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Seasonal succession of macrozoobenthic communities and environmental biological assessment in Nakaumi Lake, Japan

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ABSTRACT

Nakaumi Lake, located near the Sea of Japan, holds a significant ecological value. A detailed understanding of its intra-annual environmental variations under the broader context of global climate change is a fundamental basis for effective environmental management and the sustainable use of ecological resources. However, current research on this subject remains limited. In this study, the macrozoobenthic communities of Nakaumi Lake were investigated using a multi-index assessment approach, taking into account the lake's hydrological characteristics. This allowed evaluating seasonal environmental changes and identifying potential ecological risks. The obtained findings reveal that the macrozoobenthic community structure exhibits marked seasonal variation. Diversity peaks during the winter and spring, while it declines notably in the summer and autumn. Spatial differences in diversity levels across different lake regions are primarily attributed to habitat fragmentation driven by varying hydrological conditions. Overall, Nakaumi Lake is subject to significant environmental stress, and seasonal hydrological dynamics can cause abrupt shifts in community composition, thereby undermining the resilience of its aquatic ecosystem.

Keywords: Nakaumi Lake, macrobenthic organisms, community succession, MPI, environmental assessment.

INTRODUCTION

Nakaumi Lake is a typical brackish lake characterized by seasonal alternation between marine and freshwater inputs. This dynamic causes salinity levels to fluctuate over time, with pronounced stratification during summer when a strong halocline forms (Nakata et al., 2000). As a result, vertical mixing between surface and bottom waters is significantly reduced, leading to widespread hypoxia in bottom waters and a sharp decline in benthic biomass (Ichikawa et al., 2007). In autumn, however, the biomass gradually recovers. These seasonal fluctuations in biomass reflect the complex interactions between biological communities and environmental conditions, where the organisms' adaptation to environmental stress is often mirrored in spatiotemporal changes in community structure. Such structural shifts can effectively indicate the environmental status and ecological characteristics of Nakaumi Lake at different time points.

In lake ecosystems, organisms such as phytoplankton, benthic macroinvertebrates, and macrophytes are commonly used as bioindicators (Cottingham et al., 1998; Liu et al., 2023). Due to their close interactions with environmental conditions, these taxa are widely employed in ecological assessments. For example, Ptacnik et al. (2008) analyzed the responses of three major phytoplankton groups to eutrophication in Nordic lakes, offering important insights into regional water quality assessment. Obolewski et al. (2021) investigated how macroinvertebrate communities in shallow coastal lakes in southern Poland respond to habitat heterogeneity, providing methodological support for ecological management of such systems. Yang et al. (2018) used physiological indicators of seagrasses to evaluate nitrogen loading across coastal regions, demonstrating the potential of seagrass indicators in monitoring coastal eutrophication. However, each bioindicator has limitations based on factors such as spatial habitat positioning, environmental tolerance, and the magnitude of environmental changes. Therefore, the choice of indicator species must be made carefully, as it directly determines the appropriate evaluation method. Considering the specific characteristics of Nakaumi Lake – with a maximum depth of 16 meters and an average depth of 5.4 meters – phytoplankton, though commonly used as indicators of water quality (Chandel et al., 2024), may not accurately reflect changes in deep-water conditions due to their confinement within the euphotic zone. Currently, Nakaumi Lake is a eutrophic lake with low water transparency (Hiratsuka et al., 2007). Macrophytes such as *Zostera marina*, once widespread in the 1950s, have become extremely scarce (Yamamuro et al., 2006), with limited distribution and unstable population sizes, making them unsuitable as reliable environmental indicators. Periodic hypoxia in the bottom waters poses a major threat to the ecological stability of Nakaumi Lake and must be addressed in environmental assessments. Among potential indicators, benthic macroinvertebrates are particularly suitable due to their relatively sessile lifestyle within sediments throughout their life cycles. They are directly exposed to oxygen-depleted conditions and have limited mobility to escape environmental stress (Lyche-Solheim et al., 2013; Rossaro et al., 2011), making them sensitive indicators of bottom water quality in Nakaumi Lake.

