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Observations and Measurements of Planktonic Bioluminescence off the South Coast and Puttalam Lagoon of Sri Lanka

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Abstract – Marine bioluminescence is a unique phenomenon and widely studied around the world. However, information on bioluminescence is scarce in the Indian ocean. This study was carried out to understand the spatial and temporal variations in planktonic bioluminescence off the south coast and the Puttalm Lagoon of Sri Lanka. Planktonic bioluminescence intensity, zooplankton samples, water samples and oceanographic data were collected from sampling sites from January to December 2016 in three month intervals. Time series data were collected at a fixed sampling station, off the south coast of Sri Lanka, in order to understand the variation of bioluminescence intensity throughout the night and with respect to monsoon winds. Bioluminescence intensity was measured using the recoverable bathyphotometer and zooplankton samples were collected using WP-2 net with a 180 µm mesh size plankton net. The results revealed that most of the bioluminescence intensity peaks in the ocean were concentrated in the mixed layer depth zone. Bioluminescence and Chlorophyll profiles indicate the presence of both heterotrophic and autotrophic planktonic bioluminescence. Fixed station analysis showed variations in planktonic bioluminescence throughout the night and with respect to monsoon winds. Twenty two surface bioluminescent zooplankton species belonging to 15 families and 4 phyla were identified during this study. Variations in planktonic bioluminescence with respect to time and sampling locations were evident. The current study yielded encouraging results that should lead to further identification of planktonic distribution near Sri Lanka and key bioluminescent zooplankton in the region.

Keywords – oceanography, planktonic bioluminescence, recoverable bathyphotometer, Sri Lanka

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1. Introduction

The production and emission of visible light by living organisms is known as bioluminescence. Bioluminescent organisms are rare on land but they represent approximately 1% to 3% of biomass in the surface ocean (Haddock and Moline 2010). Copepods, euphausiids, dinoflagellates, ostracods, radiolarians, cephalopods, decapods shrimps, chaetognaths, cnidarians, ctenophores and fish are the major groups of bioluminescent organisms found in marine and brackish water environments (Morin 1983; Bradner et al. 1987; Herring 1987; Fischer and Fischer 1995; Moline et al. 2005).

The function of these luminous displays varies from organism to organism, but can be divided into some basic categories such as predator avoidance, prey attraction, physiological maintenance and intra-species communication (Morin 1983; Abrahams and Townsend 1993). Most of the bioluminescent organisms emit light by oxidizing the luciferin molecules, and there are different forms of luciferin produced by different organisms (Swift et al. 1995; Widder 2010). Light-producing reactions are assumed to be dependent on diet, photosynthetic rates (autotrophy), pH within the light organelles, interaction with the host in the case of symbionts and the organism's ability to maintain the synthetic pathways of the luciferin (Hastings 1983; Widder 2010). However, these processes and their controlling mechanisms still remain largely unknown.

Many studies have been carried out to analyse the spectral quality, flash kinetics, physiology and cellular basis of bioluminescence (Latz et al. 1988; Rees et al. 1998) and how these phenomena link with circadian rhythms (Losee and Lapota 1981), photosynthesis and diet of marine organisms (Haddock et al. 2001). Further, relationships between bioluminescence and predator avoidance, prey attraction and intra-species communication have been studied in detail (Abrahams and Townsend 1993; Rivers and Morin 2008).

Scientists have been working on ocean bioluminescence for more than two decades to understand its distribution in the world's oceans and to identify the organisms responsible for this phenomenon (Marra and Hartwig 1984; Lapota et al. 1989; Marra 1989). Many studies have shown that plankton are the dominant bioluminescent organisms in the epipelagic zone of the ocean (Losee and Lapota 1981). However, species distributions in different geographical areas, mechanisms of producing light and details on the biochemical processes remain poorly known, especially in regions where observations are scarce. One such geographical area is the southern part of the Bay of Bengal and region around Sri Lanka (Staples 1966), where primary productivity is strong during monsoon periods and bioluminescence has been reported. Furthermore, there is very little understanding of bioluminescence in lagoon ecosystems in the Indian Ocean region.

Therefore, this study focuses its investigation on the temporal variation and spatial depth distribution pattern of bioluminescence in both the offshore waters and the lagoon. Further, an attempt was made to identify and quantify the bioluminescent zooplankton in the selected offshore waters and lagoon environment.

2. Methodology

Study area

Planktonic bioluminescence was assessed off the south coast (5.763°N–6.183°N, 80.116°E–79.793°E) and the Puttalam Lagoon (8.329°N–8.504°N, 79.823°E–79.795°E) of Sri Lanka from January to December 2016. Five sampling locations off the south coast and six sampling locations from the Puttalam Lagoon were selected for this study and a description of each sampling location is summarized in Table 1, with sampling locations shown in Fig. 1.

Data collection

Planktonic bioluminescence intensity, zooplankton samples, water samples and oceanographic data were collected at each sampling location from January to December 2016 in three month frequency.

A recoverable bathyphotometer (RBPM; Teledyne-Benthos) was used to measure the planktonic bioluminescence intensity in terms of intensity counts at each sampling location. The RBPM was deployed in free-falling (1 m/s) mode and bioluminescence profiles were recorded after dusk and before dawn of the next day. The R/V Samuddrika that belongs to the National Aquatic Resources Research and Development Agency (NARA) was used to collect RBPM data in the offshore waters, while a Fiberglass Reinforced Plastic (FRP) boat powered with a 15 HP engine was used to collect lagoon samples. The RBPM was deployed up to a depth of 6 m in the lagoon and ~120 m in the ocean. If there is an external light source other than bioluminescence, the instrument records

Table 1. Details of sampling locations off the south coast and in the Puttalam lagoon of Sri Lanka

	Location	Latitude (N)	Longitude (S)	The depth of the location around (m)
Off south coast	1	6.185	79.793	980
	2	6.112	79.758	1500
	3	5.988	79.874	1050
	4	5.903	79.922	1800
	5	5.763	80.116	2300
Puttalam lagoon	1	8.504	79.79	3
	2	8.478	79.795	3
	3	8.453	79.814	3
	4	8.412	79.821	5
	5	8.374	79.829	6
	6	8.329	79.823	3
Fixed station off the south coast		6.112	79.758	1500

