



Morphometric Variation and Seasonal Polymorphism of Dinoflagellate *Triplos* in the Hooghly River Estuary Bay of Bengal

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Abstract

This study investigated morphological variation in three dominant *Triplos* spp. to validate the hypothesis of seasonal polymorphism in the Hooghly River estuarine context. Individual *Triplos* cells were assessed for raw morphological traits, such as total length, horn lengths, and transdiameter, from which shape ratios, bio-volume, surface area, and carbon content were derived using geometric approximations. Non-parametric Mann-Whitney U test on the 16 morphometric traits revealed *T. fusus* (U = 638–1334, z = 8.96–10.66, p < 0.0001), *T. furca* (U = 622–1389, z = 4.62–10.51, p < 0.0001), and *T. trichoceros* (U = 453–1647, z = 8.19–11.11, p < 0.0001) all displayed notable seasonal variations and morphometric shifts between pre-monsoon (PRM) and Post-monsoon (POM). The major patterns of these variations were documented using Principal Component Analysis (PCA). PC1 was able to capture traits (for *T. furca* 65.53%, *T. fusus* 73.36%, *T. trichoceros* 69.17% variance) related to size, like total length, bio-volume, and carbon content, while PC2 revealed intraspecific variation in morphological plasticity, which represented traits related to shape and symmetry (e.g., horn ratios). POM samples exhibited a distinct seasonal clustering, on the positive side of the PC axes, which was associated with higher cell size and biomass compared to small-sized PRM samples on the negative side of the PC axes for all *Triplos* spp. Spearman's correlation between PCA scores and water quality parameters showed a significant association, indicating that salinity, TDS, and nutrient loads are key environmental drivers.

Keywords: Correlation; Horn Length; Seasonal Form; Shape Ratios

Introduction

Genus *Triplos*, a morphologically unique group of thecate dinoflagellates under the family Ceratiaceae, of phylum Dinoflagellata. These eukaryotic unicells are found in all marine environments from tropical to cold and temperate waters and can be easily identified by their large cell size and characteristic horn-like projections. They are mixotrophs in nature and play important roles in primary productivity and nutrient cycling in the marine ecosystem (Smalley *et al.*, 2003). *Triplos* species are most common in estuarine systems and show considerable intraspecific and interspecific morphological variation. This variation can be measured through detailed morphometric analysis by looking at changes in shape, size, and horn length over time (Hasle *et al.*, 1996; Pacheco *et al.*, 1999). Most of the research on dinoflagellates in India, especially in the Bay of Bengal area, has been about species diversity, abundance patterns, and basic physical parameters like the height, breadth, and horn length of different *Triplos* spp. Furthermore, derived morphometric indices, like bio-volume measurements, surface area-to-volume ratio, and carbon content of cells, are not included as objectives (Naik *et al.*, 2011; Akhand *et al.*, 2012; Sahu *et al.*, 2014; Chitari *et al.*, 2017). Comprehensive and in-depth morphometric studies addressing seasonal polymorphism, along with correlation to environmental parameters in tropical

estuarine waters, are also lacking. The present study focuses on three distinct *Triplos* species in the Hooghly estuary near Namkhana, a biologically active eco-region impacted by freshwater inflow and tidal mixing. As a part of the Gangetic River delta, this estuary is distinguished by varying levels of salinity and nutrient concentration, caused by tidal waters. This results in a dynamic and productive ecosystem supporting various phytoplankton groups such as diatoms, dinoflagellates, chlorophytes, and cyanobacteria (Mitra *et al.*, 2015). Three species of *Triplos*—*T. furca*, *T. fusus*, and *T. trichoceros* were selected based on their high abundance and thorough persistence in the estuarine water. These dinoflagellates represent some of the most dominant taxa of the dinoflagellate community of the Hooghly River estuary (Rath *et al.*, 2021). Furthermore, these species have distinct and contrasting morphological traits, especially in the lengths of the apical and antapical spines and the general shape of the body, thereby allowing for accurate morphometric differentiation and analysis. Using multivariate approaches on seasonal variations of morphometric traits and physicochemical parameters of water across the pre-monsoon and post-monsoon season, this work validates the seasonal polymorphism hypothesis and aims to identify patterns of adaptive strategies and morphological plasticity of estuarine dinoflagellates (Morabito *et al.*, 2007; Lyakh & Bryantseva, 2014). Monsoon samples were excluded from the seasonal comparison due to the extreme low abundance of *Triplos* spp., providing insufficient morphometric data for accurate statistical analysis and interpretation.

Material and Method

Study Area and Sampling Stations

The study was carried out between October 2021 and September 2023 in the estuarine zone of the Hooghly River close to Namkhana, West Bengal, focusing on two important seasons: pre-monsoon (PRM: February to May) and post-monsoon (POM: October to January). Water samples were collected from Station 1 (21.76056°N, 88.23628°E) near Namkhana Bridge, Station 2 (21.754776°N, 88.267445°E) near Madanganj, and Station 3 (21.727693°N, 88.266245°E) near Dwariknagar Ferry Ghat. The study area (Figure 1) is a unique tidal estuary that receives fresh water from the Hooghly River and mixes it with saline water from the Bay of Bengal.

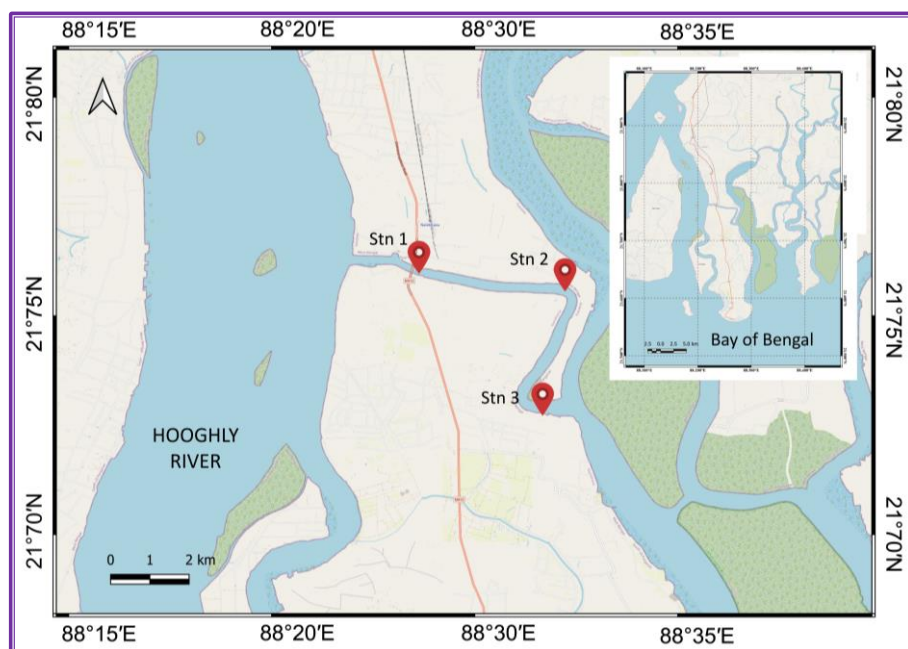


Figure 1: Map of the study area

Water Sampling, Collection, and Analysis

Phytoplankton and water samples were collected according to standard protocol and preserved. Water temperature, pH, and salinity, Total Dissolved Solids (TDS) and Electrical Conductivity (EC) were

measured in situ using a portable multi-parameter probe of HANNA, while Dissolved Oxygen (DO) and nutrient concentrations were measured in the laboratory. For determining nutrient content (nitrate, phosphate, and silicate), we have used spectrophotometric methods after sample filtration (Grasshoff *et al.*, 2009). For morphometric analysis, individual phytoplankton cells were observed under Dewinter Educator Plus and Leica DMI8 inverted microscopes, equipped with an image-capturing device.