A number of well-established methods exist for assessing aquatic environmental conditions using benthic macroinvertebrates. Common indices include the AZTI marine biotic index (AMBI), multivariate AMBI (M-AMBI) (Borja and Tunberg, 2011), biological pollution index (BPI) (Zou et al., 2017), benthic quality index (BQI) (Rossaro et al., 2006), and the macroinvertebrate pollution index (MPI), among others. These methods have been widely applied worldwide. For instance, Sun and Zhu (2020) evaluated the benthic environmental quality in Xinghua bay using AMBI, M-AMBI, and the Shannon-Wiener (H') diversity index. Shen et al. (2020) analyzed the relationship between benthic macroinvertebrates and environmental factors in the Taihu basin using BPI combined with the goodnight-whitley index (GI). Wawrzynkowski et al. (2023) developed a BQI-based assessment system to evaluate the ecological status of the Bilbao estuary.

A well-chosen assessment perspective is crucial for accurately understanding the environmental conditions of Nakaumi Lake. Such assessments can provide a scientific basis for ecosystem management and align with the United Nations Sustainable Development Goals (SDGs), specifically Goal 6 (Clean Water and Sanitation) and Goal 14 (Life Below Water), both of which emphasize the protection and sustainable use of aquatic ecosystems. Establishing a sound environmental assessment is essential for the long-term sustainability of the ecological resources of Nakaumi Lake and is a prerequisite for reversing eutrophication through future human interventions. However, studies on environmental assessments in Nakaumi Lake remain limited. Existing research has largely relied on single biological or physicochemical indicators, and systematic multi-index evaluation methods have yet to be fully applied. Moreover, few studies have explored the ecological restoration potential of Nakaumi Lake. This study, therefore, uses the data on benthic macroinvertebrates collected in 2015 (strong El Niño year) from Nakaumi Lake to assess the seasonal changes in community structure. By employing a combination of biotic indices, the study aimed to: (1) expand the application of multi-index environmental assessment methods in Nakaumi Lake; (2) understanding the potential ecological risks of Nakaumi Lake in different seasons during strong El Niño years.

MATERIALS AND METHODS

In this study, the Simpson dominance index (*C*), Shannon-Wiener diversity index (*H*`), Pielou evenness index (*J*), and Margalef species richness index (*D*) were used to analyze the diversity of the benthic animal community in Nakaumi Lake (Spellerberg and Fedor, 2003; Gamito, 2010). The relevant formulas are as follows:

$$C = \sum_{i=1}^{S} \frac{N_i(N_i - 1)}{N(N-1)} \quad (1)$$

$$H` = -\sum_{i=1}^{S} P_i \ln P_i \quad (2)$$

$$J = \frac{H`}{\ln S} \quad (3)$$

$$D = \frac{(S-1)}{\ln N} \quad (4)$$

where: N_i represents the number of individuals of the i-th species; N is the total number of individuals across all species; S denotes the total number of species; and P_i is the proportion of individuals of the i-th species to the total number of individuals.

Additionally, the Index of relative importance (*IRI*) was used to assess the relative significance of different benthic species within the community (Cui et al., 2012). The formula is as follows:

$$IRI = (N + W) \times F \quad (5)$$

where: *N* represents the relative abundance of a given species, *W* denotes its percentage biomass (wet weight was used in this study), and *F* indicates its frequency of occurrence across all sampling sites.

Due to the large number of species recorded, the analysis focused on the dominant species. First, all species recorded in each season were ranked according to their relative abundance (i.e., dominance). Then, the top five species in each season were selected for *IRI* calculation. The *IRI* values were categorized as follows:

$$IRI \geq 1000 \text{ Dominant Species}$$
$$1000 > IRI \geq 100 \text{ Key Species}$$
$$100 > IRI \geq 10 \text{ Common Species}$$
$$IRI < 10 \text{ Rare Species}$$

Regarding the assessment of environmental status, this study employed the macrobenthic pollution index (*MPI*). This index was proposed by Cai (2003) based on the macrobenthic sampling data from Shenzhen Bay, the western Xiamen sea area, Luoyuan Bay, and Xinghua Bay, and has been effectively applied in various aquatic environments. The specific calculation formula is as follows:

$$MPI = 10^{(2+k)}[\sum(A_i - B_i)]/S^{k+1} \quad (6)$$

where: A_i represents the cumulative percentage dominance of density for the i-th species when all species in the collected community are sorted by density dominance; Similarly, B_i represents the cumulative percentage dominance of biomass for the i-th species when all species in the collected community are sorted by biomass dominance; *S* denotes the total number of species collected; *k* is defined as the ratio of $\sum(A_i - B_i)$ to its absolute value.

