

VOL.67 NO.02 JULY-DECEMBER 2025 • PRINT ISSN 0025-3146 • ONLINE ISSN 2321-7898

JMBAI

**JOURNAL OF THE MARINE
BIOLOGICAL ASSOCIATION OF INDIA**



MBAI
Marine Biological Association of India





Evaluating environmental influence on *Acromitus flagellatus* Maas, 1903 (Cnidaria: Scyphozoa) blooms in the tropical estuaries and backwaters along southwest India

A. Riyas^{1,3}, K. Anoop Krishnan² and A. Biju Kumar^{3*}

¹Department of Aquaculture and Fishery Microbiology, MES Ponnani College, Malappuram-679 586, Kerala, India.

²Marine Biology Laboratory, National Centre for Earth Science Studies, Thiruvananthapuram- 695 011, Kerala, India.

³Department of Aquatic Biology and Fisheries, University of Kerala, Thiruvananthapuram- 695 581, Kerala, India.

*Correspondence e-mail: bijupzhayoram@gmail.com

ORCID: <https://orcid.org/0000-0001-5477-2119>

Received: 21 August 2025 Revised: 03 October 2025

Accepted: 10 October 2025 Published: 01 December 2025

Original Article

Abstract

Scyphozoan blooms, driven by complex interactions between biological and environmental factors, have garnered considerable attention due to their ecological, economic, and social consequences. In India, blooms of *Acromitus flagellatus* Maas, 1903 pose significant challenges for local fishers. Despite this, there is a notable gap in comprehensive research on the correlation between *A. flagellatus* blooms and hydrographic factors in the backwaters and estuaries of Kerala. This study aims to investigate the connection between *A. flagellatus* blooms and environmental parameters. Monthly data on the abundance of *A. flagellatus* were collected from 12 stations across Kerala during pre-monsoon and post-monsoon seasons through extensive field surveys and visual counts from 2016 to 2019. Principal Component Analysis (PCA) revealed relationships between *A. flagellatus* abundance and hydrographic parameters during pre- and post-monsoon seasons over the four years. Multiple regression analysis indicated a positive correlation between *A. flagellatus* abundance and factors such as temperature, chlorophyll-*a*, pH, and nitrate (NO₃⁻) concentrations in the water. The seasonal abundance of *A. flagellatus*, along with the associated ecological changes and impacts on the local estuarine fishery, is discussed. Understanding the triggers of *A. flagellatus* blooms will enable stakeholders to better predict and mitigate their impacts on fisheries, tourism, and overall ecosystem health, thereby supporting more sustainable management of these ecosystems.

Keywords: Jellyfish, Scyphozoa, bloom, estuary, hydrography, fishery

Introduction

Estuarine ecosystems are highly dynamic and mosaic habitats characterised by diverse physical, biological, and chemical processes (O'Higgins *et al.*, 2010). These ecosystems play a crucial role as nursery grounds for fish, crustaceans, and other invertebrates, providing shelter and food for juvenile species (Holsman *et al.*, 2006; Wouters and Cabral, 2009). However, the growing human population near estuaries has significantly altered their structure and functioning (Elliott and Whitfield, 2011) through nutrient loading (Bianchi *et al.*, 2000; Barletta *et al.*, 2019), toxic pollution (Tomlinson *et al.*, 1980; Roveta *et al.*, 2021), and habitat modification (Nilsson *et al.*, 2005; Lotze *et al.*, 2006). Additionally, increased organic material has heightened dissolved oxygen consumption, leading to spatiotemporal shifts along estuarine gradients (Barletta *et al.*, 2019).

Over the past few decades, jellyfish blooms have been recorded in many estuarine, coastal, and marine environments worldwide, showing significant temporal variations (Purcell *et al.*, 2007; Richardson *et al.*, 2009; Pitt *et al.*, 2018; Fernández-Alías *et al.*, 2021; Vineetha *et al.*, 2022; Fernández-Alías *et al.*, 2024). Jellyfish are vital components of many estuarine systems, often forming dominant blooms that affect ecosystem services (Schneider-Meyer *et al.*, 2018; Goldstein and Steiner, 2020). A high abundance of jellyfish can degrade estuary quality and negatively impact native species (Xian *et al.*, 2005), disrupting the food web by over-consuming zooplankton and limiting resources for indigenous species (Xian *et al.*, 2005).

Human activities and climate change have exacerbated jellyfish numbers and their ecological impacts in estuaries (Baumsteiger *et al.*, 2018). Jellyfish dynamics are mainly driven by environmental changes and are further amplified by anthropogenic factors such as global warming, eutrophication, overfishing, and ocean sprawl (Purcell, 2012; Boero, 2013; Duarte *et al.*, 2013). Alterations in river flow, which affect estuarine salinity levels (Purcell *et al.*, 1999, 2009), also influence jellyfish reproductive patterns by altering polyp feeding behaviours (Holst and Jarms, 2010) and planula larvae settlement (Conley and Uye, 2015). Massive jellyfish blooms are closely linked to environmental variability and specific species traits, often appearing and disappearing based on changing environmental conditions (Dawson and Hamner, 2009; Schnedler-Meyer *et al.*, 2018).

Research on jellyfish blooms in Indian estuaries has been relatively scarce, with most studies focusing on hydromedusae (Annandale, 1907; Vannucci *et al.*, 1970; Santhakumari, 1992; Santhakumari *et al.*, 1997, 1999). More recent studies have investigated scyphozoans in the estuarine waters of Kerala (Sandhya *et al.*, 2020; Karati *et al.*, 2021; Vineetha *et al.*, 2022) and the Sundarbans deltaic region (Siddique *et al.*, 2022; Bhowal *et al.*, 2023).

