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Long-term changes in the density and composition of profundal macrobenthos in Lake Biwa from 1966 to 2000

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ABSTRACT

Lake Biwa, the largest lake in Japan, has been affected by eutrophication and climate warming since the 20th century. To examine the effects of these environmental changes on dominant macrobenthos species in Lake Biwa, the density and composition of these organisms were determined monthly from 1966 to 2000 at an offshore station in the lake and analyzed in terms of various physicochemical factors. Annual mean bottom temperatures at the site generally remained stable (6.1-8.0 °C) until 1985, increased from 1985 (6.5 °C) to 1990 (8.3 °C), and remained high thereafter (7.4-8.3 °C). Branchiura sowerbyi dominated the oligochaete community in terms of density and biomass until 1985. Oligochaete density increased after 1986, dominated by B. sowerbyi, Limnodrilus spp., and Tubifex tubifex. Although the increase in macrobenthic density after 1986 was mainly explained by an increase in T. tubifex density (3811-8076 individuals m⁻²), total macrobenthos biomass was mainly controlled by *B. sowerbyi* $(1.9-9.5 \text{ gm}^{-2})$. Notably, the increase in *T. tubifex* density roughly coincided with density decreases in the benthic gobid fish Gymnogobius isaza (from 567 t to undetectable) and the shrimp Palaemon paucidens (from 758 to 142 t). These findings support the hypothesis that biological interactions, such as predation, play an important role in the succession of macrobenthos species in Lake Biwa.

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aquatic oligochaetes; climate warming; long-term change; predation pressure; profundal benthic community

Introduction

Long-term environmental monitoring data are useful for acquiring baseline information about complex ecological processes as well as evaluating environmental changes caused by anthropogenic disturbances (Likens and Lambert 1998). Large lakes are commonly regarded as effective sentinels of environmental change (Adrian et al. 2009) because they are closed systems and are much smaller bodies of water than marine systems. Thus, long-term data from large lakes are crucial to better manage the lakes themselves as well as to understand the effects of environmental changes on the regions where they are located.

Global threats to ecosystems and biodiversity in lakes include eutrophication, acidification, contamination, invasion by exotic species, and climate warming (Brönmark and Hansson 2002), among which eutrophication and climate warming are major threats (Meerhoff et al. 2022). Eutrophication is one of the most serious environmental changes in lakes, with extensive economic and health implications related to deterioration of water quality, deoxygenation of underlying waters, toxic cyanobacterial blooms with foul odors, and corresponding decreases in aesthetic value (Angeline et al. 1994, Paerl and Huisman 2008, 2009). Climate warming-related environmental changes in lakes can also have serious impacts, particularly in deep large lakes. In these lakes, strengthened and prolonged thermal stratification, weak and insufficient holomixis, and hypolimnetic and sedimentary oxygen depletion have been caused by climate warming since the last century (O'Reilly et al. 2003, Verburg et al. 2003, Posch et al. 2012, Ishikawa and Kumagai 2020). Because the responses of phytoplankton to environmental change are rapid, long-term monitoring in lakes has facilitated numerous studies regarding the dominant species succession of phytoplankton in the epilimnion during the process of eutrophication. This monitoring has also engendered studies concerning the reduction of primary production (O'Reilly et al. 2003, Verburg et al. 2003) and changes in dominant

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phytoplankton species (Posch et al. 2012) caused by weak and insufficient holomixis.

By contrast, few studies have examined the effects of eutrophication and climate warming on organisms living in the hypolimnion and/or sediments, particularly with respect to macrobenthos, although macrobenthic organisms have been used as indicators of environmental changes in lake sediments (Brodersen et al. 1998, Nalepa et al. 1998, White 2002). The abundance and composition of macrobenthic communities are presumably affected by eutrophication/oligotrophication (Nalepa et al. 1998, 2007, Gong and Xie 2001, Mehler et al. 2020) and/or oxygen depletion (Dermott 1988, Ohtaka et al. 2006, Dzhurtubaev et al. 2021). Because of the need to identify environmental changes in the hypolimnion and sediments in lakes, and because the responses of benthic communities to environmental change may occur slowly, long-term monitoring is particularly valuable for identifying factors that contribute to changes in the abundances and compositions of macrobenthic communities.

