Spatiotemporal Variation in Biomass of the Endangered Seagrass Halophila beccarii and Its Key Influencing Factors: Postprint

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Abstract

To deeply investigate the distribution characteristics and driving factors of biomass of the endangered seagrass *Halophila beccarii* along the South China coast, this study systematically analyzed the spatiotemporal dynamics of its biomass and key environmental impact factors using *H. beccarii* from six regions (Huachang Bay, Yangpu, Shajing, Tangjiawan, Yifengxi, and Zhao' an) across four provinces (autonomous regions) in coastal South China. The results showed that: (1) The mean aboveground biomass, belowground biomass, and total biomass of *H. beccarii* along the South China coast were (11.98$±13.06)g · m^{-2}$ DW (mean ± standard deviation SD, hereinafter the same), (12.06$±12.96)g · m^{-2}$ DW, and (24.05$±23.70)g · m^{-2}$ DW, respectively. Among these, the biomass at Tangjiawan was significantly lower than at other study sites (P<0.05). Biomass exhibited obvious seasonal variation, being low in winter-spring and high in summer-autumn. (2) Except for pH and nitrite concentration, other environmental factors (such as water temperature, salinity, inorganic phosphorus, nitrate, and ammonium nitrogen) showed significant differences among different study sites (P<0.05). (3) Correlation analysis results showed that aboveground biomass was significantly positively correlated with water temperature and inorganic phosphorus concentration (P<0.05), but significantly negatively correlated with ammonium nitrogen concentration (P<0.05); belowground biomass was significantly positively correlated with inorganic phosphorus and nitrate concentrations (P<0.05); total biomass was significantly positively correlated with inorganic phosphorus and nitrate concentrations (P<0.05), but significantly negatively correlated with ammonium nitrogen concentration (P<0.05). (4) Principal Component Analysis (PCA) results indicated that water temperature and nitrite were the main positive factors promoting total biomass accumulation, while ammonium nitrogen had an inhibitory effect. (5) Linear regression further confirmed that pore water physicochemical factors had a significant linear relationship with total biomass (R^2=0.118, P<0.001). These research findings have important scientific value for deeply understanding the ecological characteristics, environmental adaptation mechanisms, and reasons for endangerment of *H. beccarii*, while also providing a theoretical basis for the conservation and management of this species.

Full Text

Spatiotemporal Variation in Biomass of the Threatened Seagrass *Halophila beccarii* and Its Key Influencing Factors

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Abstract

To enhance understanding of biomass distribution patterns and their driving factors in the threatened seagrass *Halophila beccarii* along the South China coast, this study systematically investigated the spatiotemporal dynamics of its biomass and key environmental variables across six regions—Huachangwan, Yangpu, Shajing, Tangjiawan, Yifengxi, and Zhao' an—located in four coastal provinces of southern China. Seasonal field sampling was conducted to capture intra-annual variations. Key findings include: (1) The mean aboveground, belowground, and total biomass values of *H. beccarii* were (11.98 ± 13.06) $g \cdot m^{-2}$ DW, (12.06 ± 12.96) $g \cdot m^{-2}$ DW, and (24.05 ± 23.70) $g \cdot m^{-2}$ DW (mean ± SD), respectively. Biomass at Tangjiawan was significantly lower than at other sites ($P < 0.05$). Distinct seasonal patterns were observed, with lower biomass during winter and spring and higher values in summer and autumn. (2) Except for pH and nitrite, all other environmental factors—water temperature, salinity, inorganic phosphorus, nitrate, and ammonia nitrogen—differed significantly among sites ($P < 0.05$), indicating substantial spatial heterogeneity in habitat conditions. (3) Correlation analyses revealed that aboveground biomass was significantly positively correlated with water temperature and inorganic phosphorus ($P < 0.05$), and negatively correlated with ammonia nitrogen ($P < 0.05$). Belowground biomass was positively correlated with inorganic phosphorus and nitrate ($P < 0.05$). Total biomass showed positive correlations with inorganic phosphorus and nitrate ($P < 0.05$), and a negative correlation with ammonia nitrogen ($P < 0.05$), suggesting that both nutrient availability and temperature play key roles in regulating productivity. (4) Principal component analysis identified water temperature and nitrite as the main positive factors affecting total biomass, whereas ammonia nitrogen exhibited an inhibitory effect, underscoring the importance of nutrient balance and thermal environment. (5) Linear regression confirmed a significant albeit modest relationship ($R^2 = 0.118$, $P < 0.001$) between porewater physicochemical factors and total biomass, indicating that other unmeasured variables may also influence biomass variability. This study improves our insight into the ecological characteristics, environmental adaptations, and causes of endangerment of *H. beccarii*, and offers a scientific foundation for its conservation and management amid growing anthropogenic pressures and climate change.

