

Post-Typhoon Reorganization of Estuarine Plankton Communities in Matsu Archipelago

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Research Article

Keywords: terrestrial runoff, diatom, dinoflagellate, Noctiluca scintillans, copepod, plankton community

Posted Date: March 9th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9002362/v1>

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Additional Declarations: No competing interests reported.

Abstract

The Matsu Archipelago is a coastal marine system affected by freshwater discharge from the Minjiang River. Enhanced freshwater input from typhoons and high-intensity rainfall events can further alter local plankton communities. In this study, we divided the sampling period into (1) a freshwater-disturbed period characterized by reduced salinity and (2) a subsequent stable period, when the system began to recover. During the “Disturbed period”, we observed a brief occurrence of *Noctiluca scintillans*, although its abundance remained well below bloom levels (peaked only in 4.69 cells L⁻¹). After rainfall ceased, diatom abundance increased exponentially, driven primarily by *Chaetoceros*, which peaked at 3.7×10^7 cells L⁻¹ and was followed by a rapid rise in copepod abundance (5.3 ind L⁻¹). In contrast, dinoflagellate abundance did not differ significantly between the two periods; instead, dinoflagellate bloom (3.97×10^4 cells L⁻¹) occurred during the short transitional phase between them. Overall, this study suggests that event-scale freshwater inputs structure plankton dynamics in this coastal system, triggering a succession from the initial appearance of *Noctiluca scintillans* coincident with rainfall, through a brief dinoflagellate bloom during the transitional phase, to rapid exponential increases in diatom abundance during the subsequent “Stable period”, followed by a marked rise in copepods in the final day of the survey.

1. Introduction

Phytoplankton form the biogeochemical foundation of marine ecosystems by fixing inorganic carbon and sustaining energy flow across the global ocean (Basu and Mackey, 2018; Giraldo et al., 2024). This primary production is subsequently transferred to higher trophic levels through grazing by planktonic consumers spanning a wide range of body sizes, linking phytoplankton biomass to pelagic food webs and facilitating the transfer of energy and organic matter through marine ecosystems (Calbet, 2001; Steinberg and Landry, 2017). Therefore, microbial and planktonic processes play a central role in shaping ecosystem-level responses to environmental change.

In contrast to the open ocean, estuarine and coastal systems are characterized by intense terrestrial inputs that facilitate elevated primary productivity (Bauer et al., 2013; Cloern et al., 2014). Because these nutrient and organic matter deliveries are highly sensitive to weather, they also drive strong environmental variability within these systems (Dail et al., 2007; Cai et al., 2013; Su et al., 2018; Liu et al., 2019). Moreover, extreme weather events, such as typhoons and heavy rainfall, can abruptly alter hydrographic conditions by increasing freshwater input, enhancing vertical mixing, and elevating suspended particulate matter, which collectively increase turbidity and attenuating light penetration (Sin and Yu, 2018). Recent high-frequency observations demonstrate that, despite substantial nutrient inputs following typhoon events, sediment resuspension–driven turbidity can strongly suppress phytoplankton photosynthesis, with chlorophyll *a* concentration increasing only after several days of recovery as light conditions improve (Shi et al., 2025). Under such post-disturbance conditions, phytoplankton growth responses may be delayed or decoupled from nutrient enrichment, with cascading effects extending beyond primary producers to influence planktonic grazers and broader food-web structure (Thompson et

al., 2015; Wang et al., 2024; Baek et al., 2025; Hammond et al., 2025). For example, studies from coastal Taiwan and Japan observed a transition from dinoflagellate-dominated toward diatom-dominated assemblage within approximately one week after typhoon's passage (Chen et al., 2009; Tsuchiya et al., 2013). Complementary studies have also recorded a successional emergence of planktonic grazers, spanning diverse taxonomic groups such as heterotrophic dinoflagellate *Noctiluca scintillans* or copepods, as diatom continue to proliferates (Hoover et al., 2006; Chung et al., 2012; Li et al., 2024). Together, these evidences indicate that typhoon can rapidly reset coastal environments and drive short-term reorganization across multiple plankton groups.

Located in the northern Taiwan Strait near the mouth of the Minjiang River, the Matsu Archipelago represents a typical river-influenced coastal system that is highly sensitive to episodic meteorological forcing. Freshwater discharge from the Minjiang River, together with frequent typhoon-associated rainfall during the warm season, exerts strong control over hydrographic conditions and plankton dynamics in the surrounding waters. Previous studies in the Matsu region have documented pronounced phytoplankton responses to riverine inputs, including diatom-dominated blooms during the flood season and recurrent occurrences of bloom-forming taxa, indicating a strong coupling between hydrological variability and plankton community structure (Tsai et al., 2018; Liu et al., 2021; Lin et al., 2024). These characteristics make the Matsu Archipelago an ideal natural setting to examine how typhoon-driven disturbances rapidly reorganize plankton communities in coastal environments.

Despite growing evidence that extreme weather events can induce rapid plankton community changes in coastal systems, most previous studies have relied on before–after comparisons or temporally sparse sampling designs (Chen et al., 2009; Tsuchiya et al., 2013; Li et al., 2024). Such approaches often capture changes in one or a few dominant taxa but provide limited insight into how multiple plankton groups respond sequentially through time following disturbance. Therefore, high-frequency, continuous observations are required to resolve short-term trajectories of plankton community reorganization under extreme weather forcing.

To address this gap, we conducted intensive, high-frequency sampling in the coastal waters of the Matsu Archipelago following a typhoon-associated heavy rainfall event. By resolving phytoplankton and zooplankton communities at short time intervals, this study aims to capture the continuous reorganization of multiple plankton groups under post-disturbance conditions. We hypothesize that continuous observations will reveal coordinated and time-lagged changes across different plankton groups that cannot be resolved using temporally sparse sampling. This time-resolved perspective provides new insight into how typhoon-driven disturbances restructure coastal plankton communities in a river-influenced ecosystem.