In Lake Biwa, the largest lake in Japan, eutrophication started during the 1960s and 1970s; however, its water quality improved from the 1990s onwards (Hayakawa and Tsujimura 2020, Okuda et al. 2020). Higher water temperatures due to climate warming were detected from 1980s onwards (Endoh et al. 1999, Ishikawa and Kumagai 2020), and the effects of climate warming on lake sediments have been recorded since the 1980s (Tsugeki et al. 2010). We hypothesized that the macrobenthos species that dominated from 1960s to 1980s would have acclimated to the eutrophication of Lake Biwa, and that increased water temperatures due to climate warming would mainly determine the dominant macrobenthos species in the lake. To test these 2 hypotheses, we assessed long-term changes in the density, biomass (wet weight), and composition of macrobenthic organisms in the north basin of Lake Biwa from 1966 to 2000 and analyzed these changes in terms of various environmental factors.

Materials and methods

Study sites, sample collection, and field monitoring for environmental variables

This study was conducted in Lake Biwa (Fig. 1), 68.0 km in length, 22.6 km in maximum width, 674.4 km^2 in area, 104.0 m in maximum depth, and 41.2 m in mean depth (Horie 1984). Thermal stratification begins in May and lasts for 6–7 months (until Dec or Jan). After overturn, the dissolved oxygen concentration (DO) in water near the bottom of the lake recovers to

~11 mg L^{-1} . Areas of the lake with depths exceeding 40 m, with muddy bottoms and low year-round temperatures of around 7–8 °C, are considered the profundal zone.

Samples were collected during regular monthly monitoring at muddy-bottomed site Ie-1 (35°12′58″N, 135°59′55″E; depth ~73 m) from 1966 to 2000 (Fig. 1). This monitoring was initiated by the late Prof. S. Mori because of increasing eutrophication in Lake Biwa (Mori 1967) and conducted by the Center for Ecological Research (formerly Otsu Hydrobiological Station), Kyoto University. On a monthly basis, the research staff surveyed transparency using a Secchi disk, water and bottom temperatures using a thermistor thermometer (Tohodentan, RB-2), and DO using the



Figure 1. Sampling sites le-1, oSK-73, oSK-50, and oSK-40 in Lake Biwa.

Winkler method (Saijo and Mitamura 1995). Chlorophyll *a* and phaeopigments (collectively, Chl-*a*) have been measured since 1984 using the method established by Lorenzen (1967). Monthly areal Chl-*a* was calculated from the Chl-*a* concentration in the water column. The water samples for DO and Chl-*a* assessment were collected via a Van Dorn water sampler with a vinylon rope until 1987 and with a wire/wire gauge system after 1988. After 1988, accurate depths of water samples were recorded.

From 1966 to 1987, we collected bottom-water samples for DO measurement from a depth of 70 m. After 1988, because of the improvement of our wire/wire gauge system, we sampled from a depth of \sim 73 m (mean [standard deviation] 1.03 [0.56] m above the bottom; range 0.3– 1.6 m) as a near-bottom sample, in addition to the sample from 70 m. The mean DO at 70 or \sim 73 m each year was calculated from the values of the last 4 months in the stagnation period before overturn from September to December, or from October to January of the following year, depending on when overturn occurred.

To determine the quantity and quality of food resources for macrobenthos, loss on ignition (LI) and organic carbon and nitrogen content in sediment samples were determined. LI of the 0-2, 2-4, and 4-6cm layers of bottom sediment at Ie-1 was measured 9 times from 1995 to 1996, from 1 sample each (Supplemental Table S1); all samples were collected with modified plastic syringes (3 cm in inner diameter) using a core sampler. Sediment samples for LI were also collected at oSK-73 (35°16'70"N, 136°06'54"E, ~73 m deep) near Ie-1, oSK-50 (50 m deep), and oSK-40 (40 m deep; Fig. 1). At oSK-40, oSK-50, and oSK-73 sediment samples were collected with a dispensing spoon in 1984 and 1985; ~1 cm of the sediment surface was scooped up after collection by a grab sampler. In 1999 and 2000, the upper 1 cm of sediment was collected via plastic syringes using a core sampler (Supplemental Table S1). To determine sediment water content, the sediment samples were dried at 60 °C for at least 3 days until they maintained a constant weight. To determine LI, the dried and ground sediments were combusted at 550 °C for 3 h in an electric furnace, and the sediments were weighed twice after cooling in a desiccator. The organic carbon and nitrogen contents of the dried and ground sediment were determined using a Yanaco CN analyzer (Yanaco, Kyoto, Japan).

