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Structural characteristics and niche analysis of macrobenthic communities in Lake Nakaumi, Japan, under global climate change

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ABSTRACT

As a key component of material cycling and energy flow in Lake Nakaumi, macrobenthos play a vital role in maintaining the stability of the lake ecosystem. However, against the backdrop of global climate change, research on the macrobenthic community in this lake remains insufficient. In particular, the structural changes of this community following the impact of strong El Niño events (2014 to 2016) remain unclear. Therefore, based on macrobenthos monitoring data collected from Lake Nakaumi in 2017 and 2018, a period following the attenuation of the strong El Niño event, this study employs multivariate statistical analysis methods to comprehensively examine the community composition, diversity, ecological niches and interspecific relationships of dominant species, as well as the seasonal differentiation of the macrobenthic community. The main conclusions are as follows: The community consists primarily of 34 species belonging to 6 phyla, with annelids being the most species-rich group. Notably, there are no euryecious species (species with broad niches) within this community. The niche overlap values among dominant species exhibit interannual fluctuations, which may be attributed to the combined effects of benthic habitat fragmentation, spatiotemporal randomness in the distribution of suitable environments and resources, and environmental filtering. Temporally, the community can be distinctly divided into two seasonal groups: the winter-spring group and the summer-autumn group. In terms of diversity, the winter-spring group outperforms the summer-autumn group. This significant dissimilarity is mainly driven by seasonal indicator species and species with density differences between the two groups. Such temporal variations in community composition represent a key mechanism enabling the macrobenthic community in Lake Nakaumi to maintain stability amid extreme seasonal changes.

Keywords: macrobenthic communities, niche, structural characteristics, temporal variations, Lake Nakaumi.

INTRODUCTION

Brackish lakes in coastal regions are jointly influenced throughout the year by both riverine and marine forces. Unlike typical freshwater or saline lakes, their salinity exhibits pronounced spatial and temporal fluctuations, giving rise to a distinct type of lacustrine ecosystem. Macrobenthos are key components of aquatic ecosystems, playing an essential role in material cycling and energy flow. They generally inhabit the surface or subsurface of lakebed sediments and are mainly composed of invertebrates (Jiang et al., 2024). Because their habitats are relatively stable, macrobenthos are often used as indicators of environmental changes in lakes. Consequently, the structural characteristics of their communities are of great significance for assessing the ecological health of brackish lake ecosystems. Lake Nakaumi lies on the border between Shimane and Tottori Prefectures in Japan, facing the Sea of Japan to the north and connected to Lake Shinji to the west via the Ohashi River. It is an important transitional waterbody through which the Hii River flows before entering the sea (Tabayashi et al., 2017). The lake has been strongly affected by human activities; compared with the mid-20th century, the disappearance of submerged macrophytes has fundamentally altered its habitat conditions (Hiratsuka et al., 2007; Yamamuro et al., 2006).

Research on macrobenthos in Lake Nakaumi remains relatively limited. Yasugi et al. (1999) examined how artificial sand capping alters sediment conditions and affects macrozoobenthic community structure, demonstrating its positive role in community restoration. Yamaguchi et al. (2000) investigated the effects of installing tidal exchange pipes in the northern waterway, showing that the pipes significantly improved surrounding sediment conditions and enhanced macrobenthos diversity. Fujimoto et al. (1999) surveyed the macrozoobenthic community and environmental conditions in the Honjo area, identifying dominant species in the artificially modified habitat and their relationships with environmental variables. Hirakiuchi et al. (2019) explored how the spatiotemporal dynamics of hypoxia influence the distribution of *Anadara kagoshimensis*, highlighting the importance of oxygen-rich seawater for this species. Shinohara et al. (2016) analyzed changes in the distribution and community structure of bivalves following the removal of embankments in the Honjo area, demonstrating that embankment removal had positive effects on bivalve communities. Kurata et al. (2018) conducted a benthic survey in the summer of 2016, but their work focused only on short-term relationships between benthic organisms and environmental conditions during that season.

Therefore, given the current status of research on the macrobenthic community in Lake Nakaumi, it is crucial to systematically investigate this community and clarify its characteristics under the influence of extreme climate events. The previous strong El Niño event occurred between 2014 and 2016. In this study, we analyze two years (2017–2018) of macrobenthos monitoring data using multivariate statistical methods. Our aim is to clarify the structural characteristics of macrobenthic communities in Nakaumi Lake following the strong El Niño event, reveal interspecific relationships among dominant taxa, and elucidate temporal patterns in dominant species. The findings are expected to provide a scientific basis for the conservation and management of the Nakaumi Lake ecosystem under global climate change.