Acromitus flagellatus, a jellyfish species from the Catostylidae family, has received limited research attention despite its ecological significance. This species proliferates in Indian estuarine waters, impacting fishing activities (Sandhya *et al.*, 2020), yet its effects on ecosystem services remain largely unexplored. There is a significant gap in data on its ecology, population structure, and the hydrographic factors influencing its blooms. This study aims to investigate the population dynamics of *A. flagellatus* across tropical estuaries in southwest India, correlating these fluctuations with hydrological parameters such as surface water temperature, salinity, pH, dissolved oxygen, chlorophyll-*a*, and nutrient concentrations (phosphate, silicate, nitrite, nitrate, and ammonia).

Material and methods

Study area

Sampling activities were carried out in the twelve major estuarine and brackish waters of the Kerala coast along the southwestern Arabian Sea. Most of the estuaries along the southwest coast of India are semi-diurnal and micro-tidal, with a tidal range of 1 to < 2m. All the estuaries have a connection to the Arabian Sea, and the rivers that originate from the Western Ghats input fresh water into the estuaries. During the southwest monsoon season (June to September) and northeast monsoon (October and November), the effect of freshwater will be close to the mouth, and the intrusion of

salt water will be limited to a short distance in the estuary from the mouth (Varma *et al.*, 2002).

Sampling of jellyfish

Jellyfish abundance was monitored from 2016 to 2019 through monthly surveys conducted during the pre-monsoon (February–May) and post-monsoon (November–January) seasons. Visual counts were performed twice a month during daylight hours across estuarine and brackish waters in Kerala (Fig. 1). Abundance was quantified as the number of medusae per 9 m² area (3 m × 3 m). The monthly abundance was determined by averaging data from two bi-monthly surveys conducted at six locations within each estuary. For analysis, mean jellyfish abundance recorded from February to May was classified as pre-monsoon, while that from November to January was categorised as post-monsoon, with all values expressed as individuals per 100 m².

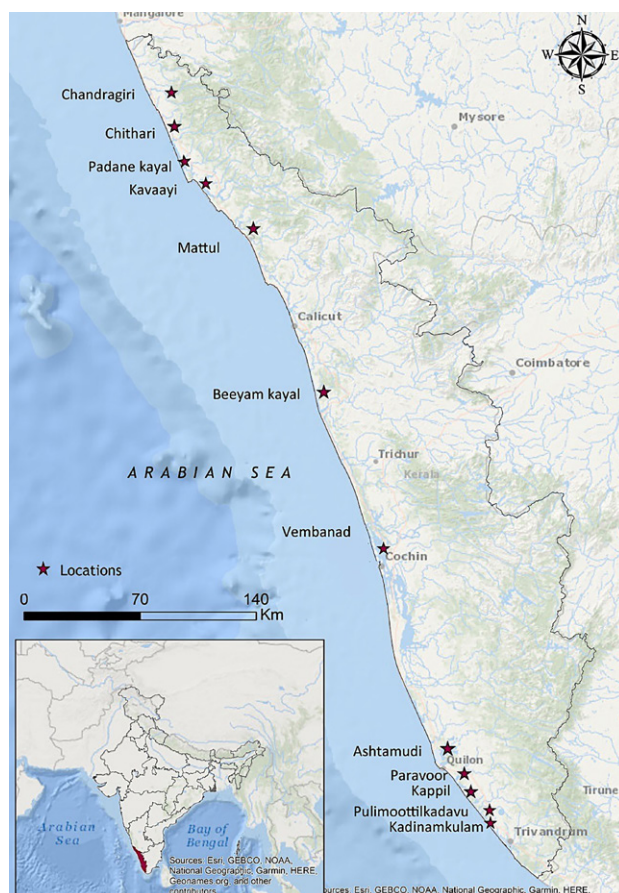


Fig. 1. Location map of selected estuaries and backwaters in Kerala, where *Acromitus flagellatus* sampled during different seasons over four years, 2016–2019; Southern estuaries (Kadinamkulam, Pulimootilkadavu, Kappil, Paravoor Lake, Ashtamudi, Vembanad, and Beeyamkayal) were sampled during the pre-monsoon season (February–May), while northern estuaries (Mattul, Kavaayi, Padane Kayal, and Chithari) were sampled during the post-monsoon season (November–January).

Hydrographic data

The collection of water quality data occurred simultaneously with the acquisition of jellyfish abundance data from the estuarine waters of Kerala. Water samples were collected using Teflon-coated Niskin samplers and decanted from the doorknob of the sampler using silicone-made rubber tubing. The water temperature was measured with a calibrated mercury thermometer with a small mercury bulb for better accuracy. Salinity, dissolved oxygen and pH were measured using a portable water quality analyser (Make: Eutech, Model: Waterproof Cyber scans PCD 650). Alkalinity was checked using the titration method with 0.01 N HCl based on the international standard method (APHA, 2012). Phosphate (PO_4^{3-}) and silicate (SiO_4^{4-}) were examined by spectrophotometry (Shimadzu, UV-1800). Total phosphorus was analysed by the ammonium molybdate method after being oxidised by potassium persulfate. Nitrite (NO_2^-) and nitrate (NO_3^-) were analysed using the α -methylamine and cadmium reduction methods. All of the above analyses were carried out using the standard methods prescribed by APHA (2012). Chlorophyll-*a* (Chl-*a*) was analysed by the acetone extraction method of Grasshoff *et al.* (1999) and detected by using a UV-Vis Spectrophotometer (630–645 nm, Shimadzu UV-1800). Hydrographic data are provided in Table 1.