Morphometric Measurements

Individual *Tripos* cells were measured for key structural parameters (Figure 2), including Total Length (TL), Midline Length (ML), Body Length (BL), Transdiameter (T), Distance between Antapical Horns (DH), Apical Horn Length (AHL), Right Antapical Horn Length (RAHL), and Left Antapical Horn Length (LAHL). From these measurement values, we have calculated several derived ratios to capture shape and proportional variability: Transdiameter to Body Length (T/BL), Left to Right Antapical Horn Length (LAHL/RAHL), Apical Horn Length to both LAHL and RAHL (AHL/LAHL, AHL/RAHL), and Transdiameter to both LAHL and RAHL (T/LAHL, T/RAHL) (Castillo *et al.*, 2003). Additionally, we have computed the cell bio-volume (μm^3), surface area (μm^2), and estimated carbon content (pg C/cell) using the available literature on standard geometric approximations for dinoflagellate shapes (Hillebrand *et al.*, 1999; Sun & Liu, 2003). For each species, more than 300 cells were measured. All the measurements were taken using captured pictures in ImageJ software and expressed in μm .

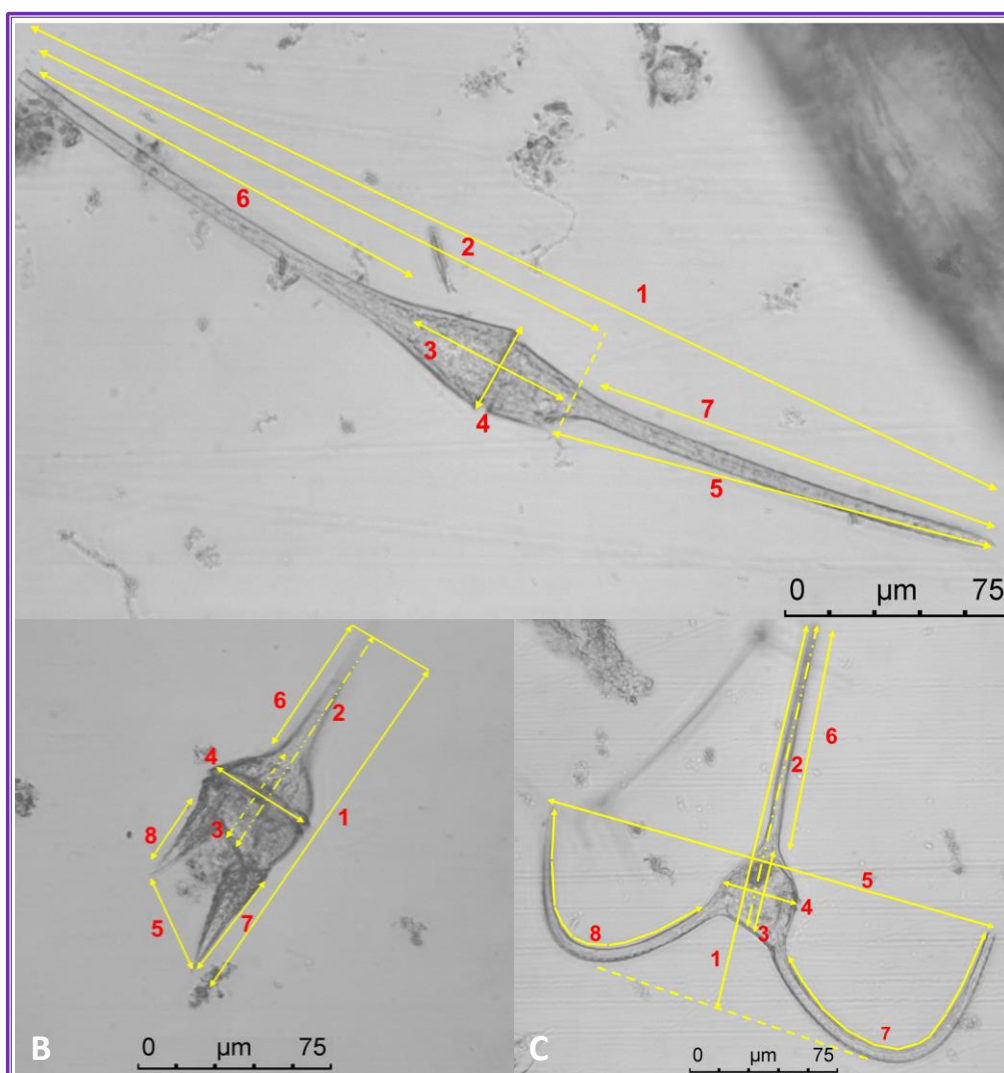


Figure 2: A) *Tripos fusus*, B) *Tripos furca*, C) *Tripos trichoceros*, showing the measured parameters 1- Total Length (TL), 2- Midline Length (ML), 3- Body Length (BL), 4- Transdiameter (T), 5- Distance between Antapical Horns (DH), 6- Apical Horn Length (AHL), 7- Left Antapical Horn Length (LAHL), 8- Right Antapical Horn Length (RAHL)

Statistical Analysis

The Shapiro-Wilk test was used to determine the normality of the morphometric datasets of the three chosen *Tripos* species. Non-parametric Mann–Whitney U test was used to assess the statistical significance of seasonal variations in morphometric parameters, as the data deviated from the normality assumption. Principal Component Analysis (PCA) was conducted to reduce dimensionality and identify principal axes of shape variation using standardized morphometric variables (z-scores) derived from both raw morphometric data and derived ratios, bio-volume, surface area, and carbon content. PERMANOVA was applied to determine the significance of PC axes. To evaluate the potential relationship between morphological variation and the water quality parameters, Spearman's rank correlation analyses were performed using the obtained principal component (PC1 and PC2) scores, and significance levels were evaluated at $p < 0.05$ (Balqis *et al.*, 2016; Saha *et al.*, 2022). All analyses were performed using MINITAB, PAST 5.0, and Microsoft Excel 2010.

Results

A detailed examination of raw morphometric parameters revealed significant seasonal variation in all *Tripos* spp. Violin plots (Figure 3) were used to visualize the distribution, central tendency, and dispersion of raw morphometric traits (TL, ML, BL, T, DH, AHL, RAHL, LAHL) across the pre-monsoon (PRM) and post-monsoon (POM) seasons. These plots demonstrated variation for each dinoflagellate species and their inter-seasonal shifts. Non-parametric Mann–Whitney U and Vargha–Delaney \hat{A} effect size tests revealed statistically significant seasonal variation across the PRM and POM seasons for all species.