2. Methodology

2.1 Sampling Time and Location

Zooplankton and water samples were collected from surface waters at Jieshou Harbor, Nangan, Matsu Islands (Fig. 1). In situ temperature and salinity were using Multiparameter Waterproof Meter (HI-98194). Sampling was conducted twice daily (day: ~08:30; night: ~20:00) from 10 to 18 July 2025. Before the sampling period, from 7 to 9 July 2025, Matsu Islands were affected by Typhoon Danas. On 9 July, the day before sampling began, the Matsu meteorological station recorded torrential rainfall with a daily total of up to 97 mm, and post-typhoon rainbands continued to bring elevated rainfall to the region over the following days (see Results, Fig. 2).

2.2 Sample Collection and Laboratory Analyses

Zooplankton were collected by horizontal tows using a 20 cm-diameter plankton net (mesh size: 150 μm) equipped with a flowmeter. Simultaneously, 2 L of unfiltered seawater were collected for phytoplankton identification and chlorophyll *a* analysis. All samples were transported to the laboratory (~ 15 minutes from the sampling site). Zooplankton and phytoplankton samples were preserved with formalin to a final concentration of 5% and 2%, respectively.

Chlorophyll *a* was determined fluorometrically (Turner Designs 10-AU-005) after filtration onto 25 mm GF/F filters (in duplicate) and pigment extraction following (Parsons et al., 1984). Daily precipitation data were obtained from the Taiwan Central Weather Administration rain gauge near the sampling site and cross-checked against local meteorological station records.

Phytoplankton (diatoms and dinoflagellates) were analyzed using the Utermöhl method (Utermöhl, 1958). Depending on sample turbidity, either 50 mL or 10 mL subsamples were settled in chambers for at least 16 hours before enumeration under an inverted microscope. Damaged or unclear cells were excluded.

Zooplankton samples were analyzed using a ZooScan digital imaging system (Gorsky et al., 2010). Samples were fractionated by one to four binary splitting steps depending on sample concentration. For most of the samples, each subsample was rinsed with freshwater and scanned. For samples that were highly concentrated, only the final two split fractions were scanned. Image processing included background removal and automatic object detection, with a practical lower size limit of ~ 0.3 mm. Objects that were physically close together were occasionally detected as a single object. These cases were reprocessed using the “separation with mask” tool in ZooProcess, although overlapping organisms could not be separated without loss of morphological detail. Zooplankton classification was performed with PlanktonIdentifier, using a reference library previously trained on samples from a different region. Incorrect classifications were corrected manually. Overlapping individuals were categorized as “Multiple,” and noted manually for abundance data. Unclear, overly small, or non-biological particles (e.g., fecal pellets, detritus, fibers) were categorized as “Reject.” Mixed calanoid and cyclopoid copepods smaller than 0.5 mm were frequently observed but could not be reliably identified, and were therefore grouped as “Small Copepods.”

The bioluminescence of *Noctiluca scintillans* has been a tourist attraction in Matsu Islands, and has been called as “Blue Tears” (Tsai et al., 2018). Due to its socio-economic importance, we treated *N. scintillans* as a separate group rather than including it within the general dinoflagellate assemblage. Methodologically, its relatively large size (~ 0.5 mm) allows it to be efficiently retained by the 150 µm plankton net and reliably detected by the ZooScan system, so *N. scintillans* was enumerated from zooplankton net-tow samples using ZooScan, whereas the smaller dinoflagellate species, although taxonomically related, were counted by inverted microscopy from unfiltered seawater samples.

Zooplankton abundance was calculated by dividing the sum of individuals (ind) to the fraction of the sample (F), then divide it again by the volume of water passes through the plankton net (Vw):

$$\text{Abundance (ind/m}^3\text{)} = \frac{\frac{\sum \text{ind}}{F}}{V_w(\text{m}^3)}$$

Volume of water passes through the plankton net (Vw) was calculated by:

$$V_w(\text{m}^3) = \text{Net opening area (m}^2\text{)} \times \text{number of revolutions of flowmeter} \times \text{filtration efficiency}$$

2.3 Data Analysis

During the study period, organism abundances exhibited near-exponential increases, particularly in the later phase, resulting in highly heterogeneous variances that violated the assumptions of parametric tests and obscured treatment effects. Although nonparametric statistics are less sensitive to differences in variance, their rank-based nature reduces the emphasis on absolute differences and does not adequately reflect the magnitude of the exponential increase in abundance. We therefore applied a logarithmic transformation, $\ln(x + 1)$, to all abundance variables prior to statistical analyses, with the addition of 1 used to accommodate zero values.

Based on the log-transformed abundance data, we conducted a series of statistical analyses, including paired and unpaired Student’s t-tests, Pearson correlation analysis. All statistical procedures were implemented in Python using custom scripts.

3. Result

3.1 Hydrographic Condition

Sampling was conducted from 10 to 18 July 2025, immediately following the passage of Typhoon Danas, which brought heavy rainfall to the Matsu Islands on 9 July. Precipitation reached 97 mm on 9 July (data not shown) and remained high during the following days, ranging from 9.5 to 29.5 mm between 10 and 13 July (Fig. 2). This rainfall event strongly influenced the hydrographic structure of the study area.

Sea surface temperature remained within a narrow range (27.6–28.7°C) throughout the sampling period. However, during 10–13 July, persistent cloudy and rainy weather suppressed the diurnal thermal amplitude, and on some days nighttime temperatures exceeded daytime values (e.g., 27.8°C during the day vs. 28.3°C at night on 10 July). After 15 July, as clear weather returned, a more distinct diel temperature contrast emerged.