The classification criteria for different calculation results are as follows:

$$MPI > 4 \text{ Severe Pollution}$$
$$4 \geq MPI \geq 0 \text{ Moderate Pollution}$$
$$0 > MPI \geq -6 \text{ Light Pollution}$$
$$MPI < -6 \text{ Clean}$$

The data used in this study were obtained from the regular monitoring of macrobenthic organisms in Nakaumi Lake conducted by the Izumo River Office (2025), including the monitoring results from February, May, August and November 2015. The regular monitoring program established four fixed sampling stations located at the central area of lake (N-6), the center of Yonago Bay (T-3), Nagami-cho (NH-1), and Kamiubeocho (NH-2). The geographical overview of the Nakaumi Lake area and the distribution of sampling sites are shown in Figure 1. The trends of water temperature and dissolved oxygen concentration changes at the four sampling sites across different seasons are shown in the Appendix. Since salinity data were not directly measured, changes in

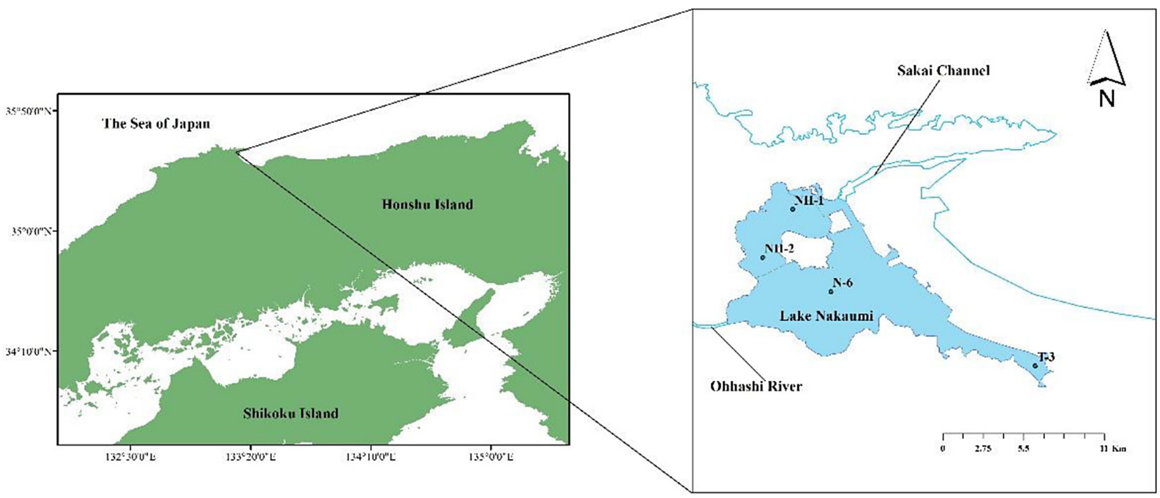

Figure 1. Overview of Nakaumi Lake

this parameter can be indirectly observed through chloride ion concentrations, the variation trends of which are presented in Figure A3.

RESULTS

Species composition

A total of 31 species of benthic macroinvertebrates were identified in the sample data. It can be seen that the benthic macroinvertebrate community in Nakaumi Lake was mainly composed of annelids, mollusks, and arthropods, with occasional occurrences of phoronids, nemerteans, and tunicates. Among them, annelids accounted for the highest proportion of species, approximately 58.07%, followed by mollusks and arthropods, which accounted for 19.36% and 12.9%, respectively. From a seasonal perspective, winter (February) and spring (May) were the two seasons with the highest species richness of benthic macroinvertebrates in Nakaumi Lake throughout the year. The number of species found in these two seasons accounted for 74% of the total number of species, although the species composition differed slightly between the two (Figure 2). The seasons with the lowest number of species were summer (August) and autumn (November), with the number of species recorded during these seasons accounting for only 22% and 29% of the total, respectively. In terms of seasonal composition, annelids made up the largest proportion of species, and in summer, their proportion exceeds 70%. Regarding the different sampling sites, among the four seasonal surveys, NH-1 was the site where species richness was relatively highest. In contrast, the site with the fewest species recorded in the same season was T-3.