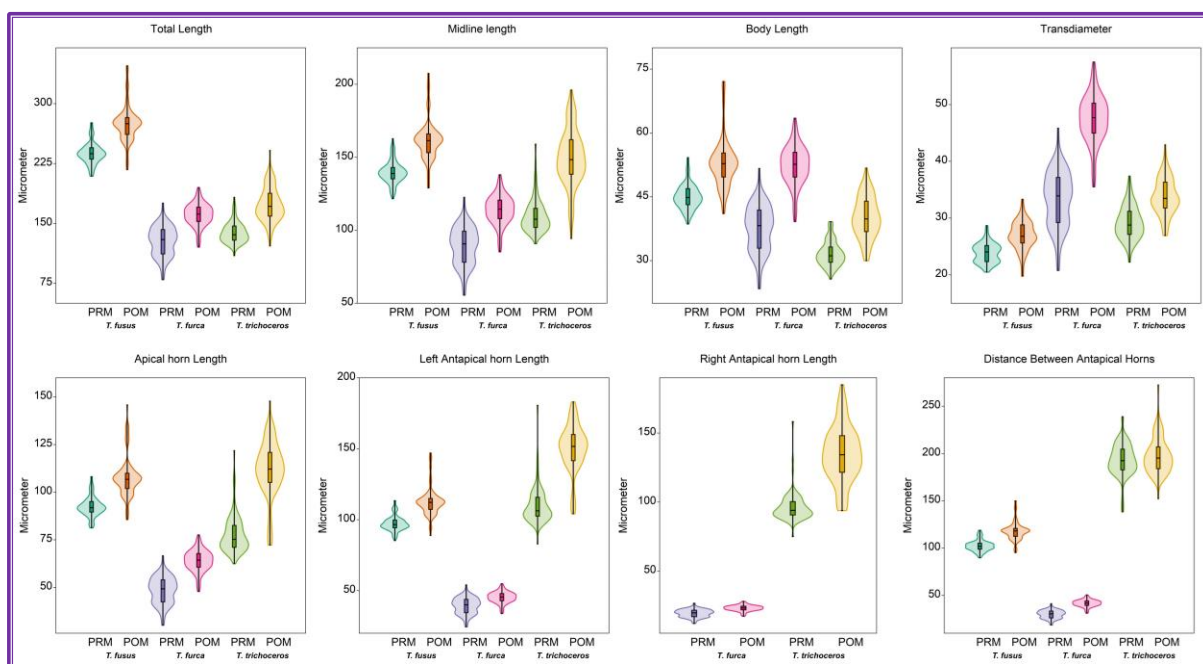


Figure 3: Violin plots of the measured morphometric parameters in pre-monsoon (PRM) and post-monsoon (POM)

In *T. fusus*, all traits showed highly significant differences ($U = 638–1334$, $z = 8.96–10.66$, $\hat{A} = 0.063–0.133$; $p < 0.0001$), indicating substantial size increases in POM. *T. furca* displayed significant divergence across most traits ($U = 622–1389$, $z = 4.62–10.51$, $\hat{A} = 0.062–0.139$; $p < 0.0001$), particularly in spines and cell dimensions. *T. trichoceros* also exhibited clear seasonal shifts ($U = 453–1647$, $z = 8.19–11.11$, $\hat{A} = 0.045–0.165$; $p < 0.0001$), except for cell depth (DH), which remained statistically non-significant ($p = 0.264$, $\hat{A} = 0.454$).

For further interpretation of morphometric variation, a set of shape ratios and biomass were calculated. Ratios such as LAHL/RAHL, AHL/LAHL, and AHL/RAHL (Figure 4) were used to investigate horn symmetry and elongation. These derived traits showed seasonal changes and interspecific variation in

horn development, which were species-specific adaptations for orientation and buoyancy. All three *Triplos* species showed a notable seasonal increase in cellular bio-volume, surface area, and carbon content in POM compared to PRM (Table. 1).

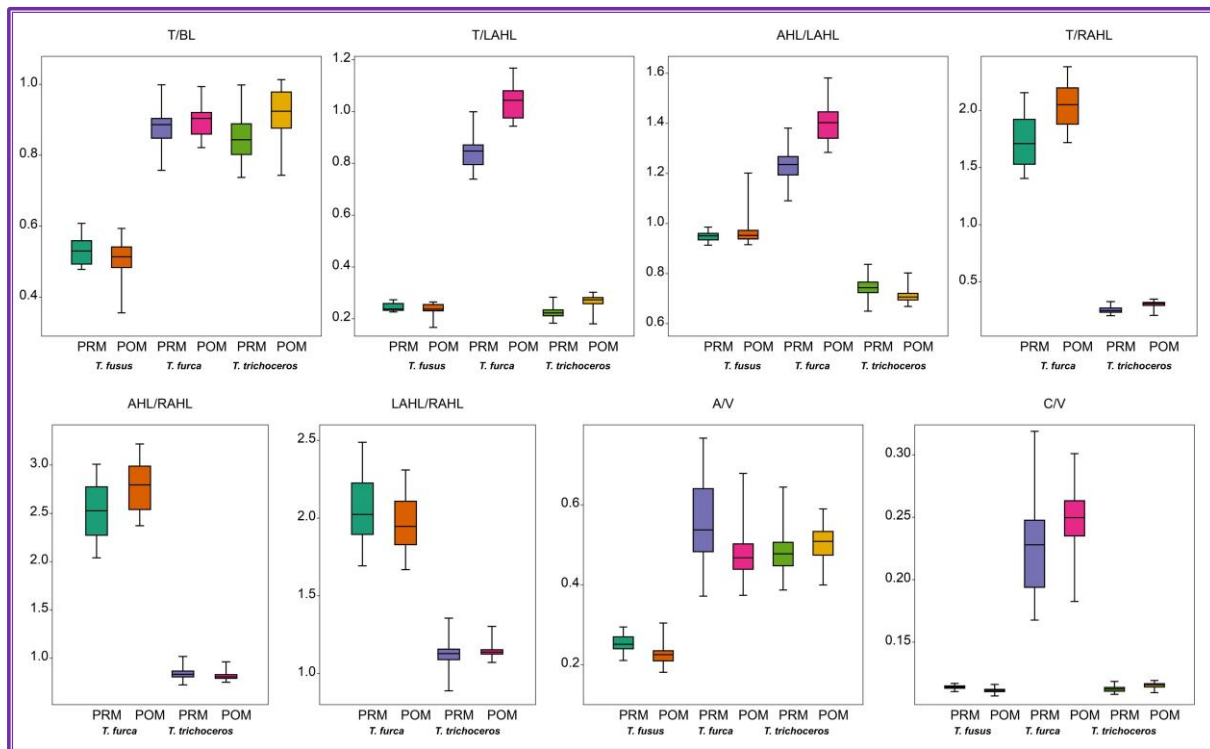


Figure 4: Derived ratio of the morphological parameters in different *Triplos* spp. in different seasons

Table 1: Bio-volume, Area, and Carbon Content of all *Triplos* Species (values in $\times 10^3$ units)