Macrobenthos sampling

Mud samples for macrobenthos monitoring were collected with an Ekman-Birge type grab sampler (15 cm $\times 15$ cm, area; 225 cm²; Rigosha, Saitama, Japan) throughout the study period. Until 1984, the mud samples were washed through a double-layer wire sieve (mesh sizes 1 and 0.5 mm), and animals on the sieves visible to the naked eye were collected using forceps while onboard the research vessel. Beginning in 1985, mud samples were washed and sieved gently through a nylon screen (0.5 mm mesh size) onboard the research vessel; remnants on the screen were transported to the laboratory in plastic bags for sorting. Sorted macrobenthic organisms were preserved in 5%-10% formalin solution for subsequent identification and counting (Supplemental Table S1). We collected macrobenthos samples from 1966 to present. Taxonomical classification of the samples is not yet available for specimens collected from 2001 onwards.

Mud samples collected using an Ekman grab were generally 9–12 cm thick. It is unclear whether these samples included all infauna in the sediment. Smalland medium-sized oligochaetes were presumably caught in the mud samples, although some large or long oligochaetes (e.g., *Branchiura sowerbyi* Beddard or *Limnodrilus grandisetosus* Nomura) may have been missed (Narita 2006). Although such oligochaetes can be found at great depths, they would likely have remained near the sediment surface because of the constant sediment temperature and limited DO of the profundal bottom.

The 2 sieving methods were compared in January 2002; 3 samples were treated using each method and then sorted as outlined above. The mean densities of all species recorded by each method were compared statistically using a 2-sample *t*-test (Supplemental Table S2).

Annual total catches of isaza (*Gymnogobius isaza* [Tanaka]) and shrimp (*Palaemon paucidens* de Hann) were obtained from the Annual Fish Catch Report of the Fisherman's Union of Shiga Prefecture (Shiga Prefecture 2023).

Species identification, food chain analysis, and statistical analyses

Macrobenthic fauna were identified in accordance with the criteria of Brinkhurst and Jamieson (1971), Ohtaka and Nishino (1995, 1999), and Kathman and Brinkhurst (1999) for oligochaetes; Wiederholm (1983) and Kitagawa (1997) for chironomid larvae; and Ueno (1973) for other taxa. Two oligochaete species, *Limnodrilus hoffmeisteri* Claparède and *L. profundicola* (Verrill), can usually be identified by the shape of the penis sheath in mature individuals. In the present study, specimens were mostly composed of immature individuals, and therefore we could not distinguish individuals at the species level. Accordingly, combined numbers of the 2 species are reported as *Limnodrilus* spp. Macrobenthic specimens collected from 1966 to 1976 were reexamined in 2011 because the oligochaetes had not been initially identified to species level (Suzuki and Mori 1967).

To examine the prey-predator relationship between *Tubifex tubifex* (Muller) and *Jesogammarus annandalei* (Tattersall), we conducted a stable isotope analysis (Yamada et al. 1998). We used the Shannon-Wiener index to examine the diversity of the annual mean density of macrobenthos. X statistics, an application of the Mann-Kendall trend test (Gocic and Trajkovic 2013), were performed using the Real Statistics Resource Pack package for Excel (Microsoft, Redmond, WA, USA) to examine temporal trends in environmental factors and macrobenthos. Spearman rank correlation analysis was performed to examine correlations between each environmental factor and species.