Statistical analysis

Principal component analysis (PCA) was performed to understand how the nine environmental parameters, namely temperature ($^{\circ}\text{C}$), salinity (ppt), chlorophyll-*a* (mg/m^3), pH, Dissolved Oxygen (mg/l),

NO_2^- ($\mu\text{mol}/\text{l}$), NO_3^- ($\mu\text{mol}/\text{l}$), PO_4^{3-} ($\mu\text{mol}/\text{l}$) and SiO_4^{4-} ($\mu\text{mol}/\text{l}$) differed for pre- and post-monsoon periods of four-year study from 2016 to 2019. PCA was performed on the correlation matrix of log-transformed data. The null hypothesis that there was no significant difference between hydrological parameters of pre- and post-monsoon seasons was tested using PERMANOVA (Anderson, 2001) employing Euclidean distances and 9999 permutations. Three environmental parameters that had low factor loading on the first PCA axis, namely salinity (ppt), Dissolved Oxygen (mg/l), and SiO_4^{4-} ($\mu\text{mol}/\text{l}$), were removed from the multiple regression analysis to understand the correlation between the dependent variable (jellyfish abundance) and independent variables (environmental parameters). Change in the abundance of jellyfish in pre- and post-monsoon seasons during the four-year study was studied using Pearson's correlation coefficient after confirming the normality of data using the Shapiro-Wilk (W) and Jarque-Bera (JB) test statistics. Statistical analysis was performed in PAST 4.10 (Hammer *et al.*, 2001).

Results

Abundance

Acromitus flagellatus is the major blooming species in the estuarine waters of Kerala (Fig. 2 a-f). For all four years, jellyfish abundance was higher in pre-monsoon than post-monsoon seasons (Fig. 3). The average abundance of *A. flagellatus* was higher (>300 ind/100 m^2) in pre-monsoon than in post-monsoon (>60 ind/100 m^2) in 2016. The average abundance of the medusa during 2017 ranged from >250 ind/100 m^2 in pre-monsoon and >100 ind/100 m^2 in post-monsoon. In 2018, the abundance of

Table 1. Seasonal variation in hydrographic parameters and their standard deviations (in brackets) across estuaries in Kerala. Pre-monsoon data represent southern estuaries, while post-monsoon data correspond to northern estuaries

Environmental Parameters	2016		2017		2018		2019	
	Pre Monsoon	Post Monsoon	Pre Monsoon	Post Monsoon	Pre Monsoon	Post Monsoon	Pre Monsoon	Post Monsoon
Temperature ($^{\circ}\text{C}$)	30.14 (0.21)	29.55 (0.14)	29.90 (0.10)	29.35 (0.07)	31.20 (0.16)	29.94 (0.07)	30.20 (0.07)	29.50 (0.26)
Salinity (ppt)	25.51 (0.31)	24.87 (0.46)	25.13 (0.29)	23.50 (0.16)	24.70 (0.25)	21.01 (0.36)	23.00 (0.55)	24.50 (0.60)
Chl- <i>a</i> (mg/m^3)	2.20 (0.18)	6.80 (0.36)	2.23 (0.19)	6.80 (0.26)	2.28 (0.18)	1.75 (0.29)	2.87 (0.13)	4.90 (0.47)
pH	7.60 (0.10)	7.10 (0.05)	7.60 (0.09)	6.89 (0.13)	7.60 (0.06)	7.45 (0.05)	7.65 (0.08)	7.30 (0.07)
DO (mg/l)	5.10 (0.27)	3.24 (0.23)	4.80 (0.15)	5.12 (0.25)	4.53 (0.17)	5.42 (0.06)	4.53 (0.10)	4.90 (0.36)
NO_2^- ($\mu\text{mol}/\text{l}$)	1.50 (0.17)	0.74 (0.09)	1.67 (0.14)	1.33 (0.14)	1.76 (0.08)	1.47 (0.07)	1.80 (0.12)	1.33 (0.15)
NO_3^- ($\mu\text{mol}/\text{l}$)	5.30 (0.18)	12.11 (0.43)	6.00 (0.29)	29.6 (0.75)	6.20 (0.40)	16.80 (0.22)	6.32 (0.20)	22.00 (0.48)
PO_4^{3-} ($\mu\text{mol}/\text{l}$)	1.60 (0.17)	2.60 (0.27)	1.50 (0.08)	2.60 (0.24)	1.95 (0.07)	2.75 (0.22)	2.10 (0.10)	2.6 (0.26)
SiO_4^{4-} ($\mu\text{mol}/\text{l}$)	33.00 (0.74)	33.8 (0.38)	31.1 (0.42)	29.00 (0.46)	31.00 (0.51)	43.00 (1.48)	31.60 (0.42)	12.00 (0.42)



Fig. 2. *Acromitus flagellatus* blooms along the estuaries of South India (a) *A. flagellatus* blooms in the Kappil estuary, Kerala; (b) *A. flagellatus* aggregation in the barmouth of Kappil estuary; (c) Caught in the fishing net; (d) *A. flagellatus* collected by fishing nets; (e) *A. flagellatus* blooms in Chithari, Kerala; (f) Group of moribund jellyfish

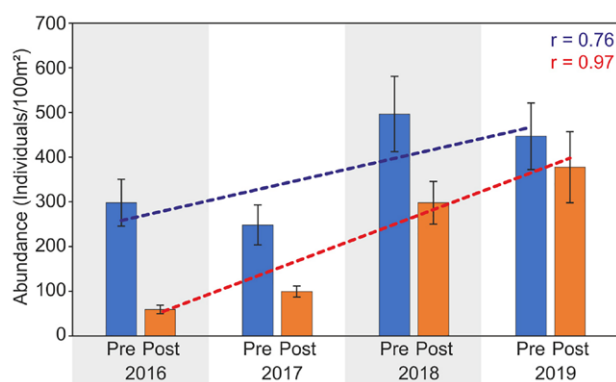


Fig. 3. Average jellyfish abundance during the pre- and post-monsoon seasons over a four-year study in estuaries along the southwest coast of India. Pre-monsoon data reflect jellyfish abundance in southern estuaries (Kadinamkulam, Pulimootilkadavu, Kappil, Paravoor Lake, Ashtamudi, Vembanad, and Beeyamkayal), while post-monsoon data represent northern estuaries (Mattul, Kavaayi, Padane Kayal, and Chithari). Error bars indicate standard errors. Abundance data for both pre ($W = 0.911$, $P = 0.4877$; $JB = 0.5272$, $P = 0.7683$) and post ($W = 0.8953$, $P = 0.4083$; $JB = 0.5391$, $P = 0.7637$) monsoon seasons were normal and showed a significant ($P < 0.05$) positive relationship

A. flagellatus was higher (>500 ind/100 m²) in pre-monsoon and (>300 ind/100 m²) in post-monsoon compared with the preceding years. Similarly, the average abundance of medusae in 2019 ranged from >450 ind/100 m² in pre-monsoon and >380 ind/100 m² in post-monsoon, which is higher compared with 2016 and 2017. The present study noticed that the abundance of *A. flagellatus* is predominant during pre-monsoon in Southern Kerala (Kadinamkulam, Pulimootilkadavu, Kappil, Paravoor lake, Ashtamudi, Vembanad and Beeyamkayal) and blooms were more during the post-monsoon season in the northern part of Kerala (Mattul, Kavaayi, Padane Kayal, Chithari, Chandragiri). There was a linear increase in jellyfish blooms in all four years (Fig. 3).