Freshwater influence was even more evident in salinity patterns. Salinity decreased markedly after consecutive rainfall and reached a minimum of 25.1 PSU. Between the morning of 14 July and the evening of 14 July, salinity rebounded sharply to 32.4 PSU and subsequently stabilized around 31.5 PSU for the remainder of the survey. Daily rainfall and salinity were significantly negatively correlated ($p < 0.01$; Fig. 3), indicating rapid hydrographic responses to rainfall-driven freshwater intrusion. Based on the pronounced early salinity fluctuation and the clear stabilization after 15 July, we defined 10–14 July as the rain-affected “Disturbed period” and 15–18 July as the post-rain “Stable period” for subsequent analyses.

3.2 Chlorophyll *a*

Chlorophyll *a* concentration ranged from 1.1 to 7.0 mg m⁻³ throughout the survey and differed significantly between the two hydrographic phases. Mean chlorophyll *a* was significantly higher during the “Stable period” than during the “Disturbed period” (t-test, $p < 0.05$). While no significant diel difference occurred during the “Disturbed period” ($p > 0.05$), a clear and significant diel change was detected during the “Stable period” ($p < 0.05$).

Chlorophyll *a* also showed significant correlations with key environmental drivers, being positively correlated with salinity ($r = 0.48$, $p < 0.05$; Fig. 3) and negatively correlated with rainfall ($r = -0.66$, $p < 0.01$; Fig. 3). These results indicate that increased chlorophyll *a* during the “Stable period” reflected recovery from rainfall disturbance and the establishment of more stable hydrographic conditions.

3.3 Biological Parameters

Diatoms ranged from 2.8×10^3 to 3.7×10^7 cells L⁻¹ throughout the study period, the increase by nearly three orders of magnitude occur toward the end of the survey. Abundance remained nearly constant during the “Disturbed period” but increased markedly during the “Stable period.” This surge was primarily driven by an exponential bloom of *Chaetoceros*, followed by *Pseudo-nitzschia*, *Thalassiosira*, *Skeletonema*, and *Leptocylindrus*. These large, chain-forming taxa far outnumbered other diatoms such as *Navicula*, *Thalassionema*, *Cylindrotheca*, and *Pleurosigma* that also constantly occur in the study area. Accordingly, diatom abundance during the “Stable period” was significantly higher than during the “Disturbed period” (t-test, $p < 0.05$). Despite this pronounced increase, no significant diel differences in diatom abundance were detected during either the “Disturbed period” or the “Stable period” ($p > 0.05$), even though nighttime abundance is higher than daytime abundance in the last two days.

Zooplankton classification using ZooScan revealed that copepod abundance was the most dominant (80.3%) among total zooplankton. Decapods (9.9%), amphipods (0.2%), and other zooplankton (9.6%) were contributed minimally to overall abundance, thus analyses focused on copepods. Total copepod abundance remained low ($0.01\text{--}0.9\text{ ind L}^{-1}$) during most of the survey with Harpacticoida as the most dominant taxa. However, total copepod increased explosively on 18 July, reaching 5.3 ind L^{-1} , with Harpacticoida and small copepods ($< 0.5\text{ mm}$ calanoid and cyclopoid copepods) cooccur as dominant taxa. Statistical analyses detected no significant diel difference, no “Disturbed period” vs. “Stable period” difference, and no significant correlations with environmental variables (all $p > 0.05$). The lack of statistical significance likely reflects the fact that the copepod bloom occurred only on the final night. Nonetheless, the bloom timing coincided with the late “Stable period” diatom bloom, suggesting that accumulated diatom biomass and increased food availability may have facilitated the copepod increase.

Dinoflagellate dynamics contrasted sharply with those of diatoms and copepods. Their bloom occurred not within either hydrographic phase but precisely at the transition, peaking on 14 July. Abundance fluctuated widely (1×10^2 to $2.13 \times 10^4\text{ cells L}^{-1}$) but rose sharply to $3.97 \times 10^4\text{ cells L}^{-1}$ on 14 July. This brief but intense peak and the subsequent rapid decline were driven mainly by the dynamics of *Alexandrium*. Dinoflagellates also exhibited a significant diel difference, although the 14 July bloom showed higher daytime abundance than nighttime, the overall pattern across the full survey revealed significantly higher nighttime abundance (paired t-test, $p < 0.05$).

Noctiluca scintillans showed yet another distinct pattern compared to other dinoflagellates. *N. scintillans* appeared mainly during the early “Disturbed period” (2.41×10^{-3} to 4.69 cells L^{-1}), declined rapidly afterward, and was nearly absent during the “Stable period” (0 to $8.35 \times 10^{-4}\text{ cells L}^{-1}$). Its abundance was strongly correlated with rainfall ($r = 0.62$, $p < 0.01$), but did not differ significantly between the “Disturbed period” and “Stable period” ($p > 0.05$), likely due to the rapid decline even during the “Disturbed period”. Additionally, no significant diel variation was observed ($p > 0.05$). These results suggest that *N. scintillans* may favor conditions resulting from freshwater input.

4. Discussion

4.1 Diatoms

The Minjiang River is a major source of terrestrial material to the Taiwan Strait (Liu et al., 2019). Although the typical flood season spans April to June, our study period experienced an additional freshwater pulse in July due to a typhoon and heavy rainfall. Such events enhance river discharge and are expected to introduce substantial nutrient loads, including silicate (SiO_4^{4-}), into the coastal waters around the Matsu Islands (Lin et al., 2024). This condition favors a marked increase in diatom abundance. Consistent with observations from the regular flood season, our samples were dominated by *Chaetoceros*, *Pseudo-nitzschia*, *Thalassiosira*, *Skeletonema*, and *Leptocylindrus* (in decreasing order). Moreover, the progression of the bloom in our study mirrored these earlier findings: *Pseudo-nitzschia* dominated

initially and later co-occurred with *Chaetoceros*, after which *Chaetoceros* became the primary dominant genus.

