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Identification and management of ecosystem vulnerability in brackish lakes based on phytoplankton primary productivity dynamics: A case study of lake Nakaumi, Japan

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ABSTRACT

Lake Nakaumi is a typical brackish lake located on the western coast of Honshu, Japan. The lake is dominated by phytoplankton, with a lack of higher aquatic organisms, resulting in relatively low ecosystem stability. The primary productivity of phytoplankton can be regarded as an important indicator of the current environmental status of Lake Nakaumi. Therefore, studying the dynamic changes in primary productivity is a crucial basis for implementing ecosystem management in the lake. This study used the mature Vertically Generalized Production Model (VGPM) and regression analysis to analyze the spatiotemporal variations of phytoplankton primary productivity (PP_{eu}) in Lake Nakaumi from March 2023 to February 2024, as well as its main driving factors. This study explored the causes of differences in PP_{eu} under different spatial and temporal conditions, summarized the key issues contributing to ecosystem instability, and identified sensitive periods and regions. Based on a comprehensive assessment, a systematic and feasible ecosystem management strategy for Lake Nakaumi is proposed.

Keywords: Lake Nakaumi, primary productivity, VGPM, spatiotemporal distribution, phytoplankton, ecosystem management, ecosystem restoration.

INTRODUCTION

Photosynthesis by autotrophs in lakes marks the starting point of energy flow within lake ecosystems (Jia et al., 2022; Sun et al., 2023). Primary production in lakes mainly comes from phytoplankton and higher aquatic plants. In lakes where higher aquatic plants are scarce, phytoplankton generally dominate primary production. Chlorophyll-a (Chl-a) is a key indicator of phytoplankton biomass. In Lake Nakaumi, a eutrophic lake, Chl-a concentration can accurately reflect fluctuations in phytoplankton biomass (Kasprzak et al., 2008). The spatiotemporal dynamics of primary productivity represent the result of interactions between phytoplankton and their environment – that is, the adaptation of phytoplankton biomass to changing environmental conditions. These variations can propagate through the food chain, influencing the distribution of resources across different trophic levels of the ecosystem (Bergamino et al., 2010; Zhang et al., 2007). Typically, high Chl-a concentrations are associated with the collapse of higher aquatic vegetation and the decline of benthic organisms – key components of lake food webs. As a result, Chl-a concentrations are generally negatively correlated with food chain length (Kelly and Schallenberg, 2019). For Lake Nakaumi, exploring the spatiotemporal dynamics of primary productivity provides an effective means to understand the current status of the ecosystem. Moreover, primary productivity serves as a sensitive indicator of eutrophication (Smith, 2007), making it especially important for developing targeted ecosystem management strategies.

Various methods have been developed to estimate primary productivity, including the light-dark bottle method, chlorophyll fluorescence, and the carbon-14 isotope method (Gilbert et al., 2000; Öquist et al., 1982; Orchardo et al., 1987). The light-dark bottle method is simple and does not require sophisticated equipment, involving only water sample collection, incubation, and dissolved oxygen measurement. However, it is not well-suited for studies across broad spatial and temporal scales. The chlorophyll fluorescence method can detect subtle variations in phytoplankton photosynthesis with high sensitivity, but its calibration and analysis are complex. The carbon-14 method directly measures carbon fixation by phytoplankton and provides accurate assessments of primary productivity, though it is costly and requires strict operational procedures. Compared to these methods, model-based approaches incorporate multiple influencing factors and allow for a comprehensive analysis of their combined effects on primary productivity. They are not only helpful for understanding complex ecological processes but also particularly convenient for large-scale spatiotemporal analysis. A representative model is the Vertically Generalized Production Model (VGPM), proposed by Behrenfeld and colleagues. This model integrates a range of environmental parameters to effectively estimate euphotic zone primary productivity in oceans and lakes, and has been widely recognized as a mature method for such estimations (Behrenfeld and Falkowski, 1997). The VGPM has been applied in diverse geographical settings. For example, Ban et al. (2024) used it to analyze temporal variation in phytoplankton productivity in Lake Qinghai; Jia et al. (2019) employed it to study net primary productivity responses to nutrient conditions in Poyang Lake and the Ganjiang River; Xiong and Liu (2018) used it to investigate the impact of saltwater intrusion on phytoplankton productivity in the Pearl River Estuary. Compared to traditional methods such as the light-dark bottle approach, VGPM has shown superior timeliness and representativeness under complex hydrodynamic conditions (Li et al., 2023; Ye et al., 2015).

Lake Nakaumi is located along the western coast of Honshu, Japan (Figure 1), covering a water area of 86.3 km², with a maximum depth of 16 meters and an average depth of 5.4 meters. A salinity stratification (halocline) exists in the lake and varies spatiotemporally (Kurata and Hiratsuka, 2018). It connects to the Sea of Japan via the narrow Sakai Channel to the northeast and is linked to Lake Shinji to the west via the Ohashi River, forming a unique "twin-lake system" (Nakata et al., 2000). Spanning the border between Shimane and Tottori Prefectures, the lake is influenced by a distinctly maritime climate, with low solar radiation in winter. Urban areas such as Matsue and Yonago are located nearby, resulting in significant anthropogenic influence (Kunii and Minamoto, 2000; Nomura et al., 2022). The brackish nature of the lake gives rise to unique habitat patterns, where interactions between internal physical, chemical, and biological processes are complex. Its semi-enclosed hydrological structure limits its