Among the four sampling sites in the lake, N-6 and NH-1 had the most diverse species composition. In spring and winter, the number of species found at these two sites accounted for more than 50% of the total species recorded in those respective seasons. In summer and autumn, however, nearly all species were found in the NH-1 area.

Dominant species in community

On an annual scale, the top five species in terms of seasonal relative abundance each accounted for over 70% of the total number of individuals collected in their respective seasons. In summer and autumn, their cumulative proportion even exceeded 97% (Figure 3). The dominant benthic macroinvertebrate species in Nakaumi Lake were *Sigambra hanaokai*, *Paraprionospio patiens, Monocorophium acherusicum, Arcuatula senhousia,* and *Eteone longa*. Seasonally, *Sigambra hanaokai* was present throughout all four seasons and served as a dominant species year-round in Nakaumi Lake—particularly in summer, where it held an absolute dominant position in the community. Among the winter-dominant species, *Eteone longa* was observed exclusively in winter (with only a few individuals found in spring). Similarly, *Arcuatula senhousia*, a dominant species in spring, was found only in that season (although a small number were recorded in winter as well). *Monocorophium acherusicum* maintained its dominance in both winter and spring but was entirely absent in summer. It reappeared in autumn, though with lower abundance and biomass. *Paraprionospio patiens* was a dominant species in winter, summer, and autumn. Especially in summer, *Sigambra hanaokai* was in an absolutely dominant position within the community. Although it was also recorded in spring, its abundance and biomass were lower, and it no longer held a dominant status in the community (Table 1).

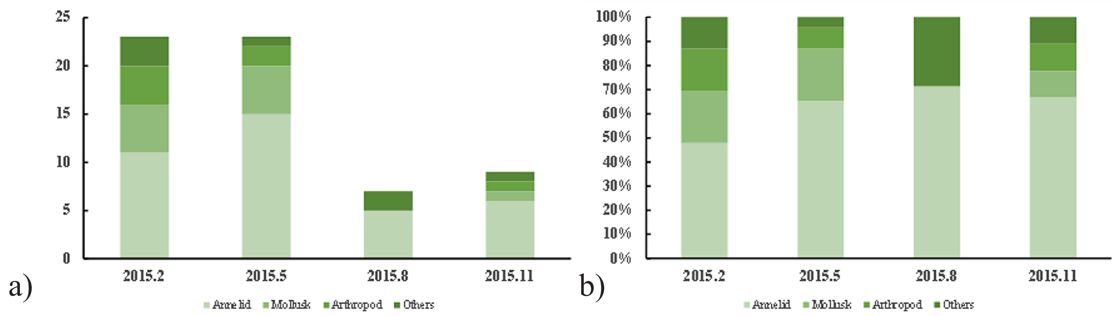

Figure 2. Temporal variations in the composition of macrobenthic communities species richness (a), percentage (b)