MATERIALS AND METHODS

The α-diversity of macrozoobenthic communities was calculated using the Shannon–Wiener diversity index (H'), Pielou's evenness index (J), and Margalef's species richness index (d) (Shannon and Weaver, 1949; Pielou, 1975; Margalef, 1958). The formulas are as follows:

$$H' = -\sum_{i=1}^{S} \frac{n_i}{n} ln \frac{n_i}{n} \tag{1}$$

$$J = \frac{H'}{\ln S} \tag{2}$$

$$d = \frac{(S-1)}{\ln n} \tag{3}$$

where: n_i is the number of individuals of species i, n is the total number of individuals in the sample, and S is the total number of species recorded in the sample.

Dominant species in the community were identified using the index of relative importance (IRI) (Pinkas et al., 1971), calculated as follows:

$$IRI = (N + W) \times F \tag{4}$$

where: N is the proportion of individuals of a given species relative to the total number of individuals, W is the proportion of biomass of that species relative to total biomass, and F is the proportion of samples in which the species occurs.

In this study, species with an IRI greater than 100 were selected for analysis. β diversity was calculated using the Sorensen dissimilarity index (Whittaker, 1960; Whittaker, 1972), expressed as:

$$\beta_{Sorensen} = 1 - \frac{2C}{A+B} \tag{5}$$

In this study, β diversity indices were used to explore temporal variations in the community. A represents the number of species in one month, B the number of species in another month, and C the number of shared species between the two months. The Sorensen dissimilarity index can be partitioned into two independent components turnover and nestedness-resultant dissimilarity, which together reveal the underlying mechanisms of β diversity variation. Turnover reflects species replacement among communities, whereas nestedness describes dissimilarity that occurs when species in the less diverse month form a subset of those in the more diverse month (Liu et al., 2025). Their calculation formulas are as follows:

$$\beta_{\text{turnover}} = \frac{\min(A,B)-C}{\frac{A+B}{2}} \tag{6}$$

$$\beta_{\text{nestedness}} = \beta_{Sorensen} - \beta_{\text{turnover}} \tag{7}$$

Niche breadth (B_i) was calculated using the Shannon index (Chi et al., 2024), according to:

$$B_i = -\sum_{j=1}^{N}(P_{ij} \ln P_{ij}) \tag{8}$$

where: P_{ij} is the proportion of species i utilizing resource j.

Species with $B_i \geq 2.0$ were classified as having a broad niche, those with $1.0 \leq B_i < 2.0$ as having an intermediate niche, and those with $0 < B_i < 1.0$ as having a narrow niche.

Eurytopic species have a wide niche breadth and exhibit broad tolerance to diverse environmental conditions and resources. Stenoniche species have a narrow niche breadth and show highly specialized demands for resources and environmental conditions. Mesoniche species have an intermediate niche breadth, representing a transitional group between the two. Niche overlap (O_{ik}) was calculated using Pianka's index (Pianka, 1973):

$$O_{ik} = \frac{\sum_{j=1}^{r}(P_{ij} \times P_{kj})}{\sqrt{\sum_{j=1}^{N} P_{ij}^2 \times \sum_{j=1}^{N} P_{kj}^2}} \tag{9}$$

where: P_{ij} and P_{kj} denote the proportions of individuals of species i and species k, respectively, associated with resource j.

The value of O_{ik} ranges from 0 to 1, with values closer to 1 indicating greater niche overlap; in general, an overlap value above 0.6 suggests substantial interspecific niche overlap (Ge et al., 2005).

All species-composition data were standardized prior to analysis. The seasonal variation in community structure was classified using hierarchical clustering (UPGMA). Non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA) were applied to test the significance of differences among groups. Similarity percentage analysis (SIMPER) was used to explain between-group differences and to identify key species responsible for seasonal variation.

The data used in this study were provided by the Izumo River Office (2025). The study area is shown in Figure 1. Sampling was conducted in February (winter), May (spring), August (summer), and November (autumn) of 2017 and 2018.

RESULTS

Community characteristics

From February 2017 to November 2018, a total of 34 species of macrobenthos were recorded in Lake Nakaumi, belonging to six phyla, Annelida, Mollusca, Arthropoda, Chordata, Phoronida, and Nemertea. Among them, 28 species were recorded in 2017 and 25 species in 2018.

