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Colonization dynamics of periphytic protozoa in a tropical marine ecosystem

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Research Article

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Abstract

For the bioassessment of tropical marine ecosystem, a survey of protozoa colonizing artificial substrate was conducted in the coastal waters of northern Bay of Bengal, Bangladesh. Protozoan samples were collected using glass slides from 1 and 2 m water depths at time intervals of 3, 7, 10, 14, 21, and 28 days during winter and monsoon seasons. Thus, the colonization processes of protozoa were assigned into three stages namely the initial (3 days), transitional (7 days), and equilibrium stages (10–28 days) at two depths in two seasons. Regression analyses demonstrated that the colonization dynamics of protozoa were well fitted to the MacArthur-Wilson model and logistic equation. Species richness reached equilibrium after 10–14 days and species abundance was maximum at a depth of 1 m. These results suggest that samples of protozoa can be collected at 1 m depth in winter season for monitoring the ecological health of tropical marine ecosystems.

Introduction

Periphytic protozoa are common at the air–water interface, where they mediate the flux of carbon and energy from lower (bacteria and microalgae) to higher (metazoans) trophic levels as a primary consumer through the microbial food chain (Zhang *et al.*, 2013; Guiet *et al.*, 2016; Zhong *et al.*, 2017*a*, 2017*b*). Therefore, they play a crucial role in maintaining both functioning process and water quality status in aquatic ecosystems (Guiet *et al.*, 2016).

Because of their cosmopolitan distribution, high abundance, fast growth rates and short generation time, functional diversity, ease of collection, sensitivity to environmental changes, the protozoa have been used as a reliable bioindicator of water quality in aquatic ecosystems (Xu *et al.*, 2009*a*, 2009*b*, 2014; Zhong *et al.*, 2014; Abdullah Al *et al.*, 2018*a*, 2018*b*). So far, however, monitoring surveys using protozoa there are relatively little information available in the context of tropical marine ecosystems exposed to a complex mixture of pollutants such as coastal engineering and dredging, fishing, aquaculture, maritime transport, agricultural activities (Micheli and Halpern, 2005; Lotze *et al.*, 2006; Duong *et al.*, 2007; Sikder and Xu, 2020).

In this study, the colonization dynamics of periphytic protozoa were studied in the coastal waters of northern Bay of Bengal, Bangladesh. The objectives were to (1) determine colonization dynamics of periphytic protozoa at two water depths during winter and monsoon seasons; (2) examine vertical and seasonal variations in protozoan colonization; and (3) suggest an optimal sampling approach for bioassessment surveys using protozoa in tropical marine ecosystems.

Materials and methods

Sampling station and samples of protozoa

The sampling station was located in the coastal waters of northern Bay of Bengal at Cox's Bazar (GPS 21°28'42.7"N 91°57'46.1"E), near the mouth of Bakkhali river (Figure 1). During the study period, the average water depth was ~4 m and the average water transparency was ~1 m.

Samples of protozoa were collected in winter (December 2020) and monsoon (July 2021) seasons using glass slides as artificial substrate after the procedure described by Xu *et al.* (2009*a*, 2009*b*) and Abdullah Al *et al.* (2018*a*, 2018*b*, 2019). In brief, 240 glass slides (each 2.5×7.5 cm = 18.75 cm^2) were fixed to 24 polyvinyl chloride frames ($5 \times 2.5 \times 7.5$ cm). Twelve frames were submerged in water in each season, six frames at 1 m depth and six frames at 2 m depth, and left for 3, 7, 10, 14, 21, and 28 days to allow periphytic protozoa to colonize on slides. These sampling depths were selected based on water transparency data. During each sampling event, two frames were randomly collected from two different depths. The PVC frames were hanged from boat jetty (act as floater) and a sinker was attached at the end of