Species	Season	Bio-volume (μm^3)		Area (μm^2)		Carbon Content (pg C/cell)	
		Mean \pm SD	Min–Max	Mean \pm SD	Min–Max	Mean \pm SD	Min–Max
<i>T. fusus</i>	PRM	22.38 \pm 4.96	13.24 – 38.12	7.07 \pm 0.93	5.15 – 9.90	2.62 \pm 0.54	1.60 – 4.33
	POM	35.66 \pm 10.01	15.21 – 72.86	9.59 \pm 1.67	5.60 – 15.49	4.06 \pm 1.07	1.83 – 7.95
<i>T. furca</i>	PRM	11.78 \pm 4.30	17.57 – 166.99	6.27 \pm 1.63	2.89 – 10.66	1.43 \pm 0.49	2.09 – 17.32
	POM	24.47 \pm 6.67	49.80 – 215.10	11.30 \pm 1.97	6.16 – 16.62	2.85 \pm 0.73	5.56 – 21.97
<i>T. trichoceros</i>	PRM	30.33 \pm 9.12	16.71 – 67.45	14.79 \pm 2.87	9.85 – 26.94	3.48 \pm 0.98	1.99 – 7.39
	POM	45.93 \pm 13.51	18.56 – 82.93	21.51 \pm 4.56	11.96 – 32.52	5.14 \pm 1.42	2.20 – 8.98

Morphometric dataset for each species was tested for sampling adequacy of PCA using the Kaiser–Meyer–Olkin (KMO) measure. The test result revealed KMO values of 0.82, 0.84, and 0.73 for *T. trichoceros*, *T. furca*, and *T. fusus*, respectively, which suggested excellent and good adequacy for appropriateness of using PCA. The biplot of *T. furca* (Figure 5) revealed that the first two components, PC1 (variance 65.53%, eigenvalue = 12.45) and PC2 (variance 13.84%, eigenvalue = 2.63), were able to explain 79.37% of the variance, indicating strong morphological structuring along these axes. The clarity of morphometric variation was improved by adding PC3 (variance 8.57%, eigenvalue = 1.63), increasing the cumulative variance to 87.94%. PCA for *T. fusus* (Figure 5) showed that PC1 and PC2 together accounted for 90.68% of the variability, with PC1 explaining 73.36% of the total variance (eigenvalue = 11.01) and PC2 contributing 17.32% (eigenvalue = 2.59). For *T. trichoceros* (Figure 5),

PC1 accounted for 69.17% of the total variation (eigenvalue = 13.14), while PC2 came in second with 11.32% (eigenvalue = 2.15). Thus, 80.49% of the variance was explained by the first two components taken together. The cumulative variance explained rose to 89.52% with the addition of PC3, which added 9.03% (eigenvalue = 1.71), suggesting a significant dimensional reduction within the first three axes. One-way PERMANOVA performed on the PC1 and PC2 scores revealed significant seasonal variation in the morphometric structure of all three *Triplos* species—*T. fusus*, *T. furca*, and *T. trichoceros*—between the PRM and POM. The results showed consistently high F-values and extremely low p-values: *T. fusus* (F = 134, p = 0.0001), *T. furca* (F = 161.9, p = 0.0001), and *T. trichoceros* (F = 169.1, p = 0.0001), suggesting a clear seasonal divergence in cell morphology.

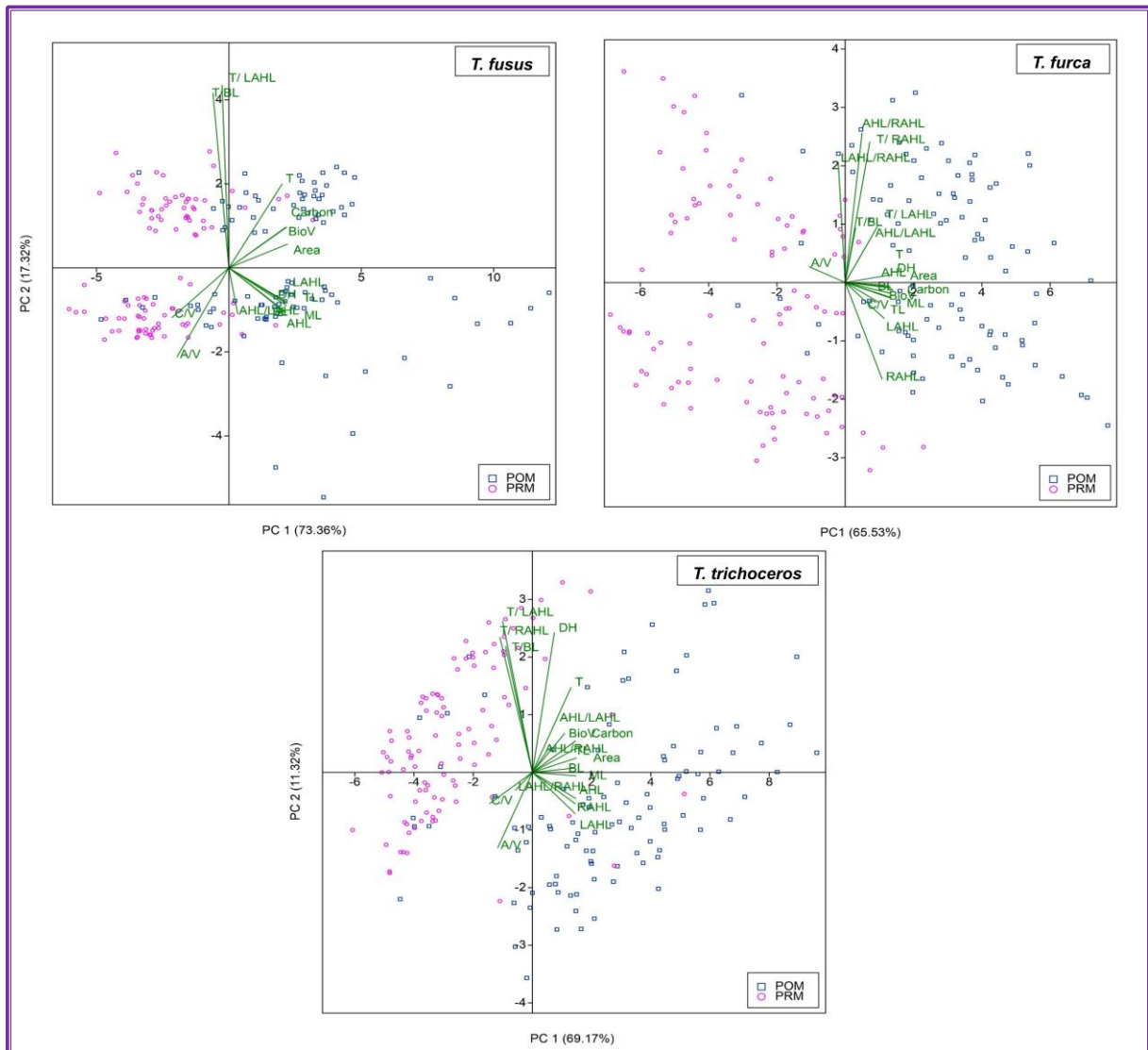


Figure 5: PCA biplot of all the *Triplos* showing first two principal components (PC1 and PC2): PC1 dominated by the size-related characteristics like body length (BL), total length (TL), carbon content, and bio-volume, and PC2 by horn lengths (LAHL, RAHL) and shape ratios (e.g., T/RAHL, LAHL/RAHL) reflecting the shape and symmetry-related parameters

