Fragmentation and separation of diatom valves in modern shallow lake sediments: a case study in Lake Kitaura, Japan

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https://hdl.handle.net/2324/7183516

Fragmentation and separation of diatom valves in modern shallow lake sediments: a case study in Lake Kitaura, Japan

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Abstract We investigated diatom-valve fragmentation and frustule separation in surface sediments in Lake Kitaura, a shallow lake in Japan, to clarify how sedimentation processes affect diatom assemblages. Twenty-two surface-sediment samples were collected from Lake Kitaura in 2014. *Aulacoseira* spp. were characteristic planktonic taxa, and *Cocconeis placentula* and *Planothidium lanceolatum* were characteristic benthic taxa, both with monoraphid valves. The fragmentation ratios of *Aulacoseira* spp., the most abundant taxon, were higher nearshore than in the central part of the lake. *Cocconeis placentula*, an epiphytic species, was widely distributed in Lake Kitaura, and its fragmentation ratios increased with distance from the lakeshore. The coexistence ratios of the two valve types of this species decreased with distance from the lakeshore and from macrophytic vegetation. *Planothidium lanceolatum*, a fluvial benthic species, was abundant at the three northernmost sites near a river mouth, and the frustules of this species were seldom separated. These results suggest that long-distance transport promotes fragmentation and separation of benthic diatom valves in shallow lakes.

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Introduction

Diatoms are common and widespread algae in aquatic environments from terrestrial to marine settings (Smol and Stoermer 2010). They form a silica frustule composed of two valves, which is preserved in sediments. The diatom communities indicate their habitat, ecology, and water environment in lakes (Bennion et al. 2010). Fossil diatom assemblages in lake sediments have been employed to reconstruct past water environments such as pH, salinity, and lake-level changes (Chiba et al. 2016; Sato et al. 2016; Vos and Wolf 1993).

Diatom assemblages in lake sediments are also altered by taphonomic factors such as chemical dissolution and the physical breakage of diatom valves (Flower 1993; Hassan et al. 2018). Dissolution

of diatom valves is primarily controlled by salinity and pH in lake waters (Ryves et al. 2001, 2009, 2013). Bioturbation (Austin et al. 2005), compaction, and long-distance transport (Kosugi 1986) play a large part in the physical breakage and fragmentation of diatom valves. Although the breakage process has been estimated from the ratio of complete to fragmented valves (Beyens and Denys 1981), our knowledge of the physical breakage and fragmentation of diatom valves during transport still needs improvement.

The robustness of diatom frustules varies between species, and thus also influences fragmentation, complicating the physical breakage process. For monoraphid diatom species, in which one valve differs from the other morphologically (i.e., they possess araphid and raphid valves), the different valves may experience different taphonomic processes (Hassan et al. 2018). The raphid and araphid valves show different distributions, as reported by Sawai (2001) for *Cocconeis scutellum*. After separation of the valves, waves, currents, and bioturbation disperse araphid valves, whereas raphid valves become concentrated near the substrata. Thus, the ratio of araphid to raphid valves is a promising indicator for assessing the transport process.

The aim of this study was to examine how diatom fragmentation and frustule separation proceed in a shallow lake. In shallow lakes, riverine inflows and waves generally affect the bottom sediment, and may also influence fragmentation and separation during the transport of diatom frustules. The diatom assemblages in Lake Kitaura sediments provide an excellent chance to assess how transportation processes alter the diatom fragmentation and separation in the shallow lake sediments through transport from riverine and lakeshore inputs and via wind-driven sediment resuspension.

Study area

Lake Kitaura is a freshwater lagoon lake located in the southeastern part of Honshu Island, Japan (Fig. 1A). The lake has an area of 35.2 km², a perimeter of 64 km, a maximum water depth of 7 m, and an average water depth of 4.5 m with the northern part relatively shallow. Among the twenty-two river inflows, the Rivers Tomoe and Hokota at the northernmost part of the lake have the highest and second-highest flow rates, with catchment areas of 131.8 and 52.7 km², respectively (Fujita et al. 2006). The River Wani is the sole outflow from Lake Kitaura to the south, and connects to Lake Sotonasakaura. Reed vegetation occurs around part of the lakeshore, particularly near the mouths of the Rivers Tomoe, Hokota, and Yamada.

The Pleistocene plain around Lake Kitaura formed mainly during the last interglacial. The incision of the River Tomoe formed the basin of Lake Kitaura during the last glacial period (Kashima 1990; Saito et al. 1990). Lake Kitaura was a bay during the mid-Holocene transgression at 10,000–5500 yr BP, and burial of the bay mouth by a tidal flood delta began at 4500–2500 yr BP. In the seventeenth century, redirection of the River Tone to its present-day path buried the bay mouth completely. As a result, the lake water changed from brackish to fresh–brackish. In the 1970s, the River Hitachi tide gate was constructed (Fig. 1A) and the lake water became fresh, with a present-day salinity of 0.06 ‰ and pH of 8.8 (Ibaraki Prefectural Government 2021; Naya et al. 2007a).

Lake Kitaura is a good model area to study shallow lake environments because of the extensive knowledge available about its sediments and diatoms. The distribution of Lake Kitaura sediments is determined by erosion, transportation, and resuspension (Naya et al. 2004a). The bottom sediments in the lake basin consist of silty clay. Sandy sediments occur in the littoral parts at 0.5–3.5 m water depth. The sediment distribution is predominantly affected by wind-induced waves, wind direction, and wind velocity because of the lake's shallowness (Naya et al. 2004a). The northeast wind prevailing around Lake Kitaura drives surface waves and thus vertical mixing of the lake water. The waves transport silty-clayey sediment particles to the lake basin, whereas sandy sediment particles are left in the littoral areas. The northern part of Lake Kitaura contains a shallow basin (water depth 2.5 m) with clay to silt deposits. The short fetch by the indented shoreline leads to deposition of fine silty clay. Except for the Tomoe River, the distribution of sandy sediment near inflowing rivers is limited, indicating a small riverine influence on the grain-size distribution (Naya et al. 2004a). The heterogeneous sediment distribution resulting from water movement can be relevant for the transport of diatoms in the lake.