Hydrography

The hydrographic parameters showed noticeable variations in post-monsoon and pre-monsoon (Table 1). In 2016, water temperature decreased from 30.14 °C (standard error ± 0.21) in pre-monsoon to 29.55 (± 0.14) °C in post-monsoon, with similar variations in succeeding years. Chlorophyll-*a* concentration increased during post-monsoon, and it declined during pre-monsoon. NO₃⁻ was high in the post-monsoon and fell sharply in the pre-monsoon. pH was higher in the pre-monsoon than in the post-monsoon. Phosphate was higher in post-monsoon as compared to pre-monsoon. In contrast, hydrographic parameters such as dissolved oxygen, sulphate and salinity do not show specific variations between post-monsoon and pre-monsoon seasons. In both seasons, salinity ranged between averages of 21.01 (± 0.36) ppt to 25.51 (± 0.31) ppt. The lowest salinity (21.01 ppt) was noticed during post-monsoon in 2018, and the highest salinity (25.51 ppt) was observed during pre-monsoon in 2017. The complex dynamics of hydrographic parameters in pre- and post-monsoon periods can be visualised using PCA analysis (Fig. 4), where the two seasons formed significantly different clusters (PERMANOVA, $F = 3.598$, $P = 0.0291$).

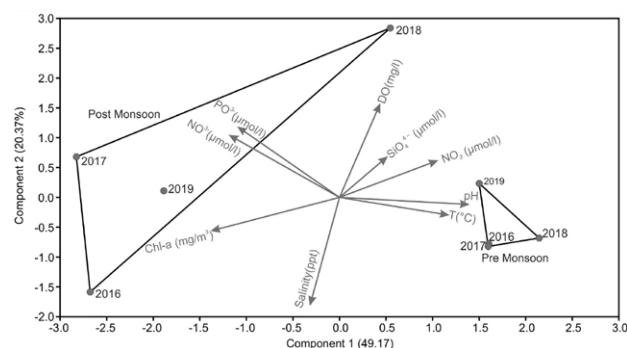


Fig. 4. Principal Component Analysis of environmental variables during pre- and post-monsoon periods from 2016 to 2019 in estuaries along the southwest coast of India. Pre-monsoon environmental variables correspond to southern estuaries, while post-monsoon variables represent northern estuaries. Values in parentheses are percentage variances explained by each principal component

There was a significant correlation between jellyfish abundance and a subset of environmental parameters (Table 2), such as temperature, chlorophyll-*a*, pH and NO₃⁻ positively influencing jellyfish abundance. NO₂⁻ and PO₄³⁻ did not affect the jellyfish abundance (Table 2). Although we removed salinity, dissolved oxygen and SiO₄⁴⁻, which were orthogonal in PCA analysis, from multiple regression, we reconfirmed their contribution to jellyfish abundance. Three further environmental factors were not correlated to jellyfish abundance (Salinity: $t = -0.86$, $P = 0.4376$; DO: $t = 0.42$, $P = 0.6934$; SiO₄⁴⁻: $t = -0.80$, $P = 0.4705$).

Discussion

This study documented blooms of *A. flagellatus* in various estuarine waters of Kerala, located on the southwest coast of India. This species has a broad distribution, spanning from the Western Indian Ocean to the Central Pacific Ocean (Jarms and Morandini, 2019), and has been reported in numerous Indian estuaries (Menon, 1930, 1936; Rao, 1931; Gravely, 1941; Panikkar and Aiyar, 1937, 1939; Nair, 1951; Jones, 1960; Chakrapani, 1984; Goswami, 1992; Haldar and Choudhury, 1995; Ramakrishna and Sarkar, 2003; Govindan and Ramanibai, 2017; Peter *et al.*, 2018; Sandhya *et al.*, 2020; Vineetha *et al.*, 2022; Siddique *et al.*, 2022).

The proliferation of *A. flagellatus* poses significant challenges to the local fishers and the fishing industry in Kerala. It clogs fishing nets, especially stake nets, severely reducing their filtering efficiency (Sandhya *et al.*, 2020). Additionally, the jellyfish damage nets and sting fishers during fishing and net-cleaning activities, with more severe reactions occurring when sensitive areas like the face, lips, or eyes are affected. The blooms also impact mussel farming in northern Kerala, where jellyfish encrust the culture racks of the mussel *Perna viridis* in the Madakkara and Padanna estuaries in Kasaragod, causing substantial economic losses.

A. flagellatus blooms were more prevalent during the pre-monsoon period than the post-monsoon period. In northern Kerala (Mattul, Kavaayi, Padane Kayal, Chithari,

and Chandragiri), blooms occurred post-monsoon, while in central (Vembanad) and southern Kerala (Kadinamkulam, Pulimoottilkadavu, Kappil, Paravoor, and Ashtamudi), blooms were more common during pre-monsoon. In the north, jellyfish were absent during pre-monsoon but began blooming at the end of post-monsoon and persisted until early pre-monsoon.