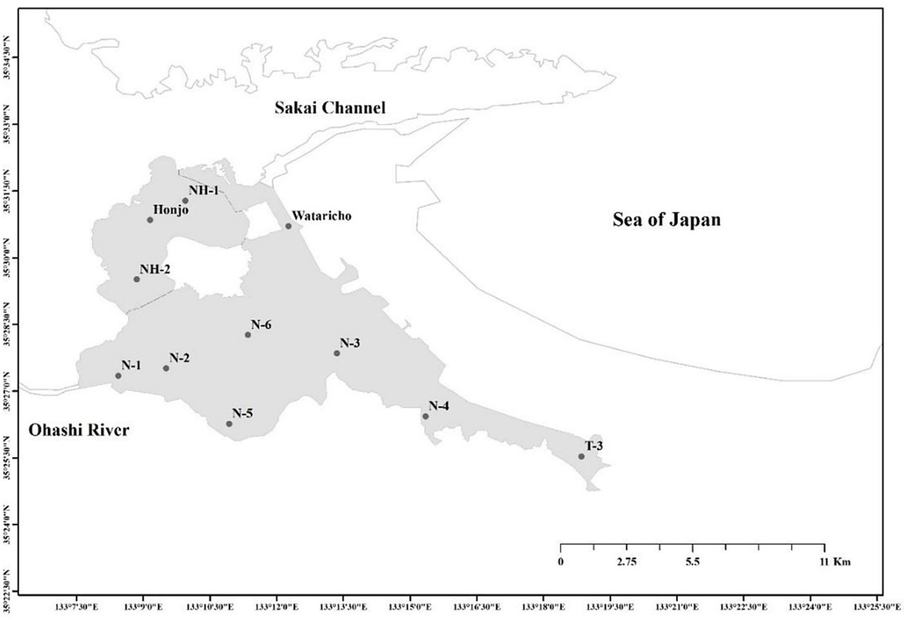

Figure 1. Distribution of water quality sampling points

ability to buffer external disturbances (Ichikawa et al., 2007; Ishida, 2015). In recent years, intensified global climate change and increasing extreme weather events have posed significant threats to lake ecosystems worldwide (Havens and Jeppesen, 2018; Mooij et al., 2005; Woolway et al., 2020). Although numerous studies have focused on freshwater or open-water lakes, research on brackish lakes remains scarce. Specifically, no comprehensive study has yet addressed the primary productivity of Lake Nakaumi. This study estimates the primary productivity of Lake Nakaumi from March 2023 to February 2024 using the VGPM in a data-driven framework. It analyzes the spatiotemporal dynamics of primary productivity and its relationship with key environmental factors. Based on the findings, this study identify the temporal and spatial characteristics of phytoplankton primary productivity, pinpoint major ecological issues and sensitive zones, and propose a systematic and feasible ecosystem management plan. The results are expected to provide a scientific basis for the sustainable use of Lake Nakaumi's ecological resources and contribute to the restoration of its ecosystem.

MATERIALS AND METHODS

The simplified expression (Huang et al., 2019) for the primary productivity of the euphotic zone PP_{eu} (mg C m^{-2}d^{-1} is:

$$PP_{eu} = 0.66125 P^B_{opt} \cdot \frac{E_0}{E_0 + 4.1} \cdot Z_{eu} \cdot C_{opt} \cdot D_{irr} \quad (1)$$

where: P^B_{opt} is the maximum photosynthetic rate of the water column (mg C m^{-2}h^{-1}), which can be expressed as a function of temperature (T):

$$P^B_{opt} = \begin{cases} 1.13 & T \leq -1.0 \\ 4.0 & T \geq 28.5 \\ P^{B'}_{opt} & -1.0 \leq T \leq 28.5 \end{cases} \quad (2)$$

When -1.0 ≤ T ≤ 28.5

$$\begin{gathered} P^{B'}_{opt} = 1.2956 + 2.749 \times 10^{-1}T + \\ + 6.17 \times 10^{-2}T^2 - 2.05 \times 10^{-2}T^3 + \\ + 2.462 \times 10^{-3}T^4 - 1.348 \times 10^{-4}T^5 + \\ + 3.4132 \times 10^{-6}T^6 - 3.27 \times 10^{-8}T^7 \end{gathered} \quad (3)$$

where: Z_{eu} is the euphotic zone depth (m), which can be calculated by the following formula through the suspended matter concentration and the chlorophyll concentration in the surface water:

$$Z_{eu} = 4.605/(0.062C_{SS} + 0.011C_{chl.a} + 1.430) \quad (4)$$

where: C_{SS} is the suspended matter concentration, and $C_{chl\text{-}a}$ is the Chl-a concentration in the surface water, C_{opt} is the Chl-a concentration at the depth where the maximum photosynthetic rate occurs, and it can be replaced by the Chl-a concentration measured in the surface water, D_{irr} is defined as light duration, E_0 is the photosynthetically active radiation intensity at the lake surface (mol m^{-2}d^{-1}), that is, the daily photosynthetically active radiation intensity Q_{PAR}. Its expression (Dong et al., 2011) in climatology is generally:

$$Q_{PAR} = \eta_Q Q \quad (5)$$

where: Q is the total radiation. In this study, the monthly average total radiation is used. η_Q is the proportion of PAR in the total radiation. There is a typical relationship between η_Q and the corrected surface water vapor pressure (Zhou et al., 1984), and this relationship can be expressed as:

$$\eta_Q = 0.384 + 0.053 \log_{10} e^* \quad (6)$$

where: e^* is the corrected surface water vapor pressure, and its expression is:

$$e^* = \frac{P_0}{P} e \quad (7)$$

In the formula, P_0 is the standard atmospheric pressure at sea level, P is the air pressure at the measuring point, and e is the surface water vapor pressure, which is taken as the monthly average value in this study.