Fig. 1 Field setting. **A** Location of Lake Kitaura, Japan. **B** Map of the sampling sites (numbered) of lakebed surface sediments in Lake Kitaura in 2014. Black solid and dashed lines denote inflowing rivers with watershed areas greater than and less than 8 km^2, respectively. The River Wani (dotted line) is the only outflowing river. **C** Lake bathymetry. Points denote the sampling sites shown in (**B**)
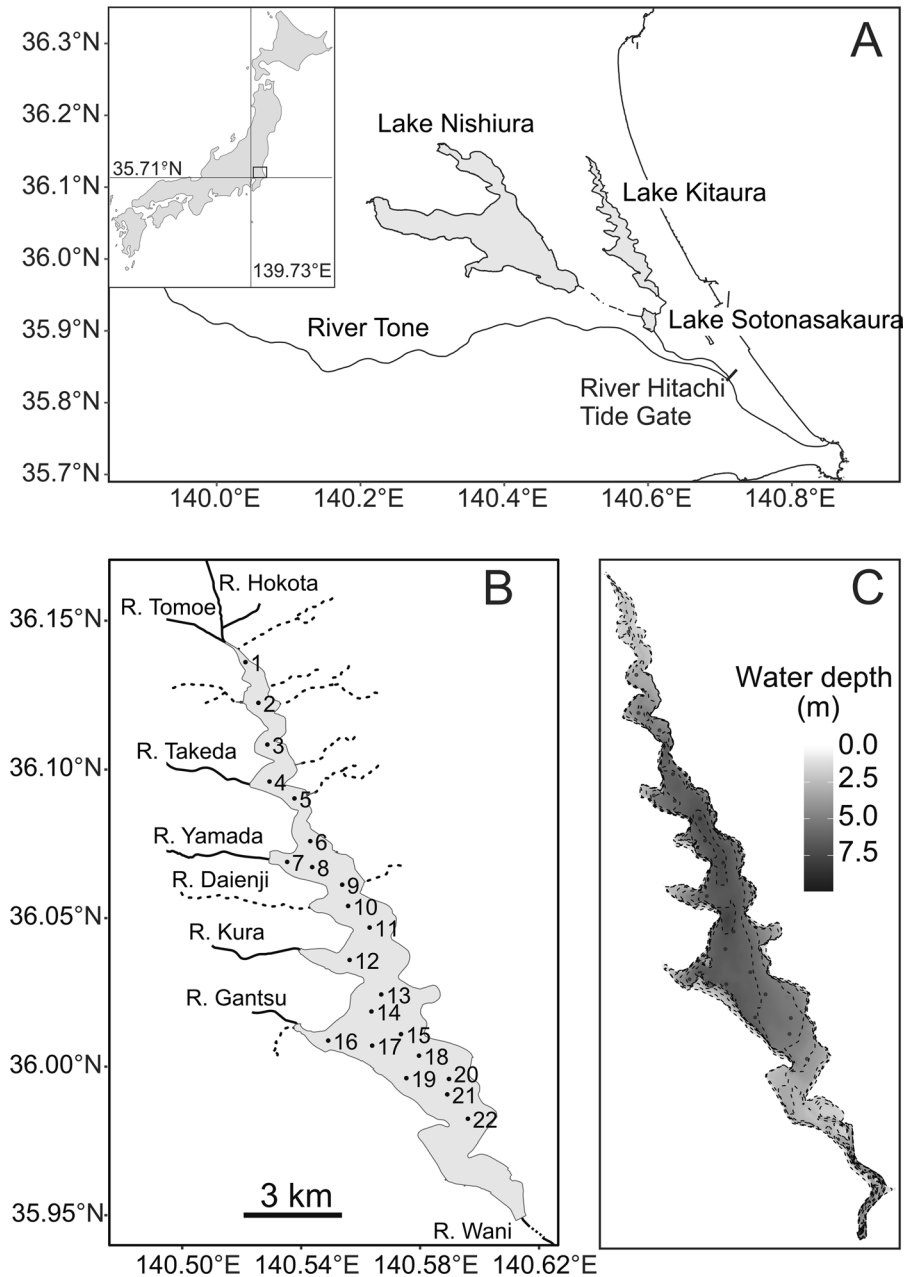
Naya et al. (2007b) reported the taxonomy and spatial distribution of diatoms in the surface sediments of Lake Kitaura and suggested that the diatom assemblages comprised a mixture of taxa that originated from different habitats (water column, shoreline macrophyte zone, and inflowing rivers). The diatom assemblages imply the existence of autochthonous and allochthonous diatoms. Autochthonous diatoms are deposited in their habitat. In contrast, allochthonous diatoms are affected by transportation. Some benthic diatoms attached to substrata in littoral areas are carried to offshore locations, and then they can be regarded as allochthonous valves. The 22 rivers that flow into Lake Kitaura carry suspended particles, including allochthonous diatom valves. A sediment-trap study demonstrated that sediments and diatom valves are resuspended and laterally transported by the wind-driven lake circulation (Naya

et al. 2004b). These reworked diatoms may also represent allochthonous valves.

Materials and methods

Surface-sediment samples were collected at 22 sites (called "kt01–kt22" from north to south) in Lake Kitaura during August and September 2014 using a gravity short corer with a diameter of 7 cm (Fig. 1B, C; Table S1). Water depths at the sampling sites were measured with a sounding lead and ranged from 1.6 to 7.3 m (Table S1). Distance of sampling sites from the nearest lakeshore (called "distance to nearshore") ranged from 100 to 930 m, and from the nearest aquatic vegetation zone (called "distance to vegetation") ranged from 114 to 1623 m (Geospatial Information Authority of Japan 2018). The top 5 cm of the sediment samples were placed in plastic bags, and each sample was stored in a laboratory refrigerator. Subsequently, they were freeze-dried (FDU-1200, EYELA, Tokyo, Japan).

Diatom analysis

Approximately 0.05 g of freeze-dried sample was put into a 50-mL plastic tube and treated with 2 mL of 15% hydrogen peroxide in a water bath at 80 °C for 1 h to decompose organic matter. The suspended sample was diluted with distilled water to 20 mL to stop the reaction. For each suspended sample, 1 mL was dropped onto a coverslip and dried at room temperature. The dried samples were mounted on glass slides with Pleurax (Mount media, Fujifilm Wako Chemicals Corp., Osaka, Japan). Three hundred diatom valves were identified on each slide using a light microscope equipped with a 100× magnification oil immersion objective lens (BX53, Evident Co, Tokyo, Japan). Diatom taxa were identified following Round et al. (1990), Idei (2000), Watanabe (2005), Kobayasi et al. (2006), and Naya et al. (2007b). The diatom lifeform and habitat were based on Naya et al. (2007b) and Vos and Wolf (1993). Each diatom valve was classified as complete or fragmented. A fragmented valve was defined as a partially broken valve if at least 60% of the valve was present. Araphid and raphid valves of monoraphid taxa (i.e., *Cocconeis* and *Planothidium*) were counted separately. Additional counting of

fifty valves of *Cocconeis placentula* was performed for each site to exclude the effect of differences in relative abundance.

We performed scanning electron microscopy (SEM) observation of the fine structures of diatom valves. The pretreated suspensions were filtered through a membrane filter (Advantech Co. Ltd., 0.45 μm pore size, 25 mm diameter) and dried at room temperature. The filtered samples were cut into 5-mm squares, taped onto an aluminum stub, and coated with OsO_4 using an osmium coater (Neoc-ST, Meiwafosis Co. Ltd., Tokyo, Japan). SEM observations were performed using a field-emission SEM (Regulus 8230, Hitachi High-Tec Co, Tokyo, Japan) with a 1 kV acceleration voltage, 10 μA emission current, and a working distance of 1.3 mm.