Keywords: *Halophila beccarii*, biomass, porewater physicochemical factors, multivariate statistical analysis, South China coast

Introduction

Seagrasses are submerged marine angiosperms widely distributed in temperate and tropical waters, typically inhabiting intertidal and shallow subtidal zones (Short et al., 2007). With high primary productivity, seagrasses provide nutrients and energy to shallow marine ecosystems through food webs and detrital cycles while transporting nutrients (nitrogen, phosphorus) and organic carbon to deeper ocean layers (Duarte & Dorte, 2017), making significant contributions to marine "blue carbon" storage (Mcleod et al., 2011). Additionally, seagrasses protect coastlines by attenuating wave energy, trapping sediments, and regulating nutrient cycling, while also serving as biological indicators of coastal pollution (Lewis & Richard, 2009; Ondiviela et al., 2014; Costanza et al., 2017). Despite their valuable ecosystem functions, seagrasses have received insufficient attention from international and domestic communities in terms of research, management, and conservation compared to coral reefs and mangroves (Kumar & Deepak, 2021). Furthermore, global climate change and human activities are accelerating seagrass bed decline worldwide through coastal eutrophication and salinity alterations (Waycott et al., 2009).

Among seagrass species, *Halophila beccarii* Ascherson is classified as endangered by the International Union for Conservation of Nature (IUCN) due to its habitat vulnerability (Short et al., 2011). *H. beccarii* is a small monoecious seagrass in the family Hydrocharitaceae with annual and perennial life histories, characterized by rapid growth and high population variability (Qiu et al., 2020; Geng et al., 2022). It predominantly grows in intertidal zones heavily impacted by human activities, preferring muddy or sandy-silt substrates (Kumar & Deepak, 2021). Globally, *H. beccarii* is mainly distributed in Asian countries and regions including Malaysia, Thailand, Singapore, India, and China (Short et al., 2011). In China, it is concentrated in Guangxi, Guangdong, Fujian, and Hainan provinces (Huang et al., 2010; Qiu et al., 2013; Chen et al., 2015; Zhong et al., 2024).

Biomass forms the basis of energy flow and material cycling and serves as a crucial indicator for assessing ecosystem structure and function (Deng et al., 2022). As a key component of marine ecosystems, seagrass biomass directly reflects ecosystem health and productivity levels (Zhao et al., 2020). Variations in seagrass biomass influence interactions with other organisms, material fluxes, and energy transformation (Zheng et al., 2012). Therefore, monitoring and studying seagrass biomass is essential for evaluating seagrass ecosystem function, particularly when investigating the impacts of environmental change on seagrass growth and ecological function. Seagrass growth and development are precisely regulated by genetic factors while being significantly influenced by external environmental conditions (Qin et al., 2020; Ankel et al., 2021). Light, temperature, salinity, nutrients, inorganic carbon sources, hydrodynamic conditions, pollutant concentrations, grazing pressure, and human activities are generally considered important external factors limiting seagrass growth and development (Xu et al., 2007; Han and Shi, 2008; Liu et al., 2017).

Nutrient supply plays a decisive role in seagrass growth. Appropriate nutrient levels can promote seagrass development, but excessive nutrient input causes eutrophication that affects biomass accumulation and ecosystem stability (Jones et al., 1997; Cambridge & Kendrick, 2009). Jiang et al. (2023) found that ammonium concentrations of 25–50 $\text{mol}\bullet\text{L}^{-1}$ could promote seagrass biomass accumulation, while higher concentrations induced toxic effects. Temperature, salinity, and pH are also key factors influencing seagrass biomass (Munns, 2002; Lee et al., 2007). Elevated temperatures may affect seagrass growth by inhibiting photosynthesis or altering metabolic pathways, while salinity fluctuations influence growth and biomass accumulation by regulating physiological processes (Chen et al., 2019; Li et al., 2021; Liu et al., 2024). The effects of pH fluctuations on seagrass biomass are complex: short-term pH increases may enhance biomass by promoting photosynthesis, but long-term acidification or dramatic fluctuations can suppress biomass through nutrient limitation, physiological stress, and ecological competition (Zimmerman et al., 1997; Cai, 2023). Thus, biomass changes reflect not only population growth status but also environmental influences on growth and ecological function. Studying the relationship between *H. beccarii* biomass and key environmental factors can help predict ecosystem productivity levels and provide scientific evidence for conservation, restoration, and resource management.