Comparatively, similar seasonal fluctuations in jellyfish abundance have been observed in other regions. For instance, *Aurelia aurita* blooms in Southampton waters lasted 3-4 months during spring and summer (Lucas and Williams, 1994). Other studies in estuarine waters have also demonstrated seasonal patterns in jellyfish abundance (Grondahl, 1988; Garcia, 1990; Lucas and Williams, 1994; Kingsford and Pitt, 1998). In Lake Wooloweyah, Australia, *Catostylus mosaicus* was absent in July but abundant in November, while in Port Stephens, Australia, medusae were present only in November and December of successive years (Kingsford and Pitt, 1998). Geographic separation did not affect recruitment timing, with asynchronous recruitment observed even at locations less than 100 km apart (Kingsford and Pitt, 1998).

Previous research suggests that climate change, fluctuating environmental conditions, and hydrographic instabilities are major contributors to increased jellyfish blooms and ecosystem shifts (Purcell, 2012; Robinson and Graham, 2013). Temperature is particularly important for the abundance of jellyfish and other gelatinous zooplankton in estuarine ecosystems (Decker *et al.*, 2007; Purcell *et al.*, 2007; Schroeter, 2008). Changes in these environmental factors may trigger biological responses, with some species reaching their physiological tolerance limits, while others, like *A. flagellatus*, proliferate (Tolan, 2007).

In this study, we found a positive correlation between the abundance of *A. flagellatus* and rising temperatures. Past studies suggest that water temperature provides environmental cues that promote the growth and reproduction of polyps, which have significant implications for the distribution and abundance of pelagic medusae (Lucas, 2001; Willcox *et al.*, 2007; Sokolowski *et al.*, 2016). Rising temperatures likely enhance the release of medusae from benthic polyps, contributing to greater jellyfish abundance in the Cochin estuary (Vineetha *et al.*, 2022). Similar studies in the Sundarbans estuaries have confirmed the influence of rising surface temperatures on the surge of *A. flagellatus* (Bhowal *et al.*, 2023; Siddique *et al.*, 2022). Higher surface temperatures accelerate jellyfish reproduction, strobilation, and population growth (Lotan *et al.*, 1994; Siddique *et al.*, 2022).

Similarly, chlorophyll-*a*, nitrate (NO₃⁻), and pH also showed significant correlations with jellyfish abundance. Increased chlorophyll-*a* during post-monsoon has been linked to higher

Table 2. Multiple regression of jellyfish abundance and environmental variables

Environmental variables	Standardised coefficients	t	P	R ²
Temperature (°C)	0.65	17.85	0.0356	0.5536
Chl- <i>a</i> (mg/m ³)	1.08	18.00	0.0353	0.4746
pH	2.49	26.97	0.0236	0.5931
NO ₂ ⁻ (μ mol/l)	-0.08	-1.75	0.3310	0.4535
NO ₃ ⁻ (μ mol/l)	1.30	16.71	0.0381	0.2008
PO ₄ ³⁻ (μ mol/l)	0.06	1.50	0.3738	0.1045

nutrient concentrations, supporting elevated phytoplankton production and jellyfish abundance (Karati *et al.*, 2021).

Vineetha *et al.* (2022) observed a significant increase in phytoplankton biomass (chlorophyll-*a*) in the Cochin estuary during the pre-monsoon period, with a more pronounced rise in larger phytoplankton, including macro- and micro-sized species, compared to smaller nano- and pico-phytoplankton. This suggests that nutrient-rich conditions during the pre-monsoon season favour the proliferation of larger phytoplankton in the estuary. Estuaries, enriched with nutrients from urbanisation and industrialisation, support primary consumers like copepods, creating food-rich environments for secondary consumers such as jellyfish (Purcell, 2012). The positive correlation between jellyfish abundance and nitrate levels likely results from increased zooplankton biomass driven by nutrient availability, particularly during the post-monsoon season (Karati *et al.*, 2021; Vineetha *et al.*, 2022).

Few studies have explored the relationship between jellyfish abundance and nitrates (Pitt *et al.*, 2009; Low *et al.*, 2016; Hubot *et al.*, 2021). Research indicates that jellyfish excrete ammonium as a metabolic waste product, which diffuses through their body surface (Low *et al.*, 2016). This ammonium serves as a key substrate for nitrifying bacteria and archaea, which oxidise it into nitrite and subsequently nitrate, generating energy in the process (Hubot *et al.*, 2021). During jellyfish blooms, elevated ammonium release can increase nitrite and nitrate levels, potentially stimulating primary production and altering phytoplankton community composition within the ecosystem (Shilova *et al.*, 2017).

Ocean acidification and changes in pH can also affect jellyfish ephyrae and behaviour (Tills *et al.*, 2016). For example, *Rhopilema esculentum* in Japanese waters can swim and feed optimally at a pH of 7.9–8.5 (Gu *et al.*, 2005). While studies on the relationship between pH and jellyfish blooms in estuarine waters are limited, further research could shed light on these dynamics.

Conclusion

This study investigated the relationship between hydrographic parameters and the abundance of *Acromitus flagellatus* in tropical estuaries along the southwest coast of India. We documented *A. flagellatus* blooms and their correlation with regional hydrographic factors, with a notable prevalence during the pre-monsoon period. This preliminary exploration lays the foundation for future research. Our findings suggest that temperature, chlorophyll-*a*, pH, and NO₃⁻ are linked to *A. flagellatus* abundance. However, to fully understand the drivers behind jellyfish blooms, a more comprehensive

investigation considering eutrophication, overfishing, artificial settlement substrates, and climate change is necessary.

Acknowledgements

We are thankful to the Kerala State Council for Science, Technology, and Environment for the financial support for the project. We are grateful to Dr Neelesh Dahanukar of the Department of Life Sciences, School of Natural Sciences, Shiv Nadar Institution of Eminence, Delhi-NCR, for his invaluable assistance in conducting the statistical analysis.

Author contributions

Conceptualisation: AR, ABK; Methodology: AR; Data Collection: AR, KAK, ABK; Data Analysis: AR, KAK; Writing Original Draft: AR; Writing Review and Editing: ABK; Funding Acquisition and Supervision: ABK.

Data availability

The data are available and can be requested from the corresponding author.