Results

Environmental factors

Annual mean, maximum, and minimum bottom temperatures increased significantly over the study period (Fig. 2, Supplemental Table S3) and generally remained stable but exhibited some annual fluctuation until 1985, increased ~1.5 °C from 1985 to 1990, and remained high thereafter (Fig. 2). The increase in bottom temperature from 1985 to 1990 coincided with the increases in water temperatures at 40, 50, 60, and 70 m in the hypolimnion (Supplemental Fig. S1).

The mean DO at 70 m decreased nonsignificantly throughout the study period (Fig. 3, Supplemental Table S3), at 70 m from 1966 to 1985 decreased significantly (Fig. 3, Supplemental Table S3), and from 1986 to 2000 showed no significant trend (Fig. 3, Supplemental Table S3). The annual minimum DO showed no interannual trend at either 70 or ~73 m (Fig. 3, Supplemental Table S3). The lowest minimum DO was 3.93 mg L⁻¹ in January 1973; annual minima in other years were not <4 mg L⁻¹ (Fig. 3).

The annual mean transparency increased significantly from 1966 to 2000 (Supplemental Table S3 and Fig. S2), but the annual mean totals of Chl-a m⁻² measured since 1984 showed no interannual trend (Supplemental Table S3 and Fig. S3).

The mean LI of the bottom sediment at Ie-1 from 1995 to 1996 was 10.55% in the upper layer (0-2 cm), 9.39% in the middle layer (2-4 cm), and 8.51% in the lower layer (4-6 cm) and did not change seasonally (Supplemental Table S4). The water contents of those sediments were also highest in the upper layer (mean 79.5%), followed by the middle (73.7%) and lower (68.9%) layers. The bottom sediment LI at oSK73,



Figure 2. Interannual variation in annual mean (black circle, thick solid line), maximum (white circle, broken line), and minimum (black circle, thin line) bottom temperatures (°C) from sampling sites le-1, oSK-73, oSK-50, and oSK-40 in Lake Biwa. Thick grey bar at the top of the figure indicates a significant increasing trend from 1966 through 2000 (Mann–Kendall trend test; Supplemental Table S3a).



Figure 3. Interannual variation in annual mean dissolved oxygen concentration (DO; black circle, solid line) during the last 4 months of the stagnation period before overturn at 70 m depth, and annual minimum DO (white circle, broken line) at 70 m depth from sampling site le-1 in Lake Biwa. Thick grey bar at the top of the figure indicates a significant decreasing trend from 1966 through 1985 (Mann–Kendall trend test; Supplemental Table S3a).

oSK50, and oSK40 was 7.89–9.54% from 1984 to 1985 and 12.26% (~73 m), 11.12% (50 m), and 10.36% (40 m), respectively, from 1999 to 2000 (Supplemental Table S4).

Nitrogen contents in the sediment were 2.0–3.3 mg g⁻¹ (0.2%–0.33% of dry sediment) at oSKs in 1984 and 1985. The carbon content of the sediment at oSKs in 1984 and 1985 was 1.51%-2.47% of dry sediment, yielding C/N ratios of 7.48–9.23 (Supplemental Table S4).

Changes in macrobenthos abundance

No statistical difference was found in the density of macrobenthos components between the wire sieve and nylon screen methods, excluding J. annandalei (Tattersall) (Supplemental Table S6). The number of taxa occurring during a given year (5-11 taxa) showed no seasonal changes or noticeable interannual trends throughout the study period (Supplemental Fig. S4 and Table S3) but decreased from 1966 to 1987 and increased from 1988 2000 to (Supplemental Fig. S4). The macrobenthos component did not change significantly during the study period (Supplemental Fig. S4). Species occurring during the study period included 27 taxa: 1 species of Turbellaria, 1 naidid, 10 tubificid Oligochaeta (excluding unidentified Naididae and Tubificidae), 1 Hirudinea (not identified), 4 Crustacea (excluding

Ostracoda), 7 chironomid larvae (excluding unidentified species), 1 insect larva, 1 Bivalvia, and 1 Gastropoda (Supplemental Table S6).