In many coastal and shelf systems, *Chaetoceros* spp. have been reported as prominent bloom-forming diatoms under high-nutrient, mixed conditions, particularly in upwelling and river-influenced environments (Loureiro et al., 2005; Montero et al., 2017; Jacob et al., 2024). In the Chuckchi Sea after strong wind events, Fukai et al. (2024) found that *Chaetoceros* spp. and their resting spores as characteristic components of the initial diatom succession stage that develops immediately after the onset of strong wind events. This propensity to dominate under nutrient-replete, turbulent conditions has been linked to several life-history traits. First, many *Chaetoceros* species produce heavily silicified resting spores that sink rapidly and accumulate in surface sediments, forming a benthic “seed bank” capable of reseeding blooms when light and nutrient conditions become favorable again (Asami and Ban, 2000; Ishii et al., 2011; Zúñiga et al., 2017). Second, the chain-forming, spiny morphologies of many *Chaetoceros* taxa increase drag, reduce sinking rates and enhance retention in the turbulent surface layer (Ishii et al., 2011; Bosak and Sarno, 2017). Together, these traits provide *Chaetoceros* with a marked competitive advantage in disturbed, nutrient-rich coastal waters and likely contributed to its rapid increase and eventual dominance in our study area following the rainfall-driven disturbance.

4.2 Copepods

Following the diatom bloom, copepod abundance exhibited a sharp spike during the night of 18 July. Such rapid increases in copepod abundance during diatom blooms have been documented elsewhere, particularly during *Chaetoceros* blooms, where grazing can quickly suppress diatom biomass (Chung et al., 2012).

Although our software only identified copepods to the order level in this study, our manual observations shows that most of the harpacticoids in this study are *Microsetella* spp., with *Euterpina acutifrons* also contributing to the community but at much lower abundance, which is numerically important components of the copepod assemblage in surface and near-surface waters (de Melo Júnior et al., 2013; Svensen et al., 2018). Both *Microsetella* spp. and *Euterpina acutifrons* are known to be important grazer for diatoms in surface water (Toullec et al., 2019; Mooney et al., 2023). Harpacticoid copepods in general are characterized by small body size, short generation times, high reproductive potential and high tolerance on wide range of salinity (de Melo Júnior et al., 2013; Punnararak et al., 2017). These traits provide a mechanistic explanation for how harpacticoid populations dominate river-influenced marine system and likely contributed to the sharp rise in copepod abundance we observed on the last night during the latter phase of the post-rainfall diatom bloom.

Although we lacked post-bloom samples to assess the immediate grazing impact on diatoms, all three major copepod orders in our samples (Calanoida, Cyclopoida and Harpacticoida) are taxa that are known to ingest diatoms, with feeding rates and preferences varying by species and environmental context (De Troch et al., 2005; Bouley and Kimmerer, 2006; Jansen and Bathmann, 2007). Their selective grazing, especially against diatoms lacking defensive traits, may explain why the abundances of

dominant diatom taxa declined on 18 July, except for *Pseudo-nitzschia*, which produces toxins that can deter grazers (Tammilehto et al., 2015).

4.3 Dinoflagellates

Dinoflagellate increase was rapid but short-lived, in contrast to the more gradual and sustained rise of diatoms. Numerous studies have shown that dinoflagellates typically perform diel vertical migration, taking advantage of their motility to ascend toward the surface during the day for photosynthesis and descend into deeper, nutrient-rich waters at night (Bollens et al., 2012; Zheng et al., 2023; Clayton et al., 2024). However, the diel pattern of dinoflagellate in our study differed from typical dynamics, with significantly higher abundance at night, except in the transitional phase between the rainfall-driven disturbance and the subsequent large-diatom bloom, where a sudden daytime increase occurred (Fig. 4B). This transient dominance is consistent with the known ecological strategy of many bloom-forming dinoflagellates, including *Alexandrium* and *Prorocentrum*, which are now recognized as mixotrophic rather than purely phototrophic. Laboratory and field studies have shown that these taxa can supplement photosynthesis by grazing on small photosynthetic prey such as nanoflagellates, picoeukaryotes and cyanobacteria, including *Synechococcus* (Jeong et al., 2005; Jeong et al., 2010; Johnson et al., 2018). Under post-disturbance conditions in which pico- and nanophytoplankton are abundant, such mixotrophic feeding may allow *Alexandrium* to exploit a temporary niche in which access to both light and prey provides a short-term growth advantage over strictly autotrophic competitors.

In addition to mixotrophy, the life cycle of *Alexandrium* includes the production of benthic resting cysts that form a sedimentary “seed bank” capable of initiating and sustaining recurrent blooms. Resting cysts of *Alexandrium catenella*, *Alexandrium tamarense*, and *Alexandrium pacificum* have been shown to germinate rapidly once dormancy is broken and hydrographic and light conditions become favorable, while at the same time sexual encystment during blooms can efficiently remove vegetative cells from the water column (Genovesi et al., 2009; Miyazono et al., 2012; Brosnahan et al., 2020; Dai et al., 2020). Field observations from various temperate and subtropical coastal systems likewise report *Alexandrium* blooms that develop quickly and persist only for days to a few weeks before collapsing (Genovesi et al., 2009; Brosnahan et al., 2020), suggesting that rapid growth, followed by encystment and biological losses, is a common pattern for this genus. Although we did not quantify cysts or identify dinoflagellates to species level, the short-lived *Alexandrium*-dominated peak observed in our study is consistent with this life-history framework. Mixotrophic exploitation of small prey and the capacity for rapid encystment together favor brief dominance during transitional conditions rather than sustained persistence through the entire post-rainfall succession.