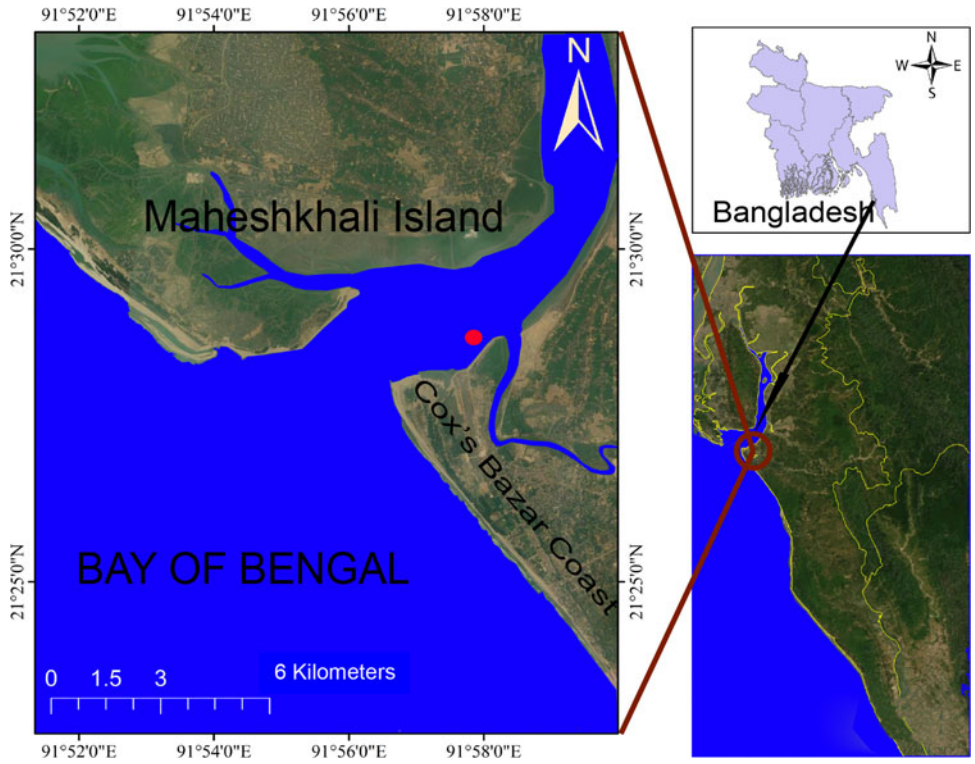

Figure 1. Map of the sampling station in the coastal waters of northern Bay of Bengal, Bangladesh.

the frames hanging rope (Xu *et al.*, 2011; Abdullah Al *et al.*, 2018*a*, 2018*b*). Therefore, the sinker maintained a stable vertical depth against wave action/tidal fluctuations.

After collection slides were transferred into Petri dishes containing *in situ* water and stored in a cool box for transport to the laboratory and then processed as soon as possible to avoid significant changes in protozoan abundance (Zhong *et al.*, 2017*b*).

Environmental parameters

Water temperature (°C), salinity (ppt), and pH were measured instantly using test kits and thermometer. DO (mg/l), TSS (mg/l), TDS (mg/l), PO_4^{2-} (mg/l), and NO_3^- (mg/l) were measured and calculated in the laboratory following APHA (1992).

Species identification and enumeration

Species identification and enumeration were carried out following the methods outlined by Xu *et al.* (2011, 2014) and Song *et al.* (2009). The individual numbers were enumerated at a 10–400-fold magnification under an inverted microscope (Wang and Xu, 2015; Xu *et al.*, 2015*a*, 2015*b*). Slides were examined to record species occurrences and abundances, using bright fields under light inverted microscope. The abundance was calculated from 10 glass slides in each season in each occasion and then averaging across all species pairs, and expressed as individual species number present per square centimetre (ind. cm^{-2}).

Data analysis

The colonization process of periphytic protozoa can be fitted to the colonization equilibrium model expressed by MacArthur and Wilson (1967):

$$S_t = S_{eq}(1-e^{-Gt})$$

where S_t = the species number at time t; S_{eq} = the estimated equilibrium species number of protozoan colonization; G = the constant value of colonization rate; $T_{90\%}$ = the time taken for reaching 90% S_{eq}. Three functional parameters (S_{eq}, G and $T_{90\%}$) were calculated using the statistical software SigmaPlot (v12.5).

Fitness tests were conducted to assess if the species numbers observed according to days fit with the MacArthur–Wilson model at the 0.05 significance level.

The increase of individual abundance over total experimental phase was tested if it was fitted to the logistic model:

$$N_t = N_{max}/[1 + e^{(a-rt)}]$$

where, N_t = the individual abundance at time t; N_{max} = the carrying capacity of individual abundance (maximum abundance); r = the growth rate constant; and a = the coefficient constant of initial individual abundance; $T_{50\%}$ = the time to reach 50% N_{max}. All parameters (e.g., N_{max} and $T_{50\%}$) were estimated using the program SigmaPlot. Fitness tests were to determine whether the individual abundance recorded at each time interval fit with the logistic model at the 0.05 significance level (Zhang *et al.*, 2012).

The multivariate analyses of the community structures were analysed using PRIMER v7.0.21 + PERMANOVA (Anderson *et al.*, 2008; Clarke and Gorley, 2015). A shade plotting analysis in terms of relative abundances of species during colonization period summarized the species distribution, from standardized species-abundance (Anderson *et al.*, 2008; Clarke and Gorley, 2015). The temporal differences in community patterns among depths and seasons during colonization period were summarized, using the submodule dbRDA (distance-based redundancy analysis). Relative abundances of species among the two water depths and seasons during colonization period summarized the vertical species distribution, from standardized species-abundance data (Anderson *et al.*, 2008; Clarke and Gorley, 2015). PERMANOVA test was used for summarizing the significant vertical community variation among two seasons during the colonization period.

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Figure 2. Shade plotting analyses showing species distribution using group-average clustering on Bray–Curtis similarities on fourth root transformed/standardized relative abundance data of each species within the protozoan communities in two seasons and at two depths.

Multivariate correlation analysis (RELATE) was used to test the best matching analysis (BEST) to identify potential driving factors for temporal and spatial structures of the periphytic protozoan communities using the routine BIOENV which were analysed using the program PRIMER (v7.0.21) + PERMANOVA add on (Anderson *et al.*, 2008; Clarke and Gorley, 2015).