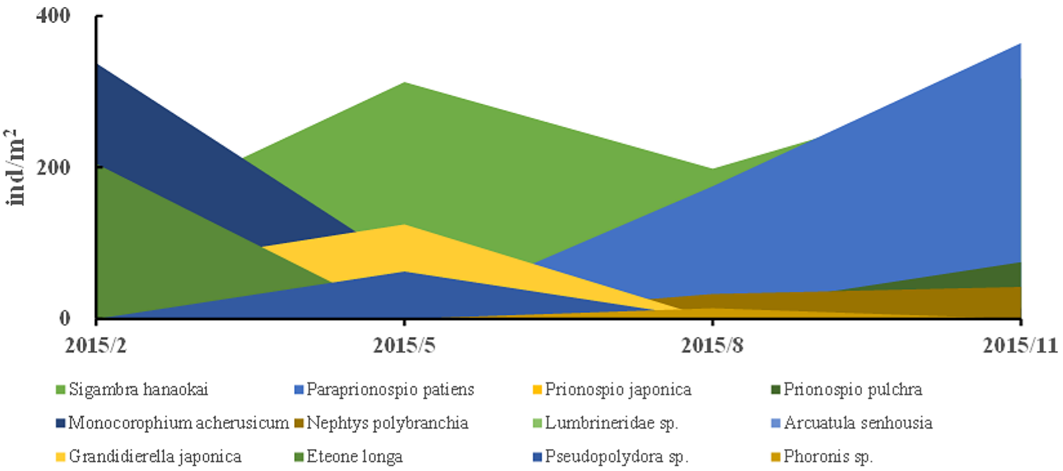

Figure 3. Abundance of dominant species in different seasons

Biodiversity

The calculated diversity indices for Nakaumi Lake are shown in Table 2. At the T-3 and NH-2 sampling sites, only a single species or no species were recorded during summer and autumn, respectively; these two cases are denoted by * and / in the table. The annual mean of the Shannon-Wiener diversity index was 1.08. The seasonal averages were higher in winter and spring, with winter having the highest mean value of the year at 1.72. In contrast, the seasonal means in summer and autumn were relatively low, around 0.5. Considering the Pielou evenness index, the average value in winter was 0.78, which was identical to that in autumn. In other words, the season with the highest diversity index (winter) had the same evenness index as the season with the lowest diversity index (autumn). The mean evenness indices for spring and summer were similar to each other, but lower than those in autumn and winter. As for the Simpson dominance index, summer

Table 1. Main species of macrobenthos in different seasons

Season	Species	N (%)	W (%)	F (%)	IRI
Winter	*Sigambra hanaokai*	9.94	1.28	75	840.89
	Paraprionospio patiens	20.25	19.39	75	2973.19
	Grandidierella japonica	4.97	3.06	75	602.20
	Monocorophium acherusicum	27.52	9.69	100	3720.98
	Eteone longa	16.69	5.36	100	2204.50
Spring	*Sigambra hanaokai*	39.06	2.22	100	4128.47
	Pseudopolydora sp.	7.81	0.68	75	637.22
	Arcuatula senhousia	8.40	13.85	75	1668.34
	Grandidierella japonica	15.63	3.76	50	969.28
	Monocorophium acherusicum	9.18	0.86	75	752.58
Summer	*Sigambra hanaokai*	44.72	19.32	100	6403.65
	Nephtys polybranchia	7.39	4.55	25	298.50
	Paraprionospio patiens	39.43	64.77	50	5210.47
	Prionospio pulchra	2.82	1.14	25	98.83
	Phoronis sp.	3.17	2.27	50	272.09
Autumn	*Sigambra hanaokai*	38.52	12.5	50	2551.00
	Nephtys polybranchia	5.12	5.00	25	253.08
	Paraprionospio patienS	44.21	76.67	50	6043.96
	Prionospio pulchra	9.11	1.67	25	269.37
	Monocorophium acherusicum	1.71	0.83	25	63.53

recorded the highest mean dominance value at 0.72, which was significantly higher than the average value of approximately 0.2 in the other seasons. The results of the Margalef species richness index showed that winter and spring were the periods with the highest average richness values of the year (approximately 1.98), far exceeding those in summer and autumn (approximately 0.40).

From the perspective of individual sites, NH-1 had the highest annual average Shannon-Wiener diversity index. Both T-3 and NH-2 experienced the episodes where only a single species was present in the community (i.e., the Simpson dominance index reached 1), or no species were recorded at all. In winter, NH-1 had the highest Shannon-Wiener diversity index among all sites in Nakaumi Lake. However, the highest evenness index during the same season was recorded at T-3. In spring, NH-2 and T-3 had similar diversity index values, both lower than those at N-6 and NH-1. Overall, during the winter–spring period, N-6 and NH-1 were the most species-rich sites in Nakaumi Lake, a finding also supported by their Margalef species richness index values. In summer, the diversity indices at all four monitoring sites showed a sharp decline, with only N-6 and NH-1 maintaining moderate values. In autumn, the Shannon-Wiener diversity index at N-6 continued to decline. However, when combined with the Pielou evenness index, it is notable that the highest evenness value at N-6 throughout the year occurred during this season. Among the four monitoring sites, only NH-1 showed an increase in its Shannon-Wiener diversity index in autumn.

