- Petridis D (1993) Macroinvertebrate distribution along an organic pollution gradient in Lake Lysimachia (Western Greece). *Arch Hydrobiol* 128:367–384
- Rasmussen JB (1993) Patterns in the size structure of littoral zone macroinvertebrate communities. *Can J Fish Aquat Sci* 50:2192–2207
- Sæther OA (1983) The larvae of Prodiamesinae (Diptera: Chironomidae) of the Holarctic region—keys and diagnoses. *Entomol Scand Suppl* 9:141–147
- Ságová-Marecková M, Kvet J (2002) Impact of oxygen released by the roots of aquatic macrophytes on composition and distribution of benthic macroinvertebrates in a mesocosm experiment. *Arch Hydrobiol* 155:567–584
- Scheffer M, Houser SH, Meijer ML, Moss B, Jeppesen E (1993) Alternative equilibria in shallow lakes. *Trends Ecol Evol* 8:275–279
- Serruya C (1978) Vertical distribution of benthic fauna. In: Serruya C (ed) Lake Kinneret. Junk, The Hague, pp 391–394
- Strayer DL, Lutz C, Malcom HM, Munger K (2003) Invertebrate communities associated with a native (*Vallisneria americana*) and an alien (*Trapa natans*) macrophyte in a large river. *Freshw Biol* 48:1938–1949
- Takamura N, Kadono Y, Fukushima M, Nakagawa M, Kim BH (2003) Effects of aquatic macrophytes on water quality and phytoplankton community in shallow lakes. *Ecol Res* 18:381–395
- Takamura N, Nakagawa M, Wakana I, Igarashi S, Tsuji N (2007) Water quality and factors influencing its distribution in Lake Takkobu (in Japanese with English abstract). *Jpn J Limnol* 68:81–95
- Taniguchi H, Nakano S, Tokeshi M (2003) Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants. *Freshw Biol* 48:718–728
- Ter Braak CJF, Šmilauer P (2002) CANOCO reference manual and Cano Draw for Windows user's guide: software for Canonical Community Ordination (v. 4.5). Microcomputer Power, Ithaca
- Tolonen KT, Hämäläinen H, Holopainen IJ, Karjalainen J (2001) Influence of habitat type and environmental variables on littoral macroinvertebrate communities in a large lake system. *Arch Hydrobiol* 152:39–67
- Tsalolikhin SJ (ed) (2004) Key to freshwater invertebrates of Russia and adjacent lands. Molluscs, polychaetes, nemerteans, vol 6. Nauka, St. Petersburg
- Ueno R, Iwakuma T, Nohara S (1993) Chironomid fauna in the emergent plant zone of Lake Kasumigaura, Japan. *Jpn J Limnol* 54:293–303

- van den Berg MS, Coops H, Noordhuis R, van Schie J, Simons J (1997) Macroinvertebrate communities in relation to submerged vegetation in two *Chara*-dominated lakes. *Hydrobiologia* 342/343:143–150
- Warfe DM, Barmuta LA (2006) Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. *Oecologia* 150:141–154
- Weatherhead MA, James MR (2001) Distribution of macroinvertebrates in relation to physical and biological variables in the littoral zone of nine New Zealand lakes. *Hydrobiologia* 462:115–129
- Webb CJ, Scholl A, Ryser HM (1985) Comparative morphology of the larval ventromental plates of European species of *Chironomus* Meigen (Diptera: Chironomidae). *Syst Entomol* 10:373–385
- Wellborn GA, Robinson JV (1991) The influence fish predation in an experienced prey community. *Can J Zool* 69:2515–2522
- Wiederholm T (ed) (1983) Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. *Entomol Scand Suppl* 19:1–457
- Wiggins GB (1996) Larvae of the North American caddisfly genera (Trichoptera), 2nd edn. University of Toronto Press, Toronto
- Yang T (ed) (1996) Annelida, Hirudinea (in Chinese with English abstract). *Fauna Sinica*. Science Press, Beijing