A univariate correlation matrix (Pearson) was used to summarize the significant relationship with environmental variables from log-transformed data.

Results

Taxonomic composition and species distribution

A total of 61 species of protozoans were identified at two depths of 1 and 2 m during the study period. Of these, 32 species occurred in winter and 58 species in monsoon season at two depths of 1 and 2 m. The species composition, species distribution in terms of present/absent and ecological types are summarized in Table S1.

In terms of relative abundance, the shade plotting analysis showed that the colonization processes of the protozoan community represented a dynamic pattern with respect to two water depths and seasons (Figure 2).

Four dendograms of the species distribution in the samples of two seasons were plotted using group-average clustering from the index of associations on square root transformed species-abundance data (Figure 3). The cluster analysis revealed 24 species at 1 m in winter falling into seven groups (I–VII) at the 50% similarity level: the protozoa of group I to V were composed of 22 dominant ciliates with high abundance and/or occurrence, and other groups represented the assemblages with low abundance and occurrence (Figure 3a). At a

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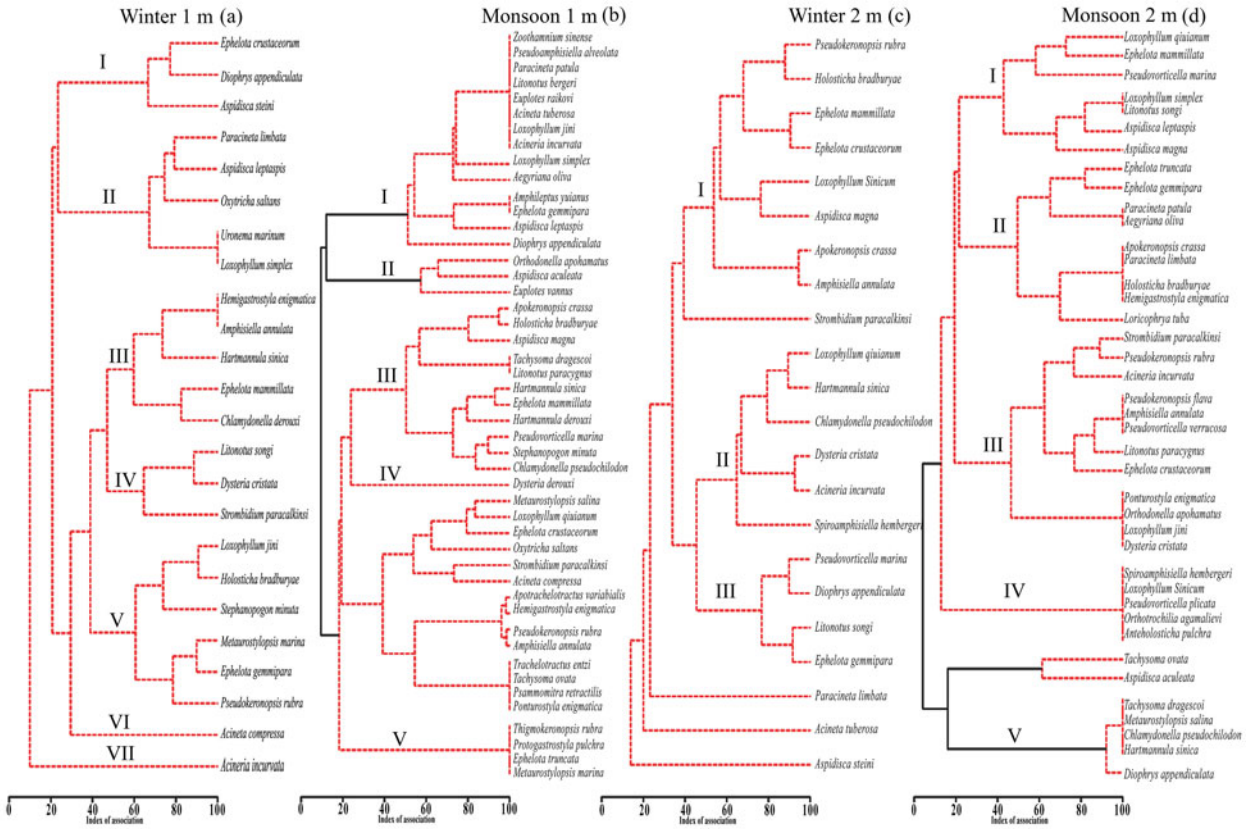

Figure 3. Dendograms of species distribution using group average clustering on index of associations on fourth-root transformed/standardize data of each species within the periphytic protozoa in two seasons and at two depths.