Discussion

The degree of shape variation differed among the three species. *T. fusus* showed the most consistent seasonal pattern, with a marked reduction in size parameters during the POM period. In contrast, *T. trichoceros* demonstrated greater intra-seasonal variability, possibly indicating a wider ecological tolerance or a response to microhabitat heterogeneity within the estuary. For example, *T. furca* exhibited longer LAHL and RAHL with moderate BL and transdiameter (T) during the PRM, while *T. trichoceros*

showed increased LAHL, RAHL, BL, and T in the POM. Such changes are indicative of morphological plasticity in response to environmental shifts, such as temperature, salinity, and nutrient availability. *T. furca* exhibited the most pronounced changes in overall body structure, with substantial increases in TL, BL, T, and DH of approximately 1.27, 1.47, 1.43, and 1.39 folds, respectively, indicating seasonal elongation and, in particular, an expansion of body width (Sastre *et al.*, 2013). On the other hand, *T. trichoceros* showed more prominent changes, especially in horn length parameters AHL, RAHL, and LAHL, with increases of 1.45, 1.39, and 1.37 folds, respectively, suggesting a morphological strategy focused on horn development, likely linked to buoyancy control or defense mechanisms. *T. fusus* presented relatively conservative but consistent seasonal changes, with moderate increases across all parameters, especially in ML at 1.15 fold and TL at 1.12 fold during the POM season (Huynh *et al.*, 2022). These results confirm strong seasonal polymorphism across all three species, with large effect sizes reflecting marked shifts in body form and size, which might be a response to changing estuarine environmental conditions (Smayda, 2000).

In case of derived ratios, a consistent asymmetry in LAHL/RAHL in *T. furca* suggests a stable morphological trait, while in *T. trichoceros* suggests plasticity probably brought on by environmental factors. Overall cell elongation in relation to horn length is indicated by ratios like T/LAHL and T/RAHL. In increased saline POM waters, these shape ratios were generally higher than PRM, indicating more slender forms that might be beneficial for vertical migration or decreased sinking. All species had the highest Surface Area to Volume (S/V) ratio in PRM, which is consistent with the requirement for optimal nutrient uptake under possibly nutrient-depleted circumstances. This ratio usually falls in POM, indicating larger, more storage-oriented forms that are in line with higher growth and nutrient-rich environments (Stanca *et al.*, 2013; Nasution *et al.*, 2021). Favourable environmental conditions, such as nutrient enrichment from runoff and variations in salinity or water column stability, might have promoted the enhanced cellular growth and carbon assimilation in all dinoflagellates (Smayda, 1997; Huang *et al.*, 2024).

PCA biplot of *T. furca* PC1 exhibited strong positive loadings for size-related variables such as TL, ML, T, bio-volume, surface area, and carbon content, indicating that it primarily represented overall body size. PC2 was associated more with shape descriptors and derived ratios, including AHL/RAHL, T/RAHL, and LAHL/RAHL, reflecting horn symmetry and shape complexity. PC Scores of POM samples showed high positive values on PC1 and formed seasonal clustering based on body size, while PRM samples revealed negative PC1 scores. PC2 emphasized intra-seasonal shape-related variability but contributed less to seasonal separation. Clustering of POM scores along the positive PC1 axis of the biplot indicated seasonal growth or favorable conditions yielding larger cells and higher carbon content. PRM cluster was positioned along the negative side of PC1, indicating smaller sizes (Vila & Masó, 2005; Baek *et al.*, 2008; Sathish *et al.*, 2022).

For *T. fusus* PCA biplot also revealed a clear separation between PRM and POM scores along PC1, indicating strong seasonal morphometric variation. The positive side of PC1 shows a strong clustering of POM scores, which indicates larger cell sizes, higher bio-volume, and more carbon content. However, PRM scores are primarily limited to the negative PC1 axis, which suggests that cells are smaller and that there is less metabolic investment (Ravelo *et al.*, 2022; Yarahmadi *et al.*, 2023).

In case of *T. trichoceros* PCA indicated that the primary morphological variation is caused by size-related parameters such as area, ML, TL, AHL, RAHL, LAHL, carbon content, suggesting that seasonal changes in environmental factors—especially salinity and nutrient availability while the PC2 highlights the influence of shape-related ratios, particularly T/LAHL, DH, T/RAHL, T/BL, pointing to variations in body proportions in relation to horns (Pradhan *et al.*, 2023).

Overall PRM and POM samples for each *Tripes* showed clear clustering in the PCA plots, indicating seasonal differentiation. POM samples moved along PC1, indicating increased cell size and biomass under POM conditions, while PRM observations were generally linked to higher PC2 values, indicating elongated and asymmetric forms. Thus, PCA effectively summarized the complex morphometric variation of *Tripes* species across seasons, revealing distinct seasonal patterns that likely reflect

phenotypic plasticity in response to changing estuarine conditions (Totti *et al.*, 2005; Smayda, 2010; Wang, *et al.* 2025).

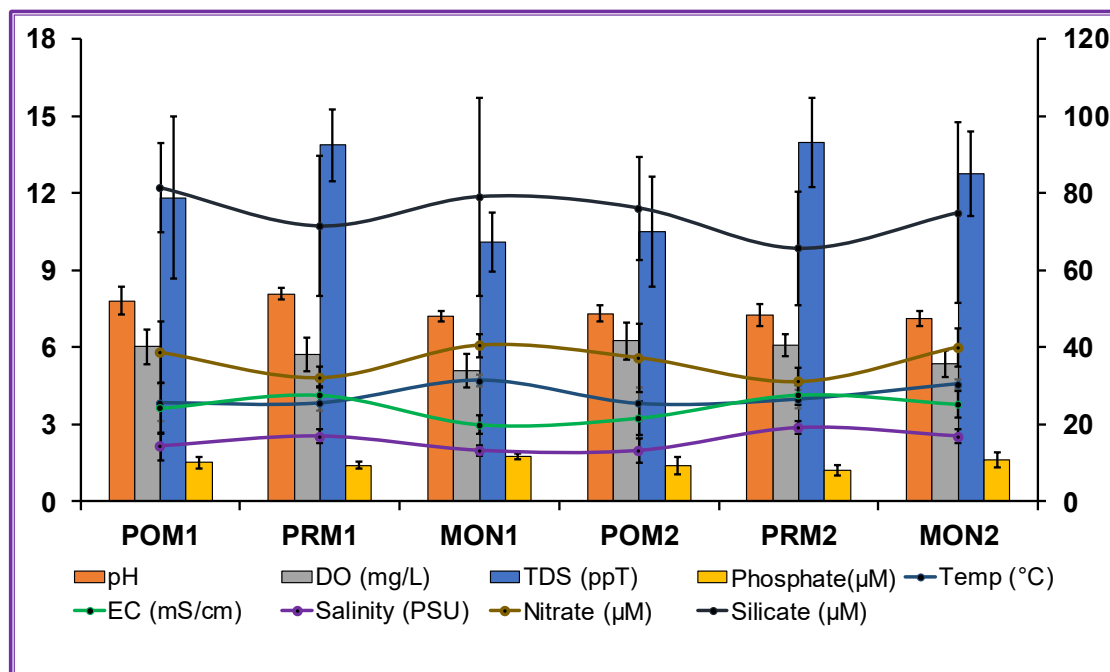


Figure 6. Water parameters of the estuary at different season of the two year study period

Physicochemical parameters showed a significant seasonal shift between the PRM and POM periods. Higher levels of salinity, Electrical Conductivity (EC), Total Dissolved Solids (TDS), and increased nutrient concentrations were found in post-monsoon waters, suggesting increased seawater intrusion and mixing. Conversely, pre-monsoon samples had relatively lower EC, TDS, and DO values and higher water temperatures (Figure 6). These hydrological shifts suggest a transition from a more stratified to a mixed estuarine environment due to monsoonal impact. Such changes likely influence nutrient dynamics and water clarity, potentially affecting the morphology, biomass, and distribution of *Triplos* spp. across seasons (Bhutia *et al.*, 2024; Souhardya *et al.*, 2025).