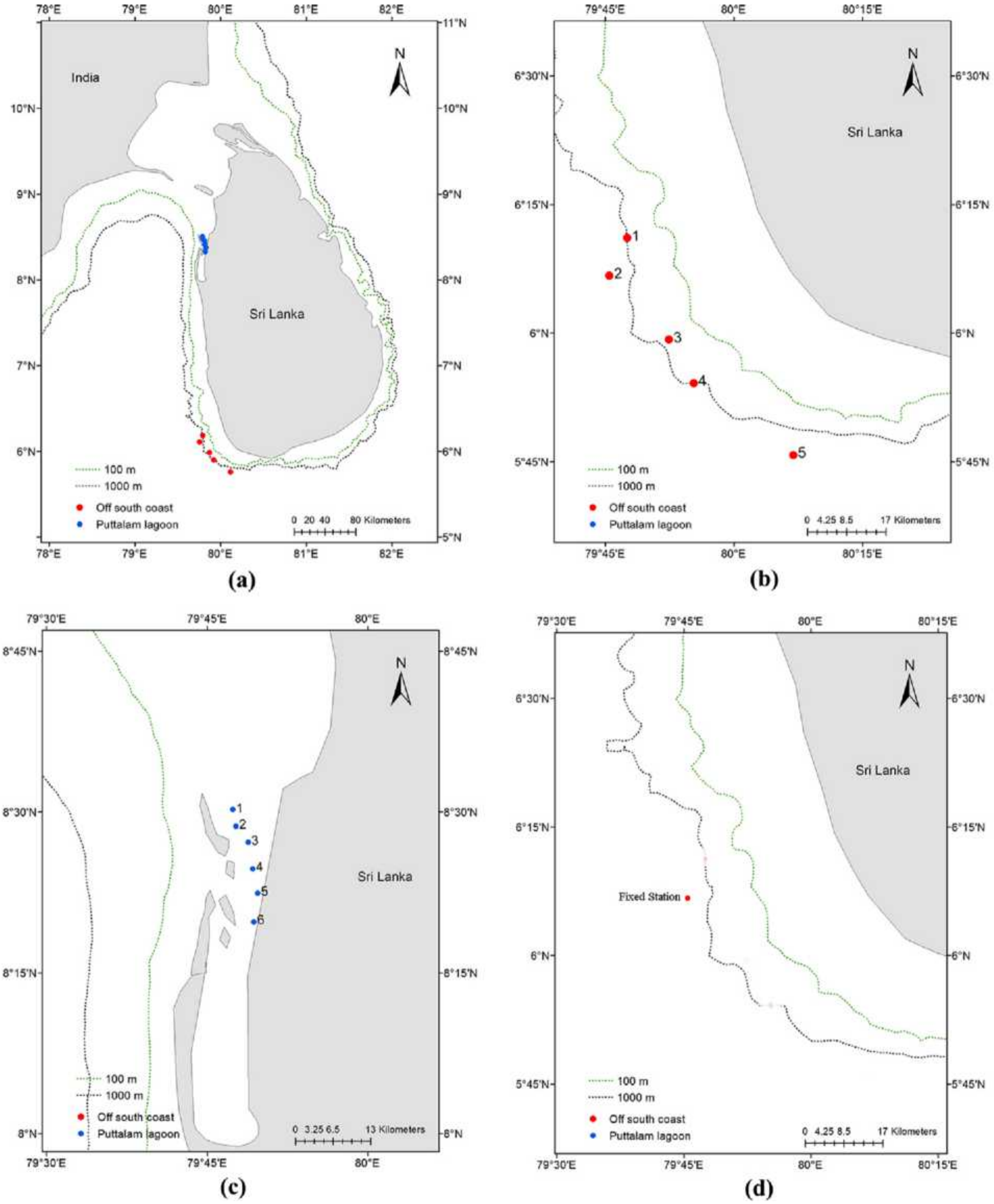

Fig. 1. Sampling plan for the measurement of planktonic bioluminescence, water and plankton samples collection off the south coast and Puttalam Lagoon of Sri Lanka from January to December 2016. (a) Two sampling areas off the south coast and Puttalam Lagoon (b) sampling locations off the south coast of Sri Lanka (c) sampling locations in Puttalam Lagoon of Sri Lanka and (d) fixed station sampling location in the south coast of Sri Lanka

it as an intensity count. Therefore, all the sampling was carried out during the new moon phase to avoid this problem. Bioluminescence intensity graphs were plotted using Grapher and MATLAB software and these graphs were used to identify the distribution of bioluminescence intensity peaks from surface to the sampling depth.

Zooplankton and water sampling

Surface zooplankton samples were collected using a 180 µm mesh size WP2 plankton net. Marine zooplankton samples were collected by towing the plankton net from 10 m depth to the surface off the south coast of Sri Lanka. Lagoon zooplankton samples were obtained by towing the net horizontally at a constant speed (1 km/h) for a specific time (5 minute) in the lagoon surface water. Four replicates of zooplankton samples were collected at each sampling location. Three samples were used to estimate the zooplankton abundance and the fourth sample was used to identify the bioluminescent zooplankton at the location. Immediately after taking the fourth sample on-board, bioluminescent zooplankton were separated by observing the naked eye (for light emitting individuals). The separated zooplankton were put into labelled sampling bottles using laboratory pipettes, and preserved in 5% buffered formalin. The other three samples were also preserved in 5% buffered formalin, labelled appropriately and transported to the laboratory of the National Institute of Oceanography and Marine Sciences (NIOMS), NARA for further analysis. At the laboratory, bioluminescent zooplankton were identified and counted using a light microscope with classification up to the lowest possible taxon using available keys (Conway et al. 2003; Razouls et al. 2005). The abundance of bioluminescent zooplankton was calculated (individuals/m^3) using the formula below proposed by Conway et al. (2003).

$$\text{Zooplankton abundance} = \frac{N}{V}$$

Where;

N - number of the zooplankton individuals

V - volume of water passed through the plankton net (m^3)

$V = a \times d$

a - surface area of the net opening (m^2)

d - depth (in ocean) or distance towed (in lagoon) (m)

Oceanographic measurements

Conductivity, temperature, Chlorophyll and depth data were collected using a Sea-Bird SBE19plus sea CAT instrument (CTD). The CTD was deployed up to 300 m and the data was recovered and processed using Sea-Bird software. The CTD was used only in the offshore waters as it could not be deployed in the lagoon waters due to its shallow depths. Grapher and Surfer software were used to identify thermocline depth, mixed layer depth and Chlorophyll maxima depth. An attempt was made to identify the distribution of bioluminescence intensity peaks in relation to oceanographic parameters.

Nutrient analysis

Three water samples were collected from each sampling location for nutrient analysis. A Ruttner sampler was used to collect surface ocean water samples and lagoon water samples were directly collected into 1 L plastic bottles. The collected water samples were immediately stored in ice and analysed for nitrate, orthophosphate and silicate within 48 hours. Analysis was carried out according to the method described by Strickland and Parsons (1972).

Fixed station data

In order to understand the variations in planktonic bioluminescence intensity throughout the night, data were collected at a fixed sampling station (6.112°N, 79.758°E, Table 1) on 20th January 2016 and 5th May 2016 in 2-hour intervals from 7.00 pm to 5.00 am on the next day. These two sampling dates were selected to represent the southwest monsoon (May to September) and northeast monsoon (December to February) periods. Bioluminescence intensity, zooplankton samples, water samples for nutrient analysis and oceanographic parameters were collected using the same methodology described previously. Variations in bioluminescence intensity with respect to the southwest monsoon and northeast monsoon were assessed.

Data analysis

Data management, data analysis and formatting were done in Microsoft Excel. All statistical analyses were done using Minitab 17 software and significant differences were considered at the probability level of 0.05. Graphical representations were done using MATLAB, Grapher and Surfer software.

3. Results

Ocean bioluminescence

Bioluminescence intensity was computed and compared off the south coast of Sri Lanka with respect to sampling locations and sampling period.

Bioluminescence intensity varied from 2 to 222 intensity counts during the period of January–March. The highest bioluminescence intensity was recorded at sampling location 2

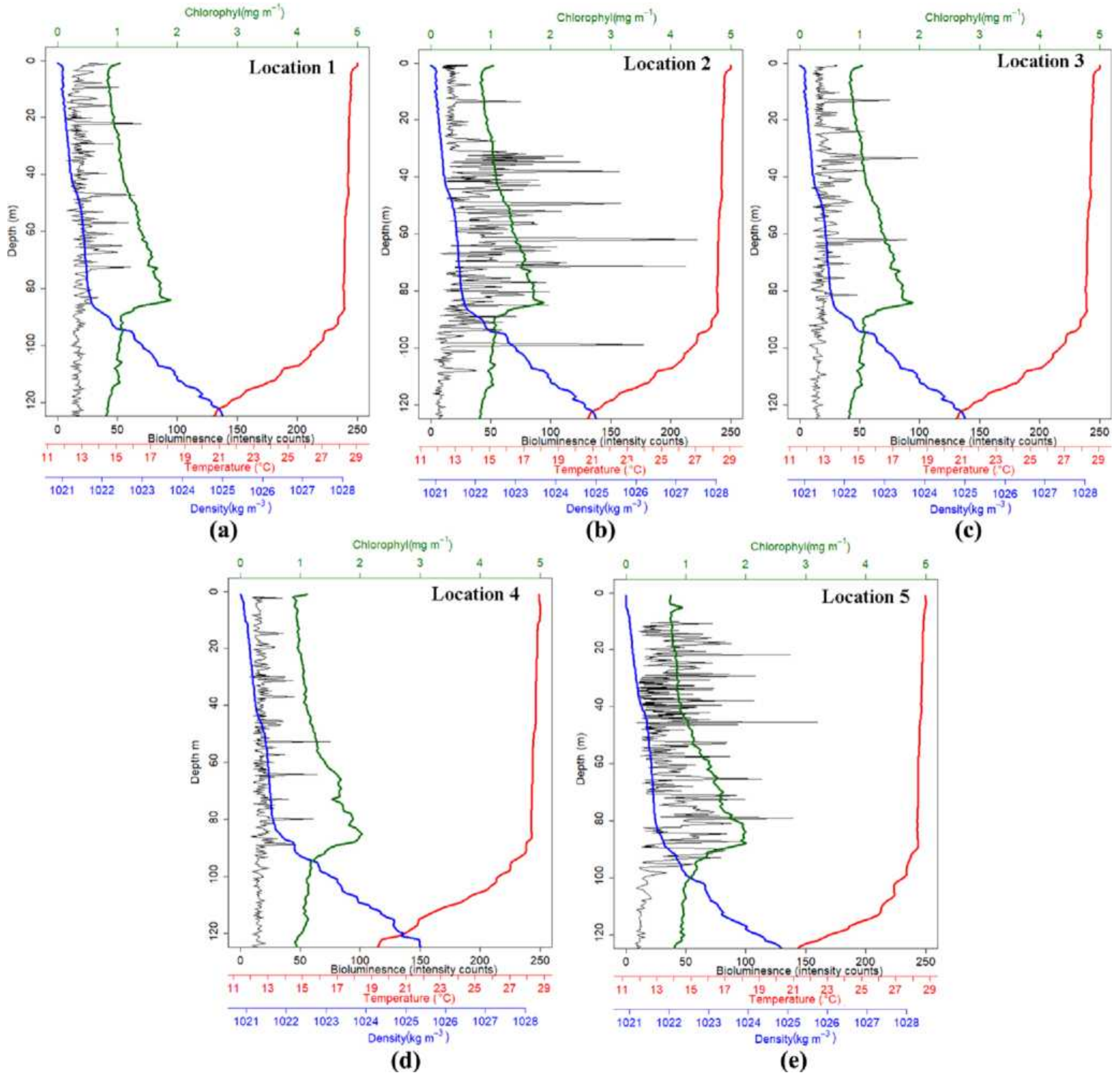

Fig. 2. Distribution of bioluminescence profile (black line), Chlorophyll profile (green line), temperature profile (red line) and density profile (blue line) at the 5 sampling locations off the South coast of Sri Lanka from January to March 2016