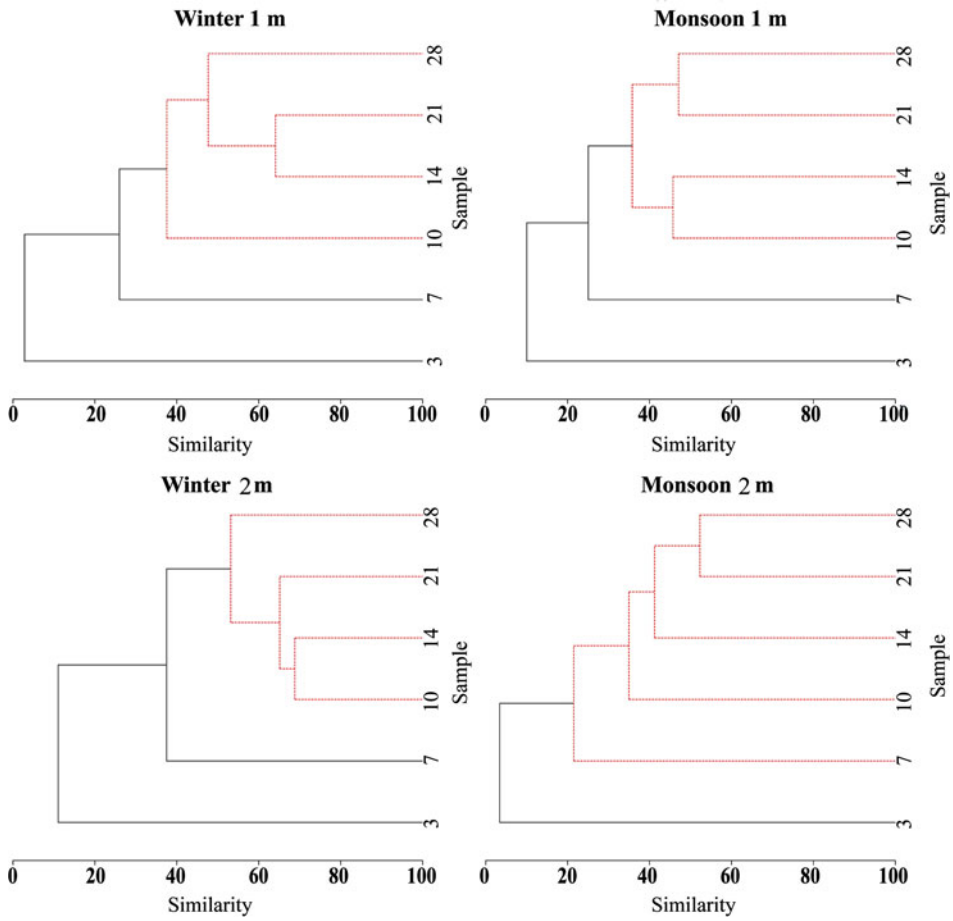

Figure 4. Cluster analyses with SIMPROF tests showing variation in each of the colonization stage in each season of periphytic protozoa during the colonization process in two seasons and at two depths.

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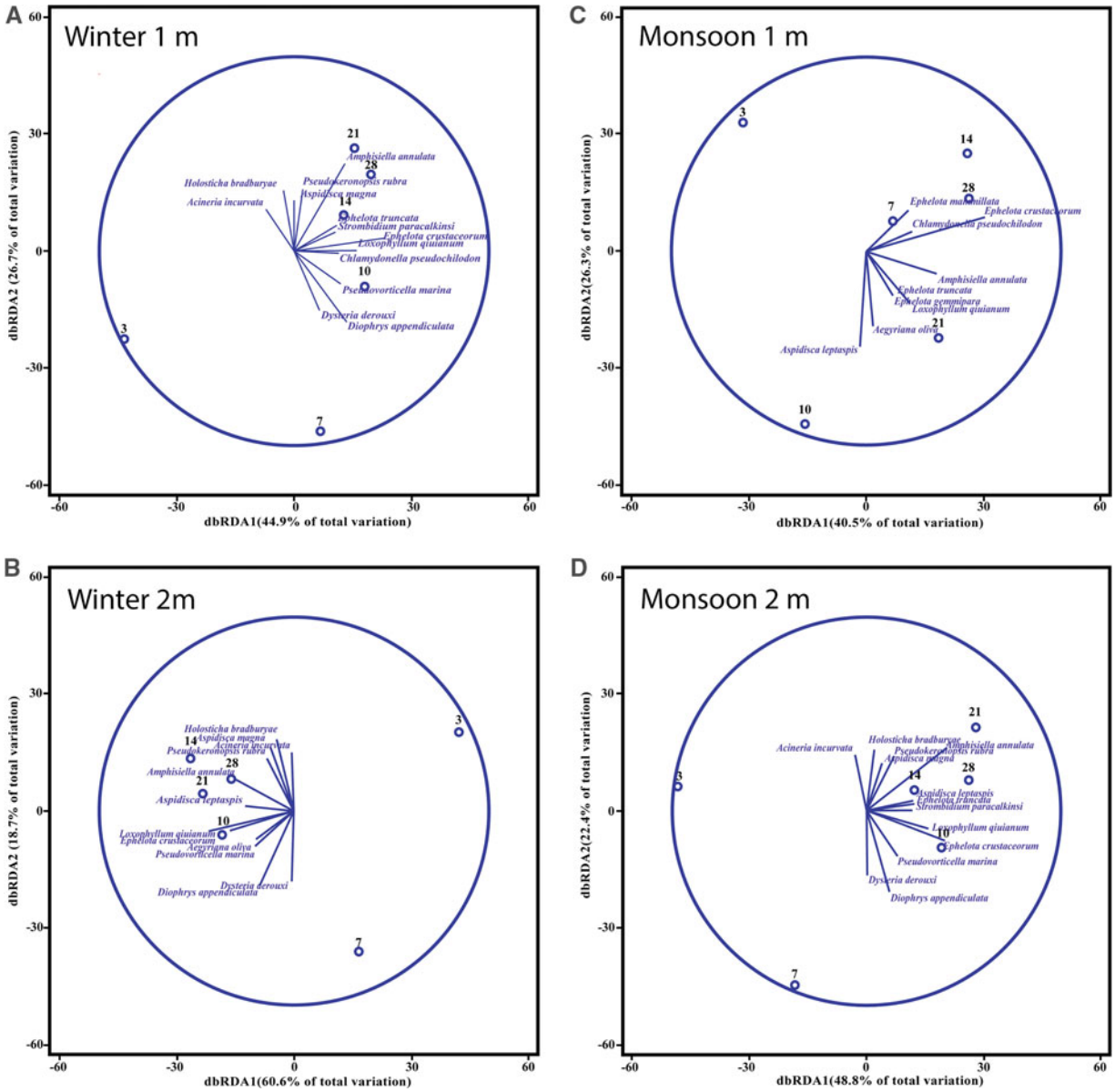