In *T. furca*, PC1 (Figure 7) showed significant positive correlations with TDS, EC, and salinity ($p < 0.001$), indicating that ionic concentration strongly influences size-related morphometry. Nitrate ($\rho = -0.429$), phosphate, and silicate were negatively and significantly correlated with PC1, suggesting a potential inverse effect of nutrient enrichment. In contrast, temperature and pH showed no significant association. PC2 displayed only weak correlations, with EC and salinity showing marginal significance. Overall, PC1 in *T. furca* is mainly shaped by salinity and nutrient-related factors, while PC2 reflects limited environmental influence (Baek *et al.*, 2006; Drakulović, *et al.*, 2024).

In *T. fusus*, PC1 (size variation) was positively impacted by salinity ($\rho = 0.334$, $p < 0.001$), TDS, EC, and negatively by nitrate ($\rho = -0.394$, $p < 0.001$), phosphate, silicate, and DO. This implies that whereas smaller or polymorphic forms were preferred in nutrient-enriched, turbid, and hypoxic PRM conditions, larger morphotypes emerged in high salinity and ionic conditions during POM. Only silicate, which represents shape/spine-related traits, exhibited a significant negative correlation with PC2, suggesting that estuarine turbidity is linked to slight shape changes (Baek *et al.*, 2009; Wang *et al.*, 2022). In contrast, PC2 exhibited mostly weak and statistically insignificant correlations (Figure 7).

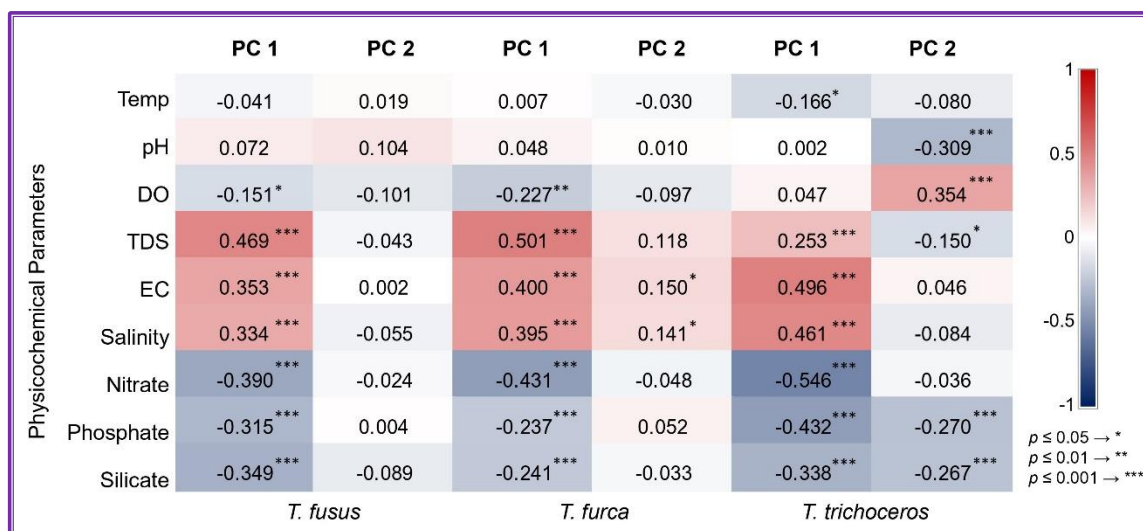


Figure 7: Correlation of the water parameters with the PC scores of different *Triplos* spp.

In *T. trichoceros*, PC1 was strongly and significantly correlated with EC, salinity, and TDS ($p < 0.0001$), indicating that ionic strength and salinity-related parameters primarily drive morphometric variation. Additionally, PC1 showed strong negative correlations with nutrients such as nitrate ($\rho = -0.547$), phosphate, and silicate, all of which were statistically significant, suggesting inverse relationships between nutrient enrichment and cell structure. A weak but significant negative correlation with temperature was also observed ($\rho = -0.166$, $p = 0.029$). In contrast, PC2 was significantly and negatively associated with pH, DO, and silicate, indicating minor but measurable effects of oxygen and alkalinity on secondary morphological axes. These findings suggest that whereas smaller polymorphic forms are preferred in nutrient-rich, turbid PRM conditions, larger morphotypes predominate in ion-rich, saline conditions during the POM (Vajravelu *et al.*, 2018; Rodrigues & Patil, 2021; Sarkar *et al.*, 2023; Baek *et al.*, 2025).

The study was limited to a single estuary with restricted sampling period and a linear set of morphometric traits, which may be insufficient to capture long-term interannual patterns and the finer morphometric variability detectable through 3D geometric imaging morphometrics. Furthermore, the analysis focused on only three species, whereas numerous other *Triplos* species with potentially significant morphometric diversity remain unexplored. Future studies on *Triplos* morphometry could combine multi-year monitoring to evaluate the influence of environmental drivers such as rising temperature, fluctuating salinity, monsoon variability, and nutrient dynamics—on morphometric variation, seasonal abundance, and adaptive responses. Incorporating advanced molecular analyses, 3D geometric imaging, alongside ecological data across additional *Triplos* species and multiple coastal and estuarine zones of the Bay of Bengal could broaden the understanding of spatial patterns and seasonal polymorphism.

Conclusion

Triplos species exhibited distinct variation in the morphometric traits, revealing a clear pattern of seasonal polymorphism driven by changing environmental conditions in the Hooghly River estuary. Larger forms with higher biomass characterized post-monsoon assemblages, while pre-monsoon populations predominantly comprised smaller, more compact forms, reflecting that size, shape, and symmetry are adaptive responses of species. The consistent and significant associations between these morphological traits and key physicochemical parameters, particularly salinity, total dissolved solids, and nutrient concentrations, highlight the major impact of environmental drivers in regulating phenotypic plasticity. Further research combining field observations and experimental approaches is necessary to unravel the complex interplay of physicochemical and biological factors shaping

morphological variability and also to predict how these dinoflagellate populations may respond to climate change in coastal ecosystems.

Conflict of Interest

Authors have declared no competing of interests.