This study employed statistical methods including the Kruskal-Wallis test (non-parametric test for multiple independent samples), the Mann-Whitney U test (non-parametric test for two independent samples), and multiple stepwise regression analysis.

The water quality data used in this study were sourced from the Izumo River Office (2025). The Izumo River Office has set up 11 monitoring points at fixed locations in Lake Nakaumi (Figure 1). All monitoring points are sampled once a month, and the sampling depth is 0.5 m from the water surface. The simultaneously sampled data include the concentration of Chl-a, nutrient concentration, water temperature, etc. The meteorological-related data were obtained from the Japan

Meteorological Agency (2025). The Japan Meteorological Agency has established a meteorological monitoring station (WMO Station ID: 47741) in Matsue City where Lake Nakaumi is located. This station can monitor local data such as sea level pressure, water vapor pressure, solar radiation, etc. All the above data are open to the public and can be queried on the websites of the Izumo River Office and the Japan Meteorological Agency.

RESULTS

Temporal and spatial distribution of PPeu in lake Nakaumi

In terms of temporal variation, both D_{irr} and Q reach their lowest values in winter. Compared to winter, these values increase significantly in spring, with the differences between the two seasons being statistically significant ($P < 0.001$). During the study period, PP_{eu} ranged from 0.07 × 10³ to 1.25 × 10³ mg C m^{-2}d^{-1}, with a median value of 0.34 × 10³ mg C m^{-2}d^{-1} and a mean value of 0.39 × 10³ mg C m^{-2}d^{-1}. Seasonally, the average PP_{eu} was 0.46 × 10³ mg C m^{-2}d^{-1} in spring, 0.40 × 10³ mg C m^{-2}d^{-1} in summer, 0.56×10³ mg C m^{-2}d^{-1} in autumn, and 0.14 × 10³ mg C m^{-2}d^{-1} in winter. The seasonal differences were statistically significant ($P < 0.001$). From March to August, PP_{eu} showed a fluctuating downward trend, with the monthly maximum value decreasing from 0.77 × 10³ mg C m^{-2}d^{-1} to 0.54 × 10³ mg C m^{-2}d^{-1}, and the minimum value declining from 0.38 × 10³ mg C m^{-2}d^{-1} to 0.19 × 10³ mg C m^{-2}d^{-1}. Between September and October, a sharp increase in PP_{eu} was observed, with the monthly average rising from 0.3 × 10³ mg C m^{-2}d^{-1} to 0.78 × 10³ mg C m^{-2}d^{-1}. Over time, the monthly averages began to decline again, reaching the lowest level of the study period in January (Figure 2).

Based on the spatial characteristics of the sampling sites, Lake Nakaumi can be divided into six distinct regions: the central lake area (N-6), the northwestern area (Honjo, NH-1, and NH-2), the area near the Ohashi River (N1, N2), the southern nearshore area (N5, N3, and N4), the Yonago Bay area (T-3), and the area nearest the Sakai Channel (Wataricho). In terms of spatial variation, significant differences ($P < 0.05$) in PP_{eu} were observed among all regions throughout the year. Seasonally, significant differences between regions were found in all seasons except autumn ($P > 0.05$). When dividing the lake along its longitudinal axis (northwest–southeast), the three subregions – the northwestern, central, and southeastern parts – also exhibited significant spatial differences during all seasons except autumn ($P < 0.05$). On a monthly scale, the most notable spatial disparities occurred in April and May. In May, PP_{eu} in the southeastern region reached 0.68 × 10³ mg C m^{-2}d^{-1}, significantly higher than in the central region (0.32 × 10³ mg C m^{-2}d^{-1}), which in turn was higher than in the northwestern region (0.23 × 10³ mg C m^{-2}d^{-1}, showing a decreasing gradient from southeast to northwest. In April, PP_{eu} values were 0.43 × 10³ mg C m^{-2}d^{-1} in the southeastern region, 0.36 × 10³ mg C m^{-2}d^{-1} in the central region, and 0.24 × 10³ mg C m^{-2}d^{-1} in the northwestern region. The seasonal spatial distribution patterns of PP_{eu} in Lake Nakaumi are illustrated in Figure 3 (only months with statistically significant differences are shown).

The relationship between the changes of important parameters and PP_{eu}

There were significant differences in Chl-a, T, TN, TP and Z_{eu} in different seasons ($P < 0.001$). The mean values and variation ranges of Chl-a,