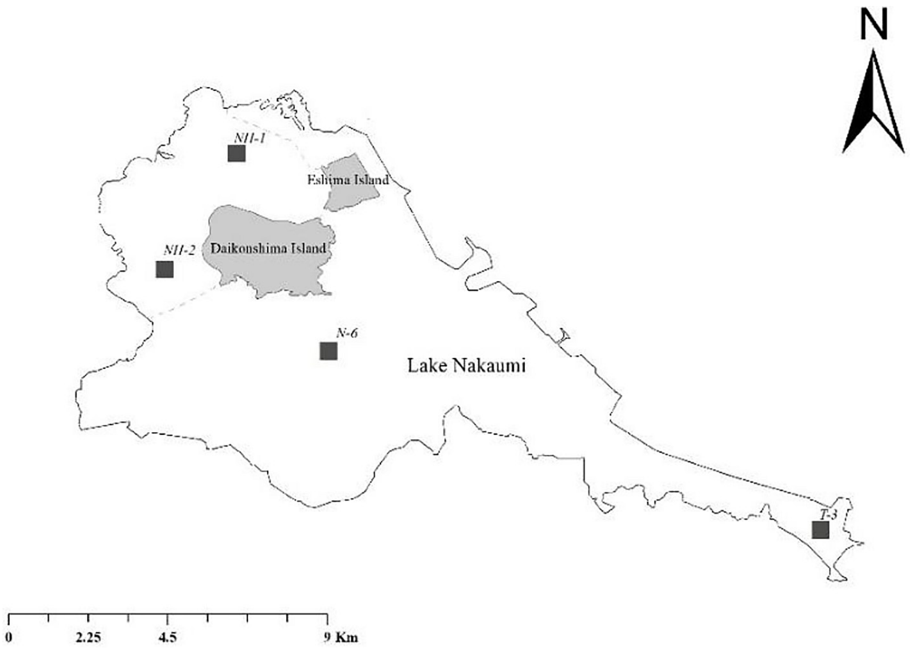

Figure 1. Study area and sampling site distribution

Nemerteans and chordates appeared only in the 2017 samples, and annelids represented the most species-rich group of macrobenthos in Lake Nakaumi. Over the course of the year, winter and spring were the seasons with the highest species richness, whereas summer and autumn were comparatively depauperate. Nearly all species recorded within a given year appeared during winter and spring, while the species occurring in summer and autumn accounted for only about 25% of the annual total (Figure 2). Annelids exhibited the highest relative abundance (85.99% in 2017 and 81.88% in 2018), far exceeding that of arthropods (6.87% in 2017 and 3.50% in 2018) and mollusks (1.03% in 2017 and 0.85% in 2018). Chordates, phoronids, and nemerteans were represented by very few species and occurred infrequently in the samples; collectively, their proportion (6.11% in 2017 and 13.76% in 2018) was also much lower than that of annelids.

The annual dominant macrobenthic species in Lake Nakaumi are listed in Table 1, and the number of species with IRI > 100 was the same in both years. Across seasons, *Sigambra hanaokai*, *Paraprionospio patiens* and *Prionospio pulchra* consistently maintained dominant status throughout all seasons in both years. *Nephtys polybranchia*, *Pseudopolydora* sp., *Raetellops pulchellus* and *Monocorophium acherusicum* were typical dominant species in the winter and spring of 2018. Additionally, *Harmothoe imbricata*, *Polydora* sp., *Prionospio japonica*, *Capitella* sp., *Pectinaria okudai*, *Arcuatula senhousia*, *Theora fragilis* and *Grandidierella japonica* were dominant only in winter or spring. During the summer and autumn of that year, *Phoronis* sp. was the only dominant species besides *Sigambra hanaokai*, *Paraprionospio patiens* and *Prionospio pulchra*. In 2017, *Pseudopolydora* sp. and *Monocorophium acherusicum* remained dominant in both winter and spring, while *Eteone longa*, *Prionospio japonica*, *Capitella* sp., *Pectinaria okudai*, *Chone* sp., *Phoronis* sp., *Arcuatula senhousia*, *Raetellops pulchellus*, and *Molgula manhattensis* were dominant in either winter or spring. Compared with the summer and autumn of 2018, the dominant species in the summer and autumn of 2017 were relatively more numerous, including *Nephtys polybranchia*, *Aonides oxycephala* and *Arcuatula senhousia*.

The overall patterns of α-diversity for macrobenthos in Lake Nakaumi during the two study years are shown in Figure 3. It is evident that diversity in winter and spring was higher than in summer and autumn. Within the winter–spring period, the Shannon–Wiener diversity index was higher in spring than in winter; within the summer–autumn period, it was higher in summer than in autumn. The Pielou evenness index showed a different pattern. Although evenness was generally higher in winter and spring than in summer and autumn,

Table 1. Annual dominant species and dominance

Number	Dominant species	IRI	
		2017	2018
S1	*Sigambra hanaokai*	1089.03	1741.52
S2	*Nephtys polybranchia*	-	169.63
S3	*Paraprionospio patiens*	2242.25	2380.55
S4	*Prionospio japonica*	256.05	-
S5	*Prionospio pulchra*	1809.76	1174.40
S6	*Pseudopolydora* sp.	134.48	341.65
S7	*Pectinaria okudai*	109.55	138.54
S8	*Phoronis* sp.	185.63	-
S9	*Arcuatula senhousia*	104.30	124.34
S10	*Theora fragilis*	-	210.90
S11	*Raetellops pulchellus*	472.17	1213.94
S12	*Monocorophium acherusicum*	223.78	401.87