(Fig. 2b) while the lowest was at sampling location 5 (Fig. 2e). During this period, a mixed layer was observed at the upper 85 m. In all these sampling locations, the highest numbers of bioluminescence peaks were in the mixed layer. However, there was an isolated strong bioluminescence peak having 177 intensity counts at around 100 m depth at sampling location 2 (Fig. 2b). But no such high intensity peaks were evidenced in other sampling locations around or below 100 m depth. The results of Chlorophyll analysis indicated a very low Chlorophyll concentration at the surface (0.8 mg/m^3) and a Chlorophyll maximum (1.9 mg/m^3) was between 80 to 90 m depth (Fig. 2). Most of the bioluminescence peaks were reported outside the Chlorophyll maximum (Fig. 2). Nitrate, orthophosphate and silicate were in the range of 0.002–0.005 ppm, 0.0006–0.01 ppm and 1.75–2.31 ppm, respectively. There were no significant variations in nutrient

Table 2. Variations in surface nutrients off the south coast and the Puttalam lagoon of Sri Lanka during the study period from January to December 2016

		January–March			April–June			July–September			October–December		
	Location	Nitrate (ppm)	Orthophosphate (ppm)	Silicate (ppm)	Nitrate (ppm)	Orthophosphate (ppm)	Silicate (ppm)	Nitrate (ppm)	Orthophosphate (ppm)	Silicate (ppm)	Nitrate (ppm)	Orthophosphate (ppm)	Silicate (ppm)
off south coast	1	0.004	0.010	2.121	0.003	0.012	3.793	0.009	0.008	0.988	0.002	0.007	1.987
	2	0.002	0.005	2.312	0.003	0.004	3.120	0.011	0.045	1.012	0.006	0.003	1.881
	3	0.003	0.001	1.910	0.004	0.001	1.900	0.009	0.007	1.277	0.005	0.002	1.951
	4	0.004	0.003	1.785	0.014	0.003	4.298	0.008	0.012	1.073	0.008	0.007	1.942
	5	0.002	0.005	1.751	0.010	0.004	8.841	0.008	0.001	0.960	0.005	0.006	1.857
Puttalam lagoon	1	0.347	0.046	12.375	0.310	0.026	15.731	0.357	0.026	12.835	0.284	0.043	10.832
	2	0.192	0.059	12.712	0.140	0.053	18.723	0.147	0.046	15.862	0.204	0.052	12.000
	3	0.301	0.051	12.711	0.250	0.040	10.732	0.281	0.044	16.832	0.241	0.045	32.000
	4	0.237	0.065	11.029	0.167	0.052	25.832	0.183	0.045	22.735	0.166	0.057	20.736
	5	0.278	0.060	14.226	0.310	0.059	22.634	0.327	0.059	18.623	0.282	0.062	15.872
	6	0.261	0.099	50.404	0.244	0.026	31.823	0.234	0.021	35.972	0.214	0.025	33.862

contents among sampling locations (Table 2).

Bioluminescence intensity was within the range of 6 -108 intensity counts off the south coast of Sri Lanka within the period from April to June. The highest intensity count was recorded at sampling location 3 (Fig. 3c). Although there is a weak mixed layer, the high level of bioluminescence intensity counts were associated with the upper 60 m of the ocean. Surface Chlorophyll concentration was ~0.65 mg/m^3 and Chlorophyll maximum (4.84 mg/m^3) was recorded at ~55 m depth. Low intensity bioluminescence peaks were highly concentrated with the Chlorophyll maximum at location 3 (Fig. 3c). However, the observed bioluminescent peaks were above the Chlorophyll maximum at other sampling locations (Fig. 3). Although nitrate (0.003–0.01 ppm), orthophosphate (0.001–0.012 ppm) and silicate (1.9–8.84 ppm) levels varied from location to location, there was no significant variation among sampling sites (Table 2).

In the third quarter of the study period from July to September,

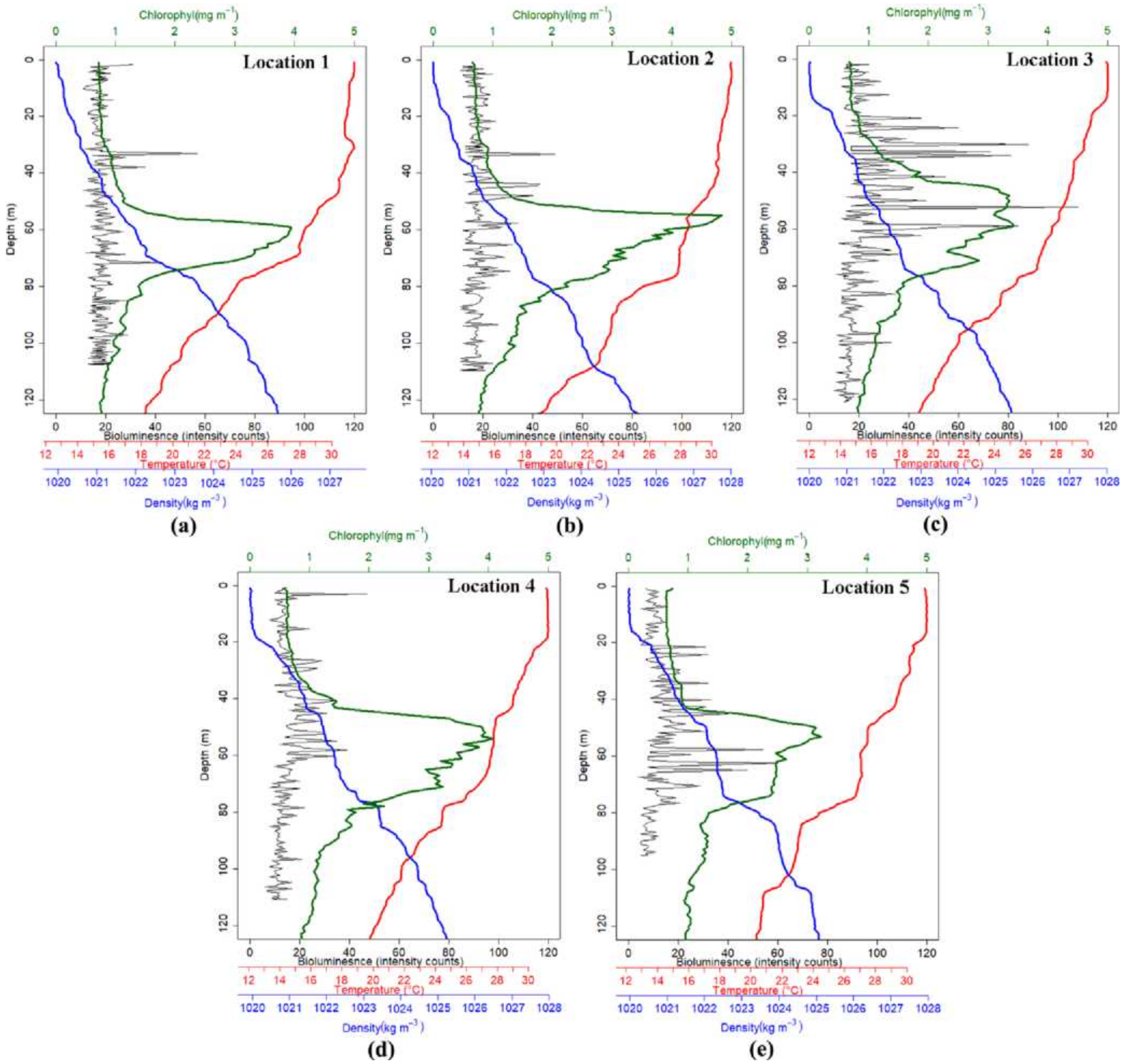

Fig. 3. Distribution of bioluminescence profile (black line), Chlorophyll profile (green line), temperature profile (red line) and density profile (blue line) at the 5 sampling locations off the South coast of Sri Lanka from April to June 2016

sampling locations 1 and 2 showed different bioluminescence distribution patterns than the other locations (Fig. 4a and b). At location 1, most of the bioluminescence peaks were concentrated in the upper 40 m, having one prominent peak at around 60 m depth while at location 2, two bioluminescence peaks were visible at the depth of 11 m and 42 m, respectively (Fig. 4). The observed highest and lowest bioluminescence intensity for this time period were 243 and 6 intensity counts, respectively. The highest bioluminescence intensity was recorded at location 1 (Fig. 4a) and the lowest was recorded at location 3 (Fig. 4c). A well-mixed mixed layer was observed from the surface to 55 m depth. Most of the bioluminescence peaks were observed in association with the Chlorophyll maximum (2 mg/m^3); however, these peaks were outside the Chlorophyll maximum at location 1. A comparatively higher orthophosphate (0.001–0.04 ppm) level was observed in all the sampling locations compared to the previous time period. Nitrate and silicate levels varied from 0.007–0.010 ppm and