Habitat density and biomass

Overall, the average habitat density of the macrobenthos in Nakaumi Lake was approximately 823.44 ind. m^{-2}. Among all sites, the most significant seasonal variation in average habitat density occurred at NH-2, where the density dropped from 1471.88 ind. m^{-2} in winter–spring to 37.5 ind. m^{-2} in summer–autumn. Seasonally, the highest average density was observed in winter, at approximately 1226.56 ind. m^{-2}, with NH-2 recording the peak value of around 1975 ind./m^2. In spring, the average density was about 800 ind. m^{-2}, with NH-1 having the highest density of approximately 1275 ind. m^{-2}. In summer and autumn, the average habitat densities were 443.75 ind. m^{-2} and 823.44 ind. m^{-2}, respectively, with NH-1 again showing the highest values for both seasons, at 1093.75 ind./m^2 and 2393.75 ind. m^{-2}, respectively. Across all seasons, annelids represented the dominant taxon in terms of density composition. Their highest seasonal proportion was in autumn, accounting for approximately 97.34% of the average density, while the lowest was in winter at around 58.85%. Looking specifically at the sampling sites with the highest seasonal densities, the proportion of annelids ranked as follows: summer (97.14%), autumn (96.35%), winter (51.58%), and spring (48.53%).

Table 2. Macrobenthic biodiversity index and MPI

Location	Season	Species richness	D	J	C	H`	MPI
N-6	Winter	12	1.93	0.76	0.21	1.88	7.60
	Spring	13	2.61	0.74	0.21	1.89	8.97
	Summer	4	0.66	0.62	0.51	0.86	11.26
	Autumn	2	0.20	0.92	0.55	0.64	21.42
T-3	Winter	4	1.25	0.91	0.24	1.26	-5.00
	Spring	7	1.51	0.71	0.30	1.39	17.44
	Summer	1	*	*	*	*	*
	Autumn	1	*	*	*	*	*
NH-1	Winter	15	2.77	0.80	0.15	2.16	-21.40
	Spring	13	2.26	0.66	0.23	1.70	-9.10
	Summer	7	1.16	0.65	0.36	1.26	-0.10
	Autumn	8	1.18	0.65	0.31	1.35	7.93
NH-2	Winter	11	1.74	0.65	0.27	1.56	-3.38
	Spring	10	1.78	0.58	0.36	1.34	1.42
	Summer	1	*	*	*	*	*
	Autumn	0	/	/	/	/	/

The average biomass of macrobenthos in Nakaumi Lake was approximately 4.62 g m^{-2}. Spring recorded the highest seasonal biomass, at about 9.14 g m^{-2}, while the lowest was in summer, at approximately 1.375 g m^{-2}. Among the sampling sites, N-6 had the highest biomass in both winter and spring, whereas NH-1 had the highest biomass in summer and autumn. In winter, although NH-2 had the highest average density, its biomass was only about 19.28% of that at N-6. Similarly, in spring, the biomass of NH-1 was only 30.38% of that at N-6 despite having the highest density. At N-6, mollusks made up 67.97% and 84.98% of the biomass in winter and spring, respectively. In contrast, mollusks accounted for 0% and 81.93% of the biomass in the high-density sites NH-2 and NH-1 during the same seasons. In summer and autumn, the biomass at NH-1 was dominated by *Paraprionospio patiens*, comprising 55.56% and 77.67% of the total biomass, respectively.