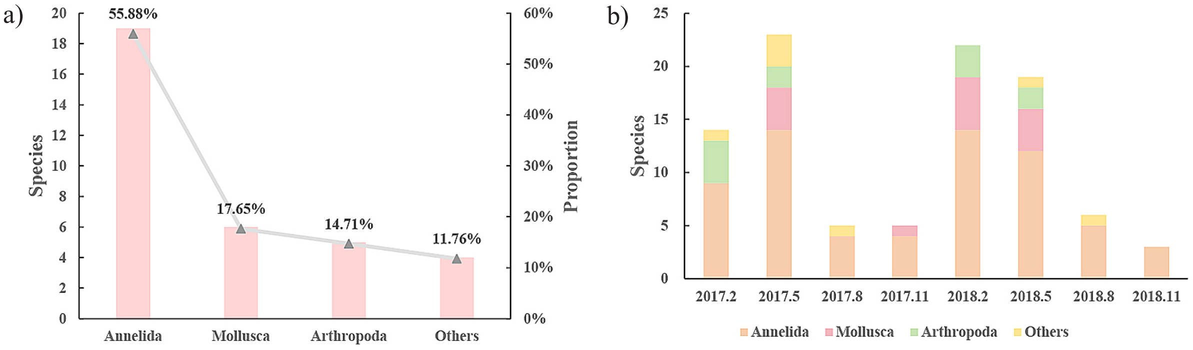

Figure 2. Species composition and dynamics: a) total proportion, b) proportion by month

the seasonal trend varied by year: in 2018, winter values exceeded those in spring, whereas in 2017 the opposite was true. Similarly, in 2018 the index was higher in summer than in autumn, while in 2017 the reverse pattern was observed.

Tables 2 and 3 show the β-diversity components of macrobenthos at different times in 2017 and 2018, respectively. Nestedness accounted for a large proportion of the variation among communities in different seasons, whereas species turnover contributed comparatively little. In the seasonal communities of 2018, nearly all pairwise comparisons were characterized by nestedness. Notably, the pattern differed between summer and autumn: turnover dominated in 2017, while nestedness dominated in 2018. According to the Sorensen index, the largest seasonal difference in community composition in 2017 occurred between spring and autumn, whereas in 2018 the greatest difference was between winter and autumn, although only slightly higher than that between spring and autumn. In terms of temporal progression, the seasonal patterns of macrobenthic community change

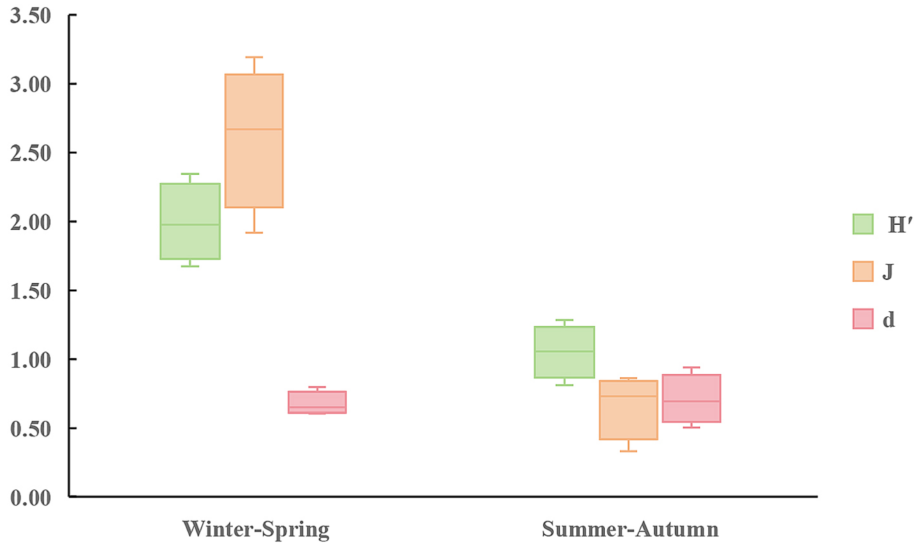

Figure 3. Patterns of α diversity

Table 2. Patterns of *β* diversity (2017)

Month	β sorensen	Turnover	Nestedness	Percentage of turnover	Percentage of nestedness
2–5	0.4595	0.2162	0.2432	0.4706	0.5294
2–8	0.5789	0.1053	0.4737	0.1818	0.8182
2–11	0.6842	0.2105	0.4737	0.3077	0.6923
5–8	0.6429	0.0000	0.6429	0.0000	1.0000
5–11	0.7143	0.0714	0.6429	0.1000	0.9000
8–11	0.4000	0.4000	0.0000	1.0000	0.0000

Table 3. Patterns of β diversity (2018)

Month	β sorensen	Turnover	Nestedness	Percentage of turnover	Percentage of nestedness
2–5	0.2195	0.1463	0.0732	0.6667	0.3333
2–8	0.6429	0.0714	0.5714	0.1111	0.8889
2–11	0.7600	0.0000	0.7600	0.0000	1.0000
5–8	0.5200	0.0000	0.5200	0.0000	1.0000
5–11	0.7273	0.0000	0.7273	0.0000	1.0000
8–11	0.3333	0.0000	0.3333	0.0000	1.0000

differed markedly between the two years. From February to May 2017, the proportion of nestedness was slightly higher than that of turnover, whereas the opposite pattern was observed in 2018. From May to August, nestedness dominated in both years. From August to November, all pairwise comparisons in 2017 were characterized by turnover, while all comparisons in 2018 were characterized by nestedness.