The diatom-valve-fragmentation ratio (*Fr*), the ratio of fragmented valves to total counted valves, was calculated for each diatom taxon (Supplementary data) as:

$$Fr = \frac{D}{Nv}$$

where *D* is the number of fragmented valves and *Nv* is the total number of valves for each diatom taxon. *Fr* values range from zero to one: zero means that no fragmented valves are present, whereas one means that all valves are fragmented. *Fr* values were calculated for species with an abundance of more than five valves in at least one sample. We selected *Aulacoseira* spp., *Cyclostephanos dubius*, *Cyclotella meneghiniana*, *Actinocyclus normanii* f. *subsalsa*, *Stephanodiscus hantzschii* f. *tenuis*, *Staurosira venter*, *Navicula* spp., *Achnanthidium* spp., *Planothidium* spp., *Psammothidium* spp, and *Cocconeis placentula* for *Fr* analysis in this study.

For monoraphid taxa, the raphid and araphid valves were counted separately. The coexistence ratio of raphid and araphid valves (*Cv*) was calculated for each taxon as:

$$Cv = 1 - \frac{|A - R|}{Nc}$$

where *A* and *R* are the counts of araphid and raphid valves, respectively, and *Nc* is the total population of each taxon (Shimoyama 1989), i.e., the greater number of araphid and raphid valves in each sample. The

Cv index ranges from zero to one. If the counts of araphid and raphid valves are the same, the *Cv* index is one. If all valves in a sediment sample are araphid (or raphid), the *Cv* index is zero. Sawai (2001) demonstrated that the distribution patterns of raphid and araphid valves of *Cocconeis scutellum* differed in a tidal marsh: raphid valves were attached to the substrata and were more abundant near habitats, whereas araphid valves were moved easily by water movements (e.g., tidal action) and were widely dispersed. The *Cv* index increases when more autochthonous diatoms accumulate near their habitat. We selected two benthic monoraphid taxa, *Cocconeis placentula* and *Planothidium lanceolatum*, for the *Cv* analysis of Lake Kitaura samples.

We conducted the following data analyses using R software (version 4.0.4) with the 'stats' and 'vegan' packages. Hierarchical cluster analysis was conducted for the relative abundances of encountered diatom taxa at the species or genus level to identify the major environmental gradient underlying variation of diatom assemblages in the lake. The Bray–Curtis dissimilarity matrix and unweighted pair group method with arithmetic mean were used for the cluster analysis. Spearman's correlation analysis was applied to examine the relationship between *Fr* and *Cv* for each diatom taxon and the distance to nearshore, water depth, and distance from macrophytic vegetation. In addition, univariate regression analysis was conducted with *Fr* or *Cv* as the independent variable and distance to nearshore as the dependent variable to show the relationships between taphonomic signatures of planktonic and benthic diatoms and environmental variables.
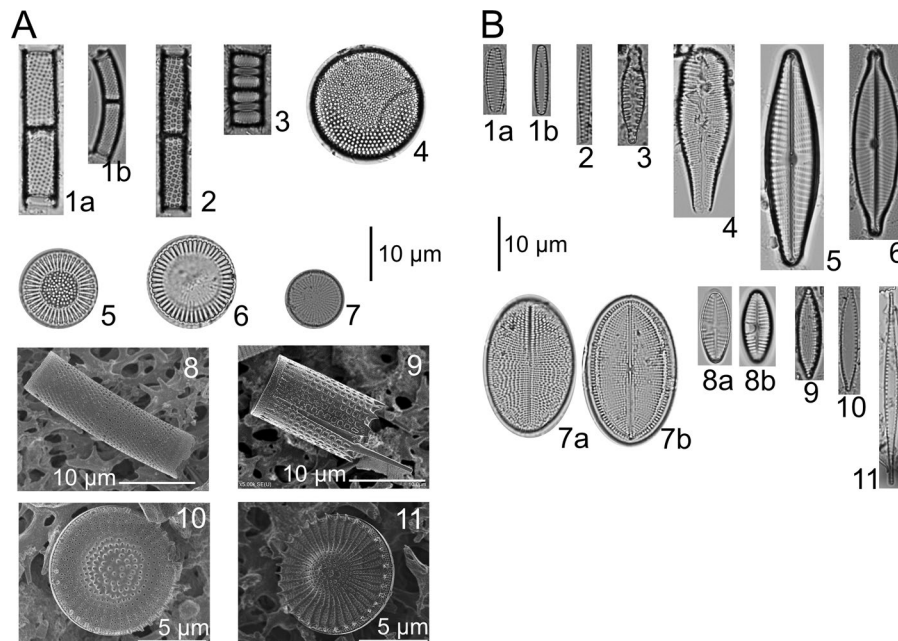

Fig. 2 Light microscopic and SEM images of diatoms from lakebed surface sediments. **A** Planktonic taxa: (*1a*, *1b*, *8*) *Aulacoseira ambigua*, sites kt02 and kt03; (*2*, *9*) *A. granulata*, kt02; (*3*) *A. pusilla*, kt08; (*4*) *Actinocyclus normanii* f. *subsalsa*, kt20; (*5*, *10*) *Cyclostephanos dubius*, kt02; (*6*) *Cyclotella meneghiniana*, kt02; (*7*, *11*) *Stephanodiscus hantzschii* f. *tenuis*, kt11 and kt02. **B** Tychoplanktonic and benthic taxa: (*1a*) *Staurosira venter*, site kt03; (*1b*) *Pseudostaurosira* spp., kt17; (*2*) *Staurosirella berolinensis*, kt21; (*3*) *Staurosira leptostauron* var. *dubia*, kt03; (*4*) *Gomphonema truncatum*, kt02; (*5*) *Navicula lanceolata*, kt02; (*6*) *Navicula amphiceropsis*, kt02; (*7*) *Cocconeis placentula*, kt02 (*a* araphid valve; *b* raphid valve); (*8*) *Planothidium lanceolatum*, kt01 (*a* araphid valve; *b* raphid valve); (*9*) *Nitzschia amphibia*, kt03; (*10*) *Nitzschia perminuta*, kt01; (*11*) *Nitzschia subacicularis*, kt02

Results

Diatom assemblages in Lake Kitaura

Fifty diatom taxa were identified in the surface sediments at 22 sites in Lake Kitaura (Fig. 2a, Fig. 2b; Table S2). Planktonic taxa dominated the surface sediments of Lake Kitaura, exceeding 70% of the assemblages except at the northern sites kt01–kt03 (Fig. 3A). The abundances of tychoplanktonic taxa increased near the River Tomoe (Fig. 3B). Similarly, the relative abundances of benthic taxa were greater than 15% in the northern part of the lake (kt01–kt03; Fig. 3C). At these three sites near the mouth of the River Tomoe, 19–57% of the diatom assemblages consisted of benthic taxa. Relatively abundant benthic taxa were found at southern sites kt20–kt22.

