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Diatom productivity since the last glacial period using *Praestephanos suzukii* cell size as supportive evidence

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Abstract A 40,000-year record of the diatom concentrations in the BIW95-4 sediment core is presented to discuss changes in diatom productivity in Lake Biwa, central Japan. Diatom productivity was estimated to have been low in the last glacial period, but high during the interglacial Holocene. *Praestephanos suzukii* is a dominant species in the core, and its size distribution changed in proportion to its valve concentrations, serving as a potential proxy of past productivity, similar to diatom concentrations that tended to be diluted by other sedimentary particles. The modes of *P. suzukii* valve diameters shifted to smaller sizes as diatom concentrations increased in the Holocene, whereas they remained relatively large in the last glacial period. The diatom productivity inferred from these proxies was highest in the mid-Holocene, declining toward the present. Further research should examine whether this declining trend has followed long-term climate changes, glacial-interglacial cycles, or recent anthropogenic global warming.

Key words: diatom productivity, cell size, last glacial period, Holocene, *Praestephanos suzukii*, Lake Biwa

Introduction

Climate exerts strong moderating control over aquatic ecosystems. Recent global warming has changed primary producers in lakes in Arctic, alpine, temperate-low-elevation, and tropical regions (Rühland *et al.*, 2015). In Lake Biwa, warming is a probable fundamental cause of the reduced oxygen supply to the hypolimnetic zone, which is having a marked ecological impact on biochemical cycles, primary production, and endemic animals in deep cold water (Yoshida *et al.*, 2018). Limnological observations of Lake Biwa begun in the early 1960s recorded the lake's eutrophication and its subsequent recovery in the 1980s, along with changes related to global warming since 1990 (Kumagai *et al.*, 2003; Hsieh *et al.*, 2011). Kishimoto *et al.* (2013) investigated 30-year phytoplankton census data and reported that the biovolume of phytoplankton, including diatoms, tended to decrease with changes in their composition.

The siliceous valves of diatoms, which are the unique fossilized components of freshwater phytoplankton, are preserved in the bottom sediments. Diatom fossils can be used to estimate the diversity of past primary producers and the ecosystem components that depend on the primary production. Tsugeki *et al.* (2010) studied a 100-year-long sediment core and found an increase in *Fragilaria crotonensis* at the expense of *Aulacoseira nipponica*, as well as higher correlations of the changes in diatom composition with meteorological parameters such as wind velocity than with nutrient loads. Kuwae *et al.* (1997, 2002) discussed 400-kyr-long changes in diatom productivity and glacial cycles using a long sediment core: high diatom productivity in interglacial periods and warm interstadial phases in contrast to low diatom productivity in glacial periods and cold stadial phases. Here, we report the changes in the diatom flora over the past 40 kyr, an intermediate time scale between these previous studies, to integrate the geological record and instrument observations. In addition, the size of planktonic diatom cells is presented as evidence of the past productivity of diatoms, although small-celled diatoms are emphasized in the context of global warming

(Rühland *et al.*, 2015).

Material and Methods

Age Model: A 16-meter-long piston core (core BIW95-4) was recovered at Site 2 off Shirahige Beach from a water depth of 67 m (Fig. 1, Yamada and Fukusawa, 1999; Hayashida *et al.*, 2007). The core was composed mainly of homogeneous bluish-gray to gray clay and silty clay, intercalated with nine volcanic ash layers. From the top to the bottom of the core, seven of the ash layers were identified as Kg, K-Ah, U-Oki, Sakate, DHg, DSs, and AT (Fig. 2). The thin silty sandy layers, darker gray clay layers, partly laminated layers, intercalated leaf fragments, and patches of vivianite crystals are illustrated in Fig. 2. The age model in this study is based on Hayashida *et al.* (2007), who constructed the age model of the same core of this study with 8 radiocarbon ages of leaves or organic material from the core and the published radiocarbon ages of 5 widespread tephra layers.