Niche breadth and niche overlap

Changes in niche breadth among the dominant macrobenthic species in Lake Nakaumi are shown in Figure 4. In 2017, niche breadth ranged approximately from 0.07 to 1.90, while in 2018 it ranged from 1.02 to 1.92. Most dominant species had a niche breadth greater than 1, indicating that they were mesoniche species. Only in 2017 did *Prionospio japonica*, *Pectinaria okudai*, *Raetellops pulchellus* and *Phoronis* sp. exhibit niche breadth values below 1, classifying them as stenoniche species. Across both years, no eurytopic species were found within the macrobenthic community of Lake Nakaumi.

Tables 4 and 5 present the niche overlap among dominant macrobenthic species in 2017 and 2018. In 2017, *Sigambra hanaokai* and *Prionospio pulchra* showed relatively high niche overlap with many of the other dominant species, whereas *Pectinaria okudai*, *Arcuatula senhousia*, *Raetellops pulchellus* and *Monocorophium acherusicum* showed little to no high niche

Figure 4. Niche breadth of dominant species: a) 2017, b) 2018

Table 4. Niche overlap value of dominant species (2017)

S	S1	S3	S4	S5	S6	S7	S8	S9	S11	S12
S1	1.00									
S3	0.70	1.00								
S4	0.30	0.10	1.00							
S5	0.92	0.55	0.30	1.00						
S6	0.33	0.26	0.94	0.26	1.00					
S7	0.80	0.35	0.61	0.83	0.55	1.00				
S8	0.08	0.00	0.96	0.06	0.91	0.36	1.00			
S9	0.47	0.20	0.97	0.49	0.90	0.73	0.88	1.00		
S11	0.85	0.50	0.20	0.97	0.17	0.68	0.00	0.40	1.00	
S12	0.56	0.74	0.21	0.41	0.46	0.41	0.10	0.27	0.30	1.00

Table 5. Niche overlap value of dominant species (2018)

S	S1	S2	S3	S5	S6	S7	S9	S10	S11	S12
S1	1.00									
S2	0.70	1.00								
S3	0.39	0.58	1.00							
S5	0.78	0.46	0.47	1.00						
S6	0.57	0.34	0.10	0.31	1.00					
S7	0.23	0.23	0.17	0.11	0.15	1.00				
S9	0.60	0.73	0.33	0.40	0.30	0.79	1.00			
S10	0.49	0.73	0.13	0.33	0.28	0.18	0.57	1.00		
S11	0.45	0.91	0.74	0.23	0.21	0.24	0.60	0.56	1.00	
S12	0.78	0.62	0.19	0.52	0.83	0.13	0.51	0.42	0.38	1.00

overlap with other dominant species. In 2018, *Sigambra hanaokai* and *Nephtys polybranchia* frequently displayed high niche overlap with other dominant species, while high overlap among the remaining dominant species occurred only sporadically.

Seasonal differences in the community

The seasonal clustering results of the macrobenthic community in Lake Nakaumi are shown in Figure 5. As illustrated, all winter and spring samples grouped into one cluster, whereas summer and autumn samples formed another. The NMDS stress value was 0.13, indicating that the ordination was reliable. PERMANOVA further confirmed significant differences between the two groups (P = 0.03, F = 6.9).

SIMPER analysis revealed that the dissimilarity between the winter–spring and summer–autumn groups was primarily driven by six species: *Monocorophium acherusicum*, *Pseudopolydora* sp., *Paraprionospio patiens*, *Prionospio pulchra*, *Prionospio japonica*, and *Sigambra hanaokai* which together accounted for 53.74% of the total dissimilarity. Among these, *Monocorophium acherusicum*, *Pseudopolydora* sp. and *Prionospio japonica* did not occur at all in the summer–autumn group, making them key indicator species differentiating the winter–spring community. In contrast, *Paraprionospio patiens*, *Prionospio pulchra* and *Sigambra hanaokai* exhibited higher average densities in the summer–autumn group than in the winter–spring group, thereby increasing the dissimilarity between the two seasonal clusters.