Figure 5. Distance-based redundancy analyses showing seasonal variations in community patterns during the colonization process in two seasons and at two depths.

depth of 1 m in monsoon season, 47 species were falling into five groups (I–V), where 42 species dominate with high abundance and/or occurrence, and other groups represented the assemblages with low abundance and occurrence (Figure 3b). At a depth of 2 m in winter season, 22 species were assigned to three groups (I–III). At 2 m in monsoon, 40 protozoans composed of five groups (I–V). In both samples, groups I to III included 19 and 28 dominant species, respectively. The assemblages of other groups represented with low abundance and occurrence (Figure 3c, d).

In terms of relative abundance, a significant seasonal and vertical variation ($P < 0.05$) in protozoan community was noted between the two depths and seasons (Fig. S1).

As for relative abundance, three types were identified: (1) those dominated by Exogenida before 21 days followed by Euplotida (at 1 m, winter season); (2) those dominated by Dysteria before 21 days followed by Urostylida (at 1 m, monsoon season); and (3) those dominated by Euplotida before 21 days followed by Exogenida (at 2 m, both in winter and monsoon seasons) (Fig. S1)

SIMPROF tests revealed that the colonization process of periphytic protozoa was clearly assigned into different stages in both seasons and depths: the initial stage (3 d), the transitional stage (7 d) (Figure 4) and the equilibrium stage (10–28 d); the latter differed among the seasons and depths (Figure 4).

The dbRDA ordinations indicated that there were different colonization patterns of protozoan communities between two seasons and depths (Figure 5). PERMANOVA test demonstrated a significant difference in colonization patterns among seasons and depths ($P < 0.05$).

Colonization curves and growth curves

The colonization curves fitness of periphytic protozoa are summarized in Figure 6. Regression analysis confirmed that the colonization processes at depths of 1–2 m were well fitted to MacArthur–Wilson model and divided into three successive stages such as initial, transitional and equilibrium, while the data were not fitted to the model at a depth of 1 m in monsoon (Figure 6). For example, colony formation on slides for reaching to equilibrium stage occurred either 10 or 14 days at 1 and 2 m in winter and at a depth of 2 m in monsoon, although regression value at a depth of 1 m in monsoon was closed to other depths and season but non-fitness to the model (Figure 7).