Diatom Analysis: Subsamples for diatom analysis were taken from cubic samples measuring 7 cm^3, which were sampled from the core at approximately 2.4-cm spacing. Each dried subsample was weighed and treated with 15% hydrogen peroxide under UV light for 1 hour to convert it into a suspension. The suspended sediments were rinsed with distilled water and diluted to 20 mL for storage in glass vials. A portion of each suspension was further diluted with distilled water and spread on a round cover slip (Matsunami no. 1, diameter 18 mm). The cover slips were mounted on glass slides (Matsunami S1215, 0.9–1.2 mm thick) with Styrax resin (Sigma Storax Gum, Sigma–Aldrich, St. Louis, MO, USA; refractive index = 1.62) on a hot plate heated at 80°C, after drying the suspension at room temperature. After fixing the resin in an oven at 80°C for several weeks, the slides from 107 of the 626 subsamples were observed on an Olympus BX-51 light microscope (LM) equipped with differential interference contrast optics. Species compositions and the number of valves per 1 g sediment were calculated for all siliceous remains that included more than 200 diatom valves (most contained over 500 valves) in radially scanned viewing areas on each slide at ×400 magnification. The diameters of 300 discoidal valves of *Praestephanos suzukii* (Tuji and Kociolek) Tuji were measured under ×400 magnification using an ocular micrometer. The measurements had a precision of 1.25 μm and were grouped into size classes at 2.5-μm intervals. Isopleths were drawn using Igor Pro for Macintosh (WaveMetrics, Lake Oswego, OR, USA). All of the material and specimens used in this study, including dry sediments (RM-009398–009997), suspensions in glass bottles (RM-029282–029908), membrane filters for scanning electron microscopy (RM-029909–029917), and LM diatom slides (MPC-031662–032287), are stored in the National Museum of Nature and Science, Tsukuba.

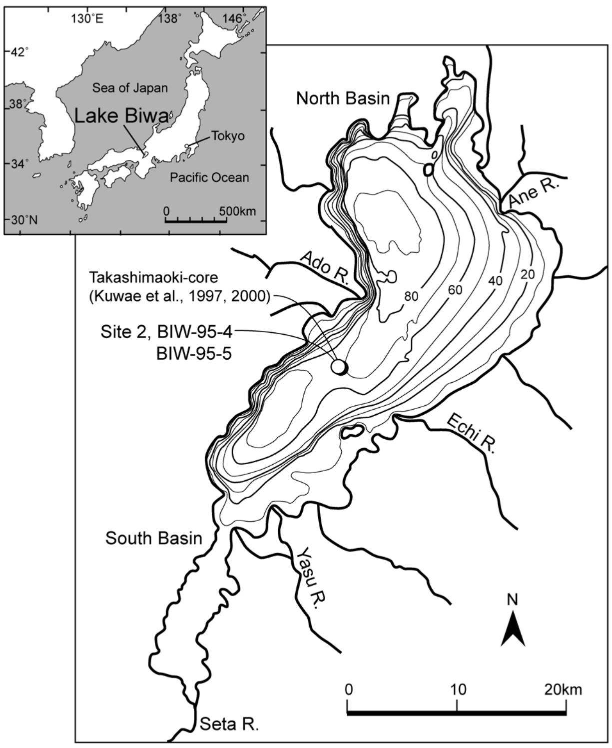

Fig. 1. Maps showing the location of Site 2 in Lake Biwa, central Japan, where the BIW95-4 (Yamada and Fukusawa, 1999; Yamada, 2004; Hayashida, 2007), BIW95-5 (Ishiwatari *et al.*, 2009), and Takashima-oki cores studied in Kuwae *et al.* (1997, 2002) were obtained.

Results

Figure 2 shows the diatom concentrations and species compositions. The abundance of diatom fossils per 1 g sediment was 2–4 times greater in the Holocene section than in the last-glacial section. Concentrations increased gradually after the U-Oki deposition to a maximum in the middle Holocene