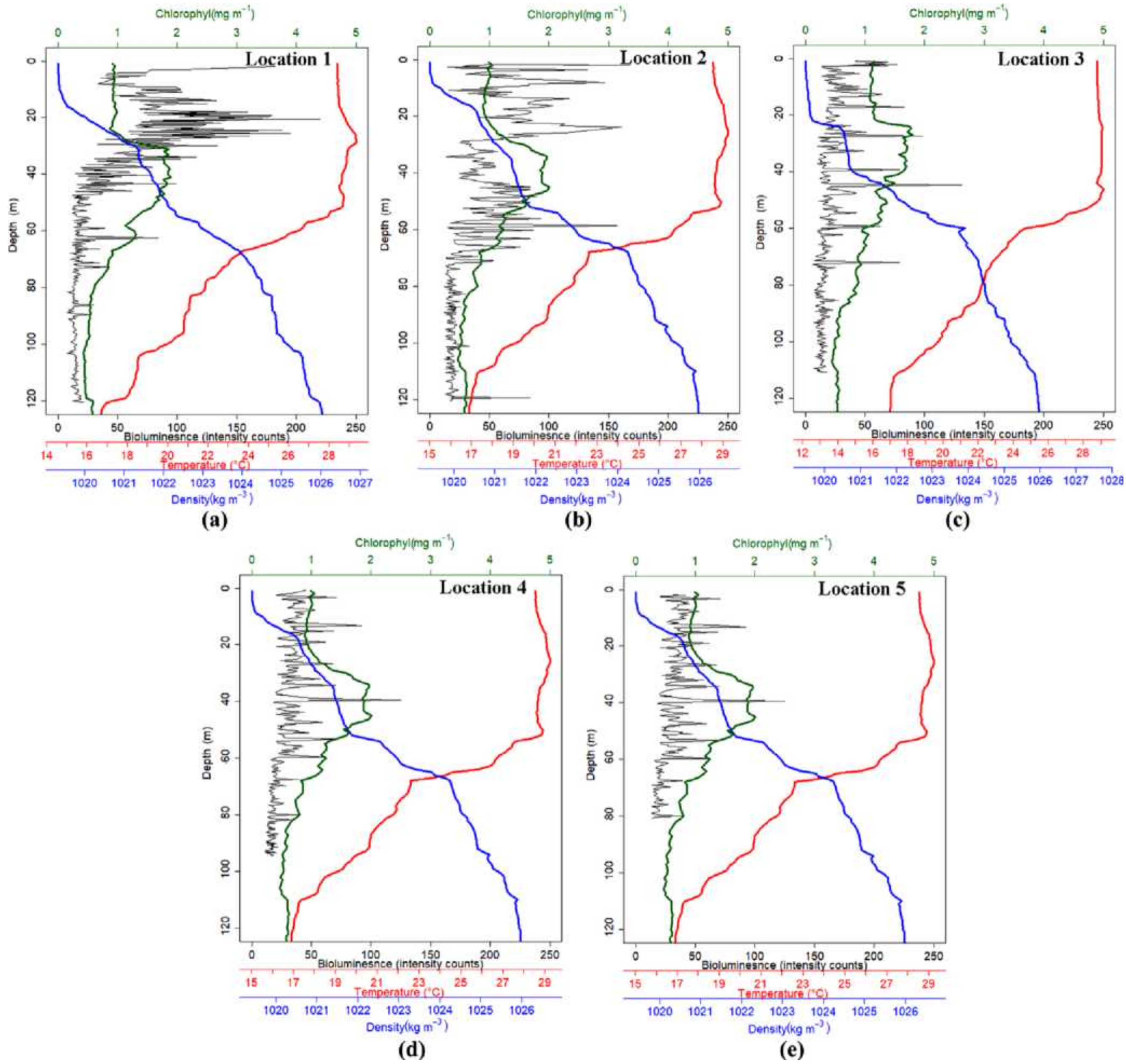

Fig. 4. Distribution of bioluminescence profile (black line), Chlorophyll profile (green line), temperature profile (red line) and density profile (blue line) at the 5 sampling locations off the South coast of Sri Lanka from July to September 2016

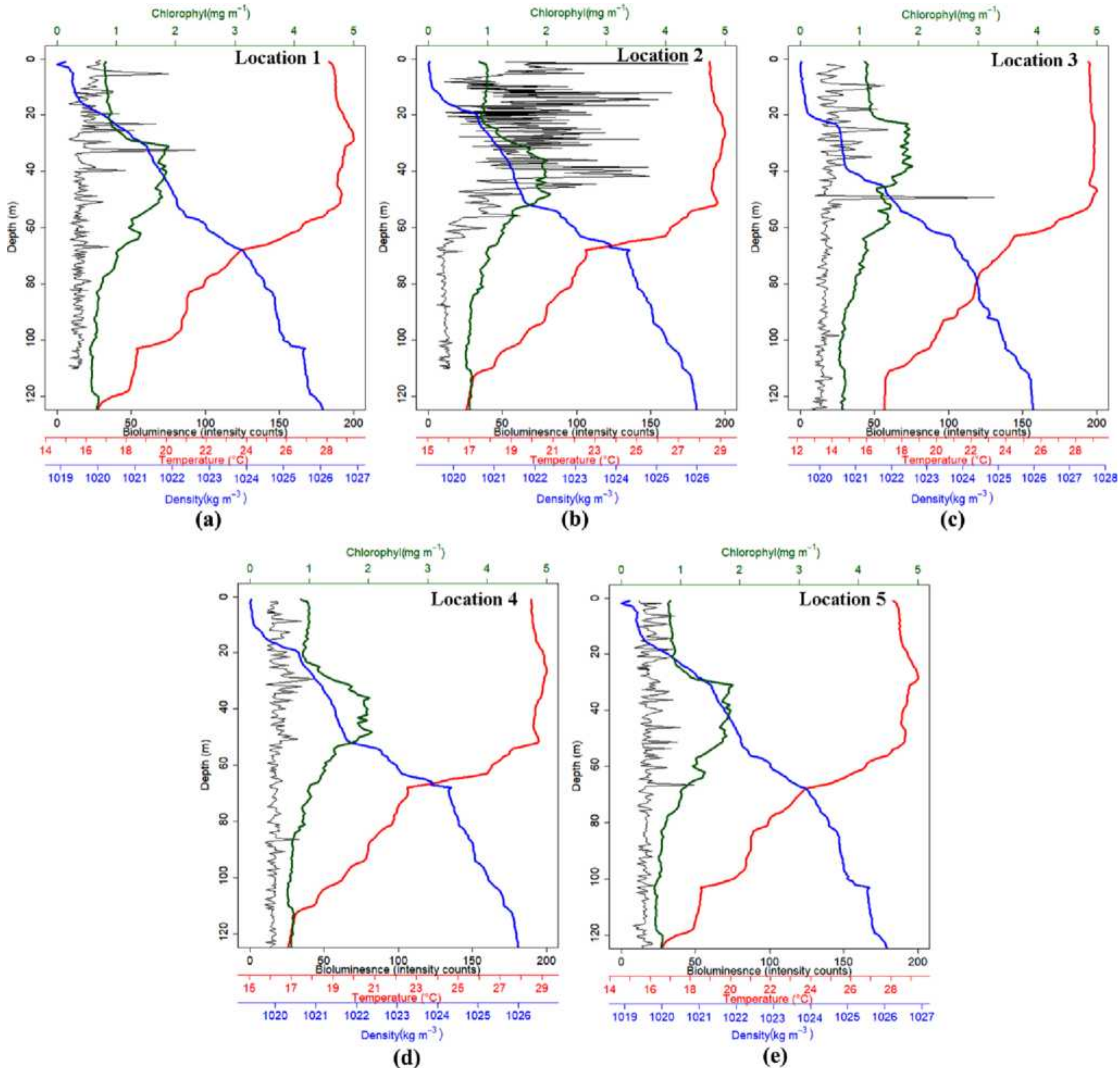

Fig. 5. Distribution of bioluminescence profile (black line), Chlorophyll profile (green line), temperature profile (red line) and density profile (blue line) at the 5 sampling locations off the South coast of Sri Lanka from October to December 2016

0.987–1.276 ppm, respectively (Table 2). However, significant variations in nutrient contents with respect to sampling locations were not evident.