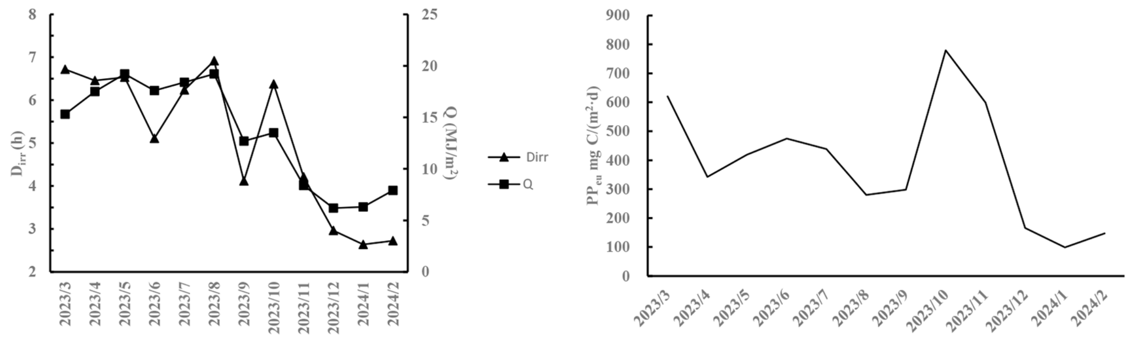

Figure 2. The monthly variations of D_{irr}（Q）and PP_{eu}

T, TN, TP and Z_{eu} within the research period were 10.24 ± 0.49 μg L^{-1} (2.6–30 μg L^{-1}), 18.55 ± 0.71 °C (6.1–32.4 °C), 0.39 ± 0.008mg L^{-1} (0.21–0.72 mg L^{-1}), 0.04 ± 0.001 mg L^{-1} (0.016–0.1 mg L^{-1}), and 2.74 ± 0.02 m (2.16–3.03m), respectively. T and Z_{eu} in spring and summer were significantly higher than those in autumn and winter, while Chl-a and TP in autumn and winter were higher than those in spring and summer. TN showed relatively small overall fluctuations (Figure 4).

After standardizing PP_{eu} and other environmental parameters using the Z-score method, univariate linear regression and multiple stepwise regression analyses were conducted. The results are shown in Figure 5 (Display only the results with highly significant relationships) and Tab. 2 There was a significant linear regression relationship between PP_{eu} and Dirr throughout the year and among different seasons. In spring, there was an extremely significant positive relationship between PP_{eu} and Chl-a, TP, and a negative relationship between PP_{eu} and TN. In summer, there was a positive relationship between PP_{eu} and Chl-a, and a negative relationship between PP_{eu} and T. In autumn, there was a positive relationship between PP_{eu} and TP, and