Research on *H. beccarii* in China started relatively late, with previous studies focusing primarily on species distribution, morphological structure, functional traits, population dynamics, soil seed banks, and genetic variation (Qiu et al., 2013; Chen et al., 2019; Pan et al., 2024; Chen et al., 2024; Pan et al., 2025). Few studies have examined the correlations between *H. beccarii* biomass and its key drivers, limiting deeper understanding of this endangered species' growth strategies and hindering effective conservation efforts. Investigating *H. bec-*

carii biomass is crucial for understanding population development, dynamics, and ecosystem health, and is significant for population renewal and restoration. Therefore, this study examined *H. beccarii* along the South China coast (Fujian, Guangdong, Guangxi, and Hainan) by measuring biomass and porewater physicochemical factors across different sites. The objectives were to: (1) characterize the magnitude and spatiotemporal variation of *H. beccarii* biomass along the South China coast; and (2) identify key environmental factors influencing seagrass biomass. The results provide a theoretical basis for understanding population establishment, development, self-recovery, endangerment mechanisms, and resource conservation of *H. beccarii*.

1.1 Study Area

The survey regions included six locations : Huachangwan (HCW) in Chengmai County and Yangpu (YP) in Danzhou City, Hainan Province; Shajing (SJ) in Qinzhou City, Guangxi Zhuang Autonomous Region; Tangjiawan (TJW) in Zhuhai City and Yifengxi (YFX) in Shantou City, Guangdong Province; and Zhao' an Bay (ZA) in Zhangzhou City, Fujian Province. Detailed characteristics of the *H. beccarii* beds at each site are provided in Table 1. ZA, YFX, TJW, and SJ experience a subtropical maritime monsoon climate with annual rainfall of approximately 1,300–2,200 mm concentrated in June–August and mean annual temperatures of 18–23°C. HCW and YP have a tropical maritime monsoon climate with annual rainfall exceeding 1,600 mm and mean annual temperatures of 22–26°C (Geng et al., 2022).

Table 1 Basic information of each research site

Research Site	Latitude	Longitude	Seagrass Coverage (%)	Macroalgae Coverage (%)	Leaf Consumption Ratio (%)
HCW	19°43 09.68 N	109°12 34.13 E	30.45 ± 9.57a	24.60 ± 11.53a	15.46 ± 4.94a
YP	19°55 07.46 N	109°58 37.57 E	23.33 ± 3.66b	21.29 ± 4.56b	5.74 ± 1.77c
SJ	21°29 19.55 N	108°34 38.24 E	20.97 ± 4.56b	9.38 ± 3.92b	10.95 ± 5.46b
TJW	22°01 51.28 N	113°35 31.12 E	2.24 ± 0.24d	2.78 ± 2.11d	5.91 ± 2.11c
YFX	23°32 33.37 N	116°53 53.74 E	25.33 ± 10.23b	5.37 ± 3.88c	7.64 ± 5.69b
ZA	23°40 05.82 N	117°13 26.13 E	10.77 ± 2.11c	4.20 ± 3.56c	0.06 ± 0.24d

Note: Data are presented as mean ± SD. Different letters (a, b, c, d) indicate *significant differences among groups (P < 0.05).*

From May 2022 to November 2023, 3–4 transects perpendicular to the seawall or shoreline were established at each site based on bed area, distribution, hydrological conditions, and proximity to seawalls, with parallel transects spaced 50–100 m apart. During low tide, three cylindrical cores (7 cm diameter, 10 cm height) were randomly collected from uniformly distributed *H. beccarii* patches along each transect using a sampling corer. Samples were sealed in plastic bags, stored in a portable cooler, and transported to the laboratory. Sampling frequency was quarterly (spring 2022 sampling was conducted only at YP and SJ, while summer 2022 sampling excluded YP). Each sample was sieved through a 50-mesh screen, and *H. beccarii* material was sorted, washed, and separated into aboveground and belowground portions. These were placed in envelopes, oven-dried at 70°C to constant weight, and weighed using an electronic balance (precision 0.0001 g) to calculate aboveground biomass (AB), belowground biomass (BB), and total biomass (TB) per unit area.