Fifteen diatom taxa each formed more than 5% of the assemblage in at least one sample of Lake Kitaura's surface sediments. Of these taxa, *Aulacoseira ambigua*, *Aulacoseira granulata*, *Aulacoseira pusilla*, *Actinocyclus normanii* f. *subsalsa*, *Cyclostephanos dubius*, *Cyclotella meneghiniana*, and *Stephanodiscus hantzschii* f. *tenuis* are planktonic; *Staurosira venter*, *Pseudostaurosira* spp., and *Staurosirella* spp. are tychoplanktonic; and *Nitzschia* spp., *Gomphonema* spp., *Navicula* spp., *Cocconeis placentula*,

Achnanthidium spp., *Planothidium* spp., and *Psammothidium* spp., are benthic (Fig. 4). *Aulacoseira ambigua* and *A. granulata* were the representative planktonic taxa in Lake Kitaura's surface sediments, but not at the four northern sites (kt01–kt04; Fig. 4A, B). The relative abundances of *A. pusilla* were lower than those of *A. ambigua* and *A. granulata* (Fig. 4C). The relative abundances of *Cyclostephanos dubius* was higher in the southern part of the lake (Fig. 4E). *Cyclotella meneghiniana* was distributed mainly in the center of the lake, and was much less abundant at sites near river mouths (kt01, kt04, kt07, kt12, and kt16) and southern sites kt20–kt22 (Fig. 4F). *Staurosira venter* was the major tychoplanktonic taxon (Fig. 4H–J). *Navicula* spp., *Achnanthidium* spp., *Planothidium* spp., and *Psammothidium* spp. were the major benthic taxa (Fig. 4M, O). *Planothidium lanceolatum* was the most abundant taxon at the three northernmost sites. *Cocconeis placentula* showed a maximum abundance at the mouth of the River Tomoe (kt02; Fig. 4N). *Navicula* spp. was abundant at site kt01 at the mouth of the River Tomoe (Fig. 4M).

The 22 sites were divided into two clusters: cluster I and cluster II, with a dissimilarity of 0.5 (Fig. 5; Table S1). The results of the hierarchical cluster analysis reflected that diatom assemblages at sites
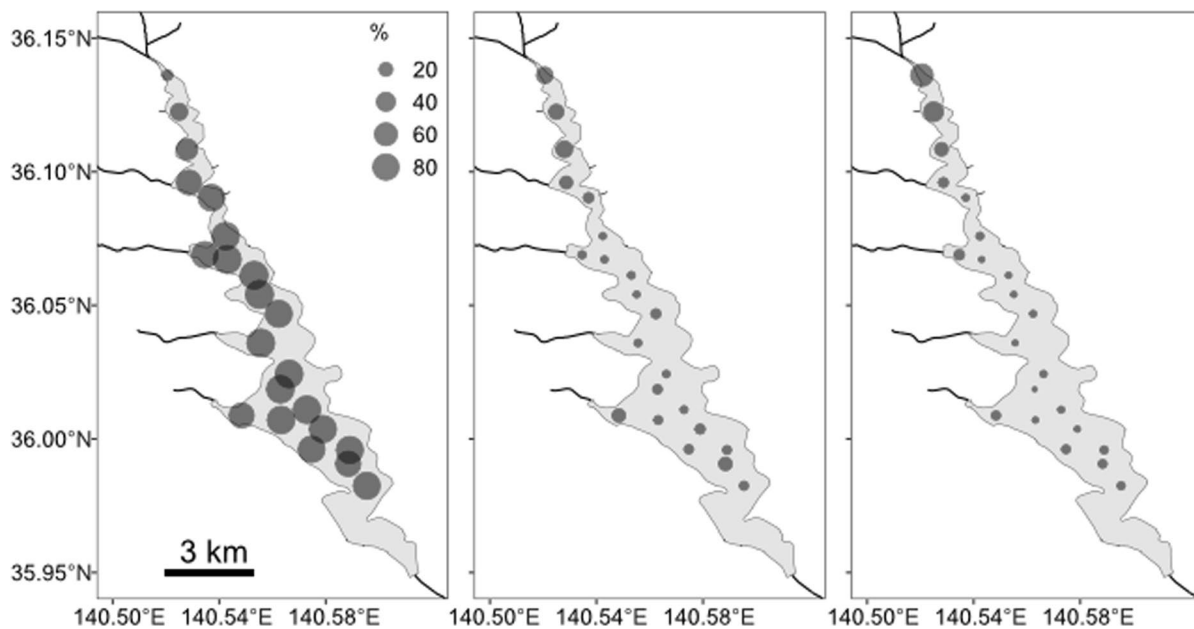

Fig. 3 Distributions of the relative abundances of **A** planktonic taxa, **B** tychoplanktonic taxa, and **C** benthic taxa in Lake Kitaura
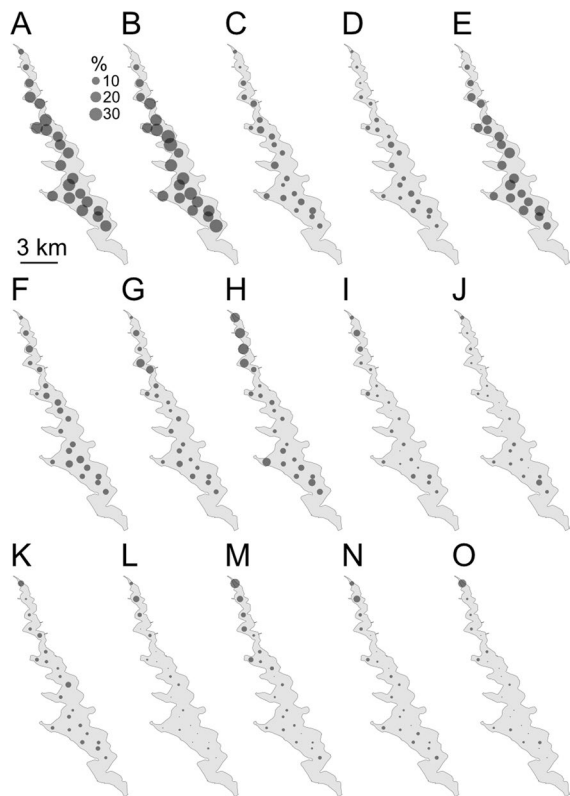
Fig. 4 Relative abundances of diatom taxa in surface sediments for taxa that constituted more than 5% of the assemblage at at least one site. Planktonic taxa: **A** *Aulacoseira ambigua*, **B** *Aulacoseira granulata*, **C** *Aulacoseira pusilla*, **D** *Actinocyclus normanii* f. *subsalsa*, **E** *Cyclostephanos dubius*, **F** *Cyclotella meneghiniana*, and **G** *Stephanodiscus hantzschii* f. *tenuis*. Tychoplanktonic taxa: **H** *Staurosira venter*, **I** *Pseudostaurosira* spp., and **J** *Staurosirella* spp. Benthic taxa: **K** *Nitzschia* spp., **L** *Gomphonema* spp., **M** *Navicula* spp., **N** *Cocconeis placentula*, and **O** *Achnanthidium* spp., *Planothidium* spp., and *Psammothidium* spp.