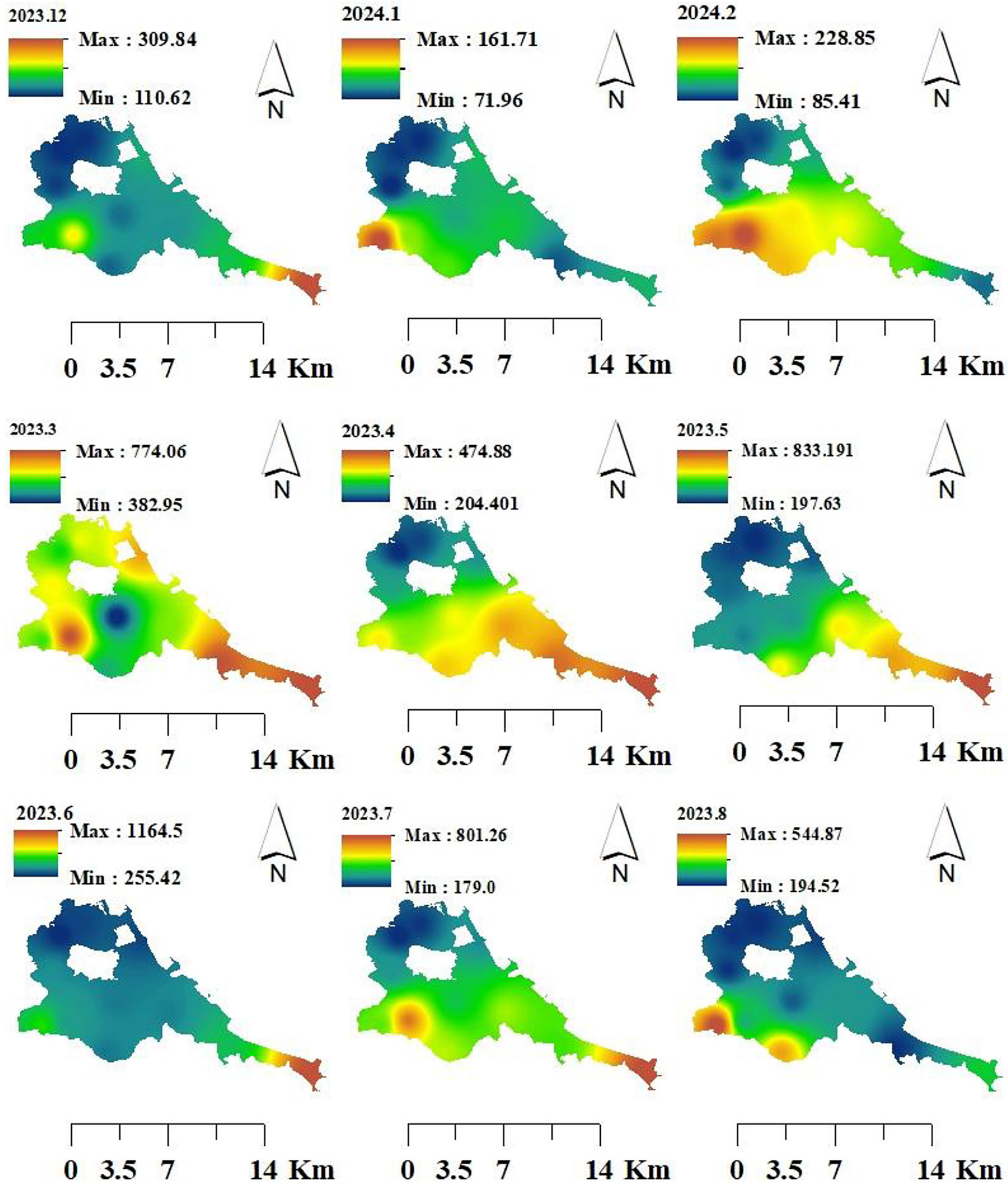

Figure 3. Spatial distribution of primary productivity

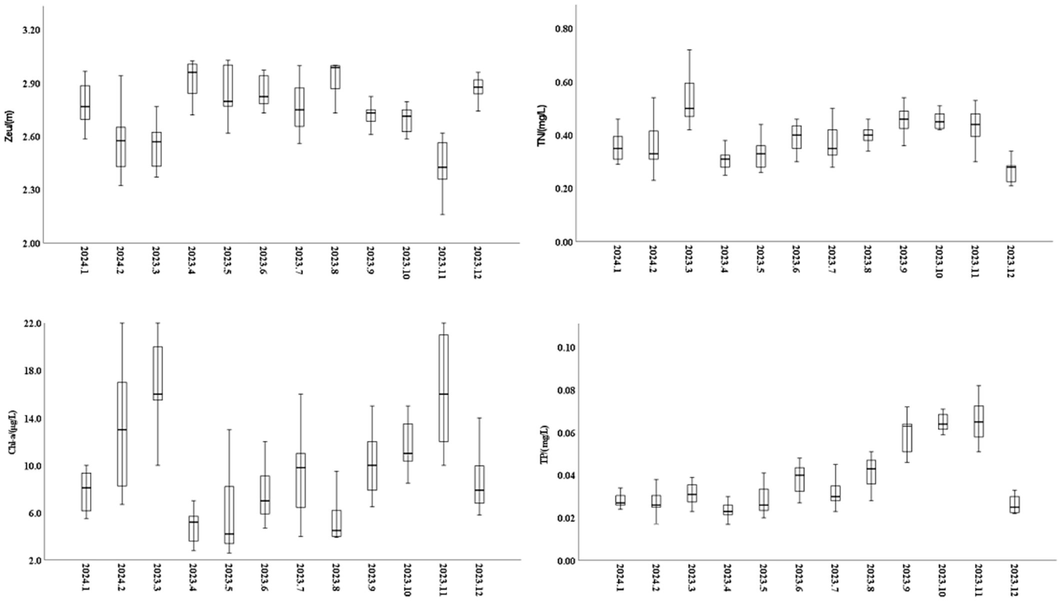

Figure 4. The monthly variations of Z_{eu}, Chl-a, TN, TP

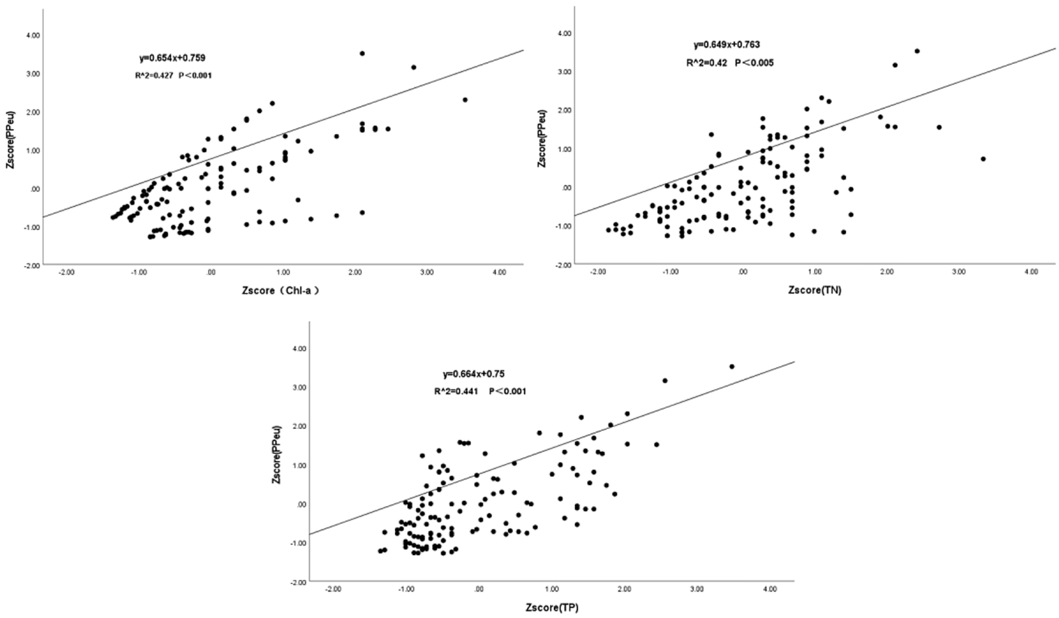

Figure 5. The results of simple linear regression analysis

a negative relationship between PP_{eu} and T. In winter, there was a positive relationship between PP_{eu} and Chl-a, T. From an annual perspective, there were positive relationships between PP_{eu} and Chl-a, TP, T (Table 1).

DISCUSSION

The causes of the spatio-temporal pattern of primary productivity in lake Nakaumi

The spatiotemporal distribution of PP_{eu} in Lake Nakaumi is closely linked to the region's climatic and hydrological conditions. Its spatial heterogeneity reflects the complex dynamics of brackish lakes, which are shaped by the interaction of both marine and fluvial influences. The variation in PP_{eu} is influenced by multiple factors, including solar radiation, photoperiod, water temperature, and Chl-a concentration. Located on the Sea of Japan side of Honshu Island, Lake Nakaumi experiences cloudy and rainy conditions during winter. Compared with other seasons, winter is characterized by shorter daylight hours and reduced solar radiation. Consequently, in winter, PP_{eu} shows significant correlations with D_{irr}, temperature, and Chl-a.