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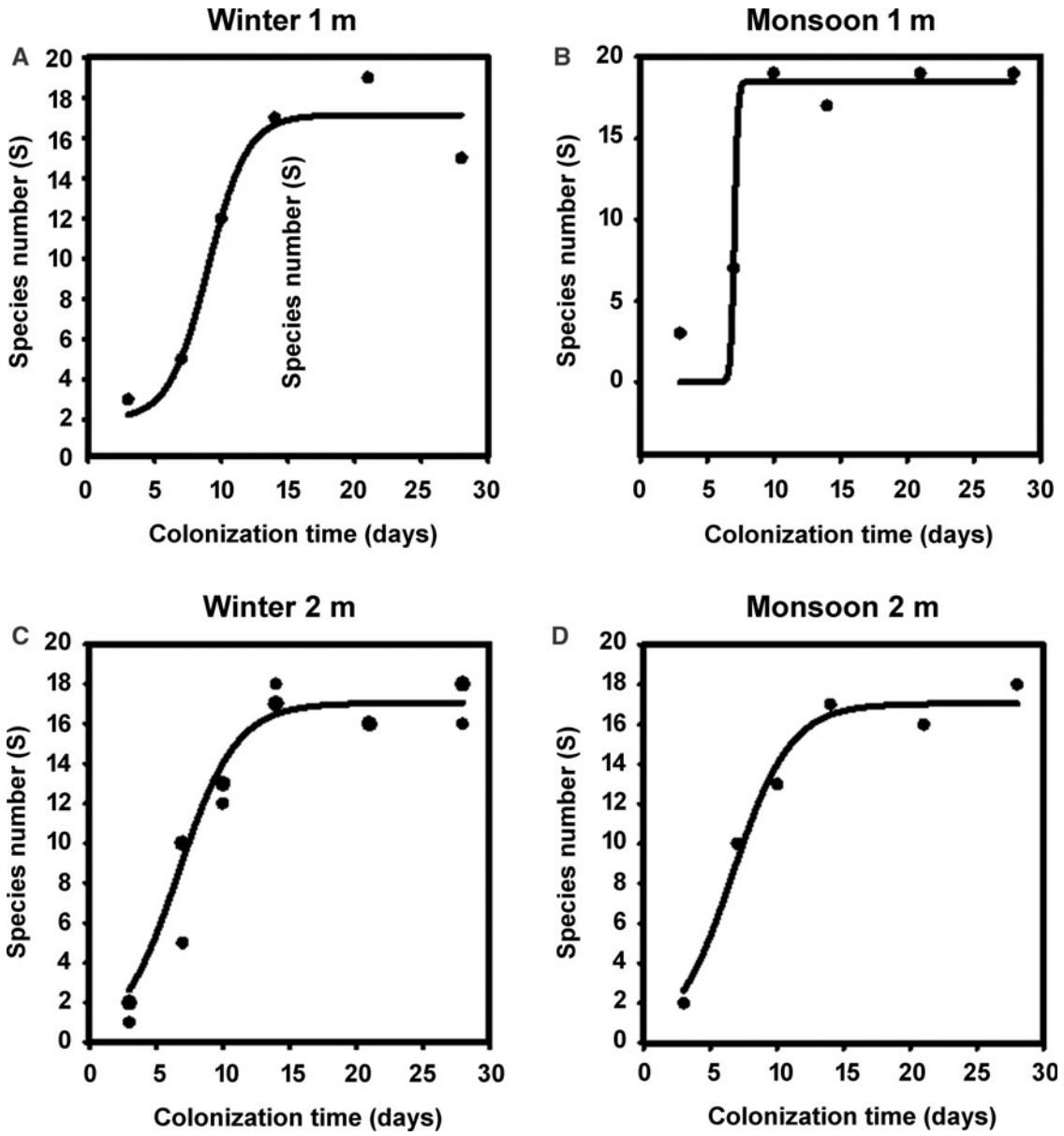

Figure 6. Colonization curves of periphytic protozoa at 1 m and 2 m in winter and monsoon seasons. (a) Winter 1 m (initial at day 3–7; transition at day 7–10; equilibrium at day 14–28); b, Monsoon 1 m (initial at day 3–7; transition at day 7–10; equilibrium at day 10–28); c, Winter 2 m (initial at day 3; transition at day 7–14; equilibrium at day 14–28); and d, Monsoon 2 m (initial at day 3; transition at day 7–14; equilibrium at day 14–28).

Three functional parameters based on the MacArthur and Wilson model, equilibrium species number (S_{eq}), colonization rate constant (G), and time required to reach 90% S_{eq} ($T_{90\%}$) are shown in Table 1. The colonization rates (G values) arranged from 0.13 to 2.17 with a short $T_{90\%}$ values (10–13 days) compared to those at a depth of 1 m in monsoon season (Table 1).

Regression analysis on growth curves revealed that the increasing process of abundances well fitted to the logistic model at two depths and seasons ($P < 0.05$). The projected maximum values of abundances (N_{max}) had a decreasing trend from depths of 1 to 2 m in different seasons, while the values levelled off (11–14 days) at depths of 1 and 2 m both in winter and monsoon seasons (Figure 7, Table 2).

Relationship between spatial pattern and environmental parameters

Multivariate correlation (RELATE) analysis suggested that there was a significant correlation between spatial patterns of environmental variables of the periphytic protozoa (correlation coefficient $\rho = 329$; $P = 0.01$). Besides, the best matching (BIOENV) analysis revealed that the spatial and vertical variation of the protozoan community were significantly driven by temperature, salinity, and transparency, either alone or combined with NO_3^-, PO_4^{2-}, TDS, TSS, and DO (Table 3).

Discussion

Previous studies have demonstrated that the ecosystem functions of protozoan fauna are well linked to environmental heterogeneity mainly due to food supply (Sonntag *et al.*, 2006; Xu *et al.*, 2018; Abdullah Al *et al.*, 2019). In this study, the distribution of protozoan species composition and community structure showed significant seasonal and vertical variations with the environmental heterogeneity in winter and monsoon seasons at different depths.