Conflict of interest

The authors declare that they have no conflict of financial or non-financial interests that could have influenced the outcome or interpretation of the results.

Ethical statement

No ethical approval is required as the study does not include activities that require ethical approval or involve protected organisms/ human subjects/ collection of samples/ protected environments.

Funding

This research was supported by the Kerala State Council of Science, Technology and Environment.

Publisher's note

The views and claims presented in this article are solely those of the authors and do not necessarily reflect the positions of the publisher, editors, or reviewers. The publisher does not endorse or guarantee any claims made by the authors or those citing this article.

References

- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral. Ecol.*, 26: 32–46.
- Annandale, N. 1907. Notes on the fresh-water fauna of India. Preliminary note on the occurrences of a medusa (*Irene ceylonensis*) in a brackish pool in the Ganges Delta, and on the hydroid stage of the species. *J. Asiat. Soc. Bengal (N.S.)*, 8 (2): 79–81.
- APHA, 2012. Standard Methods for the Examination of Water and Wastewater. In: E.W. Rice, R. B. Baird, A. D. Eaton, and L. S. Clesceri (Eds.). 22nd Edition. American Public Health Association, American Water Works Association, and Water Environment Federation, Washington, D.C., USA.
- Barletta, M., A. R. A. Lima and M. F. Coast. 2019. Distribution, sources and consequences of nutrients, persistent organic pollutants, metals and microplastics in South American estuaries. *Sci. Total. Environ.*, 651: 1199–1218.
- Baumsteiger, J., T. A. O'Rear, J. D. Cook, A. D. Manfree and P. B. Moyle. 2018. Factors affecting distribution and abundance of jellyfish medusae in a temperate estuary: a multi-decadal study. *Biol. Invasions*, 20: 105–119.
- Bianchi, T. S., E. Engelhaupt, P. Westman, T. Andr n, C. Rolff and R. Elmgren. 2000. Cyanobacterial blooms in the Baltic Sea: natural or human-induced?. *Limnol. Oceanogr.*, 45: 716–726.
- Boero, F. 2013. Review of jellyfish blooms in the Mediterranean and Black Sea. Studies and Reviews. General Fisheries Commission for the Mediterranean. No. 92. Food and