Table 1. The results of multiple stepwise regression analysis

Season	Multiple stepwise regression equation	R^2	F	P
Spring	Z_score（PP_{eu}）=0.585 Z_score（Chl-a）	0.771	104.275	＜0.001
	Z_score（PP_{eu}）=0.404 Z_score（Chl-a）+0.805 Z_score（TP）	0.899	133.322	＜0.001
	Z_score（PP_{eu}）=0.655 Z_score（Chl-a）+1.124 Z_score（TP）-0.322 Z_score（TN）	0.932	132.809	＜0.001
Summer	Z_score（PP_{eu}）=0.92 Z_score（Chl-a）	0.954	645.006	＜0.001
	Z_score（PP_{eu}）=0.886 Z_score（Chl-a）-0.243 Z_score（T）	0.975	580.791	＜0.001
Autumn	Z_score（PP_{eu}）=1.249 Z_score（TP）	0.529	34.835	＜0.001
	Z_score（PP_{eu}）=0.987 Z_score（TP）-1.12 Z_score（T）	0.716	37.784	＜0.001
Winter	Z_score（PP_{eu}）=0.226 Z_score（Chl-a）	0.662	60.775	＜0.001
	Z_score（PP_{eu}）=0.271 Z_score（Chl-a）+0.497 Z_score（T）	0.946	263.971	＜0.001
All year	Z_score（PP_{eu}）=0.664 Z_score（TP）	0.441	102.395	＜0.001
	Z_score（PP_{eu}）=0.441 Z_score（Chl-a）+0.419 Z_score（TP）	0.567	84.398	＜0.001
	Z_score（PP_{eu}）=0.603 Z_score（Chl-a）+0.284 Z_score（T）+0.229 Z_score（TP）	0.61	66.720	＜0.001

Water temperature decreases month by month during this season, and January – coinciding with the lowest effective sunshine duration – registers the lowest monthly average of PP_{eu}. The low temperature (with the seasonal minimum monthly average reaching as low as 6.76 °C) inhibits phytoplankton growth, which is reflected in the winter season having the lowest PP_{eu} values compared to the other seasons. In spring, rising temperatures and improving light conditions result in longer daylight hours, and the influence of Chl-a and nutrients on PP_{eu} becomes more pronounced. Accordingly, PP_{eu} increases significantly compared to winter. The observed negative correlation with TN may be due to the excessive uptake of nitrogen by phytoplankton during rapid growth. Lake Nakaumi also experiences a strongly seasonal halocline. In summer, this results in marked vertical heterogeneity, where the halocline limits mixing between surface and bottom layers, reducing nutrient availability in the euphotic zone. A study of Obuchi Lake, another brackish lake in Aomori Prefecture, Japan, found that vertical stratification in summer leads to differences in phytoplankton composition between layers, with surface waters favoring species adapted to low-nutrient environments(Ueda et al., 2005). Consequently, in summer, temperature and Chl-a emerge as key factors influencing PP_{eu}. According to the primary productivity calculation formula, the P_{opt}^{B} becomes constant when water temperature exceeds 28.5 °C, meaning temperature no longer contributes to productivity beyond that point. Previous studies have shown that elevated temperatures affect the activity of photosynthetic enzymes in phytoplankton(Li et al., 1984; Morris and Glover, 1974). In Lake Nakaumi, the average water temperature in August reaches 32.1 °C. Such high temperatures may reduce photosynthetic enzyme activity, increase respiration, and ultimately inhibit photosynthesis. Despite sufficient light availability in summer, nutrient limitations combined with high temperatures constrain phytoplankton growth rates and biomass, which may explain the observed positive correlation between PP_{eu} and Chl-a, and negative correlation with temperature during this season. In autumn, the weakening of the halocline allows for enhanced mixing between surface and bottom layers. This upwelling brings bottom nutrients to the surface, increasing resource availability for phytoplankton and enhancing the role of TP (total phosphorus) in influencing PP_{eu}. Phosphorus availability is known to affect phytoplankton biomass. Meanwhile, water temperatures decrease steadily from 27.27 °C at the beginning of the season to 19.35 °C at the end. Within the range of -1 °C to 28.5 °C, P_{opt}^{B} increases proportionally with temperature, but in autumn, the effect of falling temperatures on PP_{eu} appears to be offset by the increase in nutrient supply, confirming that nutrient availability plays a more critical role than temperature during this season. The sharp rise in PP_{eu} during autumn – often reaching annual peak levels – is likely due to the combined effects of favorable temperatures, sufficient nutrient inputs, and ample light availability. Over the course of the year, PP_{eu} is most strongly influenced by Chl-a, TP, and temperature, with Chl-a being the most critical factor. This highlights the tight linkage between phytoplankton biomass in the euphotic zone and primary productivity in Lake Nakaumi.

Spatially, Lake Nakaumi's northeast side connects to the Sakai Channel, which links to the Sea of Japan, while the Ohashi River – its primary freshwater source – is located on the southwest side. The spatial positioning of these features leads to distinct hydrodynamic conditions in different areas of the lake, contributing to spatial variations in PP_{eu}. In winter, areas with relatively high PP_{eu} are concentrated near the Ohashi River, where the water is shallower. Given the limited solar radiation during winter, phytoplankton in these shallower areas may be more concentrated in the euphotic zone, enhancing PP_{eu}, especially since Chl-a is the dominant influencing factor in winter. Between January and February, the high-PP_{eu} zones expand from the river mouth toward the center of the lake. Since water temperature significantly impacts PP_{eu} in winter, the relatively lower temperatures in the Ohashi River area compared to the Sakai Channel may enhance vertical mixing, facilitating nutrient upwelling that supports phytoplankton growth. In spring, nutrient availability becomes a key factor. In March, PP_{eu} tends to be higher along the shoreline while remaining low in the lake center, likely due to terrestrial nutrient inputs from snowmelt and surface runoff. Throughout spring, high-PP_{eu} zones are mainly located in the Yonago Bay area, and this spatial pattern corresponds to the temperature distribution, supporting the finding that temperature is a key factor in spring. During summer, high-PP_{eu} zones shift to the southeastern and southern regions of the lake. This pattern may be influenced by oceanic control, where seawater intrusion from the Sakai Channel restricts vertical mixing near the northeast, pushing high productivity zones away from the channel and toward the southeastern and southern regions.