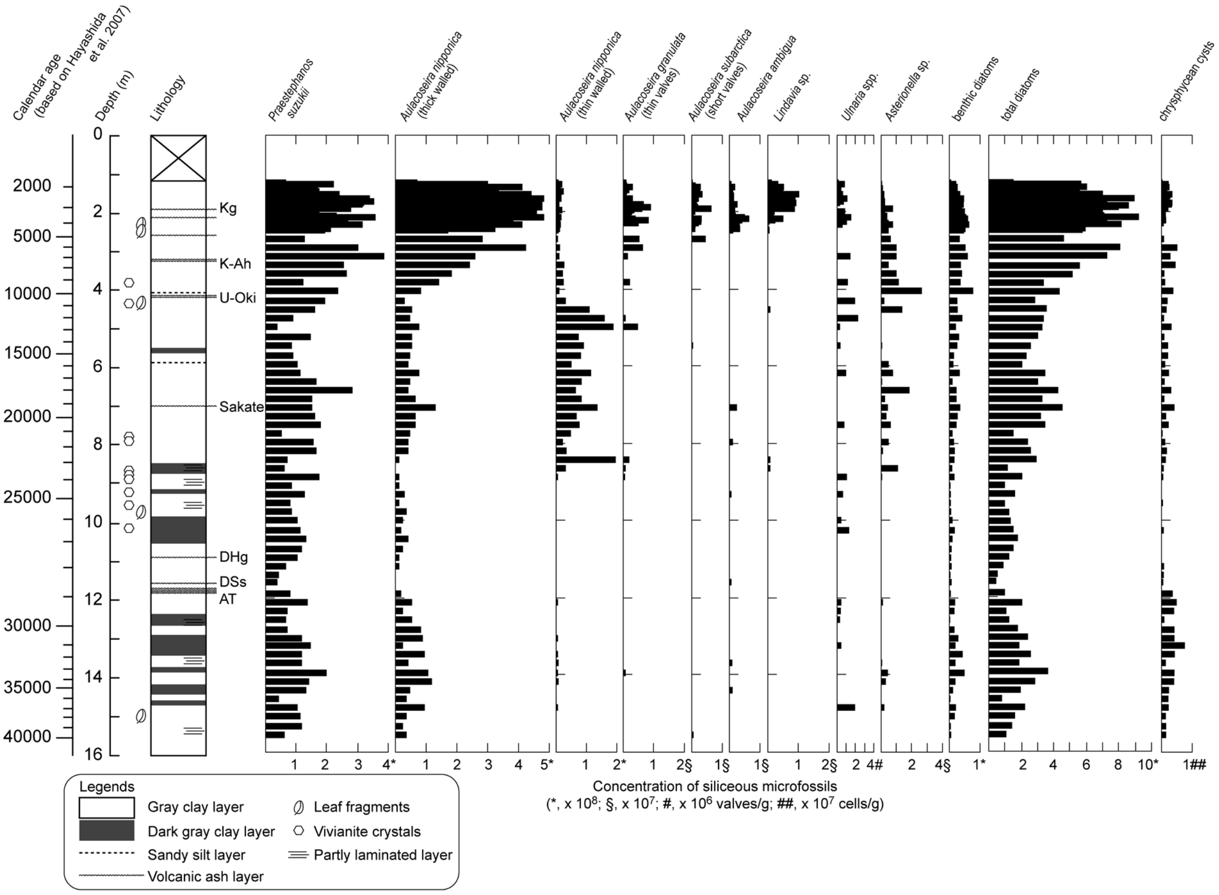

Fig. 2. Diagram showing the lithology of the BIW95-4 core and stratigraphic changes in the concentrations of siliceous microfossils.

section, 6000–4000 years BP. Most of the diatom fossils in the core were planktonic taxa such as *Praestephanos suzukii* and *Aulacoseira* spp., which comprised over 80% of the total. The Holocene increase was mainly due to increases in *Aulacoseira* species, especially thick-walled *A. nipponica*.

Figure 3 shows the changes in the size distribution of *P. suzukii* in the core. The valve diameters of *P. suzukii* were smaller in the Holocene section, especially between the onset and middle of the Holocene. Most of the valves in the population were smaller than 20 µm, with the mode at 7.5–10.0 µm. Larger valves were observed in the last glacial section. The modes of the size distribution were 7.5–12.5 µm for 40–25 ka, 17.5–22.5 µm for 25–22 ka, and 10.0–17.5 µm for 22–11 ka. The *P. suzukii* concentrations were also smaller in the last-glacial section than in the Holocene section, a trend opposite that for the mean diameter in each temporal population.