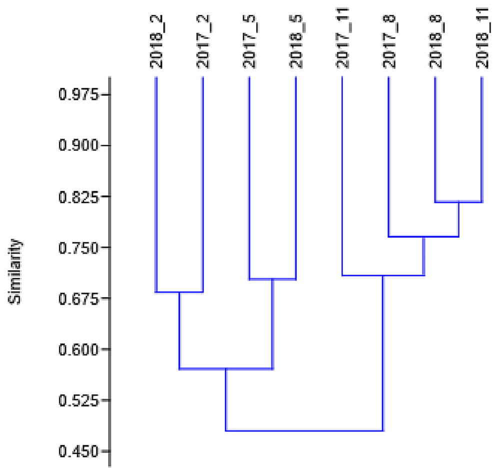

Figure 5. Results of seasonal clustering

DISCUSSION

Temporal variation in the community

Changes in habitat are the primary drivers of shifts in macrobenthic communities, and community composition reflects how macrobenthos adapt to their surroundings. The more complex the habitat, the greater the degree of niche differentiation (Czortek et al., 2021; Huang et al., 2019). The findings of this study provide direct evidence that seasonal differences in habitat play a crucial role in shaping the temporal distribution of the macrobenthic community in Lake Nakaumi. The loss of submerged macrophytes in Lake Nakaumi has simplified the ecosystem structure and reduced spatial heterogeneity on the lakebed. In addition, the seasonally occurring halocline further impedes vertical water exchange. As a result, hypoxic conditions are widespread at the lake bottom during summer, and this extreme environment severely affects the survival of macrobenthic organisms. Consequently, only a few highly stress-tolerant species, such as species *Sigambra hanaokai*, *Paraprionospio patiens* and *Prionospio pulchra*, dominate the community during summer and autumn. In winter and spring, the influence of the halocline is relatively weak, and the environmental conditions are more favorable compared with those in summer and autumn. During these seasons, numerous species, such as *Harmothoe imbricata*, *Polydora* sp., *Prionospio japonica*, *Capitella* sp., *Pectinaria okudai*, *Arcuatula senhousia* and *Theora fragilis*, appear in large numbers, leading to higher α-diversity and a more complex community structure than that observed in summer and autumn. The temporal pattern of the β Sorensen index further indicates that seasonally driven environmental changes drive shifts in the community assembly mechanisms of macrobenthos in Lake Nakaumi. In other words, the strength of environmental filtering varies with the seasons, driving changes in species dominance. Nesting dominated the transition from spring to summer, a period characterized by strong environmental stress in Lake Nakaumi. During this period, sensitive species were excluded, and only stress-tolerant species persisted. The differing patterns observed between summer and autumn across the two study years suggest that this interval represents a community recovery phase. During the transition from winter to spring, both nestedness and turnover were detected in both years, with no pronounced differences, indicating that this period is a key reproductive phase for the community.

Competition and community stability

The breadth of a species ecological niche directly reflects its adaptive capacity to the environment; the wider the niche, the stronger its ability to cope with environmental variation (Jiao et al., 2011; Meng et al., 2022). Niche indices constructed based on temporal and multi-dimensional resource use also have certain limitations. The index values are affected by the distribution of resource units in the study, coarse temporal resolution may overlook fine-scale niche differentiation, and passive dispersal or temporary occupancy of species can interfere with the accurate estimation of niche breadth, thereby introducing biases into the results of niche differentiation and species classification. Such limitations are particularly prominent in highly dynamic aquatic ecosystems, where environmental filtering often outweighs interspecific competition. The observed distribution mostly reflects differential stress tolerance among species rather than active resource partitioning, which easily leads to biased interpretation of niche differentiation, competitive intensity, and even community assembly mechanisms. In addition, intense environmental fluctuations can make the index results highly dependent on the specific sampling period, reducing the robustness and representativeness of the conclusions to a certain extent.

The absence of eurytopic species in the macrobenthic community of Lake Nakaumi indirectly indicates the strong influence of extreme seasonal environmental fluctuations. Across the two study years, only *Sigambra hanaokai* and *Paraprionospio patiens* exhibited annual niche widths greater than 1.9. Although these two species had the broadest niches within the community and their abundances were similar, they were not numerically dominant. This suggests that while both species possess broad-spectrum resource use under the seasonal environmental shifts of Lake Nakaumi, they lack competitive advantages when relying on specific resources. This pattern becomes apparent when compared with *Prionospio pulchra*: *Prionospio pulchra* may experience explosive growth during a single time period when environmental conditions or resources are favorable, which elevates its cumulative abundance but does not translate into long-term competitive superiority. Such fluctuations in abundance exemplify the variability in niche breadth within the macrobenthic community of Lake Nakaumi. In other words, the coexistence of species like *Sigambra hanaokai* and *Paraprionospio patiens*, which adopt generalized survival strategies, together with species like *Prionospio pulchra*, which exhibit a certain degree of specialization, underpins community stability under cyclic environmental changes. Narrow-niched specialists maintain community productivity through short-term population fluctuations, while broad-niched generalists provide the capacity for the community to cope with recurrent environmental extremes.