1.3 Porewater Physicochemical Factor Sampling and Measurement

During low tide, porewater was collected in situ from water-free areas of seagrass bed sediments when the intertidal beds were fully exposed. The procedure was as follows: (1) At each site, sediment profiles approximately 30 cm deep were excavated and left to stand for 5–10 minutes; (2) Porewater was slowly extracted using a syringe to obtain ~500 mL, avoiding sediment particle intake; (3) Samples were immediately transferred to brown, light-proof sealed bottles, stored on ice (4°C) in the field, filtered within 24 hours through 0.45 m membranes, and frozen at -20°C for laboratory analysis of inorganic phosphate (IP), nitrite (NO_2^--N), nitrate (NO_3^--N), and ammonia nitrogen (NH_3-N) concentrations; (4) In situ parameters including salinity, temperature, pH, and total dissolved solids (TDS) were measured using a multi-parameter water quality meter (AZ86031), with three replicate measurements per transect.

1.4 Statistical Analysis

Prior to analysis, normality of all variables was assessed using the Shapiro–Wilk test. Non-normally distributed data were log-transformed to meet analytical requirements. One-way ANOVA was used to test for differences in *H. beccarii* biomass and environmental factors among sites, followed by Tukey–Kramer HSD tests when significant differences were detected ($P < 0.05$).

To explore potential linear relationships between seagrass biomass and porewater physicochemical factors, Pearson correlation coefficients were calculated and visualized as heatmaps using Origin 2024 ($P < 0.05$ and $P < 0.01$ indicating significant and highly significant levels, respectively). Principal component analysis (PCA) was performed using IBM SPSS Statistics 25.0 to identify major patterns of variation among physicochemical factors, with components having eigenvalues > 1 retained (Kaiser, 1960). Finally, linear regression models were constructed to examine the influence of porewater physicochemical factors on total biomass, with total biomass as the dependent variable and PCA-derived components (eigenvalue > 1) as independent variables. Standardized regression coefficients (Beta) and t-test-based P-values were used to assess variable contributions (significance level = 0.05). Data processing and visualization were conducted using Excel 2007, IBM SPSS Statistics 25.0, and Origin 2024.

2.1 Spatial and Seasonal Variation in *Halophila beccarii* Biomass

Mean aboveground, belowground, and total biomass of *H. beccarii* along the South China coast were (11.98 ± 13.06) $g \cdot m^{-2}$ DW, (12.06 ± 12.96) $g \cdot m^{-2}$ DW, and (24.05 ± 23.70) $g \cdot m^{-2}$ DW, respectively. All three biomass components were lowest at Tangjiawan: (2.29 ± 2.85) $g \cdot m^{-2}$ DW, (1.57 ± 2.23) $g \cdot m^{-2}$ DW, and (3.86 ± 4.70) $g \cdot m^{-2}$ DW [FIGURE:1: A, C, E; TABLE:2]. Overall variation among sites was moderate (CV = 58.29%-142.18%), with HCW and TJW showing the highest coefficients of variation (>110.01%), while YFX exhibited the lowest variation (<75.68%) .

Biomass at Tangjiawan was significantly lower than at all other sites ($P < 0.05$) [FIGURE:1: A, C, E]. Aboveground, belowground, and total biomass showed similar seasonal trends across sites (except for belowground biomass at HCW in winter 2023 and at SJ in summer 2023), with lower values in winter and spring and higher values in summer and autumn [FIGURE:1: B, D, F].

Figure 1 Aboveground, belowground, and total biomass of *Halophila beccarii* at each research site. Data are presented as mean ± SD. Panels A, C, and E show differences in aboveground, belowground, and total biomass among sites, respectively; dashed lines indicate mean biomass values. Panels B, D, and F show spatiotemporal variation trends. Different lowercase letters indicate significant differences among sites ($P < 0.05$).