Discussion

To obtain continuous climate records since the middle Pleistocene, researchers first drilled the bottom sediments of Lake Biwa in 1971 (Horie, 1984). Many shorter cores for studies of paleoenvironmental changes during the last glacial–interglacial cycle have been taken from the lake (*e.g.* Takemura *et al.*, 2010). Yamada (2004) analyzed the mineral and chemical compositions of one core (BIW95-4) and suggested that the opal-A content and total organic carbon revealed the history of primary production in the lake. Changes in these proxies are presumed to reflect the amounts of precipitation during the summer monsoon (Yamada, 2004). The total organic carbon contents reported by Yamada (2004) were ca. 0.8% in the glacial period versus 1.5–2.0% in the Holocene. This change is similar to our results for diatom valve concentrations; the maximum observed in the mid-Holocene is synchronous with the total organic carbon (TOC) observations in Yamada (2004). Ishiwatari *et al.* (2009) reported the same trend in TOC in a 32-kyr record of the BIW95-5 core taken at the same site. The similarity of these changes might have been caused by the same basic changes in primary production in the lake.

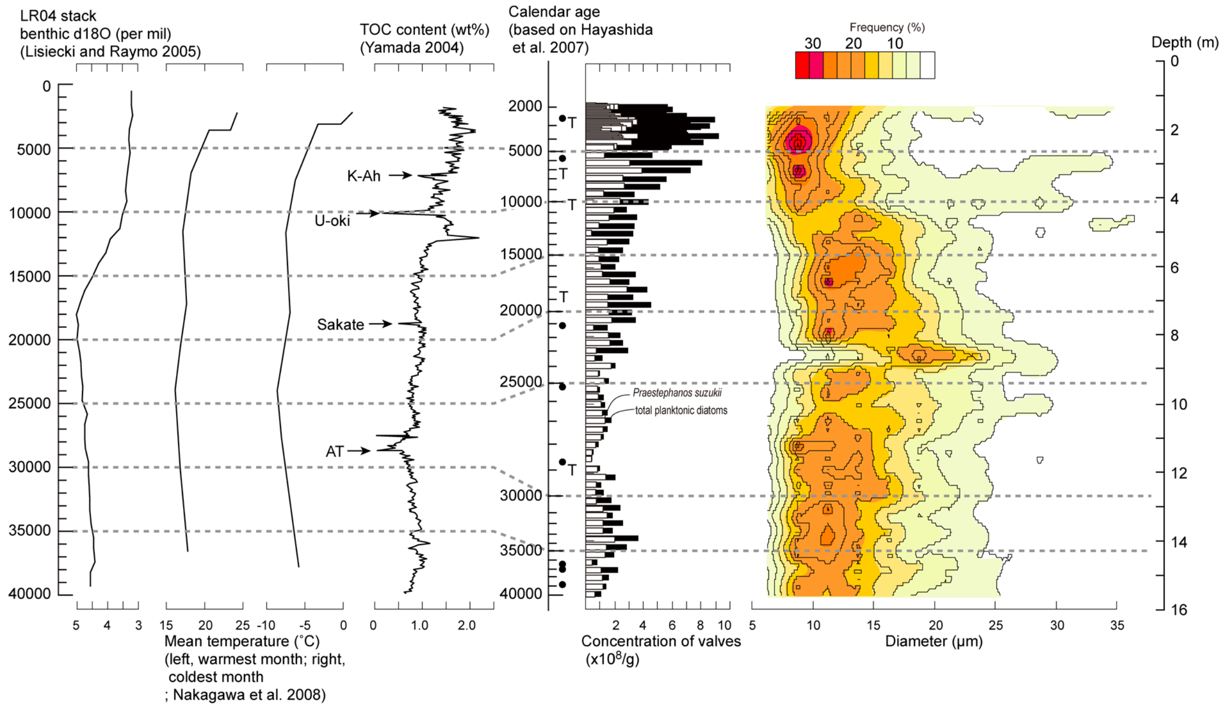

Fig. 3. Diagram showing the stratigraphic changes in valve concentrations of *Praestephanos suzukii* and total diatoms as well as in the size distribution of *P. suzukii*. On the vertical axis in the center, solid circles indicate calibrated radiocarbon dates and "T"s show ages of tephra layers adopted for age model of the core BIW95-4.