Niche overlap is a fundamental driver of interspecific competition (Yang et al., 2025; Larocque et al., 2021). In this study, we found that *Sigambra hanaokai* exhibited high niche overlap with several numerically dominant species in both 2017 and 2018. Comparing the two years, changes in its overlap values with the same dominant species reflect how different species within the community responded to interannual environmental variation. For instance, the overlap between *Sigambra hanaokai* and *Paraprionospio patiens* was 0.7 in 2017 and 0.39 in 2018; its overlap with *Prionospio pulchra* shifted from 0.92 in 2017 to 0.78 in 2018; meanwhile, overlap values with Species *Arcuatula senhousia* and *Monocorophium acherusicum* increased. Generally, such differences arise from habitat partitioning or environmental filtering, which lead to convergence in resource use. The lakebed of Lake Nakaumi is highly heterogeneous, with poor habitat continuity. This degree of habitat fragmentation results in non-continuous overlap patterns. Therefore, adaptive adjustments to environmental exclusion, combined with the stochastic occurrence of favorable resources, are likely the main drivers of the observed shifts in overlap values. It is worth noting that although many dominant species displayed niche overlap values exceeding 0.9 or approaching 0.9, such high overlap does not necessarily trigger intense competition unless resources become limiting. Under the conditions of low habitat continuity on the lakebed, these high overlap values may instead reflect a form of coexistence.

Seasonal clustering

In this study, clustering the macrobenthic community of Lake Nakaumi along the temporal dimension was primarily intended to identify the community's annual patterns of change. According to our results, the macrobenthic community in Lake Nakaumi can be clearly divided into two groups over the course of a year: a winter–spring group and a summer–autumn group. The SIMPER analysis indicates that the differences between these two groups are primarily driven by the occurrence of season-specific species and variations in their densities. *Monocorophium acherusicum*, *Pseudopolydora* sp. and *Prionospio japonica* occurred only in the winter–spring group and served as seasonal indicator species, defining the distinctiveness of this group. In contrast, *Paraprionospio patiens*, *Prionospio pulchra* and *Sigambra hanaokai* accentuated the differences between the summer–autumn and winter–spring groups, acting as key drivers of seasonal turnover in Lake Nakaumi. Overall, the winter–spring community in Lake Nakaumi is dominated by sensitive species, whereas the summer–autumn community is dominated by tolerant species. This seasonal differentiation enables efficient use of resources within the lake, and the alternating dominance of sensitive and tolerant species ensures year-round stability of ecosystem functions.

CONCLUSIONS

This study analyzes macrobenthic data from Lake Nakaumi collected between 2017 and 2018 to investigate the structural characteristics and temporal dynamics of the macrobenthic community. The results show that the macrobenthic community of Lake Nakaumi is composed of 34 species belonging to 6 phyla, with annelids being the most species-rich group. The community exhibits pronounced seasonal differences between winter–spring and summer–autumn, a pattern largely driven by the extreme nature of seasonal environmental changes in the lake. In terms of diversity, winter and spring conditions are more favorable than those in summer and autumn. Across both years, no species with a broad niche were identified in the macrobenthic community, and niche overlap among dominant species varied between years. This interannual variation is likely attributable to habitat fragmentation on the lake bottom, specifically the spatiotemporal randomness of suitable habitat and resource distribution and the effects of environmental exclusion. The differences observed between winter–spring and summer–autumn communities are mainly driven by three seasonal indicator *Monocorophium acherusicum*, *Pseudopolydora* sp. and *Prionospio japonica* as well as three species showing significant density differences *Paraprionospio patiens*, *Prionospio pulchra* and *Sigambra hanaokai*. These differences in community composition play a key role in maintaining the stability of the macrobenthic community under the lake's seasonally extreme environmental conditions. All raw data were obtained from routine environmental monitoring conducted by local governmental departments. This study has been granted formal authorization to use the monitoring data for scientific analysis. No additional destructive sampling, species collection, or other anthropogenic disturbances to natural communities were performed throughout the research. All data processing and statistical analyses in this study strictly comply with academic integrity and research ethical guidelines.