During the period from October to December, both the highest (175 intensity counts) and lowest (2 intensity counts) bioluminescence intensities were recorded at location 2 (Fig. 5b). Almost all the bioluminescence peaks were concentrated in the mixed layer, which was observed from the surface up to 55 m. Similarly, bioluminescence peaks were associated with the Chlorophyll maximum (2 mg/m^3), which was at the depth of 40 m (Fig. 5). Nutrient levels were found to be within the same range of the previous sampling time (Table 2) and there was no significant relationship with respect to nutrient variation between different locations.

Lagoon bioluminescence

Lagoon bioluminescence profiles showed intensity variations throughout the year, although the lagoon was very shallow compared to the selected offshore sampling sites in this study.

Bioluminescence intensity varied from 1 to 45 intensity counts from January to March. The highest intensity (41 intensity counts) was reported at location 1 and the lowest (1 intensity count) was at location 2 (Fig. 6a). In all the sampling locations bioluminescence peaks were highest from the surface to a depth of 3m. Larger numbers of bioluminescence peaks were observed at locations 5 and 6 than the other locations (Fig. 6). Nitrate, orthophosphate and silicate concentrations were within 0.192–0.347 ppm, 0.051–0.099 ppm and 11.029–50.404 ppm, respectively (Table 2). Nutrient parameters did not show significant variation with respect to sampling sites.

Similar to the previous observations, bioluminescence intensity peaked at the surface water during the April to June period (Fig. 6b). A notable magnitude of bioluminescence intensity, measured as 120 intensity counts, was recorded at location 2. In most of the sampling sites, bioluminescence was dominated by a single intensity peak. High magnitude bioluminescence intensity peaks were observed during this period when compared with other sampling periods of the

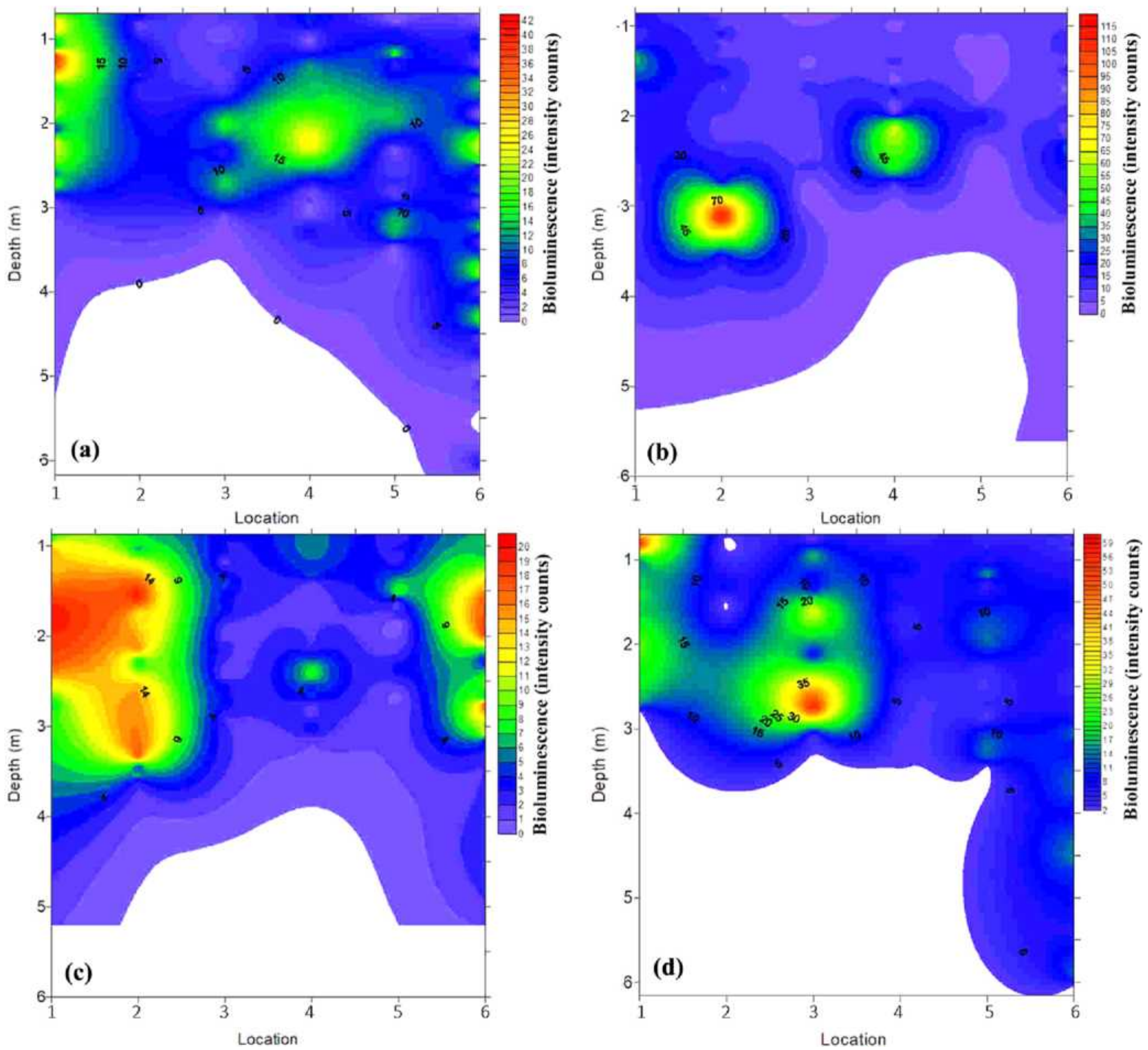

Fig. 6. Variations in bioluminescence intensity at 6 sampling locations of Puttalam Lagoon of Sri Lanka during January to March (a) April to June (b) July to September (c) and October to December (d) 2016

year. Nitrate varied from 0.140–0.310 ppm, while orthophosphate and silicate concentration was within 0.026–0.059 ppm and 10.732–31.823 ppm, respectively (Table 2).

Very low bioluminescence intensity (< 20 counts) was observed at all locations during the period of July–September (Fig. 6c). The sampling location 3 reported the lowest bioluminescence counts where peaks did not exceed 5 intensity counts. Nutrient contents were also within the similar range as observed in the April–June period (Table 2).