Table 2 Statistical description of *Halophila beccarii* biomass at different research sites

Site	Biomass Component	Median	Skewness	Kurtosis	CV (%)
YP	Aboveground	–	–	–	–
	Belowground	–	–	–	–
	Total	–	–	–	–
SJ	Aboveground	–	–	–	–
	Belowground	–	–	–	–
	Total	–	–	–	–
ZA	Aboveground	–	–	–	–
	Belowground	–	–	–	–
	Total	–	–	–	–
TJW	Aboveground	–	–	–	–

Site	Biomass Component	Median	Skewness	Kurtosis	CV (%)
	Belowground	–	–	–	–
	Total	–	–	–	–
YFX	Aboveground	–	–	–	–
	Belowground	–	–	–	–
	Total	–	–	–	–
HCW	Aboveground	–	–	–	–
	Belowground	–	–	–	–
	Total	–	–	–	–

Note: Original table data were incomplete in the source material.

2.2 Spatial Variation in Porewater Physicochemical Factors

Except for pH and nitrite, which did not differ significantly among sites ($P > 0.05$) [FIGURE:2: C, F], all other porewater physicochemical factors showed significant spatial variation ($P < 0.05$) [Figure 2: see original paper]. Salinity was highest at HCW and lowest at YFX, following the pattern HCW > ZA > YP > TJW > SJ > YFX [FIGURE:2: A]. Water temperature was highest at YFX and lowest at SJ, following YFX > TJW > YP > HCW > ZA > SJ [FIGURE:2: B]. Total dissolved solids were highest at ZA and lowest at TJW, following ZA > HCW > SJ > YP > YFX > TJW [FIGURE:2: D]. Inorganic phosphorus was highest at ZA and lowest at TJW, following ZA > HCW > YP > YFX > SJ > TJW [FIGURE:2: E]. Nitrate was highest at TJW and lowest at HCW, following TJW > ZA > YP > YFX > SJ > HCW [FIGURE:2: G]. Ammonia nitrogen was highest at YP and lowest at TJW, following YP > HCW > ZA > SJ > YFX > TJW [FIGURE:2: H].

Figure 2 Comparison of environmental factors among different research sites. Data are presented as mean ± SD. Panels A-H represent differences in salinity, water temperature, pH, total dissolved solids, inorganic phosphorus, nitrate, nitrite, and ammonia nitrogen content in porewater among sites. Different lowercase letters indicate significant differences among sites ($P < 0.05$).

2.3 Multivariate Statistical Analysis of *Halophila beccarii* Biomass and Porewater Physicochemical Factors

Pearson correlation analysis [Figure 3: see original paper] showed that total biomass was highly positively correlated with both aboveground and belowground biomass ($r = 0.91$, $P < 0.01$), while aboveground and belowground biomass were significantly positively correlated ($r = 0.66$, $P < 0.01$). pH, salinity, total dissolved solids, and nitrite were not significantly correlated with biomass metrics ($P > 0.05$). Inorganic phosphorus was significantly positively correlated with all biomass metrics ($P < 0.01$). Nitrate was positively correlated with belowground biomass ($r = 0.10$) and total biomass ($r = 0.11$) ($P < 0.05$).

Ammonia nitrogen was highly significantly negatively correlated with aboveground biomass ($P < 0.01$) and significantly negatively correlated with total biomass ($P < 0.05$). Water temperature was significantly positively correlated with aboveground biomass ($r = 0.16$, $P < 0.01$).

Principal component analysis identified four components with eigenvalues > 1, cumulatively explaining 77.19% of variance. The eight variables were reduced to four integrated dimensions: PC1 primarily reflected water mineralization, closely associated with total dissolved solids, salinity, and pH; PC2 reflected nitrogen cycling microbial activity, associated with nitrite, nitrate, and ammonia nitrogen; PC3 represented temperature-driven nutrient release, associated with water temperature, inorganic phosphorus, and ammonia nitrogen; and PC4 indicated interactions between nitrogen forms and acidity/alkalinity, reflecting pollution input characteristics, associated with ammonia nitrogen, nitrate, and pH. Key porewater physicochemical factors influencing total biomass included total dissolved solids, salinity, nitrite, water temperature, and ammonia nitrogen. Linear regression analysis revealed that PC3 and PC2 were key promoting factors for total biomass, with PC3 contributing most . PC1 and PC4 had weak promoting and inhibiting effects on total biomass, respectively . The total biomass regression model explained 11.8% of variance with high statistical reliability ($F = 11.95$, $P < 0.001$) .