4.4 Noctiluca scintillans

During April–June, high densities of *Noctiluca scintillans* (> 1000 cells L^{-1}) commonly occur in the Matsu Archipelago, where they play an important role as grazers of diatoms (Tsai et al., 2018). However, *N. scintillans* declines rapidly when temperatures exceed $27^{\circ}C$, leading to their disappearance in early July. In our study, the highest density of *N. scintillans* observed was only 4.69 cells L^{-1} (on 10 July), and the

population collapsed shortly thereafter. Throughout our sampling period, surface temperatures remained above 27°C, but a relative temperature minimum associated with the rainfall event occurred at the beginning of the survey. We therefore infer that the brief occurrence of *N. scintillans* likely reflects a remnant population transported into the area by the Minjiang River plume that could persist only during this short, slightly cooler phase; once temperatures increased again, local survival and reproduction became unfavorable and the population declined to undetectable levels. These temperature constraints may also explain why, unlike the April–June conditions described by (Tsai et al., 2018), we did not observe strong top-down control of diatoms by *N. scintillans* in this study. During the later phase of our survey, when large diatoms and copepods both increased markedly, *N. scintillans* remained rare or absent, suggesting that the diatom bloom was grazed primarily by copepods rather than being co-amplified with heterotrophic dinoflagellates.

4.5 Sucession

In our short-term survey, the rainfall-driven transition between the “Disturbed period” and the “Stable period” influenced not only hydrographic conditions but also the responses of multiple plankton groups. Although chlorophyll *a* was significantly correlated with the ln-transformed abundances of diatoms ($r = 0.56$, $p < 0.05$) and dinoflagellates ($r = 0.71$, $p < 0.01$), its temporal pattern did not mirror the exponential increase of diatoms during the final few days or the dinoflagellate bloom on 14 July. These results indicate that, in this coastal system, bulk chlorophyll *a* was not controlled primarily by the biomass of large diatoms and dinoflagellates. Instead, the weak response of chlorophyll *a* to the rapid build-up of these microplankton points to a stronger contribution from small photosynthetic plankton to the pigment pool during most of our survey. Previous work in Taiwanese coastal waters has shown that pico-sized cyanobacteria such as *Synechococcus* exhibit pronounced diel variability and play an important role in coastal primary production (Tsai et al., 2005). In the same Matsu coastal ecosystem, Tsai et al. (2021) further reported that during the warm season ($\sim 27.5^\circ\text{C}$) the $> 20\ \mu\text{m}$ phytoplankton fraction typically accounts for more than 70% of total chlorophyll *a*, whereas the $< 20\ \mu\text{m}$ fraction dominates primary production during the cold season. Taken together with our observation that bulk chlorophyll *a* remained relatively stable while large diatoms increased exponentially only near the end of the survey, these findings suggest that unmeasured small phytoplankton ($< 20\ \mu\text{m}$) likely made a major contribution to the chlorophyll *a* pool during the immediate post-rainfall period, and that the rapid build-up of large diatoms in the final days of sampling marked the onset of a more typical warm-season state in which the $> 20\ \mu\text{m}$ size fraction becomes dominant.

Considering previous studies from this coastal region that have documented a strong seasonal dominance of diatoms under the influence of Minjiang River flooding (Lin et al., 2024), it is likely that our observations captured only the initial stage of a diatom-dominated successional sequence following the rainfall event. Event-scale studies from other estuarine and coastal systems have likewise shown that freshwater inputs and associated changes in stratification and nutrient supply can drive lagged phytoplankton responses and shifts in community dominance, with small, fast-growing cells often responding first and larger diatoms increasing later as conditions stabilize (Thompson et al., 2015; Wang

et al., 2024; Baek et al., 2025; Hammond et al., 2025). This delay is likely occurred because freshwater inflow lowered salinity and delivered high loads of suspended sediments that initially reduced light availability, suppressing the growth of large-celled diatoms despite elevated nutrient concentrations (Sin and Yu, 2018). Although we lacked direct measurements of size-fractionated chlorophyll *a*, light and turbidity, we infer that disturbed, rain-affected conditions at the beginning of our sampling favored small, disturbance-tolerant phytoplankton that dominated the bulk chlorophyll *a* signal. As post-rainfall conditions evolved and the water column partially stabilized, large diatoms then increased rapidly in abundance, consistent with the diatom-dominated warm-season state described for the Matsu region (Tsai et al., 2021; Lin et al., 2024). Within this broader framework, the short-lived dominance of dinoflagellates and the subsequent sharp rise in copepod abundance can be viewed as transient stages embedded in a rainfall-triggered, multi-trophic successional sequence from small phytoplankton to large diatoms and their grazers in the Matsu coastal waters.

In contrast to previous studies that have reported pronounced diel differences in plankton communities, we did not detect significant day–night differences for most groups except dinoflagellates (Garcia-Herrera et al., 2022; Jia et al., 2023). However, we observed that abundances were higher at night during the final two days of exponential diatom growth and on the final night of rapid zooplankton increase. The appearance of clearer nocturnal dominance during the high-biomass phase may indicate that diel differences become more detectable at higher abundances, or that trophic interactions and behavioral responses become more evident in stable condition.

Overall, our results are consistent with a rainfall-triggered, multi-stage successional sequence in the Matsu coastal waters. We hypothesize that immediately after disturbance, the phytoplankton community is likely dominated by small pico- and nanophytoplankton that contribute most of the chlorophyll *a* signal. These small cells, including cyanobacteria such as *Synechococcus* (although we did not quantify them directly), may provide a rich prey field that supports a short-lived increase in mixotrophic dinoflagellates dominated by *Alexandrium*. As post-rainfall conditions continue to stabilize and sufficient silicate is supplied large diatoms then become dominant, and their biomass in turn fuels the sharp increase in copepod abundance observed during the “Stable period”. To our knowledge, this high-frequency, event-scale survey is the first to resolve such a rapid, rainfall-driven sequence from pico-sized phytoplankton through a dinoflagellate-rich transitional assemblage to a large-diatom-dominated community in the Matsu region, highlighting the value of short-term intensive observations for understanding ecosystem responses in this river-influenced coastal system.