Naidid oligochaetes were rarely caught, but they might have been overlooked (particularly with the wire sieve) because of their tiny and transparent bodies. Meiobenthos such as nematodes, ostracods, and copepods (Cyclopoida, Harpacticoida) were occasionally collected but were not identified or counted. The shrimp *P. paucidens* was seldom collected by the grab, presumably because of its speed and mobility.

Macrobenthos exhibited no seasonal changes in total density or total biomass. Total macrobenthos density increased over the study period (Fig. 4, Supplemental Table S3) because of the dramatic increase in oligochaete density after 1986 (Fig. 4), particularly T. tubifex (Fig. 5, Supplemental Table S3). Oligochaetes were dominant in terms of macrobenthic density (mean 95.3% of annual mean total density), with 3 predominant species: B. sowerbyi, Limnodrilus spp., and T. tubifex (90.0%). The B. sowerbyi density showed no significant trend throughout the study period, increasing from 1966 to 1977, decreasing from 1978 to 1983, and gradually increasing again from 1984 onwards with fluctuations (Fig. 5, Supplemental Table S3). The increasing trend in Limnodrilus spp. density during the study period was significant (Supplemental Table S3). The T. tubifex density showed an increasing trend



Figure 4. Interannual variation in annual mean density for each taxonomic group (individuals m^{-2}) from sampling site le-1 in Lake Biwa. Thick grey bar at the top of the figure indicates a significant increasing trend from 1966 through 2000 (Mann–Kendall trend test; Supplemental Table S3b).

from 1966 to 1985 and remained high after 1986 (Fig. 5). The mean percentages of the dominant oligochaetes (in total density) were 41.0% for *B. sowerbyi*, 17.7% for *Limnodrilus* spp., and 23.2% for *T. tubifex* during 1966–1985; these percentages were 3.6% for *B. sowerbyi*, 4.8% for *Limnodrilus* spp., and 87.5% for *T. tubifex* during 1986–2000.

The annual mean biomass of total macrobenthos increased noticeably from 1966 to the end of 1970s, decreased toward the mid-1980s, and then increased slowly (Fig. 6, Supplemental Table S3). Oligochaetes also dominated the total macrobenthic biomass, with mean percentages of 92.9% in 1966–1985 and 88.8% in 1986–2000. The 3 dominant oligochaetes comprised a



Figure 5. Interannual variation in the annual mean density of 3 dominant oligochaete species (individuals m^{-2}): from sampling site le-1 in Lake Biwa: *Branchiura sowerbyi* (left vertical axis) and *Tubifex tubifex* (right vertical axis). Thick bars at the top of the figure indicate a significantly increasing trend (Mann–Kendall trend test for each period; Supplemental Table S3b).



Figure 6. Interannual variation in the annual mean biomass of taxonomic groups (g wet weight m⁻²).

large proportion of the total macrobenthic biomass (mean 87.9%) during 1966 to 2000. *Branchiura sowerbyi*, a large-bodied oligochaete, dominated the biomass during 1966–1985 (mean 65.8%). After 1986, the mediumsized *T. tubifex* predominated in terms of density and affected the total biomass; it increased from a mean of 3.2% during 1966–1985 to 41.5% during 1986–2000. Spearman rank correlation analysis showed that the

B. sowerbyi density controlled changes in total macrobenthic biomass (Table 1, Supplemental Table S5).

Jesogammarus annandalei, an endemic amphipod, also increased in density during the study period (Fig. 7), particularly after 1985. The mean biomass of this species increased in biomass from 0.17 g m⁻² (mean 1.5% of the total macrobenthic biomass) from 1966 to 1984 to 1.39 g m⁻² (12%) from 1985 to 2000, which

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Table 1. Spearman's rank correlation analysis results for 1966–2000. Significant positive and negative relationships are indicated in
bold red and blue text, respectively. Asterisks indicate that analyses were applied to a subsection of the study period (*1984–1997,
**1966–1985). Empty cells were not included in analyses.