Kuwae *et al.* (1997, 2002) studied a longer core, the Takashima-oki core (Fig. 1), to determine diatom concentrations over the last 400 kyr. They found high concentrations in warm periods and low concentrations in cold periods, synchronous with the so-called Milankovitch glacial–interglacial cycles. Our results (Fig. 2) support their work and fill in their Holocene record. Based on Kuwae *et al.* (1997, 2002), high diatom concentrations were correlated with coarser grains that were transported and deposited during warm periods with much precipitation and much erosional force (Kashiwaya *et al.*, 1987). Diatom concentrations remained high even with dilution by these terrestrial grains, implying high diatom production maintained by increased nutrient supplies, which might have resulted from intensified erosional processes under high precipitation (Kuwae *et al.*, 1997, 2002).

The valve diameter of *P. suzukii* (Fig. 3) is a proxy independent of the amounts of terrigenous grain deposition that dilute the diatom concentrations. The valve diameters of *P. suzukii* generally showed an inverse relationship with total diatom valve concentrations (Fig. 4). When relatively high diatom concentrations were observed, the modal valve diameter of *P. suzukii* was relatively small.

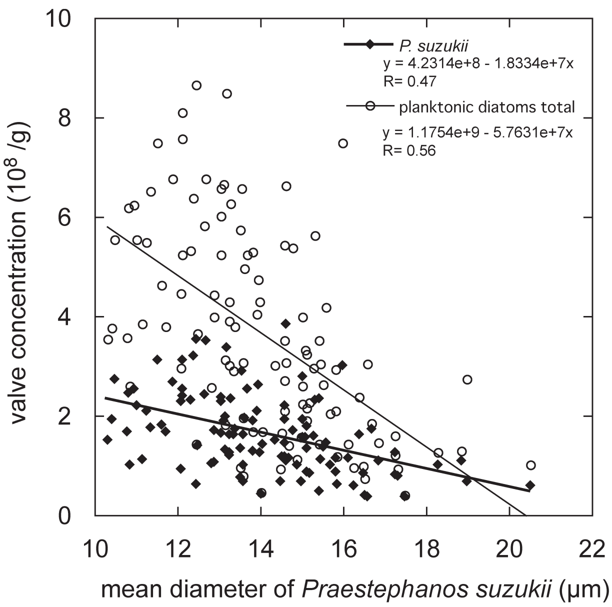

Fig. 4. Diagram showing the correlations between the mean diameter and valve concentration of *Praestephanos suzukii* and those of planktonic diatoms as a whole.

Even the range of the changes in the valve concentrations of *P. suzukii* was smaller than those of *Aulacoseira* species and total diatoms, most of which were *Aulacoseira* spp. The valve diameters of *P. suzukii* obviously fluctuated and they could be therefore served as a sensitive proxy for the paleoenvironment. Correlation coefficients between valve diameters and concentrations, however, do not show high values, R = 0.47 for *P. suzukii* and R = 0.56 for total planktonic diatoms (Fig. 4). One of the reasons of such low correlation coefficients could be that the valve concentrations had been diluted from original diatom production by terrigenous grains. Taphonomic losses of diatom valves would also have diluted the original diatom production. If we had better estimates of the past sedimentation rates and amount of taphonomic losses, the original amount of diatom production could be calculated and could show a better correlation with the size of diatoms.

The diatom concentrations during the glacial period examined in this study do not show a declining pattern unlike the marine oxygen isotope record (LR-04 stack in Lisiecki and Raymo, 2005), but show repeated, slight increases and decreases (Figs. 2 and 3), whereas the modal valve diameters of *P. suzukii* shift gradually to larger sizes during the last glacial period. This pattern of changes resembles the pollen-based climatic changes reported by Nakagawa *et al.* (2008). Their results indicate that the mean temperature of the warmest month (MTWA, Fig. 3) in the last glacial period was 7–10°C lower than that at present as well as that of the coldest month (MTCO, Fig. 3) was 10–12°C lower. This cold climate regime lasted from 80 to 10 ka, showing a barely recognizable decline. In comparison, the global ice volume reflected in the marine oxygen isotope record (*e.g.* Lisiecki and Stern, 2016; LR-04 stack in Lisiecki and Raymo, 2005; Fig. 3) shows a gradual but obvious decline during glacial periods and abrupt rises at the ends of these periods. Climate has strong moderating influences on water column properties, including ice cover, thermal stability, and stratification, which affect the duration of the growing season and the availability of resources such as light and nutrients for the phytoplankton community (Rühland *et al.*, 2015). The valve diameter of *P. suzukii* generally shows a pattern rather similar to the marine oxygen isotope record (Fig. 3), which might reflect original diatom productivity decreasing gradually during the last glacial period.