Fig. 5 Dendrogram of diatom assemblages in Lake Kitaura calculated by hierarchical cluster analysis. Sample dissimilarities of each sample calculated by the Bray–Curtis distance for diatom abundance

kt01–kt03 were abundant benthic and tychoplanktonic taxa (Fig. 4; Table S3). Cluster I consists of samples from water shallower than 4 m depth. Cluster II contains sites deeper than 4 m water depth on a flat plain: kt06-k22.

Valve fragmentation and frustule separation

The range of *Fr* in Lake Kitaura sediments differed among diatom species and sampling sites (Fig. 6). *Aulacoseira* species and *Stephanodiscus hantzschii* f. *tenuis* showed low *Fr* values compared to the other planktonic taxa, i.e., *Cyclostephanos dubius*,
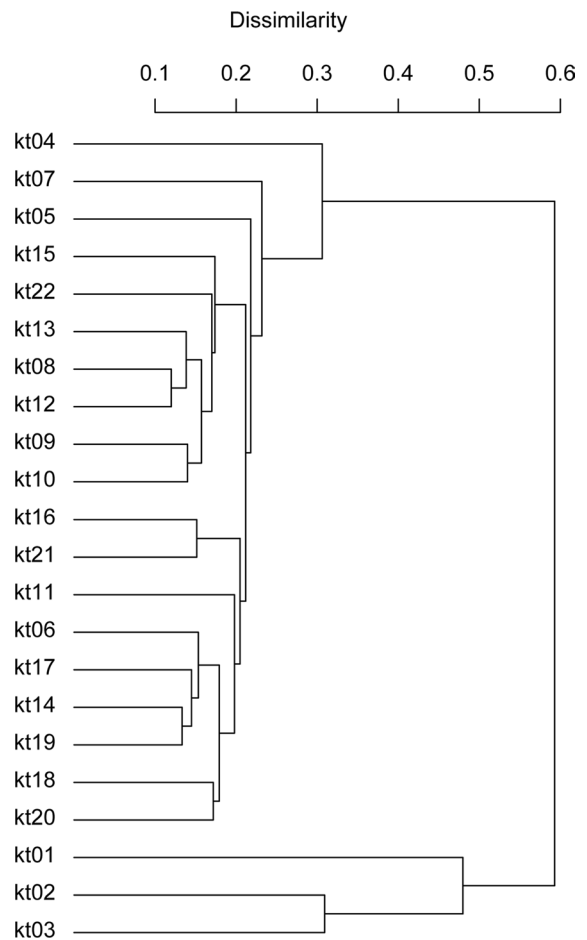
Cyclotella meneghiniana, and *Actinocyclus normanii* f. *subsalsa* (Fig. 6). *Staurosira venter* had a low *Fr* value (<0.1) at almost all sites. *Navicula* spp. and *Cocconeis placentula* were highly fragmented. The spatial patterns of the *Fr* values of *Aulacoseira ambigua* and *A. granulata* showed that they tended to increase at relatively shallow sites (Fig. 7). The *Fr* values of *Aulacoseira ambigua* and *A. granulata* showed peaks at the rivers Tomoe (kt02) and Gantsu (kt16), and at the southern littoral site (kt20). *Fr* of *A. ambigua* was also high at site kt10.

The *Cv* variations in *C. placentula* and *P. lanceolatum* showed different patterns (Fig. 7C, D). The *Cv* values of *C. placentula* were highest at the northern site kt03 and the southernmost site kt22. In contrast,
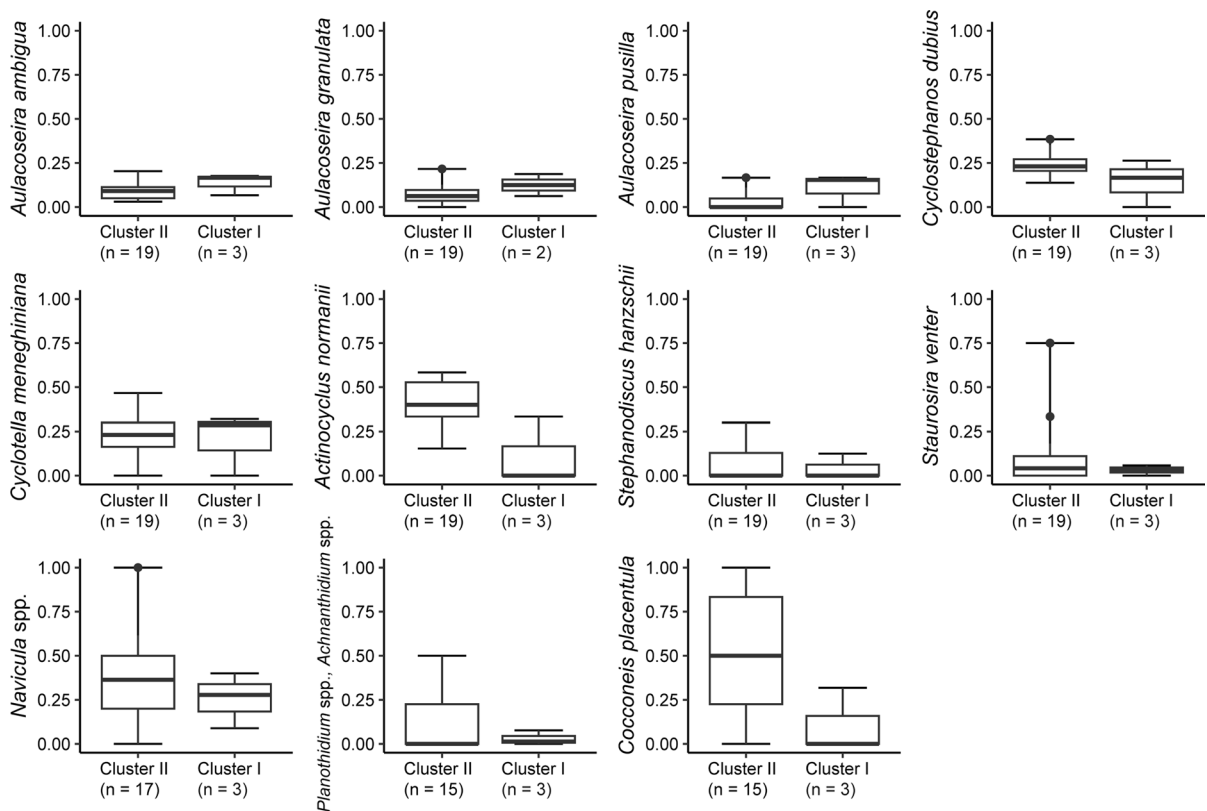
Fig. 6 Boxplots of *Fr* values in dominant diatom species. Boxes denote 25–75 percent quartiles. Vertical lines show the median. Error bars indicate maximum and minimum values. The *n* values denote sample sizes in clusters I and II

Planothidium lanceolatum showed sporadically high *Cv* values at sites kt01, kt07, kt17, and kt20.