		Branchiura	Tubifex	Limnodrilus	Jesogammarus	Diversity	Catch of isaza	Mean bot temp	Mean DO_70 m	Transparency
Branchiura										
Tubifex		-0.433								
Limnodrilus		0.265	0.358							
Jesogammarus		-0.229	0.703	0.209						
Number of species						-0.005				
Total biomass		0.687	0.031	0.306	0.050		0.031			
Catch of isaza		0.077	-0.617	-0.299	-0.537	0.618				
Catch of shrimp		0.427	-0.344	0.034	-0.559					
Mean bot temp		0.025	0.316	0.125	0.279		-0.612			
Transparency		-0.118	0.209	0.153	0.211			0.046		
Chl & Phaeo	*	-0.125	0.015	0.037	-0.332			0.270	-0.363	0.086
Mean DO_70 m	**	-0.088	-0.327	-0.382	-0.174		0.211	-0.207		0.104

Branchiura: density of Branchiura sowerbyi.

Tubifex: density of Tubifex tubifex.

Limnodrilus: density of Limnodrilus spp.

Jesogammarus: density of Jesogammarus annandalei.

Mean bot temp: Annual mean bottom temperature from 1966 to 2000. Chl & Phaeo: Annual mean amount of chlorophyll *a* and phaeopigments.

Chi & Phaeo. Annual mean amount of chiorophyli a and phaeophyliel Maan DQ, 70: Maan disashud suuran santant at 70 m water danth

Mean DO_70: Mean dissolved oxygen content at 70 m water depth.



Figure 7. Interannual variation in the annual mean density of *Jesogammarus annandalei* and *Asellus hilgendorfii* (individuals m⁻²). Thick grey bar at the top of the figure indicates a significantly increasing trend from 1966 through 2000 (Mann–Kendall trend test; Supplemental Table S3b).

slightly influenced the increase in total macrobenthic biomass after the mid-1980s.

Results of statistical analyses

Spearman rank correlation analysis showed a significant negative correlation between the B. sowerbyi and T. tubifex densitiy, and no correlation between the B. sowerbyi density and any other environmental factor (Table 1, Supplemental Table S5). The T. tubifex density correlated positively with that of Limnodrilus spp. and J. annandalei and negatively with the catch rates of isaza (an endemic profundal benthic gobid fish; Table 1, Supplemental Table S5). The Limnodrilus spp. density correlated negatively with mean DO at 70 m, and the J. annandalei density correlated negatively with the isaza catch. The annual total catches of isaza and shrimp decreased markedly during the 1980s and 1990s (Fig. 8, Supplemental Table S3) and correlated negatively with bottom temperature, transparency, and total oligochaete density (Table 1, Supplemental Table S5).

We detected a marked decrease in macrobenthos diversity estimated using the Shannon-Wiener index after 1986 (Supplemental Fig. S5). Macrobenthos diversity was positively correlated with *B. sowerbyi* density and the isaza catch rate and negatively with *T. tubifex* and *J. annandale*i density, but was not correlated with the number of species (Table 1, Supplemental Table S5).

Discussion

In this study, we found a succession of the dominant macrobenthos species from *B. sowerbyi* to *T. tubifex* between 1966 and 2000. The study period is important because Lake Biwa exhibited significant eutrophication during the 1960s and 1970s or 1980s (Hayakawa and Tsujimura 2020, Okuda et al. 2020) and because climate warming continuously affected the lake ecosystem throughout the study period (Tsugeki et al. 2010, Ishikawa and Kumagai 2020). Based on our hypotheses, we examined single and synergistic effects of eutrophication and climate warming on the density and composition of macrobenthos species in Lake Biwa.

Environmental conditions for macrobenthos ecology

A ~1.5 °C increase in bottom temperature from 1985 to 1990 coincided with increases in water temperature at 40, 50, 60, and 70 m in the hypolimnion (Supplemental Fig. S1). The rise of water temperatures in the hypolimnion and at the bottom may have been caused by increasing air temperatures after the 1980s (Endoh et al. 1999, Kumagai 2008, Hsieh et al. 2010).