Declarations

Funding

This research was supported by the Ministry of Science and Technology, ROC (Taiwan), grant number : MOST 114-2611-M-002-006.

Author Contribution

RFP: Methodology, Investigation, Data curation, Writing – original draft, Writing – review & editing
CFC: Visualization, Writing – original draft, Writing – review & editing
MO: Methodology, Writing – review & editing
CNA: Methodology, Investigation
PWC: Formal analysis, Writing – review & editing
ANT: Conceptualization, Investigation, Resources, Data curation, Formal analysis, Project administration, Funding acquisition, Writing – review & editing.

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Figures

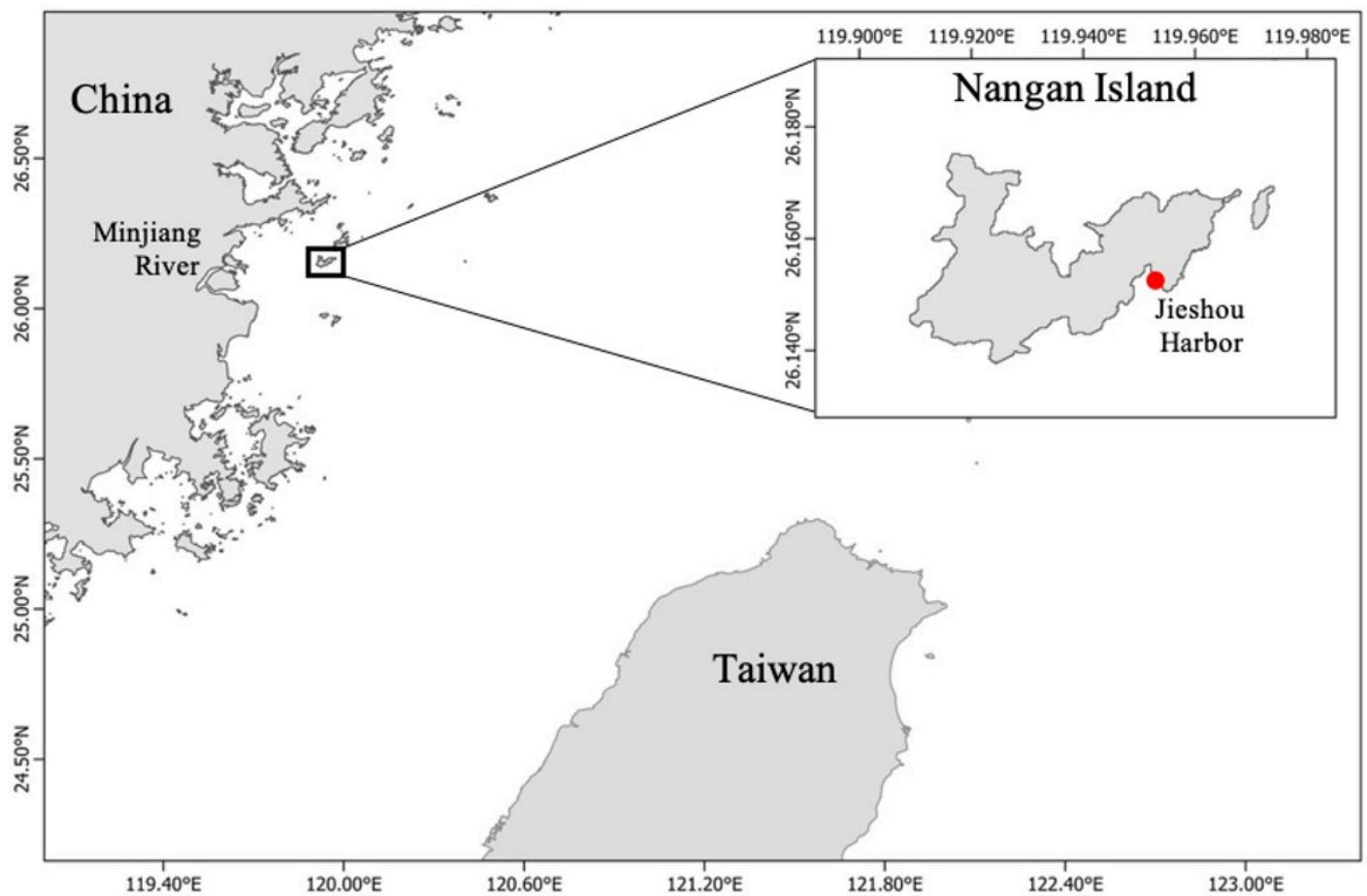


Figure 1

Study site during 10 July 2025 to 18 July 2025, Jieshou Harbor (red dot) located in Nangan Island of Matsu Archipelago.