The community structures of periphytic protozoa can be shaped by water depths despite mixing of water among different layers in coastal waters (Franco *et al.*, 1998; Abdullah Al *et al.*, 2018*a*, 2018*b*). The abundances of microalgae in biofilms are high in surface layers with high sunlight intensity, while the

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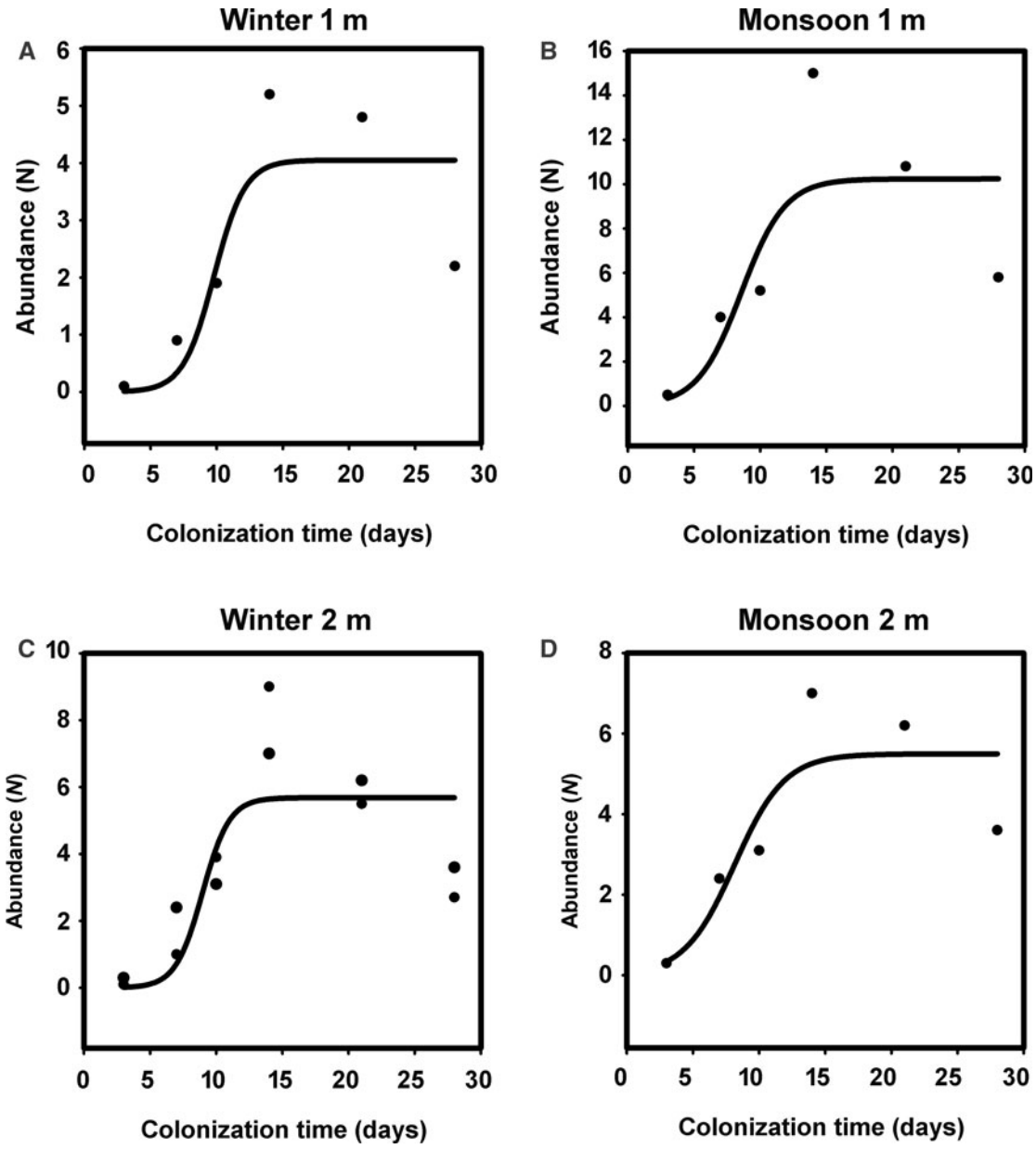

Figure 7. Growth curves of periphytic protozoa at 1 m and 2 m in winter and monsoon seasons. a, Winter 1 m; b, Monsoon 1 m; c, Winter 2 m; and d, Monsoon 2 m.

Table 1. Colonization curve fitness to the Mac-Arthur and Wilson model for periphytic protozoa at depths of 1 and 2 m during winter and monsoon seasons

Parameters	Winter 1 m	Monsoon 1 m	Winter 2 m	Monsoon 2 m
S_{eq}	15	18	16	17
G	1.47	0.13	1.54	2.17
$T_{90\%}$	1.57	17.71	1.50	1.06
R^2	0.96*	0.95*	0.98*	0.97*

S_{eq}, the estimated equilibrium species number of ciliates colonization; G, the growth colonization rate constant; $T_{90\%}$, the time (days) taken for reaching 90% S_{eq}; R^2, regression coefficients; *significant difference at 0.05 level.