Environmental status assessment

According to the MPI index shown in Table 2, environmental conditions in Nakaumi Lake varied significantly across time and space. The overall mean MPI value was 2.47, indicating a moderately polluted state. By season, winter had a mean MPI of -5.55, corresponding to a mildly polluted condition. Among the four monitoring sites, only N-6 was classified as severely polluted, while NH-1 exhibited the most favorable environmental quality. In spring, the mean MPI rose to 4.68, indicating a severely polluted state. Notably, T-3 showed the most drastic change, deteriorating from mildly polluted to severely polluted. The environmental status at the other sites also declined. During summer, only a single species was detected at T-3 and NH-2, with the seasonal mean MPI recorded at 2.79, still indicating moderate pollution. The environmental conditions at N-6 and NH-1 continued to worsen compared to spring. In autumn, no species were detected at NH-2, and only one species was found at T-3. The seasonal mean MPI reached 9.78. The conditions at N-6 and NH-1 further declined compared to summer. When comparing annual MPI fluctuations at N-6 and NH-1, N-6 showed a larger change, with an estimated variation rate of approximately 181%. For both sites, the environmental status during winter and spring was better than in summer and autumn. NH-1 exhibited the highest relative seasonal change, with a variation rate of about 125% between the colder and warmer halves of the year.

DISCUSSION

Community succession

The number of macrobenthic species recorded in Nakaumi Lake was significantly lower than that observed in estuarine environments at similar latitudes, such as the Yellow River Estuary (109 species) and the Yangtze River Estuary (124 species) in China (Yan et al., 2020; Yang et al., 2023). Unlike these open estuaries, Nakaumi Lake, though located near a river mouth, is only narrowly connected to the Sea of Japan via the Sakai Channel. Due to the small tidal range in the Sea of Japan, water exchange is limited, resulting in a relatively enclosed environment. This isolation, along with the seasonal formation of a halocline and variations in bottom water salinity (Nomura, 2003; Katsuki et al., 2008), prevents the development of complex transitional habitats across spatial gradients. Instead, drastic environmental changes tend to occur at the same location across seasons. This restricts the dispersal of marine species from the sea into the lake and causes seasonal disappearance of stenohaline species.

In contrast to estuaries like the Yellow River, where terrestrial organic input dominates, the organic matter in Nakaumi Lake primarily originates from aquatic organisms, with limited allochthonous input (Sampei et al., 2019). The organic detritus derived from aquatic organisms decomposes more easily and consumes large amounts of dissolved oxygen during decomposition, exacerbating seasonal extremes in bottom water conditions. The extreme temporal variability and spatial homogeneity of habitats are likely the main reasons for the significantly lower species richness in Nakaumi Lake compared to other estuaries at similar latitudes. Throughout the year, the species richness of macrobenthic communities in Nakaumi Lake followed a high–low–high seasonal pattern, which corresponded closely with seasonal changes in bottom water conditions. In winter and spring, the influence of the halocline is relatively weak, and species richness peaks. During this period, the community was mainly composed of euryhaline and freshwater species. In contrast, summer and autumn communities were dominated by stenohaline species due to the influx of seawater in summer, followed by a return to freshwater dominance in autumn. Comparison of community composition between autumn and summer showed the reappearance of euryhaline and freshwater species, indicating environmental recovery.

Spatially, species were more evenly distributed across the four sampling sites in winter and spring, with each site hosting a certain number of taxa. However, in summer and autumn, extreme differences emerged between sites. At T-3 and NH-2, only a single species or no species were found, indicating that bottom environments at these locations changed more drastically than those at N-6 and NH-1. The dominance of *Paraprionospio patiens* across different seasons reflects these seasonal environmental shifts. This species exhibited absolute dominance in winter, summer, and autumn, with particularly high importance values (IRI) in summer and autumn – indicative of its tolerance to extreme conditions and salinity variations. The biodiversity patterns across sites showed relatively high diversity levels in winter and spring, with T-3 consistently having the lowest. The limited number of species and individuals at T-3 may indicate site-specific environmental stress. The dominant species – *Arcuatula senhousia*, *Pseudopolydora sp.*, *Monocorophium acherusicum* – are all pollution-tolerant or opportunistic euryhaline species. This area is subject to intensive human activities, which likely contributes to the observed patterns. In summer and autumn, the biodiversity at all sites declined. T-3 and NH-2 were dominated by *Sigambra hanaokai*, a species highly tolerant of pollution and capable of surviving in severely hypoxic conditions. This suggests that extreme hypoxia pushed these habitats to ecological thresholds. Even at N-6 and NH-1, species richness declined by over 50%, indicating a broader structural degradation and functional loss of the macrobenthic community. However, NH-1 maintained higher diversity than N-6, possibly due to intermittent or localized water exchange that mitigated hypoxia. Consequently, species with varied environmental requirements coexisted at this site. By autumn, freshwater had regained control of the lake. Although community structure at T-3 and NH-2 remained unchanged, biomass increased markedly at N-6 and NH-1, with the reappearance of previously absent euryhaline species at NH-1, suggesting the most noticeable environmental improvement occurred here. The sharp increase of *Sigambra hanaokai* and *Paraprionospio patiens*, both considered "pioneer species" in recovering hypoxic environments, marked the early stages of community recovery – evident from their relative abundance and species richness compared to winter.