Major ecological issues in lake Nakaumi

The primary productivity of phytoplankton in Lake Nakaumi exhibits marked seasonal fluctuations, with the lowest values observed in winter. In spring and autumn, there is a noticeable increase compared to winter and summer, with a particularly sharp rise in autumn. This surge reflects the vulnerability of Lake Nakaumi's ecosystem to seasonal hydrological changes, indicating an imbalance in system structure and relatively low ecological stability. One of the key reasons for this instability is the current dominance of macroalgae in the lake, while seagrass species remain scarce (Yamamuro et al., 2006). Higher aquatic plants play a critical role in maintaining the stability of lake ecosystems. This is reflected in their inhibitory effect on phytoplankton reproduction through competitive interactions and their ability to reduce sediment resuspension (Nõges et al., 2003). Both of these processes influence water transparency. From August to November, the concentration of suspended solids in Lake Nakaumi increases significantly, with monthly averages rising from 1.27 mg L^{-1} in August to 4.55 mg L^{-1} in November. Correspondingly, the water transparency at multiple monitoring sites shows a sharp decline in November compared to August. High water transparency allows more light to penetrate deeper into the lake, which enhances the photosynthetic activity of higher aquatic plants and facilitates oxygen release. The presence of abundant macrophytes is beneficial for maintaining biodiversity in aquatic ecosystems. In the case of Lake Nakaumi, the lack of seagrass means that in the absence of higher plants, phytoplankton receive most of the available resources, becoming the dominant contributor to primary production. A phytoplankton-dominated system is prone to hypoxia in bottom waters (Li et al., 2018; Mallin et al., 2006; Rabalais et al., 2001). Every summer, Lake Nakaumi experiences periodic limitations in vertical mixing. During these periods, the lack of higher aquatic vegetation exacerbates the impact of hydrological stratification, significantly increasing the risk of hypoxia in bottom waters. Over the long term, severe hypoxia may lead to shifts in the structure of aquatic communities and a reduction in ecosystem functional diversity. In autumn, vertical stratification weakens, removing barriers to the exchange of nutrients between surface and bottom waters. This allows large quantities of nutrients to rise to the surface, resulting in a substantial increase in surface nutrient concentrations. TP levels are particularly elevated during this season compared to others, increasing the risk of harmful algal blooms, especially red tides. Therefore, from a year-round perspective, summer and autumn are the most ecologically vulnerable periods for Lake Nakaumi.

During the summer, special attention should be given to the areas near the Ohashi River, Yonago Bay, and the southern nearshore zones. All three areas are located in the southern or southeastern part of Lake Nakaumi, surrounded by densely populated cities and characterized by frequent industrial and agricultural activities. During summer, when vertical water exchange is weak, anthropogenic impacts may exacerbate eutrophication in these regions, further deteriorating water quality. In autumn, when PP_{eu} reaches its annual peak, the Ohashi River region warrants particular attention. Although relatively shallow, this area holds a geographically unique position: during summer, saline bottom water flows into the Ohashi River via this region; in autumn, as marine influence recedes, large volumes of freshwater flow back into Lake Nakaumi through the same channel. As a result, surface waters in this region are simultaneously influenced by both riverine inputs and bottom water upwelling, making it especially susceptible to eutrophication.

Recommendations for ecosystem management

Effective management of the Lake Nakaumi ecosystem requires not only harmonizing the relationship between local socio-economic activities and ecological integrity, but also ensuring the long-term sustainability of the ecosystem. Historically, when the lake was still dominated by seagrass species, *Zostera marina L.* was widely distributed across the lake. However, due to herbicide pollution and land reclamation projects, this species has nearly disappeared (Hiratsuka et al., 2007). Therefore, reintroducing suitable macrophytes and adjusting the current ecological structure of Lake Nakaumi should be a top priority in ecosystem management. At present, the lake is a turbid water body where phytoplankton holds a dominant position. Since *Zostera marina L.* requires relatively high water quality and transparency, the current conditions are not favorable for its survival (Katsuki et al., 2008). For example, during autumn—a peak season for phytoplankton proliferation—the average water transparency at three monitoring points in the southern nearshore area decreases by approximately 33% in November compared to August. The limited light availability in the bottom layer makes it difficult for *Zostera marina L.* to compete with phytoplankton. In summer, hypoxic conditions near the sediment further inhibit root development, preventing plant survival.

A phased restoration of seagrass beds is a suitable approach. In the initial phase, the introduction of pioneer species that are tolerant of pollution, low light, and capable of rapid growth is recommended to acclimate to the environment. These pioneers serve as indicators of environmental tolerance. Given Lake Nakaumi's hydrological and environmental characteristics, pioneer species should first be introduced into shallow regions such as the Ohashi River area, where light conditions near the lakebed are relatively favorable. These conditions support the rapid growth of submerged pioneers, which can help stabilize sediment and improve transparency. Additionally, this area is adjacent to the Ohashi River and experiences relatively dynamic water flow. Pioneer species should be able to compete effectively with phytoplankton for nutrients. This would help gradually reduce the sharp seasonal rise in PP_{eu} observed in autumn, and improve bottom water oxygen levels during summer, contributing to a more stable ecosystem structure. However, it is crucial that the pioneer plant communities also provide suitable habitats for benthic organisms and epiphytes. This is essential for enhancing the benthic food web, which plays a key role in the resilience of the Lake Nakaumi ecosystem.