Table 2. Increase curve fitness to the logistic model for periphytic protozoa at depths of 1 m and 2 m during winter and monsoon seasons

Parameters	Winter 1 m	Monsoon 1 m	Winter 2 m	Monsoon 2 m
N_{max}	4	10	6	5
$T_{50\%}$	10	9	10	8
R^2	0.72*	0.62*	0.61*	0.73*

N_{max}, the carrying capacity of abundance or maximum abundance; $T_{50\%}$, time (days) for the half of the maximum abundance; R^2, regression coefficients; *significant difference at 0.05 level.

periphytic and planktonic bacteria are abundant in deep layers (Coppellotti and Matarazzo, 2000; Eisenmann *et al.*, 2001; Petchey *et al.*, 2008; Abdullah Al *et al.*, 2018*a*, 2019). Abdullah Al *et al.* (2019) considered the abundances and composition of food supply as the driver to shift the community patterns of periphytic protozoa at different layers of water columns in coastal waters. In the present study, the colonization processes of protozoan communities represented different dynamics at depths of 1 and 2 m during winter and monsoon seasons. This implies that water depths and different seasons might be alternated the colonization process of protozoan communities due to influence of food supply under different sunlight conditions in water columns in different seasons.

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Table 3. Summary results of the biota-environment matching analysis (BIOENV) showing the 10 best matches of environmental variables with spatial variations of the periphytic protozoa with respect to two water depths and seasons

Rank	ρ value	Environmental Variables
1	0.781	Temp, PO_4^{2-},
2	0.780	Temp, Salinity, PO_4^{2-},
3	0.726	Temp, Transparency, PO_4^{2-},
4	0.717	Temp, NO_3^-, PO_4^{2-},
5	0.712	Temp, PO_4^{2-},TSS
6	0.707	DO, PO_4^{2-},TSS
7	0.691	PO_4^{2-},TDS,TSS
8	0.691	Temp, Salinity, Transparency, PO_4^{2-}
9	0.689	Temp, Salinity, NO_3^-, PO_4^{2-}
10	0.686	Temp, Salinity, PO_4^{2-}, TSS

ρ, Spearman coefficient; Statistical significant level at 0.05 ($P < 0.05$).

Multivariate approaches are effective tools for summarizing seasonal and vertical variations in community patterns (Anderson *et al.*, 2008; Clarke and Gorley, 2015; Abdullah Al *et al.*, 2019; Sikder *et al.*, 2019*a*). In this study, dbRDA ordinations revealed that the colonization process at a depth of 1 m both in winter and monsoon seasons was clearly categorized into three successive stages. This finding was consistent with the reports of Xu *et al.* (2009*a*, 2009*b*), Mieczan (2010) and Zhang *et al.* (2012, 2013). However, PERMANOVA test revealed that the colonization patterns represented a significant difference between both depths in winter than monsoon. Thus, these findings suggest that a depth of 1 m in winter is the best sampling strategy for bioassessment surveys using protozoa in tropical marine ecosystems.

The functional parameters based on colonization analysis are valuable indicators for assessing the carrying capacity with external organic load/toxic levels of tropical marine ecosystems (Zhang *et al.*, 2012, 2013). For example, the lower the levels of pollution, the higher the values of S_{eq} and G (Xu *et al.*, 2009*a*, 2009*b*; Burkvoskii *et al.*, 2011; Zhang *et al.*, 2012, 2013, Sikder *et al.*, 2019*b*, 2019*c*). In this study, the colonization rate (G), S_{eq}, and N_{max} showed a clear vertical and seasonal variability from a depth of 1–2 m in water columns. The highest values of colonization rates (G), equilibrium species number (S_{eq}), and carrying capacity (N_{max}) were found at 1 m depth, while the lower values were measured at 2 m depth. However, these parameters generally levelled off at stable values at both depths. Thus, this implies that availability of food supply due to light intensity in deeper water might influence the colonization succession with lower abundance and higher variability at different depths. Another reason might be due to organic load since higher organic pollutants can minimize the carrying capacity of an ecosystem (Burkovskii and Mazei, 2001; Burkvoskii *et al.*, 2011).

In summary, the colonization processes of protozoa were generally assigned into three stages at two depths in two seasons: the initial (3 days), transitional (7 days), and equilibrium (10–28 days) stages. The regression analyses demonstrated that the colonization dynamics were fitted to the MacArthur–Wilson model and logistic equation. The species richness reached an equilibrium after 10–14 days and maximum abundances were high at a depth of 1 m. These findings suggest that a depth of 1 m in winter is comparatively more useful reference for bioassessment surveys using protozoa in tropical marine ecosystems.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315423000528.

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Author's contributions. M. J. H. B. and M. N. A. S. carried out the field works and laboratory experiments (sample collection, preparations, identification, data collection etc.). M. N. A. S., S. M. B. H., A. S. M. S., and S. A. U. compiled the whole data sets and completed the analyses. M. N. A. S. and H. X. wrote the manuscript. S. M. S. reviewed and edited the manuscript.

Competing interest. None.

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