Figure 3 Correlation analysis heatmap.

Table 3 Eigenvalues and principal component matrix

Component	Initial Eigenvalues	Variance (%)	Cumulative (%)	Variables	Component Score Coefficient Matrix
—	Total	—	—	Salinity	—
—	—	—	—	Total dissolved solids	—
—	—	—	—	Water temperature	—
—	—	—	—	Inorganic phosphorus	—
—	—	—	—	Nitrite	—
—	—	—	—	Nitrate	—
—	—	—	—	Ammonia nitrogen	—

Table 4 Principal components regression results for total biomass (TB)

Regression Model	Independent Variable	–
–	–	–

3.1 Analysis of Biomass Variation in *Halophila beccarii*

Biomass directly reflects plant primary productivity and serves as a key indicator for assessing ecosystem health and energy flow (Tang, 2018). This study found that mean aboveground, belowground, and total biomass of *H. beccarii* along the South China coast were (11.98 ± 13.06) $g \cdot m^{-2}$ DW, (12.06 ± 12.96) $g \cdot m^{-2}$ DW, and (24.05 ± 23.70) $g \cdot m^{-2}$ DW, respectively, with significant variation among sites. Tangjiawan exhibited significantly lower biomass than other locations, reflecting growth and distribution differences under varying environmental conditions closely related to habitat characteristics, growth cycles, and water/nutrient availability—consistent with findings by Yang et al. (2024). Pan et al. (2025) reported that Tangjiawan experienced the highest human disturbance (>70%), while other sites had relatively lower disturbance (20%-39%), with human disturbance showing significant negative correlations with both aboveground and belowground biomass. Additionally, large latitudinal spans among sites and significant differences in porewater nutrients, temperature, and salinity contributed to biomass variation.

Biomass variation in *H. beccarii* is influenced by both environmental factors and population growth characteristics (Qin et al., 2020; Ankel et al., 2021). This study revealed consistent seasonal patterns of lower biomass in winter/spring and higher biomass in summer/autumn. Observations indicated substantial temporal variation in growth status (coverage and density) across sites, representing an important cause of spatiotemporal biomass variation. For example, during the survey period (November 2022-November 2023), Tangjiawan and Shajing showed low coverage and density, with vegetation degradation observed. Tangjiawan entered a decline phase after February 2023, while Shajing declined after August 2023; subsequent monitoring showed vegetation recovery only after March 2024. This demonstrates the critical influence of vegetation coverage and density on biomass dynamics.

3.2 Correlation Analysis Between *Halophila beccarii* Biomass and Porewater Physicochemical Factors

This study found that aboveground biomass was significantly positively correlated with water temperature and inorganic phosphorus but negatively correlated with ammonia nitrogen; belowground biomass was significantly positively correlated with inorganic phosphorus and nitrate; and total biomass was significantly positively correlated with inorganic phosphorus and nitrate but negatively correlated with ammonia nitrogen. These results indicate complex interactions between temperature and nutrients (nitrogen, phosphorus) during seagrass growth. Water temperature emerged as the strongest comprehensive promoting factor, directly influencing growth seasons and biomass accumulation by affecting cellular enzyme activity, photosynthetic efficiency, and photosynthate accumulation (Li et al., 2011; Li et al., 2014). Specifically, elevated porewater temperature accelerates microbial metabolism in sediments, promoting mineralization and nitrification of nitrogen and phosphorus, leading to ammonia nitrogen and inorganic phosphorus accumulation (Yu et al., 2012; Liu et al., 2016). High ammonia nitrogen concentrations are toxic to seagrasses, potentially inhibiting photosynthesis and damaging cell membranes, thereby affecting biomass accumulation (Yu et al., 2012). In contrast, increased inorganic phosphorus can alleviate ammonia toxicity and promote seagrass growth (Liu et al., 2016). Similarly, nitrate, as the end product of nitrification, effectively promotes biomass accumulation (Huang et al., 2017). Nitrite may act as an intermediate in nitrogen cycling or covary with other key factors (e.g., nitrate), associating with high-biomass regions in the multivariate PCA space despite lacking significant simple linear correlations.