Ecological risk

The stability and functionality of an ecosystem are rooted in its biodiversity. As a critical component of the benthic system, macrobenthic communities in Nakaumi Lake exhibit pronounced seasonal fluctuations that can compromise the resilience of the ecosystem to disturbances. Their recovery is often driven by a few opportunistic species, casting doubt on the functional integrity and consistency of the ecosystem. In summer, the loss of biodiversity among macrobenthos led to food web simplification and decreased nutrient cycling efficiency. During winter and spring, except for T-3, the other sampling sites showed similar diversity levels, with abundant euryhaline and freshwater species evenly distributed. However, as seawater influx intensified in summer, the spatial distribution of these species contracted, and community composition became increasingly site-specific. Homogenization of macrobenthic communities at individual sites and fragmented bottom habitats caused by hypoxia and salinity changes posed serious threats to ecosystem stability. The consequences of habitat fragmentation became evident in autumn. Despite freshwater regaining control, only N-6 and NH-1 showed biomass recovery. T-3 and NH-2, in contrast, exhibited no improvement – NH-2 even had no detectable species. Notably, NH-2 had similar species composition to NH-1 during winter, suggesting that fragmentation delayed population dispersal and recovery. Interestingly, in winter and spring, the sites with the highest densities (NH-1 or NH-2) did not correspond to those with the highest biomass (N-6), with considerable discrepancies. Such high-density but low-biomass communities are often observed in disturbed environments. This pattern reversed in summer, likely due to widespread hypoxia. The primary species causing biomass differences was *Raetellops pulchellus*, indicating that NH-1 and NH-2 were dominated by detritus-based food chains and opportunistic small-sized species. These communities likely exhibited lower energy transfer efficiency and incomplete trophic structures, limiting their capacity for environmental regulation. With ongoing disturbance, further eutrophication in these areas is likely. The MPI index also reflected considerable environmental pressure in Nakaumi Lake, which intensified during seawater-dominated periods and eased slightly during freshwater control, confirming the seasonal nature of ecological stress in the lake.

CONCLUSIONS

The macrobenthic communities in Nakaumi Lake exhibit significant spatial and temporal variation. Overall, their species composition is far less diverse than that of estuarine systems at similar latitudes, primarily due to hydrological constraints. On the basis of annual trends, the year can be divided into two distinct periods. During the winter–spring period, species richness peaked across all four sampling sites, with relatively high biodiversity, biomass, and habitat density. In contrast, in summer–autumn, macrobenthic diversity declined sharply, with T-3 and NH-2 exhibiting either single-species dominance or complete absence of detectable species. Seasonal changes in hydrology may disrupt the continuity of bottom habitats. Hypoxia and salinity fluctuations not only constrain the survival of certain species but also segment the lake bottom into isolated areas, impeding or delaying species dispersal. These seasonal hydrological changes have led to large-scale fluctuations in community composition, posing serious threats to ecosystem stability. Currently, Nakaumi Lake's macrobenthic communities are dominated by small-bodied opportunistic species. This composition renders them less resilient to external disturbances. If adverse seasonal hydrological conditions coincide with intensified human activity, the macrobenthic community may undergo functional collapse – potentially leading to a broader ecological breakdown of the entire lake system.

As a widely applied assessment method, MPI is particularly well-suited to exploring the changes in aquatic environments through the lens of variations in macroinvertebrate communities. While Japan is home to a large number of brackish lakes, the practical application of this research method in such contexts still requires further expansion through additional case studies. Moving forward, the emergence of more application examples will help illuminate the causes behind environmental changes in brackish lakes across different regions, thereby providing support for the conservation of brackish lake environments on a global scale.

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