We focused on the valve fragmentation and frustule separation of *Cocconeis placentula*, which occurred ubiquitously in the sediments of Lake Kitaura. *Fr* and *Cv* values were calculated from data on 50 *C. placentula* valves for each sample (Fig. 8). The *Fr* values increased from north to south, and the lowest values were found at sites kt02 and kt07, which are close to river mouths. The *Fr* values of araphid valves exhibited a trend similar to that of *Fr* of whole valves, but *Fr* of raphid valves was different. The *Cv* values were higher at river mouths (kt02 and kt07) and the southernmost site (kt22). The spatial pattern of *Fr* values was a mirror image of that of the *Cv* values ($R = -0.64$).

The relationships of valve fragmentation, frustule separation, and environmental variables

The *Fr* values of *A. ambigua* and *A. granulata* showed a weak negative correlation with distance to nearshore ($R = -0.25$ and -0.44, respectively; Fig. 9A, B, Table 1). The highest correlation with *Fr* of *A. granulata* was distance to nearshore (Fig. 9B). In addition, *Fr* and *Cv* of *C. placentula* were correlated with water depth ($R = 0.42$ and -0.30, respectively), distance to nearshore ($R = 0.80$ and -0.47, respectively), and distance from neighboring aquatic macrophytic vegetation (distance to vegetation, $R = 0.57$ and -0.52, respectively). Thus, the highest correlation with *Fr* of *C. placentula* was distance to nearshore (Fig. 9C).
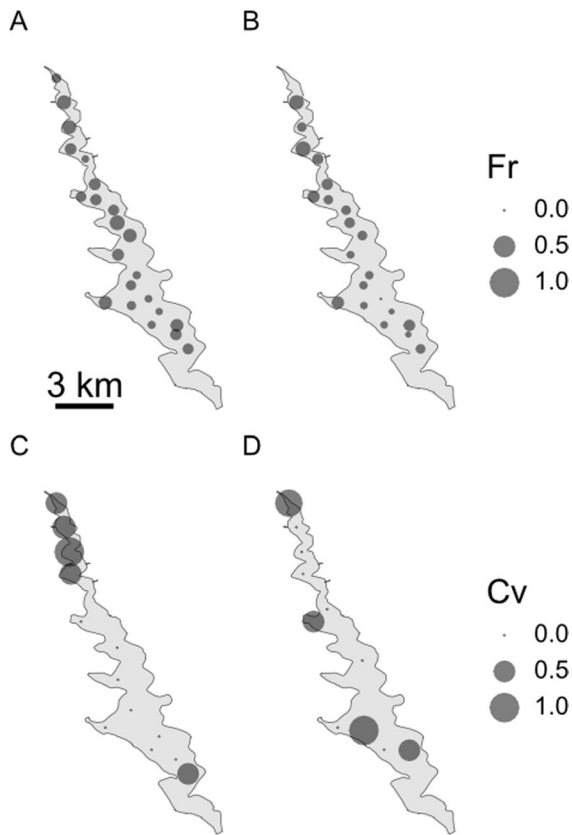
Fig. 7 *Fr* values of **A** *Aulacoseira ambigua* and **B** *A. granulata*, and *Cv* values of **C** *Cocconeis placentula* and **D** *Planothidium lanceolatum* at each sample site. Gray circles show the *Fr* and Cv values

Fig. 8 *Cv* and *Fr* values for *Cocconeis placentula*. **A** *Cv* values obtained by counting 50 valves in each sample. **B** *Fr* values obtained by counting 50 valves in each sample. **C** *Fr* values of the araphid valves. **D** *Fr* values of the raphid valves

Discussion

Diatom distribution in Lake Kitaura

Diatom assemblages in the surface sediments of Lake Kitaura were composed of autochthonous and allochthonous specimens. Abundant *Aulacoseira* at most sites indicate a high contribution of autochthonous planktonic taxa in the diatom assemblages. Naya et al. (2007b) also reported that *Aulacoseira* taxa were the dominant diatoms in the surface sediments of Lake Kitaura, suggesting that this group is the major primary producer. A sediment-trap study observed flux peaks of both vegetative cells and empty valves of *Aulacoseira* taxa during spring and fall (Naya et al. 2004b). *Aulacoseira* taxa (*A. ambigua*, *A. granulata*, and *A. pusilla*) form resting spores after the spring bloom, which sink to the lake bottom in the
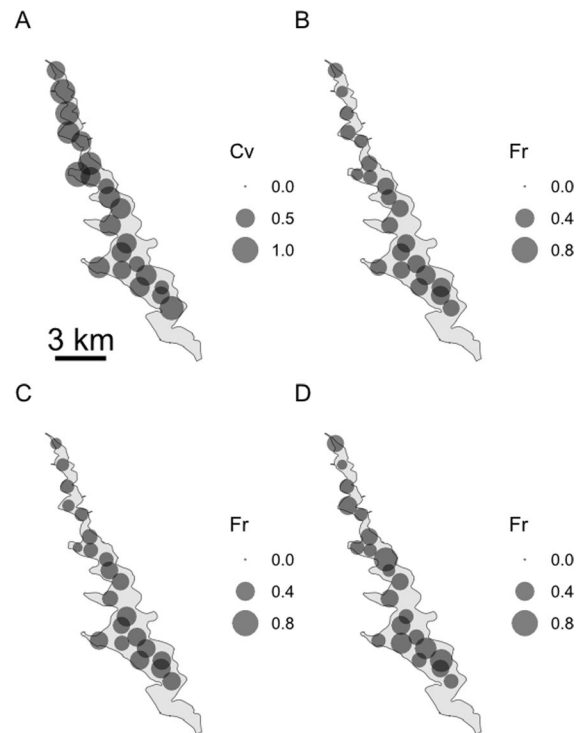
oligotrophic summer (Kilham and Kilham 1975; Tsukada et al. 2006). The restarting of lake-water circulation in the fall brings the *Aulacoseira* resting spores to the surface water, where they revert to vegetative cells. Therefore, *Aulacoseira* taxa in Lake Kitaura's sediments are a mixture of autochthonous specimens that have sunk directly from the surface water and reworked valves that were transported by lake-sediment resuspension.