Previous studies have demonstrated a decreasing tendency of DO in the bottom environments of Lake Biwa (Kumagai 2008). The DO in the macrobenthic habitat,



Figure 8. Interannual variation in annual total catches of shrimp (*Palaemon paucidens*) and isaza (*Gymnogobius isaza*) in the north basin of Lake Biwa. Thick bars at the top of the figure indicate significantly decreasing trends (Mann–Kendall trend test for each period; Supplemental Table S3d). Data obtained from the Annual Fish Catch Report of the Fisherman's Union of Shiga Prefecture.

which extends from the water-sediment interface to ~ 20 cm above the bottom, may be lower than that of the near-bottom water sampled in this study; however, we do not have DO data specifically for these habitats.

The bottom sediment LI near Ie-1 in 1963 was ~10% (10.7% in May, 9.8% in July; Horie 1964), which is comparable with our values at Ie-1 in 1995 and 1996 (Supplemental Table S4). The mean LI of 8 points in the deep profundal bottom (60.5-86.7 m depth) was $8.71 \pm 1.97\%$ (May and July 1963; n = 16 in total; Horie 1964), which is comparable with our values at oSKs in 1984 and 1985. Nitrogen content in the sediment was 2.0–2.5 mg g^{-1} at Ie-1 in 1963 (Horie 1964) and 4.0–6.0 mg g^{-1} in the deep bottom of the north basin (Koyama et al. 1980) in the 1970s, both of which are comparable with our values $(2.0-3.3 \text{ mg g}^{-1})$; Supplemental Table S4). In terms of organic matter quantity and food quality for macrobenthos, the bottom sediment environment of Lake Biwa was likely stable throughout the study period.

Changes in macrobenthos abundance and food webs of profundal benthic animals

The *T. tubifex* density remained high (Fig. 5) after 1986 when mean bottom temperatures were relatively high (Fig. 2) and mean DO at 70 m was relatively low (Fig. 3). We examined the validity of our second hypothesis regarding *T. tubifex* density but detected no significant relationship between *T. tubifex* density and either

mean bottom temperature or mean DO at 70 m (Table1, Supplemental Table S5); therefore, our second hypothesis was not supported. Interestingly, T. tubifex density was affected by biological interactions rather than abiotic factors. The T. tubifex density correlated negatively with isaza and shrimp catches (Table 1, Supplemental Table S5), suggesting food linkages between T. tubifex and isaza and shrimp. The increase in J. annandalei density since the mid-1980s (Fig. 7) coincided with an increase in T. tubifex density (Fig. 5), but the increase in J. annandalei density presumably was not caused by J. annandalei predation on T. tubifex; our stable isotope analyses of macrobenthos at Ie-1 revealed δ^{15} N values of 9–11.5‰ for *J. annandalei* and 11.6‰ for T. tubifex (TN, unpubl. data). These findings suggest J. annandalei and T. tubifex belong to the same trophic level and do not have a prey-predator relationship in the profundal zone of the lake.

The sharp decrease in macrobenthos diversity after 1986 (Supplemental Fig. S2) was not caused by the decrease in the number of species in a given year (Table 1, Supplemental Table S5), but may have been caused by the predominance of *T. tubifex* after 1986 (Fig. 5), which caused unevenness in the macrobenthos community. The relatively high temperature (Fig. 2) and low DO (Fig. 3) in the profundal environment of Lake Biwa likely favored *T. tubifex*. High temperature can favor the reproduction of all animals, and previous studies have demonstrated that prolonged hypoxia may be advantageous for hypoxiatolerant or short-term anoxia-tolerant animals, such as *T. tubifex* (Palmer 1968, Volpers and Neumann 2005).

During the period of eutrophication in Lake Biwa, B. sowerbyi maintained high density. However, B. sowerbyi density was not correlated with any factors related to eutrophication, such as mean DO at 70 m or Chl-a and phaeopigment content (Table 1. Supplemental Table S5); therefore, our first hypothesis was also not supported. Previous studies have demonstrated that increased organic matter supply to bottom sediments due to eutrophication favored the dominance of B. sowerbyi (Yan and Wang 1999, Dornfeld et al. 2006, Wang et al. 2018). We also found that Limnodrilus spp. and T. tubifex density levels were positively correlated (Table 1, Supplemental Table S5). Those 2 oligochaetes are thought to tolerate low DO environments (Palmer 1968, Volpers and Neumann 2005), and we found Limnodrilus spp. density was negatively correlated with mean DO at 70 m (Table 1, Supplemental Table S5). Therefore, despite nonsignificant relationships between B. sowerbyi density and environment factors related to eutrophication (Table 1, Supplemental Table S5), we conclude that the increase in B. sowerbyi density during the 1960s to mid-1970s was caused by eutrophication in Lake Biwa.