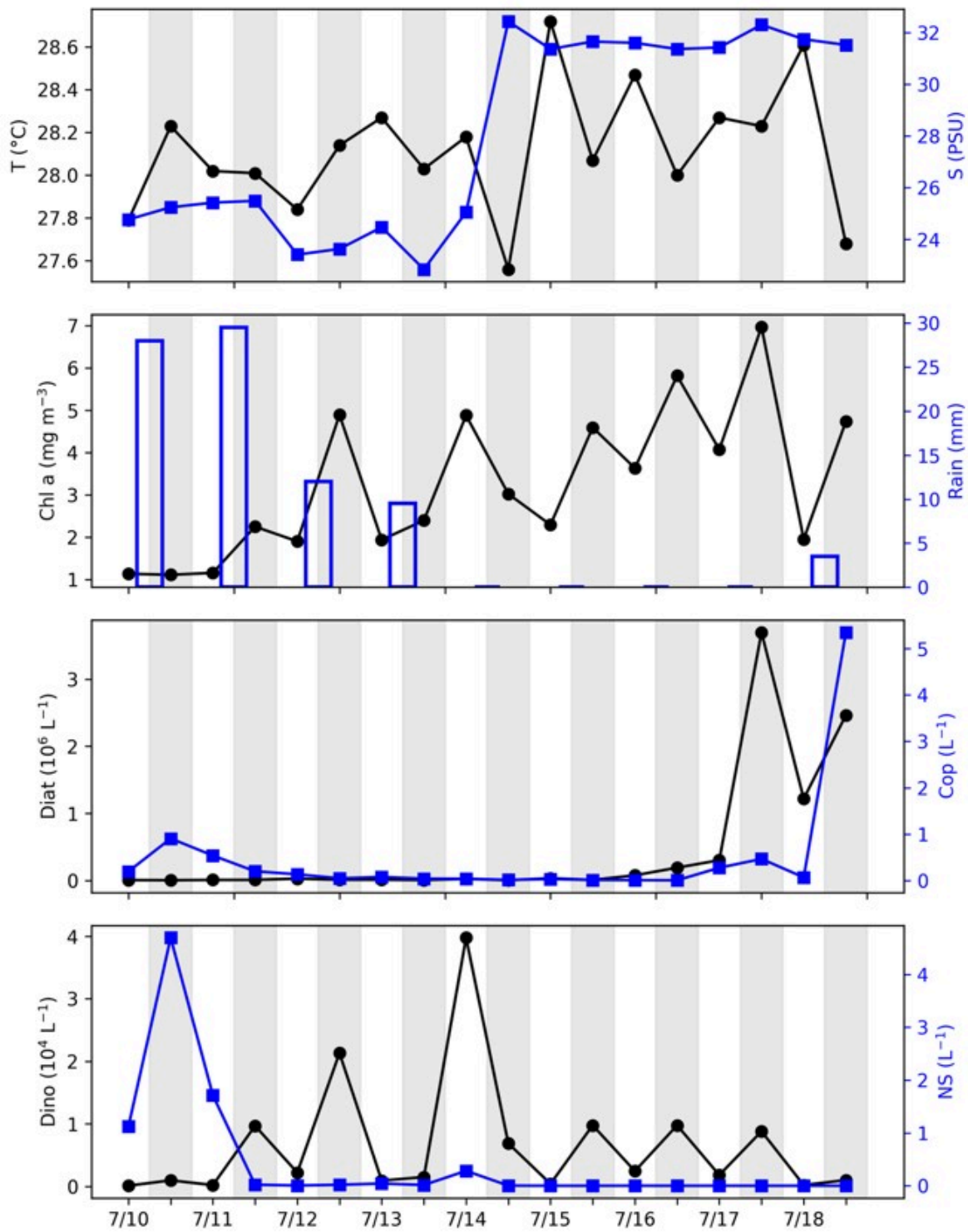


Figure 2

The dynamics of environmental parameters and plankton groups from 10 July 2025 to 18 July 2025 at Jieshou Harbor. (A) Temperature (black) and Salinity (blue), (B) Chlorophyll *a* concentration (black) and Rainfall (blue bar), (C) Diatom abundance (black) and Copepod abundance (blue), (D) Dinoflagellate abundance (black) and *Noctiluca scintillans* abundance (blue). Grey bars represent nighttime sampling.