High variability in bioluminescence intensity was evident

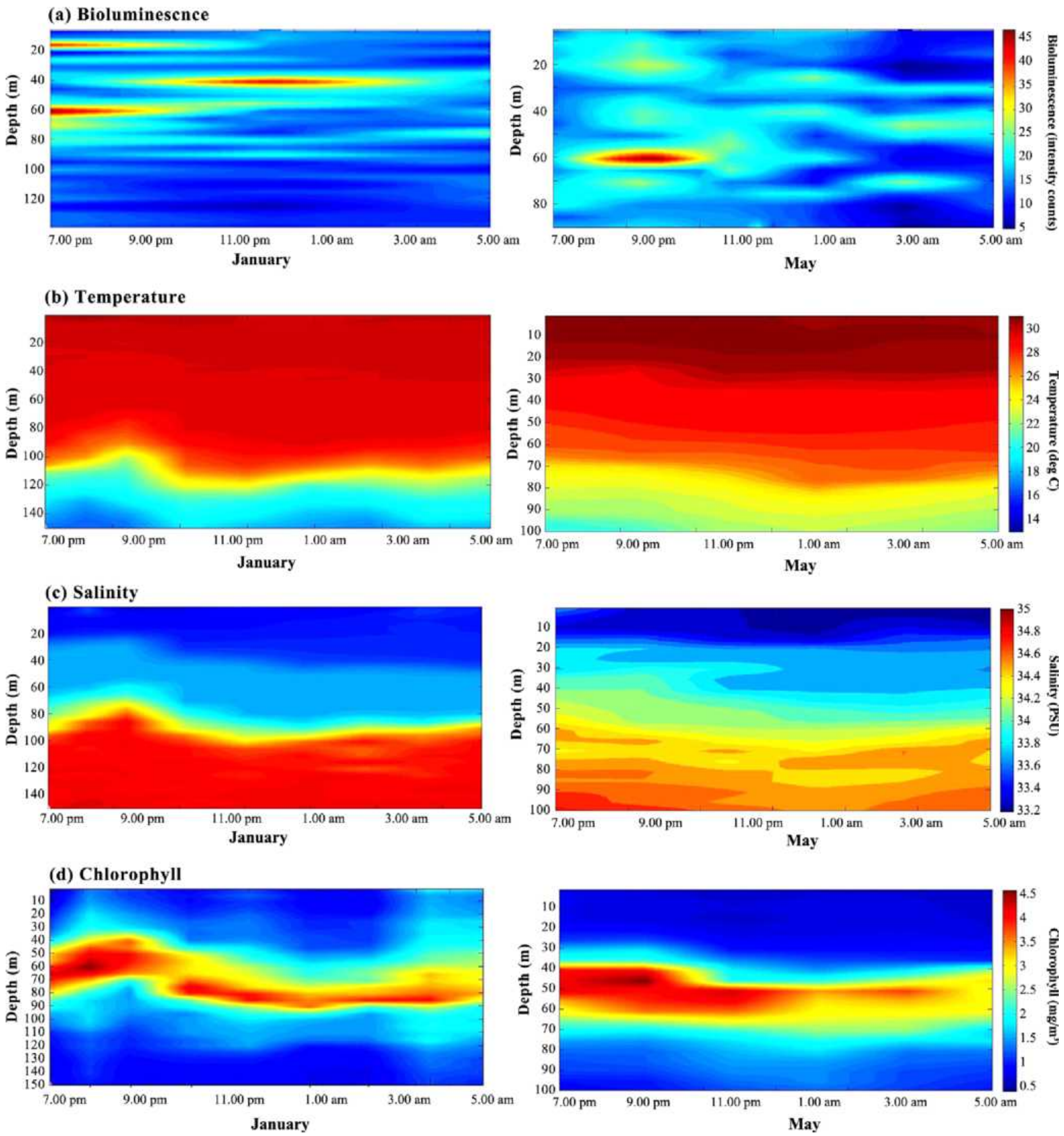

Fig. 7. Variations in bioluminescence intensity (a), Temperature (b), Salinity (c) and Chlorophyll concentration (d) at fixed sampling location off the south coast of Sri Lanka on 20th January and 5th May 2016 from 7.00 pm to 5.00 am

from October to December. The locations 1 and 3 exhibited an intensity range from 1 to 60 intensity counts. Although large number of peaks were recorded at location 6 (Fig. 6d), their magnitudes were relatively low (< 16 counts). The nutrient parameters were within the similar range observed in the previous time period (Table 2).

Variations of bioluminescence intensity at fixed sampling location

The results of the fixed station data analysis showed that the highest bioluminescence intensity was generally from dusk to midnight (7.00 pm to 12.00 am) and the lowest intensity was at dawn (5.00 am). However, variations in bioluminescence intensity counts with respect to time and depth were evident in relation to monsoon winds. During the northeast monsoon period (January), a peak bioluminescence (169 intensity counts) was observed at 11.00 pm at around 40 m (Fig. 7a) while it was at 9.00 pm around 60 m depth during the southwest monsoon (108 intensity counts) period. A "thin layer" (less than 4 m in total thickness) of bioluminescence was observed around 80 m over a 10 hour period during the northeast monsoon (Fig. 7). However, the responsible organisms for this thin layer formation were not identified.

Variations in mixed layer depth and halocline depth demonstrated differences with respect to monsoon winds (Fig.7b and c). The thermocline depth during the northeast monsoon period was ~80 m, but it was around 50 m during the southwest monsoon period. All the bioluminescence peaks were associated above the thermocline depth irrespective of the monsoon winds. However, the Chlorophyll maximum (2.2 mgm^3) was observed around 50–90 m depth during the northeast monsoon period, and 40–60 m depth (4.6 mgm^3) during the southwest monsoon period (Fig. 7d). Bioluminescence peaks were not associated with the Chlorophyll maximum during the northeast monsoon period although the peaks were associated with the Chlorophyll maximum during the southwest monsoon.

Diversity and abundance of surface bioluminescent zooplankton off the south coast and the Puttalam Lagoon of Sri Lanka

Abundance of surface bioluminescent zooplankton was assessed off the south coast and in the Puttalam Lagoon of Sri Lanka. Twenty two surface bioluminescent zooplankton species belonging to 15 families and 4 phyla were identified during this study. Out of which 8 species were recorded in the lagoon and 21 species were identified in the ocean. Seven bioluminescence zooplankton species; *Acrocalanus longicornis, Paracalanus indicus, Pleuromamma indica, Macrosetella gracillis, Oithona similis, Triconia conifer* and *Oikopleura dioica* were recorded in both lagoon and ocean.

The most abundant bioluminescent zooplankton species off the south coast of Sri Lanka was *Triconia conifer* and its average abundance was 7 individuals/m^3. This species was observed throughout the year and the highest abundance was reported in the October to December period mainly at sampling location 4 (Table 3). *Acrocalanus longicornis* (3 individuals/m^3) was the second most dominant species and it was also reported throughout the year showing the highest abundance in the October to December period (Fig. 8). *Macrosetella gracilis,* Dana, 1848 and *Oikopleura dioica,* Fol, 1872 were also observed throught the year but their abundance was very low compared with *Triconia conifer and Acrocalanus longicornis* (Table 3).

Less abundant zooplankton species include: *Diphyes dispar,* Chamisso & Eysenhardt, 1821; *Centropages furcatus,* Dana, 1849; *Clausocalanus arcuicornis,* Dana, 1849; *Pleuromamma indica,* Wolfenden, 1905; *Pleuromamma gracilis,* Claus, 1863; *Pontellina* sp, *Scolecithricella minor,* Brady, 1883; *Temora stylifera,* Dana, 1849; *Tomopteris helgolandica,* Greeff, 1879; *Undinula vulgaris* ,Dana, 1849; *Corycaeus (Onychocorycaeus) latus* Dana, 1849; *Corycaeus (Corycaeus) speciosus* Dana, 1849; *Oithona similis,* Claus, 1866.

Although there were variations in bioluminescent zooplankton abundance with respect to sampling locations (Fig. 8), it was not significant ($p > 0.05$; Kruskal–Wallis test). However, bioluminescent zooplankton abundance exhibited significant difference ($p < 0.05$; Kruskal–Wallis test) with respect to the sampling season where the highest and lowest abundance was reported during October-December and April-June, respectively (Table 3).

According to fixed station data, the highest abundance of surface bioluminescent zooplankton was reported around 1.00 am during the northeast monsoon period (Table 4) and around 9.00 pm during the southwest monsoon. *Triconia conifer* was the highly abundant bioluminescence zooplankton during the northeast monsoon period and it was *Oikopleura dioica* during the southwest monsoon period. The lowest species abundance was observed at dusk and dawn for both sampling dates.

Bioluminescent zooplankton species were also observed throughout the year in the Puttalam Lagoon similar to the

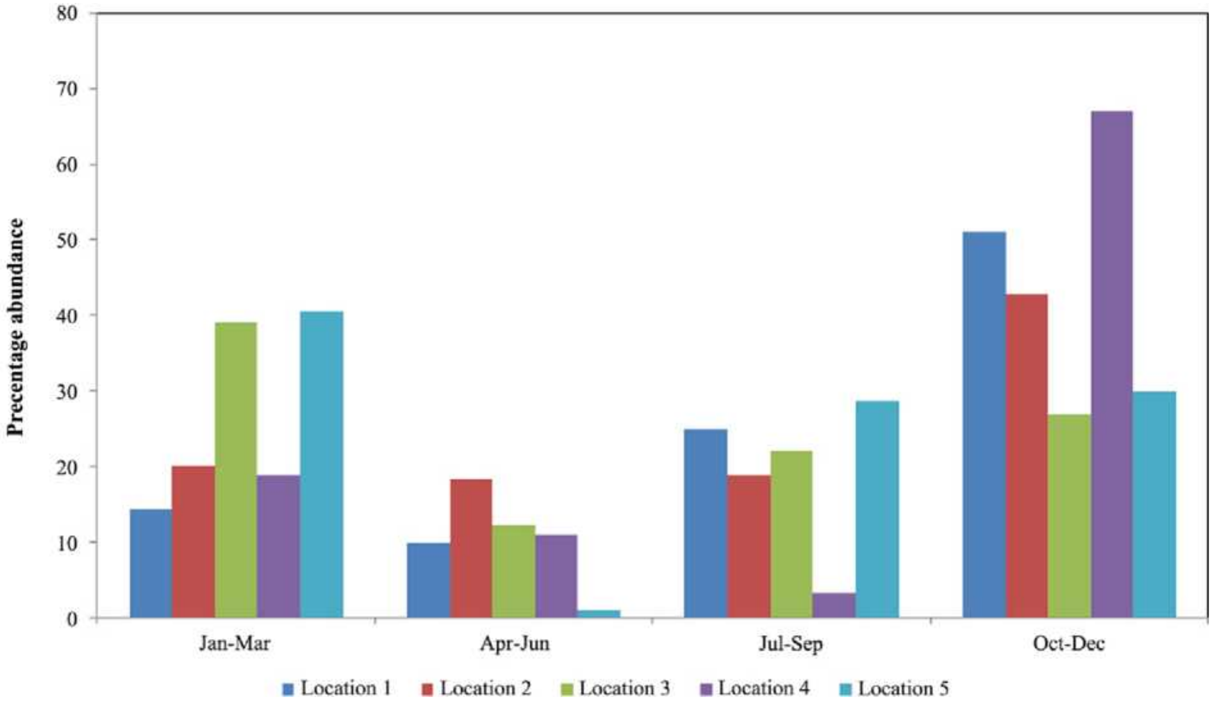

Fig. 8. Percentage abundance of surface bioluminescent zooplankton at 5 sampling locations off the south coast of Sri Lanka during 2016

observations made off the south coast of Sri Lanka. *Vargula hilgendorfii* reported the highest average abundance (11.2 individuals/m^3) in the lagoon (Table 5) and this species was reported at all the sampling locations in much higher densities than the other species. Although *Oikopleura dioica* (3 individuals/m^3) was also observed throughout the year at all the sampling locations, the abundance was lower than *V. hilgendorfii*. *Acrocalanus longicornis* was the second highest abundant (6 individuals/m^3) species in the lagoon but the distribution was mostly restricted to the sampling locations close to the open ocean. *Pleuromamma indica* (0.08 individuals/m^3) and *Oncaea conifer* (1 individuals/m^3) were identified as the least abundant species (Table 5) in the Puttalam Lagoon. The abundance of bioluminescent zooplankton in the Puttalam Lagoon did not show significant variation with respect to sampling time and sampling location ($p > 0.05$; Kruskal–Wallis test).