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References

- Akhand, A., Maity, S., Mukhopadhyay, A., Das, I., Sanyal, P., & Hazra, S. (2012). Dinoflagellate *Ceratium symmetricum pavillard* (Gonyaulacales: ceratiaceae): its occurrence in the Hooghly-Matla estuary and offshore of Indian Sundarban and its significance. *Journal of Threatened Taxa*, 4(7), 2693-2698. <http://dx.doi.org/10.11609/JoTT.o2530.2693-8>
- Baek, S.H., Lee, C.H., Kim, M., Hong, S., & Lim, Y.K. (2025). Seasonal effects of Nakdong River freshwater inflow and coastal environmental changes on phytoplankton community structure, including harmful species, in Eastern Jinhae Bay, Korea. *Journal of Marine Science and Engineering*, 13(4), 1-19. <https://doi.org/10.3390/jmse13040669>
- Baek, S.H., Shimode, S., & Kikuchi, T. (2006). Reproductive ecology of dominant dinoflagellate, *Ceratium furca*, in the coastal area of Sagami Bay. *Coastal Marine Science*, 30(1), 344-352. <https://repository.dl.itc.u-tokyo.ac.jp/record/40806/files/KJ00004354628>
- Baek, S.H., Shimode, S., Han, M.S., & Kikuchi, T. (2008). Growth of dinoflagellates, *Ceratium furca* and *Ceratium fusus* in Sagami Bay, Japan: The role of nutrients. *Harmful Algae*, 7(6), 729-739. <https://doi.org/10.1016/j.hal.2008.02.007>
- Baek, S. H., Shimode, S., Shin, K., Han, M. S., & Kikuchi, T. (2009). Growth of dinoflagellates, *Ceratium furca* and *Ceratium fusus* in Sagami Bay, Japan: The role of vertical migration and cell division. *Harmful algae*, 8(6), 843-856. <https://doi.org/10.1007/BF03022431>
- Balqis, A. R. S., Yusoff, F. M., Arshad, A., & Nishikawa, J. (2016). Seasonal variations of zooplankton biomass and size-fractionated abundance in relation to environmental changes in a tropical mangrove estuary in the Straits of Malacca. *Journal of Environmental Biology*, 37(4), 685. https://www.jeb.co.in/journal_issues/201607_jul16_spl/paper_07.pdf
- Bhutia, R. N., Abhilashwodeyar, K., Devadas, D., Mandal, U. K., Sreekanth, G. B., Landge, A. T., ... & Burman, D. (2024). Dynamics of phytoplankton community in relation to environmental variables in tropical mangrove estuary, Sundarbans, India. *Journal of Environmental Biology*, 45(6), 654-665. <http://dx.doi.org/10.22438/jeb/45/6/MRN-5369>
- Chitari, R. R., Anil, A. C., Kulkarni, V. V., Narale, D. D., & Patil, J. S. (2017). Inter-and intra-annual variations in the population of *Triplos* from the Bay of Bengal. *Current Science*, 1219-1229. <https://doi.org/10.18520/cs/v112/i06/1219-1229>
- Drakulović, D., Huter, A., Pestorić, B., Marković, O., & Šuković, D. (2024). Phytoplankton Dynamics in an Oligo-mesotrophic Environment along the Montenegrin Coast (South-East Adriatic Sea). *Turkish Journal of Fisheries and Aquatic Sciences*, 24(4), TRJFAS24835. <https://doi.org/10.4194/TRJFAS24835>
- Grasshoff, K., Kremling, K., & Ehrhardt, M. (Eds.). (2009). *Methods of seawater analysis*. John Wiley & Sons. <https://doi.org/10.1002/9783527613984>
- Hasle, G. R., Syvertsen, E. E., Steidinger, K. A., Tangen, K., & Tomas, C. R. (1996). *Identifying marine diatoms and dinoflagellates*. Elsevier, 5-38. <https://doi.org/10.1016/B978-0-12-693015-3.X5000-1>
- Hillebrand, H., Dürselen, C. D., Kirschtel, D., Pollinger, U., & Zohary, T. (1999). Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology*, 35(2), 403-424. <https://doi.org/10.1046/j.1529-8817.1999.3520403.x>
- Huang, X., Liu, K., Ding, X., Liu, S., Cui, Z., Zhao, Y., & Chen, N. (2024). Dinoflagellate *Triplos* species composition and seasonal dynamics in Jiaozhou Bay revealed through 18S rDNA V4-based metabarcoding analysis. *Journal of Applied Phycology*, 36(4), 1939-1952. <https://doi.org/10.1007/s10811-024-03239-5>
- Huynh, N. D. T., Nguyen-Ngoc, L., Voss, M., & Doan-Nhu, H. (2022). Dinoflagellate *Triplos furca* and *Triplos fusus* niches in the South China Sea: Maximum entropy assessment of environmental factors. *Regional Studies in Marine Science*, 55, 102601. <https://doi.org/10.1016/j.rsma.2022.102601>