- Agriculture Organization of the United Nations, Rome, Italy. 53 pp. <https://www.fao.org/4/i3169e/i3169e.pdf>
- Bhowal, A., A. Siddique, H. Prasad J. Purushothaman and D. Banerjee. 2023. Comparison of microzooplankton community structure before and during *Acromitus flagellatus* swarm in the estuarine waters of northern Bay of Bengal. *Reg. Stud. Mar. Sci.*, 61: 102864.
- Chakrapani, S. 1984. Studies on marine invertebrates scyphomedusae of the Indian and adjoining seas (PhD thesis). University of Madras, India. <https://shodhganga.inflibnet.ac.in/handle/10603/243098>
- Conley, K. and S. Uye. 2015. Effects of hyposalinity on survival and settlement of moon jellyfish (*Aurelia aurita*) planulae. *J. Exp. Mar. Biol. Ecol.*, 462: 14-19.
- Dawson, M. N. and W. M. Hamner. 2009. A character-based analysis of the evolution of jellyfish blooms: adaptation and exaptation. *Hydrobiologia*, 616: 193-215.
- Decker, M. B., C. W. Brown, R. R. Hood, J. E. Purcell, T. F. Gross, J. C. Matanoski, R. O. Bannon and E. M. Setzler-Hamilton. 2007. Predicting the distribution of the scyphomedusa *Chrysaora quinquecirrha* in Chesapeake Bay. *Mar. Ecol. Progress. Ser.*, 329: 99-113.
- Duarte, C. M., K. A. Pitt, C. H. Lucas, J. E. Purcell, S. I. Uye, K. Robinson, L. Brotz, M. B. Decker, K. R. Sutherland, A. Malej, L. Madin, H. Mianzan, J. M. Gilli, V. Fuentes, D. Atienza, F. Pagés, D. Breitburg, J. Malek, W. M. Graham and R. H. Condon. 2013. Is global ocean sprawl a cause of jellyfish blooms? *Front. Ecol. Environ.*, 11: 91-97.
- Elliott, M. and A. K. Whitefield. 2011. Challenging paradigms in estuarine ecology and management. *Estuar. Coast. Shelf. Sci.*, 94(4): 306-314.
- Fernández-Álías, A., C. Marcos and A. Pérez-Ruzafa. 2024. The unpredictability of scyphozoan jellyfish blooms. *Front. Mar. Sci.*, 11: 1349956.
- Fernández-Álías, A., C. Marcos and A. Pérez-Ruzafa. 2021. Larger scyphozoan species dwelling in temperate, shallow waters show higher blooming potential. *Mar. Pollut. Bull.*, 173: 113100.
- García, J. R. 1990. Population dynamics and production of *Phyllorhiza punctata* (Cnidaria: Scyphozoa) in Laguna Joyuda, Puerto Rico. *Mar. Ecol. Prog. Ser.*, 64:243-251.
- Goldstein, J. and U. K. Steiner. 2020. Ecological drivers of jellyfish blooms – The complex life history of a 'well-known' medusa (*Aurelia aurita*). *J. Anim. Ecol.*, 89: 910-920.
- Goswami, B. C. B. 1992. Marine fauna of Digha coast of West Bengal, India. *J. Mar. Biol. Assoc. India*, 34: 115-137.
- Govindan, S. and R. Ramanibai. 2017. Report on cnidarians from Pulicat Lagoon. *Fish and Ocean Opj.*, 4 (2): 555632.
- Grasshoff, K., K. Kremling and M. Erhardt. 1999. Methods of Seawater Analysis, third ed. Wiley-VCH Verlag: Germany, 600p.
- Gravely, F. H. 1941. Shells and other animal remains found on the Madras beach. I. Groups other than snails, etc. (Mollusca, Gastropoda). Bulletin of the Madras Government Museum. 5 (1): 112.
- Gröndahl, F. 1988. A comparative ecological study on the scyphozoans *Aurelia aurita*, *Cyanea capillata*, and *C. lamarckii* in the Gullmar Fjord, western Sweden, 1982 to 1986. *Mar. Biol.*, 97: 541-550.
- Gu, L., M. Guo, H. Liu J. Liu, Z. Sun and Y. Lei. 2005. The physical-chemical factors affecting jellyfish *Rhopilema esculenta* breeding. *J. Dalian Fisher. Univ.*, 20(1): 41-44.
- Haldar, B.P., and A. Choudhury. 1995. Medusae: Cnidaria Estuarine ecosystem series, Part 2: Hugli Matla Estuary ZSI: Calcutta.
- Hammer, Ø., D. A. T. Harper and P. D. Ryan. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontol. Electron.* 4(1): 9
- Holsman, K. K., P. S. McDonald and D. A. Armstrong. 2006. Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Mar. Ecol. Prog. Ser.*, 308: 183-195.
- Holst, S. and G. Jarms. 2010. Effects of low salinity on settlement and strobilation of Scyphozoa (Cnidaria): is the lion's mane *Cyanea capillata* (L.) able to reproduce in the brackish Baltic Sea? *Hydrobiologia*. 645: 53-68).
- Hubot, N. D., S. L. C. Giering, J. Füssel, J. Robidart, A. Birchill, M. Stinchcombe, C. Dumousseaud and C.H. Lucas. 2021. Evidence of nitrification associated with globally distributed pelagic jellyfish. *Limnol. Oceanogr.*, 66 (6): 2159-2173.
- Jarms, G. and A.C. Morandini. 2019. World Atlas of Jellyfish. Dölling und Galitz Verlag, 816.
- Jones, S. 1960. Notes on Animal Associations. 2. The Scyphomedusa, *Acromitus flagellatus* Stiasny and young *Seleroides leptolepis* (Cuvier & Valenciennes) with the latter forming a vanguard. *J. Mar. Biol. Assoc. India*, 2 (1): 51-52.
- Karati, K. K., C. R. Ashadevi, N. V. Harikrishnachari, S. Valliyodan, M. Kumaraswami, S. A. Naidu and M. A. Ramanamurthy. 2021. Hydrodynamic variability and nutrient status structuring the mesozooplankton community of the estuaries along the west coast of India. *Environ. Sci. Pollut. Res.*, 28: 42477-42495.
- Kingsford, M. J. and P. A. Pitt. 1998. Research on the Timing of Reproduction, Abundance, Stock Assessment and Genetics of the Edible Jellyfish *Catostylus mossaicus* in New South Wales Waters. Sydney, Australia: University of Sydney.
- Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson and J. B. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*. 312: 1806-1809.
- Lotan, A., M. Fine and R. Ben-Hillel. 1994. Synchronization of the life cycle and dispersal pattern of the tropical invader scyphomedusan *Rhopilema nomadica* is temperature dependent. *Mar. Ecol. Prog. Ser.*, 109 (1): 59-65.
- Low, P., K. Molnár and G. Kriska. 2016. Atlas of animal anatomy and histology. *Springer*, 413 pp.
- Lucas, C. H. and J. A. Williams. 1994. Population dynamics of the scyphomedusa *Aurelia aurita* in Southampton Water. *J. Plankton. Res.*, 16: 879-895.
- Lucas, K.H. 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia*. 451: 229-246.
- Menon, M.G.K. 1930. The scyphomedusae of Madras and the neighbouring coast. Bulletin of the Madras Government Museum, 3(1): 1-26.
- Menon, M. G. K. 1936. Scyphomedusae of Krusadai Island. Bulletin of the Madras Government Museum, 1 (2): 1-9.
- Nair, K. K. 1951. Medusa of the Trivandrum coast. Part I-Systematics. Bulletin of the Central Research Institute, University of Travancore, Series C. *Natural Sciences*, 2: 47-75.
- Nilsson, C., C. A. Reidy, M. Dynesius and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. *Science*. 308: 405.
- O'Higgins, T. G., S. P. Ferraro, D. D. Dantin, S. J. Jordan and M. M. Chintala. 2010. Habitat scale mapping of fisheries ecosystem service values in estuaries. *Ecol. Soc.*, 15(4): 7.
- Panikkar, N. K. and R. G. Aiyar. 1937. The brackish-water fauna of Madras. *Proc. Indian. Acad. Sci. Section B, Springer India*, 6 (5): 284-337.
- Panikkar, N. K. and R.G. Aiyar. 1939. Observations on breeding in brackish-water animals of Madras. *Proc. Indian. Acad. Sci., Section B*, 9 (5): 343-364.
- Peter, S., B. Manojkumar and D. Pillai. 2018. First record of *Eutonia indicans* (Romanes, 1876) from Kerala waters, India. *Indian J. Mar. Sci.*, 47 (08): 1636-1639.
- Pitt, K. A., C. H. Lucas, R. H. Condon, C. M. Duarte and B. Stewart-Koster. 2018. Claims That Anthropogenic Stressors Facilitate Jellyfish Blooms Have Been Amplified Beyond the Available Evidence: A Systematic Review. *Front. Mar. Sci.*, 5:451.
- Pitt, K. A., D. T. Welsh and R. H. Condon. 2009. Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. *Hydrobiologia*, 616: 133-149.
- Purcell, J. E. 2012. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. *Ann. Rev. Mar. Sci.*, 4: 209-235.
- Purcell, J. E., R. A. Hoover and N. T. Schwarck. 2009. Interannual variation of strobilation by the scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity, and light conditions in situ. *Mar. Ecol. Progr. Ser.*, 375: 139-149.
- Purcell, J. E., S. Uye and W. T. Low. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Mar. Ecol. Progr. Ser.*, 350: 153-174.
- Purcell, J. E., J. R. White, D. A. Nemazie and D. A. Wright. 1999. Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. *Mar. Ecol. Progr. Ser.*, 180: 187-196.
- Ramkrishna and J. Sarkar. 2003. On the Scyphozoa from east coast of India, including Andaman and Nicobar Islands. *Rec. Zool. Surv. India*, 101 (1-2): 25-56.
- Rao, H. S. 1931. Notes on Scyphozoa in the Indian Museum. *Rec. India. Mus.*, 33: 25-62.
- Richardson, A. J., A. Bakun, G. C. Hays and M. J. Gibbons. 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends. Ecol. Evol.*, 24: 312-322.
- Robinson, K. L. and W. M. Graham. 2013. Long-term change in the abundances of northern Gulf of Mexico scyphomedusae *Chrysaora* sp. and *Aurelia* spp. with links to climate variability. *Limnol. Oceanogr.*, 58: 235-253.
- Roveta, C., A. Anna, A. Afghan, C. Barbara, G. Cristina, C. G. Di Camillo, C. Gregorin, S. Illuminati, T. Pulido Mantas, C. Truzzi and S. Puce. 2021. "Biomonitoring of Heavy Metals: The Unexplored Role of Marine Sessile Taxa". *Appl. Sci.*, 11 (2): 580.
- Sandhya, K. M., G. Archana, S. Chinnadurai and R. Saravanan. 2020. Jellyfish menace in estuarine Stake nets operated off Kochi, Kerala. *Fish. Tech. Rep.*, 6 (1): 6-8.
- Santhakumari, V. 1992. Ecology and distribution of hydromedusae from Beypore and Korapuzha, tropical estuaries of southwest coast of India. Proceedings of 4th Kerala Science Congress, p. 280-281
- Santhakumari, V., N. Ramaiah and V. R. Nair. 1997. Ecology of hydromedusae from Bombay Harbour-Thana and Bassein Creek estuarine complex. *Indian J. Sci.*, 26: 162-168.
- Santhakumari, V., L. R. Tiwari and V. R. Nair. 1999. Species composition, abundance and distribution of hydromedusae from Dharamtar estuarine system, adjoining Bombay harbor. *Indian J. Mar. Sci.*, 28: 158-162.
- Schnedler-Meyer, N. A., S. Pigolotti and P. Mariani. 2018. Evolution of Complex Asexual Reproductive Strategies in Jellyfish. *Am. Nat.*, 192 (1): 72-80.
- Schroeter, R. E. 2008. Biology and long-term trends of alien hydromedusae and striped bass in a brackish tidal marsh in the San Francisco Estuary (Ph. D Thesis). University of California, Davis. <https://escholarship.org/uc/item/5gh43754>
- Siddique, A., C. Praveen Raj, A. Bhowal, J. Purushothaman, A. Athira and A. S. Azeez. 2022. The first record of *Acromitus flagellatus* (Maas, 1903) (Cnidaria: Scyphozoa) swarm from the world's largest deltaic ecosystem, the Sundarbans, India. *Reg. Stud. Mar. Sci.*, 55: 1-9.
- Shilova, I. N., M. M. Mills, J. C. Robidart, K. A. Turk-Kubo, K. M. Björkman, Z. Kolber, I. Rapp, G. L. van Dijken, M. J. Church, K. R. Arrigo, E. P. Achterberg and J. P. Zehr. 2017. Differential effects of nitrate, ammonium, and urea as N sources for microbial communities in the North Pacific Ocean. *Limnol. Oceanogr.*, 62: 2550-2574.
- Sokolowski, A., D. Brulin'ska, M. Olenycz and M. Wolowicz. 2016. Does temperature and salinity limit the asexual reproduction of *Aurelia aurita* polyps (Cnidaria: Scyphozoa) in the Gulf of Gdansk (southern Baltic Sea)? An experimental study. *Hydrobiologia*. 773: 49-62.