The only obvious difference from the other proxies is that *P. suzukii* valve diameters show a significant short-term shift to an extremely large size at 25–22 ka (Fig. 3). The air temperature estimated on the pollen record (Nakagawa *et al.*, 2008) suggests the coldest climate in this period whereas the diatom concentration revealed in this study is the smallest during 40 kys in this period. Both of these variables show a general decline with the gradual beginning and ending, whereas the *P. suzukii* valve diameter shows an abrupt shift in this period. No other mineralogical or chemical proxies show this pattern (Yamada and Fukusawa, 1999; Yamada, 2004; Ishiwatari *et al.*, 2009). A speculative hypothesis to explain this change in diatom size is that a drastic change related to diatoms' life-cycle strategy and productivity occurred at that time as a result of changes in the physical properties of the water column. A shortened growing season with restricted vertical mixing is one possible interpretation. Monomictic overturn occurs in January–March in the present north basin of Lake Biwa, with blooms of the major diatom species (Tezuka, 1984); even anthropogenic disturbances have been observed recently (Ikeda *et al.*, 2018). Under the colder climate during the last glacial period, the winter vertical mixing was interrupted because the temperature of the lake surface water was below 4°C; ice may have covered most of the lake. The growth of diatoms in winter could have been disturbed. Simultaneously, with weakened thermal stratification, diatoms might have grown in a completely different season, i.e., during summer. However, the resource supply was limited throughout the growing season, and their productivity was suppressed at low levels, as estimated by the diatom concentrations in this study (Figs. 2 and 3). Under such environmental conditions, *K*-selected phytoplankton with a low surface-to-volume ratio could dominate (Reynolds, 2006), including large diatoms at the opposite end of the scale from small diatoms with an *r*-selected strategy.

Bramburger *et al.* (2017) provided data supporting the above hypothesis based on sediment cores of Laurentian Great Lakes, revealing that the mean cell size of diatoms decreased by 587 μm^3 over the last ~115 years of lake warming. Even though the rate of decrease is small, the decrease of the cell size is due not only to an increased number of small-sized diatoms in the communities but also to a demographic shift toward smaller individuals within species (Bramburger *et al.*, 2017). Although

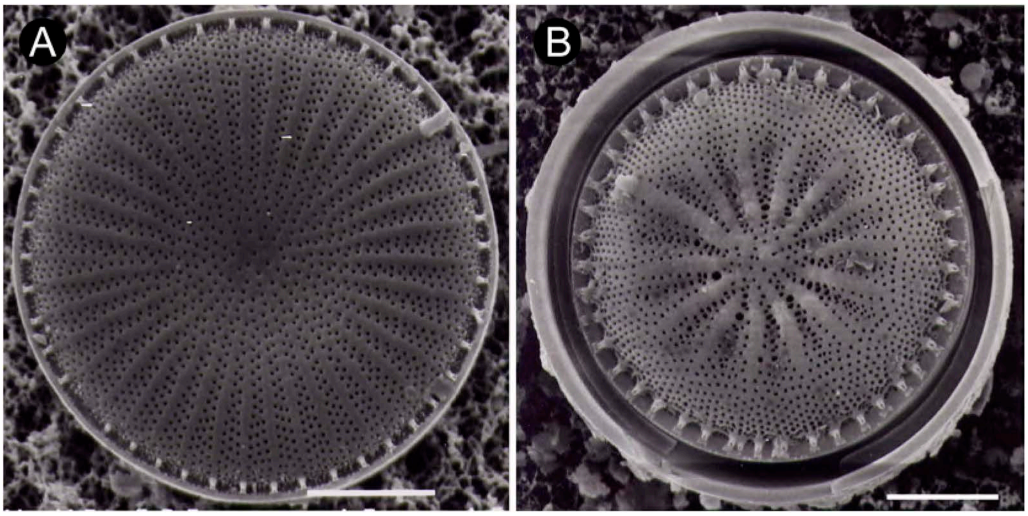

Fig. 5. Scanning electron microscope images of thin-(A) and thick-walled (B) valves of *Praestephanos suzukii*.