The J. annandalei density was likely also regulated by biological interactions. The increase in J. annandalei density since the mid-1980s coincided with a decrease in catches of isaza (Fig. 7, 8, Table 1, Supplemental Table S5), which is a principal predator of J. annandalei (Nakanishi and Nagoshi 1984). Ishikawa et al. (2004) also demonstrated the control on J. annandalei density by isaza predation. The negative correlation of the isaza catch with bottom temperature (Table 1, Supplemental Table S5) suggests that the temperatures of near-bottom sediments were unfavorable for the fish. The decrease in isaza abundance since the mid-1980s (Fig. 8) likely resulted in increases in T. tubifex and J. annandalei density caused by the release of predation pressure, but the reason for the decrease in isaza abundance remains unknown. Overfishing, alien predatory species, environmental deterioration such as DO depletion in near-bottom sediments, and synergistic effects are all possible explanations.

DO depletion and macrobenthos ecology in relation to climate warming

The warm climate has led to both insufficient winter cooling and an increase in water temperature of the hypolimnion and sediments; these forcings tend to suppress reoxygenation of water column and accelerate biological oxygen consumption (Kumagai 2008, Ishikawa and Kumagai 2020). Thus, increasing bottom temperature may increase the rate of oligochaete reproduction while prolonged hypoxia may be advantageous for hypoxia-tolerant or short-term anoxia-tolerant animals, such as T. tubifex, Limnodrilus spp., and Asellus hilgendorfii Bovallius (Palmer 1968, Volpers and Neumann 2005, Inoue 2020). According to the Ohtaka et al. (2021) intensive monitoring study of 3 depths (50, 70, and 90 m) in the profundal zone of Lake Biwa from 1992 to 2019, macrobenthos composition and abundance at a given site did not change significantly over time; however, macrobenthos abundance was lowest at the deepest point, where DO was significantly lower. These authors concluded that only bottom water DO depletion affected macrobenthos abundance. We found that macrobenthos composition was similar between Ie-1 in this study since 1986 and at a depth of 90 m according to Ohtaka et al. (2021), suggesting that the macrobenthos fauna at Ie-1 had already shifted to a less DO-tolerant type by 1986.

Although both of our hypotheses were contradicted by our findings, this study demonstrated the importance of biological interactions such as predation for the succession of dominant macrobenthos species in Lake Biwa. Causal mechanisms influencing the dynamics of profundal macrobenthic fauna may include synergistic effects of organic matter enrichment at the bottom (Nalepa 1987, Johnson and Winderholm 1990), DO depletion near the bottom (Bazzanti and Seminara 1987, Harman 1997, Ohtaka et al. 2021), and predation pressure (Nalepa 1987, Nalepa et al. 2007). Warming air temperatures elevate water temperatures in the epilimnion, hypolimnion, and bottom, which in turn causes a prolonged stagnation period and weak and insufficient holomixis, ultimately resulting in increasing hypoxia near the bottom (Table 1, Supplemental Table S5). This scenario is possible under climate warming, which delays or suppresses holomixis in the profundal bottom of the lake (Yamada et al. 2021). If the mixing regime of Lake Biwa becomes meromictic (Yamada et al. 2021), DO near the bottom will be seriously depleted, making benthic environments unfavorable to predators, discouraging them from inhabiting the profundal zone. This change in predator habitats would cause increases in low DO-tolerant prey species. Eventually, even low DO-tolerant macrobenthic organisms could be removed from the profundal zone under serious anoxia, and some processes other than biological interactions would become important for determining the dominant macrobenthos species. Continued environmental monitoring of lake ecosystems is needed to understand the potentially widespread impacts of climate warming.

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Disclosure statement

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