Seagrasses growing in sandy or organic-rich sediments are typically nitrogen-limited, while those in carbonate sediments are generally phosphorus-limited; under certain conditions, dual nitrogen and phosphorus limitation may occur (Fourqurean & Zieman, 2002). Moderate nutrient concentrations promote seagrass growth, and nutrient-limited beds may show increased biomass with nutrient addition. Zhao et al. (2020) found that nitrogen and phosphorus were not limiting factors for *Thalassia hemprichii* around Sanya, as nutrients only increased shoot height without significantly improving biomass or productivity. However, Yu et al. (2012) and Liu et al. (2016) reported that excessive nitrogen input increased the N:P ratio in Hainan’ s Li’ an Port seagrass beds, exacerbating nutrient limitation effects. Our results suggest that low porewater inorganic phosphorus concentration may limit *H. beccarii* growth at Tangjiawan, Zhuhai; inorganic phosphorus and nitrate may be primary limiting factors at Shajing, Qinzhou; and nitrate may be the main limiting factor at Huachangwan, Chengmai. The significant influence of nitrogen and phosphorus on *H. beccarii* biomass along the South China coast aligns with conclusions by Orth et al. (2006).

Although salinity, total dissolved solids, and pH were not significantly correlated with biomass, salinity and total dissolved solids were highly positively correlated, while pH was significantly negatively correlated with both. Water temperature was significantly positively correlated with pH but negatively correlated with salinity and total dissolved solids. This occurs because increased temperature reduces CO_2 solubility, raising pH and inhibiting ion dissolution (Peng and Xu, 2019). High salinity and total dissolved solids indicate evaporative concentration, while heavy rainfall during hot seasons introduces freshwater inputs that dilute porewater, causing synchronous decreases in salinity and total dissolved solids. *H. beccarii* distribution areas are typically estuarine regions under monsoon climate influence, where rainfall events and riverine freshwater input reduce nearshore salinity (Sánchez-Lizaso et al., 2008). Reduced salinity decreases osmotic regulation energy costs, allowing more energy allocation to growth. *H. beccarii* is considered euryhaline, with a salinity tolerance range of 0–30 and optimal growth at 10–20 (Yang et al., 2024; Pan et al., 2025). The studied porewater salinity (mean = 17.54) fell within this optimal range, and the non-significant correlation suggests salinity was not a primary limiting factor within the species' tolerance range. Overall, salinity and total dissolved solids exert weak positive effects on biomass by influencing ion balance, osmotic regulation, or indirectly affecting other key factors.

Although the linear influence of porewater physicochemical factors on total biomass was significant ($P < 0.001$), confirming detectable effects of the included factors (total dissolved solids, salinity, nitrite, temperature, ammonia nitrogen), the explanatory power was modest ($R^2 = 0.118$), suggesting non-linear relationships or complex interactions. Zhang et al. (2018) found that eutrophication and salinity reduction synergistically decreased *Zostera japonica* biomass, with combined effects exceeding individual factor impacts. Additionally, light limitation, sediment characteristics, biological interactions, hydrodynamics, genetic variation, and other limiting nutrients also influence seagrass biomass, partially reducing the model' s explanatory power. Nevertheless, while porewater physicochemical factors may not be the primary drivers, they participate in seagrass growth regulation through indirect pathways such as modulating nutrient availability or stress intensity. Future studies should integrate non-linear modeling approaches and strengthen multi-dimensional monitoring of sediments, water, and organisms to better resolve sources of variation in seagrass growth.

This study revealed spatiotemporal distribution patterns and key drivers of *H. beccarii* biomass along the South China coast. The species exhibited spatial heterogeneity and seasonal adaptability. Except for pH and nitrite, other porewater physicochemical factors differed significantly among sites. Water temperature, inorganic phosphorus, ammonia nitrogen, nitrite, and nitrate were closely associated with biomass variation, playing important roles in growth and accumulation. PCA identified water temperature and nitrite as key promoting factors for total biomass accumulation, while ammonia nitrogen significantly inhibited biomass growth. These findings provide new insights into growth patterns and adaptive mechanisms under specific environmental conditions, offering novel perspectives for seagrass bed conservation and restoration: (1) establishing nitrogen load monitoring systems and implementing nitrogen reduction measures to mitigate ammonia nitrogen threats; and (2) prioritizing restoration sites with suitable temperatures and moderate nutrient concentrations. Our results can directly inform conservation planning, transplantation restoration, and ecological management of *H. beccarii.*

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