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REFERENCES

1. Chi, S., Hu, J., Zheng, J., et al. (2024). Characteristics of community structure and niche analysis of benthic macroinvertebrates in the upper reaches of Jinsha River. *Journal of Lake Sciences*, *36*: 1192–1203. https://doi.org/10.18307/2024.0444
2. Czortek, P., Orczewska, A., Dyderski, M. K. (2021). Niche differentiation, competition or habitat filtering? Mechanisms explaining co-occurrence of plant species on wet meadows of high conservation value. *Journal of Vegetation Science*, *32*: e12983. https://doi.org/10.1111/jvs.12983
3. Fujimoto, M., Takayasu, K., Yamaguchi, K., Sonoda, T. (1999). Benthic fauna and environmental characteristics in Honjo-Area of Lake Nakaumi. *Laguna, 6*: 107–117.
4. Ge, B., Bao, Y., Zheng, X., Cheng, H. (2005). The structure of the macrobenthic community and niche analysis at a tidal flat of Linkun Island. *Acta Ecologica Sinica*, *25*: 3037–3043.
5. Hiratsuka, J., Yamamuro, M., Ishitobi, Y. (2007). Long-term change in water transparency before and after the loss of eelgrass beds in an estuarine lagoon, Lake Nakaumi, Japan. *Limnology*, *8*: 53–58. https://doi.org/10.1007/s10201-006-0198-5
6. Hirakiuchi, H., Sasaki, T., Semura, H., et al. (2019). Effect of hypoxic water mass in summer on the distribution of ark shells, *Anadara kagoshimensis*, in Lake Nakaumi, Japan. Japanese *Journal of Benthology*, *74*: 16–24. https://doi.org/10.5179/benthos.74.16
7. Huang, L., Xue, W., Herben, T. (2019). Temporal niche differentiation among species changes with habitat productivity and light conditions. *Journal of Vegetation Science*, *30*: 438–447. https://doi.org/10.1111/jvs.12741
8. Izumo River Office. (2025). Environmental Monitoring for Ohashi River Renovation Project. Izumo River Office: https://www.cgr.mlit.go.jp/izumokasen/
9. Jiang, H., Guo, D., Liu, M., et al. (2024). Diversity of macroinvertebrates and ecological niche in Zhongyangzhan Black-Billed Capercaillie National Nature Reserve. *Wetland Science*, 22: 508–517. https://doi.org/ 10.13248/j.cnki.wetlandsci.2024.04.004
10. Jiao, H., Shi, H., You, Z., Huang, B. (2011). Niche analysis of dominant species of macrobenthic community at a tidal flat of Yushan Island. *Acta Ecologica Sinica*, *31*: 3928–3936.
11. Kurata, K., Sonoda, T., Yamaguchi, K., Seto, K. (2018). Benthic fauna of Lake Nakaumi in summer of 2016. *Laguna*, *24*: 49–63.
12. Liu, S., Zhou, Z., Lv, Q., et al. (2025). Biodiversity pattern and its driving factors of macrobenthic communities in island-type coastal salt marsh. *Acta Ecologica Sinica*, *45*: 7696–7709. https://doi.org/10.20103/j.stxb.202408282053
13. Larocque, S. M., Johnson, T. B., Fisk, A. T. (2021). Trophic niche overlap and abundance reveal potential impact of interspecific interactions on a reintroduced fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*: 765–774. https://doi.org/10.1139/cjfas-2020-0204
14. Margalef, R. (1958). Information theory in ecology. *General Systems*, *3*: 36–71.
15. Meng, Z., Chen, K., Liu, L., et al. (2022). Niche and interspecific association with respect to the dominant phytoplankton species in different hydrological periods of Lake Wuchang, China. *Frontiers in Environmental Science*, *10*: 985672. https://doi.org/10.3389/fenvs.2022.985672
16. Pinkas, L., Oliphant, MS., Iverson, ILK. (1971). Food habits of albacore, bluefin tuna, and bonito in California waters. *Fishery Bulletin*, *152*: 1–105.
17. Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics*, *4*: 53–74.
18. Pielou, E. C. (1975). Ecological diversity. John Wiley & Sons.
19. Shannon, C. E., Weaver, W. (1949). *The mathematical theory of communication.* The University of Illinois Press.
20. Shinohara, R., Yamaguchi, K., Seto, K., Kurata, K. (2016). Influence of partial removal of reclamation dikes on the bivalve distribution in the Honjo Area of Lake Nakaumi, Southwest Japan. *Japanese Journal of Benthology*, *71*: 1–10. https://doi.org/10.5179/benthos.71.1
21. Tabayashi, Y., Miki, K., Godo, T., Yamamuro, M., Kamiya, H. (2017). Multi-tracer identification of nutrient origin in the Hii River watershed, Japan. *Landscape and Ecological Engineering*, *13*: 119–129. https://doi.org/10.1007/s11355-016-0307-5
22. Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr*, *30*: 279–338.

23. Whittaker, R.H. (1972). Evolution and measurement of species diversity. *Taxon*, *21*: 213–251.
24. Yasugi, S., Nakamura, M., Miura, S., Nakao, S. (1999). Successional changes of macro benthos community on the artificial bottom in Lake Nakaumi. *Aquaculture Science*, *47*: 181–190. https://doi.org/10.11233/aquaculturesci1953.47.181
25. Yamaguchi, K., Fujimoto, M., Takayasu, K., Sonoda, T. (2000). Effect of tidal−flow induction on macrobenthic animal community in an enclosed channel of Lake Nakaumi, Southwest Japan. *Laguna*, *7*: 37–44.
26. Yamamuro, M., Hiratsuka, J. I., Ishitobi, Y., Hosokawa, S., Nakamura, Y. (2006). Ecosystem shift resulting from loss of eelgrass and other submerged aquatic vegetation in two estuarine lagoons, Lake Nakaumi and Lake Shinji, Japan. *Journal of oceanography*, *62*: 551–558. https://doi.org/10.1007/s10872-006-0075-1
27. Yang, Q., Zhao, R., Qiu, X. (2025). Analysis of ecological niche and interspecific associations among dominant zooplankton species in the major lakes of Yinchuan City, China. *Scientific Reports*. https://doi.org/10.1038/s41598-025-29974-4