Benthic diatom taxa, such as *Navicula*, *Cocconeis*, *Achnanthidium* spp., *Planothidium* spp., and *Psammothidium* spp., in Lake Kitaura's sediments were transported from inflowing rivers and littoral areas. In particular, notable contributions of autochthonous benthic taxa were found at the northern sites (cluster I) near the mouth of the River Tomoe (Figs. 4, 5). In contrast, the allochthonous valves are transported offshore (Naya et al. 2007b). *Planothidium lanceolata* and *Cocconeis placentula* dwell on substrata of inflowing rivers or on macrophytes. Thus, the presence of these benthic taxa can indicate transport of
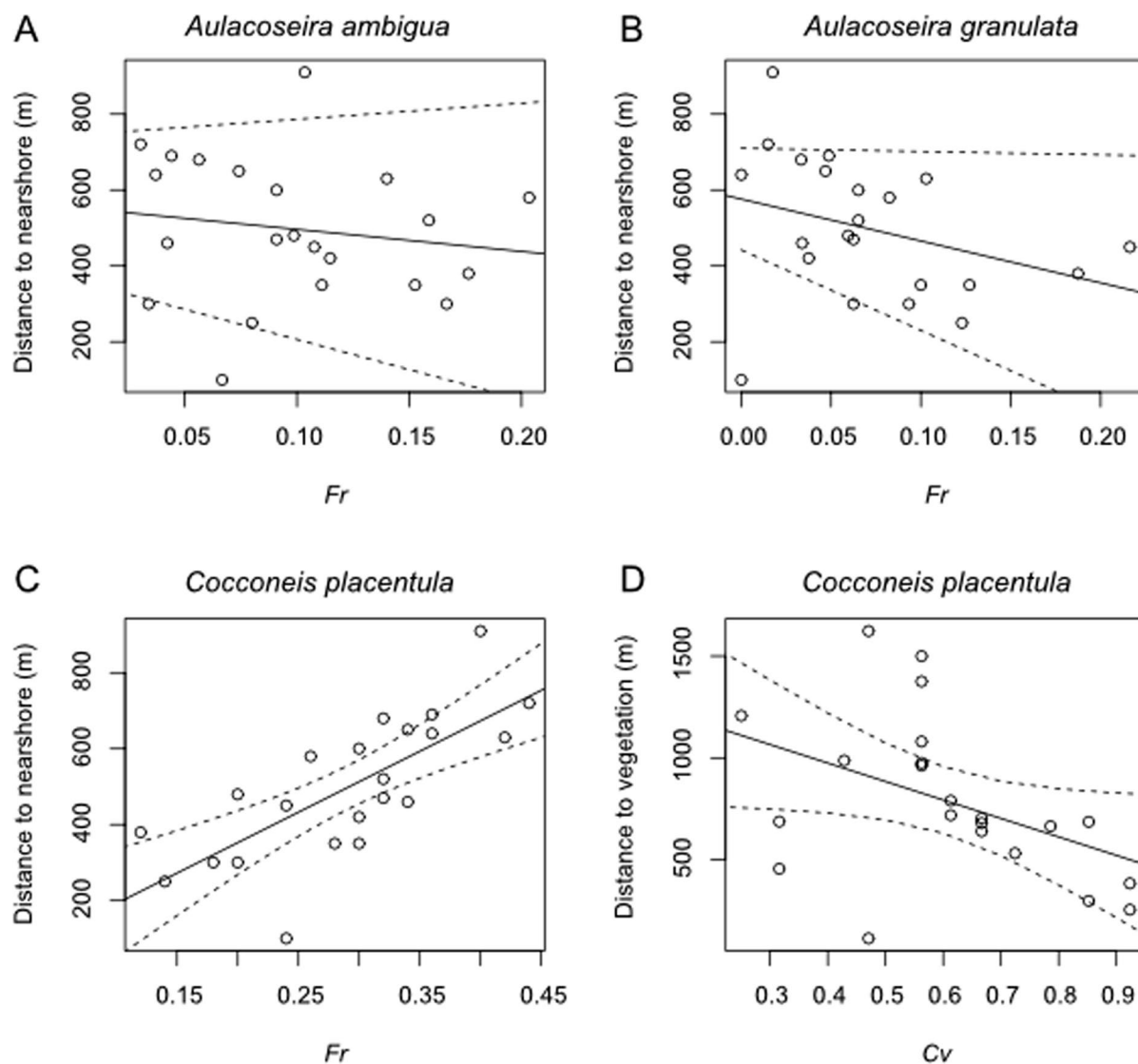
Fig. 9 Univariate regression of distance to nearshore and *Fr* values of **A** *Aulacoseira ambigua*, **B** *Aulacoseira granulata*, and **C** *Cocconeis placentula*. **D** Univariate regression of distance to vegetation and *Cv* values of *Cocconeis placentula*. The solid lines show the regression lines, and the dotted lines denote 95% confidence intervals

Table 1 Spearman's correlation coefficients between taphonomic signatures (*Fr* and *Cv*) of *Cocconeis placentula* and *Aulacoseira* taxa and water depth, distance to nearshore, and distance to vegetation

	Fr of *Cocconeis placentula*	Water depth (m)	Distance to nearshore (m)	Distance to vegetation (m)
Fr of *Cocconeis placentula*	–	0.42	0.80	0.57
Cv of *Cocconeis placentula*	− 0.62	− 0.30	− 0.47	− 0.52
Fr (Araphid valve)	0.83	0.34	0.74	0.57
Fr (Raphid valve)	0.65	0.33	0.43	0.24
Fr of *Aulacoseira ambigua*	–	− 0.04	− 0.25	–
Fr of *Aulacoseira granulata*	–	− 0.22	− 0.44	–

material from rivers and littoral areas. The presence of autochthonous diatoms (*Planothidium* and *Cocconeis*) in an assemblage can be explained by transport by inflowing water and valve fragmentation and frustule separation.

Fragmentation of planktonic diatoms

We discuss the sedimentation of *Aulacoseira* taxa as representative of planktonic diatoms in Lake Kitaura. The *Fr* values of *Aulacoseira* taxa were lower than those of other planktonic taxa—*Cyclostephanos dubius*, *Cyclotella meneghiniana*, and *Actinocyclus normanii* f. *subsalsa* (Fig. 6)—because of differences in valve shape and silicification. *Aulacoseira* taxa have heavily silicified cylindrical valves, whereas the other planktonic taxa have less silicified discoid valves, leading to selective valve fragmentation and dissolution (Ryves et al. 2001). Remains of *Aulacoseira pusilla*, which is a small species with valves measuring less than 10 μm in both diameter and height, were less fragmented than remains of *A. ambigua* and *A. granulata*. The *Fr* values of the discoid valves of *Stephanodiscus hantzschii* f. *tenuis* are lower than those of the discoid valves of other planktonic taxa such as *Cyclostephanos dubius*, *Cyclotella meneghiniana*, and *Actinocyclus normanii* f. *subsalsa*. Naya et al. (2007b) reported that the relative abundances of *A. pusilla* and *Stephanodiscus* species were positively correlated with sand content, and were high in littoral areas despite disturbance by wave erosion. *Aulacoseira pusilla* and *Stephanodiscus* spp. may be less influenced by wave action than other taxa (Naya et al. 2007b), and so the *Fr* values of these taxa were lower. Among the *Aulacoseira* taxa, the *Fr* values of *A. ambigua* and *A. granulata* were weakly correlated with distance to nearshore (Fig. 9A, B; Table 1). Naya et al. (2004a) suggested that lake currents and waves resuspend sediments in the lake basin; however, the *Fr* values of *Aulacoseira* taxa were lower in the center of the lake (sites kt13–kt15, kt17, and kt19) regardless of the influence of resuspension. The ecological features of requirement of turbulence (Anderson 2010; Hassan et al. 2013, 2018) and formation of resting spores (Schelske et al. 1995) suggest that vertical mixing is unimportant for valve fragmentation of *Aulacoseira* taxa. *Aulacoseira* valve fragmentation is likely to take place in river mouths and littoral areas where littoral erosion and wave-related transport

occur (Fig. 7). However, the correlation between *Fr* and distance to nearshore was not strong (Fig. 9A. B). *Aulacoseira* taxa can also be found as tychoplanktonic species (Kobayasi et al. 2006), which may have caused the weak correlation between *Aulacoseira Fr* and distance to nearshore.