- Lyakh, A. M., & Bryantseva, Y. V. (2014). Seasonal polymorphism of the Black Sea dinoflagellates from genus *Ceratium*: *C. furca*, *C. fusus*, *C. tripos* (Dinophyceae). *Modern Phytomorphology*, 5, 209-214. <http://dx.doi.org/10.5281/zenodo.161026>
- Castillo, M. E. M. D., Resendiz, M. E. Z., Okolodkov, Y. B., & Ugarte, I. H. S. (2003). *Ceratium balechii* sp. nov. (Dinophyceae: Gonyaulacales) from the Mexican Pacific. *Hidrobiológica*, 13(1), 75-90. https://www.scielo.org.mx/scielo.php?script=sci_arttext&pid=S0188-88972003000100009
- Mitra, A., Trivedi, S., Zaman, S., Pramanick, P., Chakraborty, S., Pal, N., Fazli, P., & Banerjee, K. (2015). Decadal variation of nutrient level in two major estuaries in Indian Sundarbans. *Jordan Journal of Biological Sciences*, 8(2), 231-236. <https://jjbs.hu.edu.jo/files/v8n3/Paper%20Number%2012m.pdf>
- Morabito, G., Oggioni, A., Caravati, E., & Panzani, P. (2007). Seasonal morphological plasticity of phytoplankton in Lago Maggiore (N. Italy). *Hydrobiologia*, 578(1), 47-57. <https://doi.org/10.1007/s10750-006-0432-5>
- Naik, R. K., Hegde, S., & Anil, A. C. (2011). Dinoflagellate community structure from the stratified environment of the Bay of Bengal, with special emphasis on harmful algal bloom species. *Environmental Monitoring and Assessment*, 182(1), 15-30. <https://doi.org/10.1007/s10661-010-1855-z>
- Nasution, A.K., Takarina, N.D., & Thoha, H. (2021). The presence and abundance of harmful dinoflagellate algae related to water quality in Jakarta Bay, Indonesia. *Biodiversitas Journal of Biological Diversity*, 22(5) 2909-2917. <https://doi.org/10.13057/biodiv/d220556>
- Pacheco, J. L. P., Álvarez Borrego, J., Orellana Cepeda, E., & Cortés Altamirano, R. (1999). Diffraction pattern applicability in the identification of *Ceratium* species. *Journal of Plankton Research*, 21(8), 1463-1474. <http://dx.doi.org/10.1093/plankt/21.8.1455>
- Pradhan, S.P., Nayak, S., Sharma, S.N., Nayak, P., Muduli, N., & Patnaik, L. (2023). Diversity of *Ceratium* Schrank (Dinophyceae) species in the surface waters of Dhamra, Odisha, Eastern India. *Journal of Environmental Biology*, 44(6), 784-794. <http://doi.org/10.22438/jeb/44/6/5141>
- Rath, A. R., Mitbavkar, S., & Anil, A. C. (2021). Response of the phytoplankton community to seasonal and spatial environmental conditions in the Haldia port ecosystem located in the tropical Hooghly River estuary. *Environmental Monitoring and Assessment*, 193(9), 548. <https://doi.org/10.1007/s10661-021-09255-z>
- Ravelo, S. F., Yap-Dejeto, L. G., Silaras, M. L. S., Amparado, M. L. L., Ocampo, J. A., Abria, E. G., & Albina, M. B. (2022). A snapshot on the distribution of coastal phytoplankton communities in five HAB-affected bays in Eastern Visayas, Philippines. *Frontiers in Marine Science*, 9, 730518. <https://doi.org/10.3389/fmars.2022.730518>
- Rodrigues, R. V., & Patil, J. S. (2021). Salinity changes may influence dinoflagellate cyst morphometry: data from monsoon-influenced tropical coastal ecosystems. *Journal of Plankton Research*, 43(6), 853-864. <https://doi.org/10.1093/plankt/fbab072>
- Saha, S., Chukwuka, A. V., Mukherjee, D., Saha, N. C., & Adeogun, A. O. (2022). Hydrological connectivity, surface water quality and distribution of fish species within sub-locations of an urban oxbow lake, East India. *Watershed Ecology and the Environment*, 4, 44-58. <https://doi.org/10.1016/j.wsee.2022.04.001>
- Sahu, G., Mohanty, A. K., Samantara, M. K., & Satpathy, K. K. (2014). Seasonality in the distribution of dinoflagellates with special reference to harmful algal species in tropical coastal environment, Bay of Bengal. *Environmental Monitoring and Assessment*, 186(10), 6627-6644. <https://doi.org/10.1007/s10661-014-3878-3>
- Sarker, S., Haque, A. B., Chowdhury, G. W., & Huda, A. S. (2023). Environmental Controls of phytoplankton in the river dominated sub-tropical coastal ecosystem of Bangladesh. *Regional Studies in Marine Science*, 66, 103114. <https://doi.org/10.1016/j.rsma.2023.103114>
- Sastre, M.P., Sánchez, E., Flores, M., Astacio, S., Rodríguez, J., Santiago, M., Olivieri, K., Francis, V., Núñez, J. (2013). Population fluctuations of *Pyrodinium bahamense* and *Ceratium furca* (Dinophyceae) in Laguna Grande, Puerto Rico, and environmental variables associated during a three-year period. *Revista de Biología Tropical*, 61(4), 1799-1813. https://www.scielo.sa.cr/scielo.php?pid=S0034-77442013000500019&script=sci_arttext
- Sathish, T., Nazrin, A. K., Thomas, L. C., & Padmakumar, K. B. (2022). Seasonal dynamics of dinoflagellates with special emphasis on potentially harmful species in a tropical estuarine system along the southwest coast of India. *Journal of Oceanography*, 78(5), 397-408. <https://doi.org/10.1007/s10872-022-00648-3>
- Smalley, G. W., Coats, D. W., & Stoecker, D. K. (2003). Feeding in the mixotrophic dinoflagellate *Ceratium furca* is influenced by intracellular nutrient concentrations. *Marine Ecology Progress Series*, 262, 137-151. <https://doi.org/10.3354/meps262137>
- Smayda, T.J. (1997). Harmful algal blooms: Their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnology and Oceanography*, 42(5, Part 2), 1137-1153. https://doi.org/10.4319/lo.1997.42.5_part_2.1137
- Smayda, T.J. (2000). Ecological features of harmful algal blooms in coastal upwelling ecosystems. *African Journal of Marine Science*, 22(1), 91-110. <http://dx.doi.org/10.2989/025776100784125816>

Smayda, T.J. (2010). Adaptations and selection of harmful and other dinoflagellate species in upwelling systems: Morphology and adaptive polymorphism. *Progress in Oceanography*, 55(1–2), 53-70. <https://doi.org/10.1016/j.pocean.2010.02.004>

Souhardya, S.M., Kumar, U., Iqbal, M.M., Kabir, I. E., Billah, M.M., Das, C., Barman, S., Das, S., Shawlin, J.F., Ahmed, S.I., & Das, J. (2025). Phytoplankton in contrasting ecosystems of the southeastern coast of Bangladesh: Effects of seasonality and environmental factors. *Environmental Monitoring and Assessment*, 197(3), 260. <https://doi.org/10.1007/s10661-025-13699-y>

Stanca, E., Cellamare, M., & Basset, A. (2013). Geometric shape as a trait to study phytoplankton distributions in aquatic ecosystems. *Hydrobiologia*, 701(1), 99-116. <https://doi.org/10.1007/s10750-012-1262-2>

Sun, J., & Liu, D. (2003). Geometric models for calculating cell biovolume and surface area for phytoplankton. *Journal of Plankton Research*, 25(11), 1331-1346. <https://doi.org/10.1093/plankt/fbg096>

Totti, C., Cangini, M., Ferrari, C., Kraus, R., Pompei, M., Pugnetti, A., Romagnoli, T., Vanucci, S., Socal, G. (2005). Phytoplankton size-distribution and community structure in relation to mucilage occurrence in the northern Adriatic Sea. *Science of the Total Environment*, 353(1–3), 204-217. <https://doi.org/10.1016/j.scitotenv.2005.09.028>

Vajravelu, M., Martin, Y., Ayyappan, S., & Mayakrishnan, M. (2018). Seasonal influence of physico-chemical parameters on phytoplankton diversity, community structure and abundance at Parangipettai coastal waters, Bay of Bengal, South East Coast of India. *Oceanologia*, 60(2), 114-127. <https://doi.org/10.1016/j.oceano.2017.08.003>

Vila, M., & Masó, M. (2005). Phytoplankton functional groups and harmful algae species in anthropogenically impacted waters of the NW Mediterranean Sea. *Scientia Marina*, 69(1), 31-46. <https://doi.org/10.3989/scimar.2005.69n131>

Wang, X., Sun, J., & Yu, H. (2022). Distribution and environmental impact factors of phytoplankton in the Bay of Bengal during autumn. *Diversity*, 14(5), 1-12. <https://doi.org/10.3390/d14050361>

Wang, Y., Liu, Z., Qi, Y., Chen, Y., Zhang, H., Liu, X., & Su, D. (2025). Temporal dynamics of summer phytoplankton communities and their response to environmental changes in the northern Yellow Sea (2011–2020). *Frontiers in Marine Science*, 11(1), 1-18. <https://doi.org/10.3389/fmars.2024.1481701>

Yarahmadi, Z., Archangi, B., Savari, A., & Nabavi, S.M.B. (2023). Combined morphological and molecular phylogenetic analysis of the genus *Tripos* (Dinophyceae) from the Persian Gulf. *Plant, Algae, and Environment*, 7(1), 969-987. <https://doi.org/10.48308/jpr.2023.231640.1045>