Therefore, the pioneer community should exhibit vertical spatial complexity. Ideal pioneer species should have a stratified growth form, with root systems capable of stabilizing the soft sediment of the lake. Rather than introducing a single species, mixed planting of various growth forms is recommended to increase habitat heterogeneity and enhance the stability of the plant community under Lake Nakaumi's complex hydrological conditions. Based on environmental adaptability, pioneer species should be selected and categorized by function. Since this is a mixed planting strategy, it is not necessary for each introduced species to fulfill both nutrient absorption and structural functions simultaneously. Once the pioneers have improved water quality and stabilized the environment, native macrophyte species should be reintroduced on a larger scale. However, care must be taken to avoid excessive interspecies competition. At the same time, it is essential to regulate the use of agricultural chemicals in the watershed and promote ecological farming practices. The Lake Nakaumi region experiences frequent rainfall during winter, which increases the risk of herbicides entering the lake via surface runoff and negatively impacting pioneer plants – making chemical regulation critical for their survival. Regular monitoring of interactions between pioneer plants, phytoplankton, and benthic organisms is necessary. Adjustments to the composition of pioneer species should be made when necessary. From a horizontal spatial perspective, pioneer planting should be carried out in stratified layers from shallow nearshore areas toward deeper zones, using species with complementary functional traits. This will enhance community resilience, gradually improve habitat conditions, and reduce spatial variability in PP_{eu} during the summer and autumn months. Planting zones should be designated according to depth gradients. In shallow nearshore areas, species that grow rapidly, photosynthesize efficiently, and absorb nutrients quickly, such as *Vallisneria asiatica* and *Hydrilla verticillate* are recommended for rapid sediment stabilization. These species are tolerant of high water temperatures and have strong nutrient uptake capabilities. Given the autumnal phytoplankton bloom in Lake Nakaumi, a small proportion of *Potamogeton crispus* which thrives in cooler temperatures – may be co-planted. This species grows vigorously during autumn and can compete with phytoplankton for nutrients during peak bloom periods. In deeper transitional zones, euryhaline species such as *Ruppia maritima* should be introduced to buffer the impacts of seasonal hydrological changes from the nearshore zone. For deep-water regions, where bottom water conditions are initially poor, suspended, low-light-tolerant species such as *Stuckenia pectinata* and *Ceratophyllum demersum* may be mixed and introduced. Attention must be paid to changes in biomass of the introduced species. At the early stage of planting, artificial improvements to the sediment and installation of flow barriers may be necessary to prevent hydrodynamic disturbance. For floating or suspended species, periodic harvesting and replanting should be implemented. Lake Nakaumi has already established successful practices of using harvested aquatic plants as fertilizer in nearby agricultural areas. This not only prevents excessive shading and additional stress on bottom waters, but also offers a potential source of economic value.

CONCLUSIONS

The spatiotemporal variation of PP_{eu} in Lake Nakaumi exhibits significant heterogeneity, closely tied to the lake's unique environmental conditions. During spring and summer, PP_{eu} fluctuates, while autumn marks a phase of rapid increase, and winter maintains a relatively stable and low level. The main influencing factors of PP_{eu} vary by season: in spring, PP_{eu} is significantly correlated with Chl-a, TP, and TN; in autumn, it is mainly influenced by TP and temperature; in summer and winter, Chl-a and temperature are the dominant factors. Across the entire year, Chl-a, TP, and temperature are identified as the principal drivers of PP_{eu} variation. The spatial heterogeneity of PP_{eu} is largely shaped by the complex hydrological conditions resulting from the alternating influence of riverine and marine inputs. Except for autumn, significant spatial differences are observed in other seasons. In winter, relatively high PP_{eu} values are concentrated near the Ohashi River area (southwest). In spring, they shift to the Yonago Bay area (southeast), and in summer, they are mainly found in the southeast and southern regions, away from the northeast Sakai Channel area.

The hypoxia in bottom water during summer and the sudden increase in PP_{eu} in surface water during autumn are both highly detrimental to the stability of Lake Nakaumi's ecosystem. In summer, particularly in the areas near the Ohashi River, Yonago Bay, and the southern coastal zone, these three regions exhibit relatively high PP_{eu} values. Since the surrounding areas of Lake Nakaumi are densely populated, eutrophic substances from industrial, agricultural, and domestic activities enter the lake through surface runoff. Therefore, close attention must be paid to the nutrient dynamics in these three regions. In autumn, the surface water near the Ohashi River is influenced by both riverine replenishment and bottom water replenishment, making its eutrophication level particularly noteworthy.

The structural instability of the Lake Nakaumi ecosystem is primarily due to the absence of macrophytes and the dominance of phytoplankton. The key to ecosystem management lies in reintroducing macrophytes and rebuilding aquatic plant communities. However, direct large-scale reintroduction is currently unfeasible due to environmental constraints and human disturbances. A phased restoration strategy is thus recommended: initially introducing pioneer species to stabilize water quality and reconstruct habitat structure, followed by the reintroduction of native species. This approach aims to enhance the resilience of the Lake Nakaumi ecosystem. Although this study proposes a feasible strategy for restoring ecosystem structure, implementing effective ecosystem management remains a highly complex task that will require extensive long-term practice and validation. It should be noted that this study has not yet conducted experiments on the phased restoration of macrophytes or related risk assessments. However, carrying out such experiments and assessments will bridge the gap between the current research findings and the actual ecological management needs, and will contribute to further exploring effective strategies for the management of the ecosystem of Lake Nakaumi.

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