- Tills, O., X. Sun S. D. Rundle, T. Heimbach, T. Gibson, A. Cartwright, M. Palmer, T. Rudin-Bitterli and J. I. Spicer. 2016. Reduced pH affects pulsing behaviour and body size in ephyrae of the moon jellyfish, *Aurelia aurita*. *J. Exper. Mar. Biol. and Ecol.*, 480: 54-61.
- Tolan, J. M. 2007. El Niño Southern Oscillation impacts translated to the watershed scale: estuarine salinity patterns along the Texas Gulf Coast, 1982 to 2004. *Estuar. Coast. Shelf. Sci.*, 72: 247-260.
- Tomlinson, D. L., J. G. Wilson, C. R. Harris and D. W. Jeffrey. 1980. Problems in the assessment of heavy-metal levels in estuaries and the formation of a pollution index. *Helgolander Meeresunters*, 33: 566-575.
- Varma, K. K., C. J. Cherian, P. S. Mrithunjayan, N. N. Raman and P. Joseph. 2002. Characteristics of temperature and salinity fluctuations in a south Indian estuary. *Earth. Syst. Monit.*, p. 9-14.
- Vannucci, M., V. Santhakumari and E. P. Dos Santos. 1970. The Ecology of Hydromedusae from the Cochin Area. *Mar. Biol.*, 7: 49-58.
- Vineetha, G., V. Kripa, K. M. Karati, N. V. Madhu, P. Anil and M. S. Vishnu Nair. 2022. Surge in the jellyfish population of a tropical monsoonal estuary: A boon or bane to its plankton community dynamics? *Mar. Pollut. Bull.*, 182: 113951.
- Willcox, S., N. A. Moltschaniwskyj and C. Crawford. 2007. Asexual reproduction in scyphistomae of *Aurelia* sp.: effects of temperature and salinity in an experimental study. *J. Exp. Mar. Biol. Ecol.*, 353: 107-114.
- Wouters, N and H. Cabral. 2009. Are flatfish nursery grounds richer in benthic prey? *Estuar. Coast. Shelf. Sci.*, 83(4): 613-620.
- Xian, W., B. Kang and R. Liu. 2005. Jellyfish blooms in the Yangtze Estuary. *Science*, 307: 41. doi:10.1126/science.307.5706.