4. Discussion

Bioluminescence is ubiquitous in the world's ocean and an essential factor in marine ecology (Haddock et al. 2010). Although many studies have been carried out to study the abundance, distribution, chemical process of bioluminescence organisms in many parts of the world, only a few studies have described bioluminescence communities and their distribution in the Indian Ocean (Shanware et al. 2013). However, no work has been done to study any aspect of bioluminescence in Sri Lankan waters until the current effort.

In this study, bioluminescence was measured using the recoverable bathyphotometer (RBPM) which is a new instrument used in the field of bioluminescence (Fucile 2003). Due to its small structure and the attached mesh grid to the lower part of the instrument, large animals such as jellyfish and fish are prevented from entering and passing through the instrument. Thus, the RBPM only measures the light emitted by small organisms such as phytoplankton and zooplankton. According to Tett and Kelly (1973), pump-through bathyphotometers only collect smaller zooplankton which cannot or do not swim away from the suction current of the intake hose. Therefore, pump-through bathyphotometers underestimate the contribution of zooplankton to the bioluminescence profiles. However, this is does happen with regard to RBPM as it records all the animals in the water column while being deployed in a free falling method.

This study presents the first bioluminescence intensity profiles in Sri Lankan waters and the results revealed that bioluminescence occurs throughout the year off the southern

Table 3. Variations in the abundance of surface bioluminescence zooplankton (individuals /m^3) off the south coast of Sri Lanka during the study period from January to December 2016

Species	January–March abundance (individuals/m^3)					April–June abundance (individuals/m^3)					July–September abundance (individuals/m^3)					October–December abundance (individuals/m^3)				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Diphyes dispar	0	0	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4
Acrocalanus longicornis	0	4	12	28	8	3	2	6	25	1	12	3	0	3	25	18	24	12	60	16
Paracalanus indicus	0	0	0	16	4	0	11	2	0	0	0	0	3	0	0	0	0	0	20	20
Centropages furcatus	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	6	0	0	10	0
Clausocalanus arcuicornis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	90	0
Pleuromamma indica	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromamma gracilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pontellina plumata	0	0	0	4	8	3	0	2	5	0	0	0	0	0	0	0	8	0	0	0
Pontellina sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0
Pontellafera sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scolecithricella minor	0	0	0	0	0	8	6	2	0	0	8	0	0	0	0	0	0	0	0	4
Temora stylifera	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	4	0	0	4
Tomopteris helgoladica	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Undinula vulgaris	0	0	4	0	0	3	0	0	0	0	0	6	9	0	0	0	0	0	0	0
Euchaeta marina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corycaeus latus	0	0	0	0	0	0	3	0	0	1	0	0	0	0	10	0	0	0	0	0
Corycaeus speciosus	0	0	0	4	4	0	0	4	0	0	0	12	0	0	0	6	0	0	0	0
Triconia conifer	12	0	32	20	60	0	5	4	5	0	40	9	24	12	15	84	32	28	190	20
Macrosetella gracilis	0	8	8	0	0	10	2	0	15	0	0	0	0	0	15	6	0	0	0	0
Oithona similis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Oikopleura dioica	80	20	8	28	0	0	0	0	10	0	16	0	0	0	0	0	0	0	0	0

Table 4. Variations in the abundance of surface bioluminescence zooplankton (individuals/m^3) at the fix sampling location off the south coast of Sri Lanka during the northeast(January) and southwest (May) monsoon periods

Species	January abundance (individuals/m^3)						May abundance (individuals/m^3)					
	7.00 pm	9.00 pm	11.00 pm	1.00 am	3.00 am	5.00 am	7.00 pm	9.00 pm	11.00 pm	1.00 am	3.00 am	5.00 am
Diphyes dispar	0	0	0	4	4	0	4	0	0	0	0	0
Tomopteris helgolandica	0	0	0	0	4	0	0	4	0	0	0	0
Undinula vulgaris	0	0	4	0	0	0	12	12	0	10	0	0
Centropages furcatus	0	0	0	0	0	0	0	0	0	10	0	0
Pleuromamma gracilis	4	0	0	0	0	0	0	0	0	0	0	0
Acrocalanus longicornis	0	4	12	28	8	18	4	54	8	10	0	0
Paracalanus indicus	0	0	0	16	4	0	0	24	20	0	16	0
Pontella fera	0	0	0	0	0	0	0	0	4	0	0	0
Potellina plumata	0	0	0	4	8	0	12	6	0	10	0	0
Temora stylifera	20	0	0	0	0	0	4	0	0	0	0	0
Macrosetella gracilis	0	8	8	0	0	0	0	0	4	0	4	0
Corycaeus speciosus	0	0	0	4	4	0	0	0	0	0	0	3
Triconia conifer	12	0	32	20	60	6	0	0	0	0	8	0
Oikopleura dioica	8	20	8	28	0	0	4	48	16	20	4	12

Table 5. Variations in the abundance of surface bioluminescence zooplankton (individuals/m^3) in the Puttalam lagoon Sri Lanka during the study period from January to December 2016

Species name	January–March abundance (individuals/m^3)						April–June abundance (individuals/m^3)						July–September abundance (individuals/m^3)						October–December abundance (individuals/m^3)					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Acrocalanus longicornis	0	2	6	0	0	0	10	8	14	18	0	0	10	8	11	16	0	0	5	0	8	20	0	0
Paracalanus indicus	0	0	1	4	0	0	0	0	8	6	0	0	0	0	4	2	0	0	7	0	14	16	0	0
Pluromamma indica	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Macrosetella gracillis	0	0	0	0	0	0	0	0	2	1	0	0	4	2	8	0	0	0	0	2	5	0	0	0
Oithona similis	0	0	8	0	8	4	0	0	0	16	0	8	0	0	8	18	2	6	0	0	3	11	2	5
Triconia conifer	1	0	4	0	0	0	0	0	0	4	0	0	0	0	0	2	0	0	0	0	4	2	0	0
Vargula hilgendorfii	8	21	18	6	10	14	3	5	6	2	1	5	10	18	15	20	12	8	15	6	8	16	22	20
Oikopleura dioca	0	2	1	1	1	1	1	0	0	1	0	1	2	8	6	8	2	1	4	5	8	4	0	1

coast of Sri Lanka and the Puttalam Lagoon in varying degrees of intensity. Physical oceanographic dynamics in off-shore and coastal waters could be the main reason for this intensity variation and similar observations have been previously reported by Marra (1989) in the Northeast Atlantic. From an oceanographic perspective, Sri Lanka is situated in a unique location in the Indian Ocean. This uniqueness is mainly due to the presence of bi-annual reversing monsoon winds in two different seasons of the year (Schott and Mccreary 2001). The southwest monsoon is generally from May to September and the northeast monsoon is from December to February. There are additional two seasons named as first inter monsoon (March to April) and second inter monsoon (October to November) which are considered as transitional periods of wind. This bi-directional monsoonal wind is responsible for the changes in the physical and chemical properties of the ocean which greatly affect plankton biomass in the water column (Marra 1989). Similarly, monsoon winds also change the physical characteristics of Puttalam Lagoon (Silva et al. 2013). During the southwest monsoon, the lagoon exhibits rough conditions due to high winds but it is calm during the northeast monsoon period (Durairatnam 1963).

The observed high bioluminescence intensity counts in the bioluminescence intensity profiles off the south coast especially during January to March and July to September periods could be due to monsoonal wind driven water currents, as explained by Lynch (1981). According to the results of this study, high intensity bioluminescence peaks were mostly reported at sampling locations 2 and 4 during this study period. The high bioluminescence intensity records in these two locations could be due to high abundance of planktonic organisms in those areas. Although surface nutrient concentrations did not show any significant changes among locations, vertical nutrient distribution could have made some contribution to this observation (Gunasekara 2016).