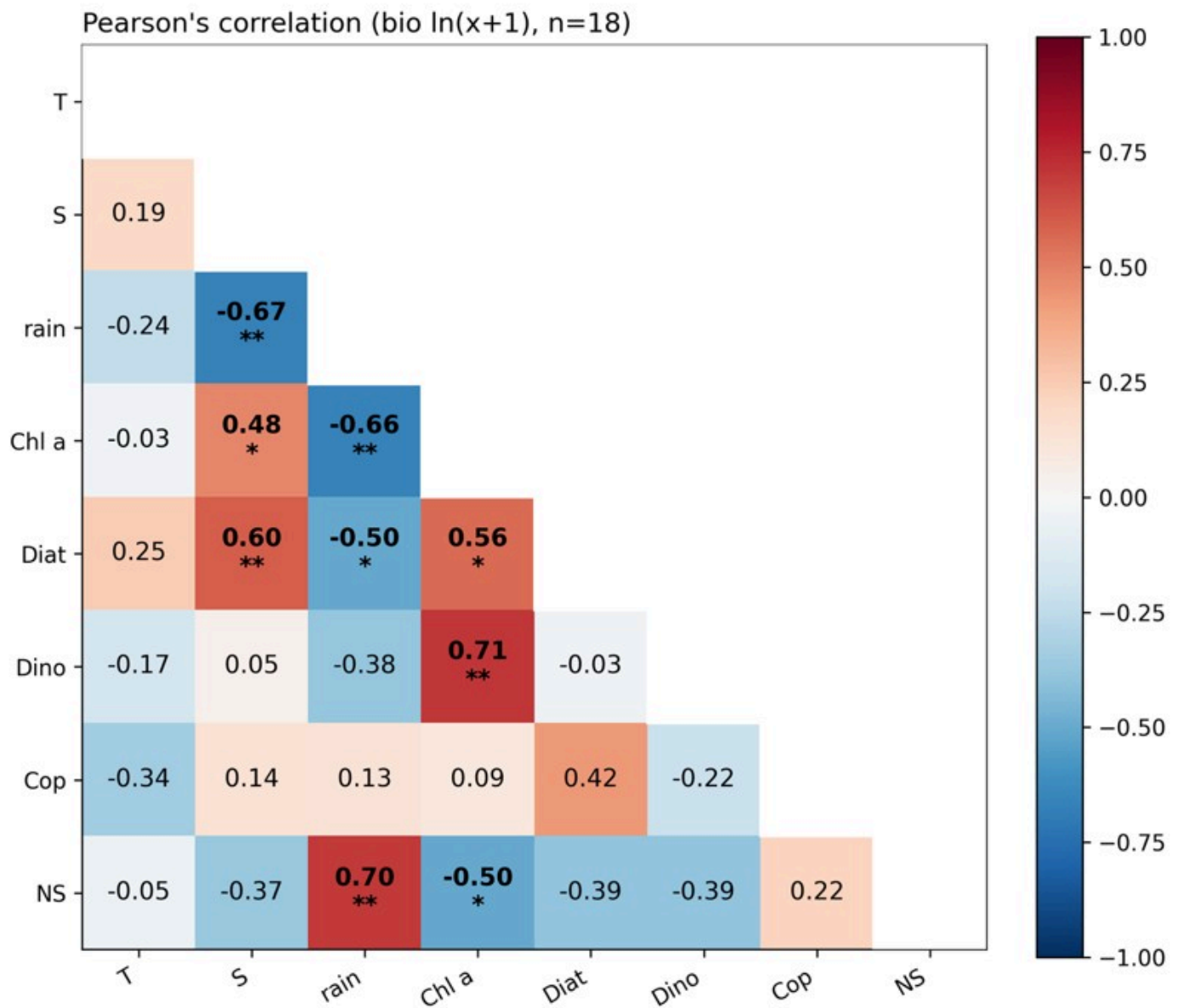


Figure 3

Pearson's correlation test showing correlations between environmental parameters and plankton groups (T: Temperature; S: Salinity; rain; Cop: Copepod; NS: *Noctiluca scintillans*; Diat: Diatom; Dino: Dinoflagellate; Chl-a: Chlorophyll *a*). The abundance value of Cop, NS, Diat, and Dino were converted into ln(x+1). (*: p<0.05; **: p < 0.01).

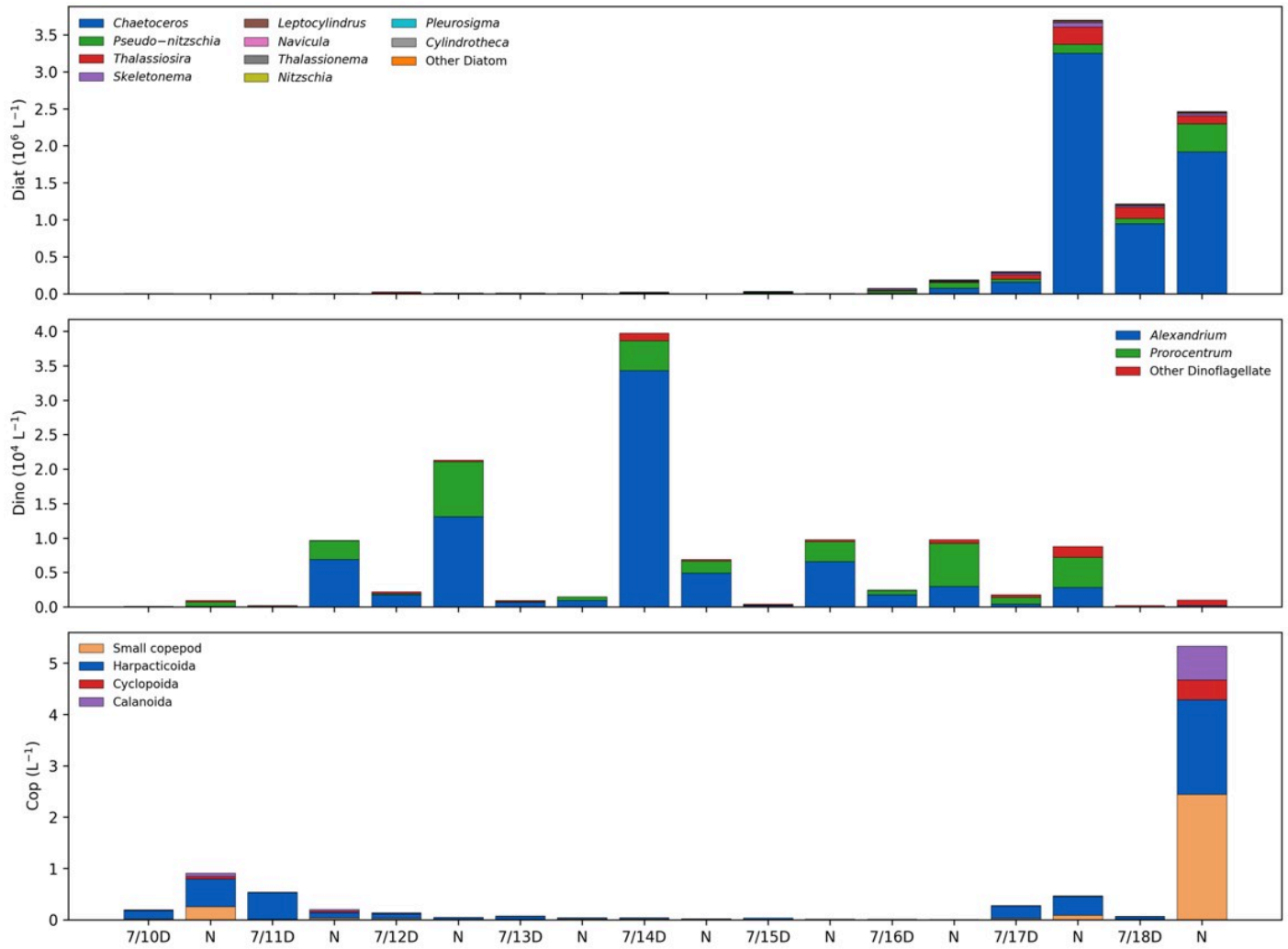


Figure 4

The abundance and composition of plankton groups from 10 July 2025 to 18 July 2025 at Jieshou Harbor. (A) Diatom, (B) Dinoflagellate, and (C) Copepods. D: daytime sampling, N: nighttime sampling.