Transportation of benthic diatoms

Monoraphid diatom species provide clues for estimating the transport of allochthonous diatoms because of the differing in the attachment to the substrata between the raphid and araphid valves (Sawai 2001). The high abundances and *Cv* values of *P. lanceolatum* at sites near river mouths suggest transport of this species from the inflowing rivers, such as the rivers Tomoe and Hokota (kt01; Fig. 7). *Planothidium lanceolatum* may be attached to the substrata by the raphid valve in streams (Chen et al. 2017). The decrease in both *Cv* and abundance from kt01 to kt02 suggests frustule separation (Fig. 7). The high *Cv* values of *P. lanceolatum* in the offshore sites (kt17 and kt20; Fig. 7) indicate transport of valves as frustules. In contrast, the wide distribution of *C. placentula* suggests that remains of this species are transported from the inflowing rivers and littoral areas. The southernmost site (kt22) showed a high *Cv* value that is comparable to those of the northern sites (kt02 and kt07; Fig. 8). *Cocconeis placentula* lives attached to macrophytes by its raphid valve (Rojas and Hassan 2017), and has been demonstrated to dominate emergent, submersed, and rooted floating macrophytes in a shallow eutrophic lake (Hassan et al. 2018). The reed vegetation of Lake Kitaura is a potential habitat for *C. placentula* and source of autochthonous valves. Overall, the *Cv* trends reflect the origin and transport of *P. lanceolatum* and *C. placentula* in the lake sediments.

The negative correlation between *Fr* and *Cv* of *C. placentula* in Lake Kitaura indicates that transport affects the valve fragmentation and frustule separation. The difference between the *Fr* values of raphid and araphid *C. placentula* valves suggests that valve fragmentation mainly occurs during transport. Diatom-valve fragmentation is controlled by long-distance transportation (Dawson 2007; Kosugi 1989), bioturbation (Austin et al. 2005), and chemical dissolution (Ryves et al. 2006). Hassan et al. (2018) showed that the preservation of *C. placentula* was better in the macrophyte zone than in open-water

environments. Bioturbation should not affect the araphid and raphid valves selectively, and chemical dissolution is unlikely in freshwater lakes with a near-neutral pH. Considering the correlation between *Fr* of the araphid valve and distance to nearshore, we suggest that valve fragmentation of *C. placentula* in Lake Kitaura is mainly caused by long-distance transport, demonstrating the importance of *Fr* and *Cv* as autochthonous indicators.

Diatom taphonomic process and implications for shallow lakes

The *Fr* and *Cv* values of benthic diatom taxa in surface sediments, particularly for monoraphid taxa such as *Planothidium* and *Cocconeis* species, are feasible indicators of the provenance and transport of diatom valves. The monoraphid *Cocconeis* and *Planothidium* taxa are often found in sediment samples from shallow lakes (Dong et al. 2007; Rojas and Hassan 2017; Ryves et al. 2009). These diatoms are attached to substrata, especially macrophytes, so they are a means of detecting the localities where those diatoms live. The high *Cv* values of *C. placentula* based on counting 50 valves per sample showed that autochthonous valves accumulated at sites near river mouths (Figs. 7, 8A). The *Fr* index is helpful for indicating the transport distance: higher values suggest a greater transport distance. However, the *Fr* values of the raphid valves were weakly correlated with distance to nearshore because these valves, being attached to macrophytes, are difficult to transport. The positive correlation between the araphid valve *Fr* values and distance to nearshore suggests that these valves become fragmented during transport.

The *Fr* values of *Aulacoseira* taxa indicate the sedimentation process in the shallow lake regardless of the complex ecology. *Aulacoseira* taxa commonly live in shallow freshwater lakes (Anderson and Odgaard 1994; Dong et al. 2007; Flower 1991; Ryves et al. 2013). They dominate in the lake center but also dwell in littoral areas (Kobayasi et al. 2006). *Aulacoseira ambigua*, *A. granulata*, and *A. pusilla* form thick, robust resting spores (Kilham and Kilham 1975; Tsukada et al. 2006). In shallow lakes, resuspension causes reworking of diatom assemblages (Hassan et al. 2018; Naya et al. 2004b). The consistently low *Aulacoseira Fr* values suggest that most *Aulacoseira* specimens in Lake Kitaura are

autochthonous. A slight increase in the *Fr* values of *Aulacoseira* in the littoral area reflects lateral movement of valves by resuspension. *Aulacoseira* taxa grow in the water column and are deposited in central areas of the lake as autochthonous valves. The reworked valves of *Aulacoseira* were transported to a littoral area with fragmentation. However, *Aulacoseira* taxa can live in the littoral area as tychoplankton, and thus, the *Aulacoseira Fr* patterns can sometimes be equivocal compared to those of benthic taxa (kt01; Fig. 7).

Benthic diatom taxa can help to understand diatom taphonomy in shallow lakes because of their specific habitats and behaviors related to riverine inflow and aquatic vegetation. Benthic diatoms living in shore regions or rivers are transported into the lake and spread to the lake center. Autochthonous valves of benthic diatoms are mainly deposited near areas of reed vegetation (Flower 1993) and are well preserved (Hassan et al. 2018). Without vegetation in littoral areas, fine-grained benthic diatom valves are readily washed out by waves. Monoraphid benthic diatom taxa demonstrate how transport of benthic diatoms from the lakeshore to offshore regions results in selective removal of the araphid valves, causing the coexistence ratio of the paired valves to decrease (Sawai 2001). The *Cv* and *Fr* taphonomic indices can help to interpret diatom-assemblage data, and thus improve paleoenvironmental reconstructions based on diatom assemblages from sediments of shallow lakes.

Conclusions

We studied diatom assemblages in surface sediments from Lake Kitaura, and found that valve fragmentation and frustule separation differed by species, habitat, and ecology. Valve fragmentation of *Aulacoseira* taxa likely occurs in river mouths and lakeshore areas, not the lake center. Vertical mixing and resuspension in the water column are unlikely to promote fragmentation of *Aulacoseira* valves. Benthic diatom taxa for which both valves coexist in river mouths and lakeshore areas are autochthonous. The raphid valves of *Cocconeis placentula* were restricted to areas near the shore with reed vegetation, whereas the araphid valves were spread from the shore to offshore. The species' ecology and habitat caused both valves to behave differently and become separated. The *Fr* of

C. placentula was more sensitive to the distance from the nearest shore and can be a good indicator of diatom transport from littoral areas. The *Cv* values also indicated transport of diatoms from their life habitat. However, the relationships between diatom transport processes and sediments need to be clarified. In the future, sedimentological and chemical analyses should be conducted to confirm diatom transport processes.

Author contributions KK, NY, and YO designated the study. NY collected sediment samples. KK carried out microscopic observation and wrote the draft. All authors contributed to the data analysis and manuscript writing, and approved the manuscript contents.

Declarations

Conflict of interest The authors declare no competing interests.

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