Bramburger *et al.* (2017) did not discuss possible *r*-selection of smaller cells in the community or population, extended open water and stratified seasons would be manifested as a demographic shift toward smaller frustules within a species (i.e., decreased taxon-specific mean cell size). Regardless of the environmental factor responsible for such a size change, the valve diameters of *P. suzukii* behaved as if they had exceeded an ecological threshold at 25 ka and then dropped below that level at 22 ka, as reported for the lake diatom responses to warming (Rühland *et al.*, 2015), although further investigations are required to test the hypothesis with sensitive proxies for the mixing or stratification of lake water or with plausible models of the physical profile of the lake.

During the shift of the *P. suzukii* valve diameter toward a larger size at 25–22 ka, dome-shaped initial valves were observed with a high frequency as well (Saito-Kato and Hayashi, 2010). Initial valves are formed after the auxopore formation in the last stage of the sexual reproduction of the diatom life cycle (Round *et al.*, 1990). The auxopore is the largest cell and the earliest stage in the life cycle. Its high frequency in the population means a high frequency of sexual production and/or a low frequency of vegetative cell division that may result in low productivity. Robust valves with thicker walls (Fig. 5) were observed during this period and the earlier section of the core (unpublished data). The life cycle of *P. suzukii* could have been flexibly altered responding to the environmental changes during the last glacial periods, although no supportive evidence has not been presented.

Global warming is the greatest concern that the world faces today. Regarding Lake Biwa, a stagnant water mass with less oxygen as a result of the current warming trend will have severe influences on its ecosystem. A prediction model presented the vertical temperature profiles of the lake under global warming (Yamashiki *et al.*, 2010). It has been estimated that reduced mixing has already reduced primary production by diatoms including *P. suzukii* (Tsugeki *et al.* 2010). During last 40 kyr, the time period of greatest productivity of diatoms and *P. suzukii* observed was in the middle Holocene (Figs. 2 and 3), with a subsequent gradual decrease. Using pollen data, Takahara *et al.* (2000) demonstrated a similar geographical distribution of the biome at present and at 6 ka, respectively, although the climate in the Japanese middle Holocene was estimated to have been warmer in some studies (*e.g.* Kawahata *et al.*, 2009). The diatom flora in the middle Holocene (Fig. 2) appears similar to the present one, i.e., high productivity supported by active vertical mixing or abundant available resources from the catchment area. The vertical mixing in winter–spring may have been promoted by the marked seasonality with cold windy winters. The result of the present study does not contradict Kuwae *et al.* (1997, 2002) in which diatom productivity was regarded reflecting changes in precipitation but also supports Tsugeki *et al.* (2010) in which the vertical mixing was regarded as the factor for changes in diatom productivity. Diatom productivity might be controlled by precipitation that brings nutrients from the catchment area at first, followed by vertical mixing under enough resources during the Holocene.

The mode of valve diameters shifted toward larger sizes in the late Holocene, implying decreasing diatom productivity toward the present. This decreasing trend is consistent with the 100-year sedimentary record (Tsugeki *et al.*, 2010) and recent observations of plankton (Kishimoto *et al.*, 2013), although careful evaluations of diatom concentrations in sediment and of plankton biovolumes in water are needed. If the decreasing trend of diatom productivity has continued from the late Holocene, the recent global warming might not be its sole driver. Because the valve concentration in the sediment is dependent on the effect of dilution by other sedimentary particles as well as taphonomic processes, direct comparison of the core data with recent observations of plankton samples is not plausible. Further search of proxies independent of such effects is necessary. The size changes of *P. suzukii* in recent decades would offer a test whether global warming benefits smaller-celled species and/or smaller individuals in a population (Winder *et al.*, 2009; Selbie *et al.*, 2011; Bramburger *et al.*, 2017), both of which are characterized by a high surface-to-volume ratio.

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