In most of the bioluminescence profiles, the highest bioluminescence peaks were found in the mixed layer. It has been reported that temperature and salinity are fairly constant in the mixed layer. However, layers below mixed layer continuously inject nutrient rich water to the mixed layer (Kara et al. 2003). Therefore, high productivity is evidenced in the mixed layer due to high level of plankton growth. Thus, the high abundance of plankton in the mixed layer could be a reason for the high concentration of bioluminescence peaks in this layer compared to other layers. According to Lapota et al. (1989), well-mixed water with relatively uniform temperature is vital for the existence of the planktonic bioluminescence species in the mixed layer and this study also supports their findings. Furthermore, the observed high bioluminescence intensity counts in the mixed layer off the south coast especially during January to March and July to September periods could be due to changes in the mixed layer plankton population as a result of monsoon variation, as explained by Lynch (1981) and Marra (1989).

The changes in the mixed layer depth are caused by a wind driven phenomenon and chages in mixed layer depth is mainly associated with monsoonal changes (Keerthi et al. 2013, 2016). This may be the reason for the observed slight changes in the mixed layer depth during this study period. It is well documented that the mixed layer depth ranges from the surface to ~60 m in tropical oceans, while it varies seasonally in temperate oceans (Gitelson and Levin 1989). Therefore, the observed high number of bioluminescence peaks around 60 m depths can be explained, as Sri Lanka is situated in a tropical region. Similar observations were reported for vertical bioluminescence profiles obtained from many parts of the world (Gitelson and Levin 1989). For example, high bioluminescence has been reported around 70 m depth, which is within the mixed layer depth, in the Arctic Ocean. Other scientists (Lapota et al. 1989; Lapota and Losee 1984) have confirmed the occurrence of high numbers of high intensity bioluminescence peaks in the mixed layer of the ocean due to the presence of light-emitting dianoflagellates and zooplankton. However, this study faced difficulties in quantifying the type of bioluminescent organisms and their intensities due of the lack of depth related plankton sampling. However, it can be assumed that the observed bioluminescence peaks are mainly due to planktonic organisms as the instrument employed only allows planktonic organisms to enter the bathyphotometer chamber.

Fixed station bioluminescence profiles indicated differences in bioluminescence intensity during January (northeast monsoon) and May (southwest monsoon). The observed differences in bioluminescence intensity with respect to monsoon winds could be due to changes in bioluminescent species abundance in the sampling area. The high number of bioluminescence peaks in May compared to January could be a result of high bioluminescent species abundance stemming from the high productivity of the ocean during May. The occurrence of high intensity bioluminescence peaks were found to vary with time with respect to the two sampling periods. The exact reason for this observation could not be established, but this could be due to variations in water currents or differences in species composition. A similar study was carried out in the US Pacific Northwest waters by Mcmanus et al. (2003) and they reported that bioluminescence intensity was high during 10.00 pm to 4.00 am - similar to the findings of this study.

This study also demonstrated that changes in bioluminescence intensity and the abundance of bioluminescent organisms occurred with respect to the sampling time of the day and the sampling season at the fixed station, off the south coast of Sri Lanka. The observed bioluminescence intensity variations with respect to time could be due to intermittent increases and decreases created by vertical migration of plankton. It has been well reported that many species of zooplankton such as copepods, euphausiids and ostracods undertake diurnal vertical migration (Roe 1972; Ambler and Miller 1987). Migration of bioluminescent zooplankton can easily alter the number of flashes, mean intensity of the flashes and intensity distribution in near-surface waters at night (Sweeney et al. 1959; Batchelder et al. 1992; Buskey 1992; Swift et al. 1995). Similar observations were reported previously by Lieberman et al. (1987), Clarke and Kelly (1965), Clarke and Backus (1957) for different regions of the world.

This study confirms the occurrence of a thin layer of bioluminescence at the fixed station especially during 7.00 pm to 5.00 am in January 2016 at around 80 m depth. As per the explanation made by Mcmanus et al. (2003), this thin layer may be a result of the aggregation of planktonic organisms (both phytoplankton and zooplankton). According to Mcmanus et al. (2003), organisms in this thin layer belong to several orders and they are more abundant than in the water immediately above or below it. Further, it has been reported that this thin layer can persist for much more extended periods than other plankton communities, and this was also observed in this study. The thin layer produce a unique physical, chemical and biological environment for plankton community and preserve and maintain species diversity (Mcmanus et al. 2003). This type of planktonic aggregation is important to maintain productivity in the pelagic oceans (Mcmanus et al. 2003) and more importantly it can be directly observed through RBPM using the bioluminescence ability of organisms.

Only a few studies have been carried out to assess the lagoon bioluminescence in the world. A few authors such as Ratheesh (2016) and Zimberlin (2013) made attempts to identify the patterns of bioluminescence in different lagoons previously and the findings of this study will enhance existing knowledge and information. The observed high intensity bioluminescence peaks in the lagoon profiles during the April to July period might be due to the increase of wind driven wave action in the lagoon in response to the first inter-monsoon. Pinckney et al. (2018) also highlighted the role of wind driven variability in bioluminescence in mangrove lagoons in the United States.

According to the findings of this study, it seems that the entire Puttalam Lagoon acts as one unit with high bioluminescence dispersed throughout the lagoon. The lack of differences in the bioluminescence intensity along the lagoon could be due to its shallowness. Although high bioluminescence peaks were observed during monsoonal winds, they did not show any consistent pattern across the lagoon. A study carried out in Kavaratti Lagoon in India revealed that although fluctuations in tide and salinity proved to be the major factors affecting bioluminescence variations in the lagoon, lagoon nutrients did not exert any influence (Ratheesh 2016).

The observed bioluminescence profiles off the south coast and Puttalam Lagoon could be due to bioluminescent phytoplankton or zooplankton species or a combination of both as the mesh net in the RPBM only allows planktonic organisms to pass through it. However it is hard to distinguish phytoplankton and zooplankton bioluminescence separately only by looking at bioluminescence profiles. Lieberman et al. (1987) suggested comparing bioluminescence profiles and Chlorophyll profiles to identify the responsible organism or group that produce bioluminescence peaks.

Accordingly, it can be assumed that bioluminescence peaks in the regions where bioluminescence and Chlorophyll peaks overlap are due to bioluminescent phytoplankton mainly from dianoflagellates, as revealed by many authors previously (Lapota et al. 1989; Swift et al. 1995) Bioluminescence in the regions where bioluminescence peaks and Chlorophyll peaks did not overlap could be due to heterotrophic plankton such as zooplankton or heterotrophic dianoflagellates. However, some studies have reported a non-systematic correlation between bioluminescence and Chlorophyll fluorescence (Lapota et al. 1989). Neilson et al. (1995) explained that the relationships between bioluminescence and Chlorophyll fluorescence in the North Atlantic Ocean are mainly due to differences in organism assemblage.

When analysing the bioluminescence and Chlorophyll profiles off the south coast of Sri Lanka, it was shown that large autotrophic and heterotrophic plankton populations were present in this area during the study period. However, this study did not collect plankton samples along the depth profile due to practical difficulties, hence it is difficult to make conclusions regarding the type of bioluminescent phytoplankton species responsible for bioluminescence peaks.

Batchelder et al. (1992) emphasized that zooplankton are responsible for at least two-thirds of the ocean flashes and around 60% of bioluminescence occurs in the ocean surface (Batchelder et al. 1992). Rudyakov and Voronina (1967) also suggested that zooplankton are just as important as phytoplankton in the surface waters of the Gulf of Aden and the Red Sea. Furthermore, they reported those bioluminescent zooplanktons are largely responsible for the bioluminescence in vertical profiles. They also noted that different zooplankton organisms are responsible for bioluminescence at different depths. Moreover, bioluminescent phytoplankton were found to be generally persisting over a vast region and that they are more abundant in numbers and uniform in distribution. Zooplankton (i.e., copepods) were found to be fewer in numbers than phytoplankton in an equivalent volume, but their flash intensity was reported to be much higher. These differences are believed to have caused the many variations in bioluminescence outputs observed in this study.This study demonstrated the presence of seasonal and perennial zooplankton species along the south coast of Sri Lanka. Seasonality of zooplankton, including bioluminescent zooplankton, has been reported by several studies in Sri Lanka (Wijetunge and Ranatunga 2015) as well as in other parts of the world (Khalil and El-Rakman 1997). Although zooplankton are able to swim, their horizontal distribution largely depends on water currents. Similar to this study, high abundance of *Triconia conifer* and *Acrocalanus longicornis* was reported in the Sargasso Sea (Swift et al. 1983), North Atlantic (Herring et al. 1993) as well as in other parts of the world (Herring 1988).

5. Conclusion

This study provides the first scientific evidence of the presence of bioluminescence in the marine and lagoon waters of Sri Lanka and preliminary results regarding intensity variations with respect to space and time. This information will be useful to update existing regional and global information; however, more detailed studies will be needed in the future to understand such variations around Sri Lanka and to utilize bioluminescent organisms for commercial purposes in a sustainable manner.

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