Spatio-temporal variation of microphytoplankton in the upwelling system of the south-eastern Arabian Sea during the summer monsoon of 2009*

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Abstract

The phytoplankton standing crop was assessed in detail along the South Eastern Arabian Sea (SEAS) during the different phases of coastal upwelling in 2009.

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During phase 1 intense upwelling was observed along the southern transects (8°N and 8.5°N). The maximum chlorophyll *a* concentration (22.7 mg m $^{-3}$) was observed in the coastal waters off Thiruvananthapuram (8.5°N). Further north there was no signature of upwelling, with extensive *Trichodesmium erythraeum* blooms. Diatoms dominated in these upwelling regions with the centric diatom *Chaetoceros curvisetus* being the dominant species along the 8°N transect. Along the 8.5°N transect pennate diatoms like *Nitzschia seriata* and *Pseudo-nitzschia* sp. dominated. During phase 2, upwelling of varying intensity was observed throughout the study area with maximum chlorophyll *a* concentrations along the 9°N transect (25 mg m^{-3}) with *Chaetoceros curvisetus* as the dominant phytoplankton. Along the 8.5°N transect pennate diatoms during phase 1 were replaced by centric diatoms like *Chaetoceros* sp. The presence of solitary pennate diatoms *Amphora* sp. and *Navicula* sp. were significant in the waters off Kochi. Upwelling was waning during phase 3 and was confined to the coastal waters of the southern transects with the highest chlorophyll *a* concentration of 11.2 mg m^{-3}. Along with diatoms, dinoflagellate cell densities increased in phases 2 and 3. In the northern transects (9°N and 10°N) the proportion of dinoflagellates was comparatively higher and was represented mainly by *Protoperidinium* spp., *Ceratium* spp. and *Dinophysis* spp.

1. Introduction

The phytoplankton community in a coastal upwelling system is influenced by the temporal variations in physicochemical factors associated with the progression of upwelling processes. Factors like temperature (Goldman & Mann 1980), illumination (Ryther 1956), turbidity (Estrada & Berdalet 1997) and nutrients (Sanders et al. 1987) have significant effects on the distribution of phytoplankton in such regions. The phytoplankton community in the various upwelling regions of the World Ocean has been assessed in numerous research works. It is usually the case in an upwelling ecosystem that phytoplankton of the class Bacillariophyceae (diatoms) flourish during intense upwelling conditions with enhanced nutrient levels, but is replaced by dinoflagellates (class: Dinophyceae) during the relaxation period of the more or less stratified water column. Earlier studies in upwelling areas off north-west Africa (Estrada & Blasco 1985) revealed an abundance of diatoms belonging to the genera *Chaetoceros*, *Thalassiosira* and *Rhizosolenia* in the phytoplankton community. Recent works have identified certain functional groups of phytoplankton in upwelling regions. According to Tilstone et al. (2000) diatom dynamics in a coastal upwelling system is greatly influenced by physical processes; hence, the upwelling that initiates several biogeochemical responses can be treated as forces shaping the phytoplankton community. Lassiter et al. (2006) examined the diatom community response to upwelling events along the coasts of northern California and stated that *Chaetoceros* sp. together with other centric diatom genera such as *Thalassiosira*, *Asterionella* and *Rhizosolenia* comprise a functional group in these coastal upwelled waters.

The south-eastern Arabian Sea (SEAS), one of the most productive regions of the World Ocean, is influenced by coastal upwelling mainly during the summer monsoon period. Phytoplankton production along the SEAS is found to be intense during the summer monsoon upwelling that extends from May–June to September (Bhattathiri et al. 1996), and the vertical flux of inorganic nutrients during this period triggers phytoplankton production, leading to high biological productivity (Ryther et al. 1966, Qasim 1982). During the wind-driven upwelling process, surface nutrient levels increase and nitrate concentrations in surface waters reach $\sim$ 2–4 μM in the area (De Sousa et al. 1996). According to Subrahmanyan (1958), phytoplankton along the SEAS was most abundant during the south-west monsoon period, with the composition varying with season. Previous studies (Qasim & Reddy 1967, Radhakrishna 1969, Subrahmanyan et al. 1975, Rajagopalan et al. 1992, Bhattathiri et al. 1996, Habeebrehman et al. 2008) quantified strong changes in the chlorophyll patterns during this period. Roy et al. (2006) studied the spatial variation of phytoplankton pigments along the SEAS towards the end of the upwelling event, and found that chlorophyll *a* was the most abundant of all the pigments.

Upwelling begins at the southern tip of India during May–June and subsequently propagates northwards. However, the process along the southern tip of India as well as the south-west coast are highly localized features with different forcing mechanisms, so it cannot be treated as a uniform wind-driven upwelling system (Smitha et al. 2008). Upwelling along the southern tip of the Indian peninsula (Cape Comorin) is purely wind-driven and strong (Smitha et al. 2008). Off the west coast, alongshore wind stress plays the major role along the Cape Comorin-Kollam sector, and further north the process is due to the combined action of alongshore wind stress and remote forcings from the Bay of Bengal which include the propagation of Kelvin and Rossby waves (Shankar & Shetye 1997). The maximum offshore extent of the process is recorded in the Kollam-Kochi region (Haugen et al. 2002). Biological responses tend to vary according to the intensity of the upwelling event in both coastal and offshore waters (Habeebrehman et al. 2008). However, detailed studies of the phytoplankton composition in the area during this period are few. In this scenario, an attempt was made to understand the influence of upwelling events on the phytoplankton community in the inshore as well as shelf waters of SEAS during the upwelling period of the summer monsoon of 2009.

2. Materials and methods

There was evident variability in the phytoplankton responses during three sampling phases along four latitudinal transects, namely, off Cape Comorin (8°N), off Thiruvananthapuram (8.5°N), off Kollam (9°N) and off Kochi (10°N). The transects are treated separately with respect to spatial variation in the physical process of upwelling and phytoplankton production, and a general overview of the phytoplankton community of the whole area is given. In situ observations were made on board FORV Sagar Sampada as a part of the Marine Living Resources (MLR) programme to assess environmental parameters and productivity patterns in the Indian EEZ. The studies were done in three phases: phase 1 (June 2009), phase 2 (August 2009) and phase 3 (September 2009) along the south-eastern Arabian Sea (SEAS). Sampling was carried out in four latitudinal transects: 8°N (off Cape Comorin), 8.5°N (off Thiruvananthapuram), 9°N (off Kollam) and 10°N (off Kochi). Figure 1 shows the study area and sampling locations. Stations were fixed at three locations along each transect at 30 m, 50 m and 100 m station depths and a total of twelve stations were sampled during each phase.

Vertical profiling of parameters like temperature, salinity and density was done using the CTD (Seabird 911 plus CTD) attached sensors to understand the oceanic processes. The depth of the 25°C isotherm is considered the reference value for tracing upwelling and is termed D25. The

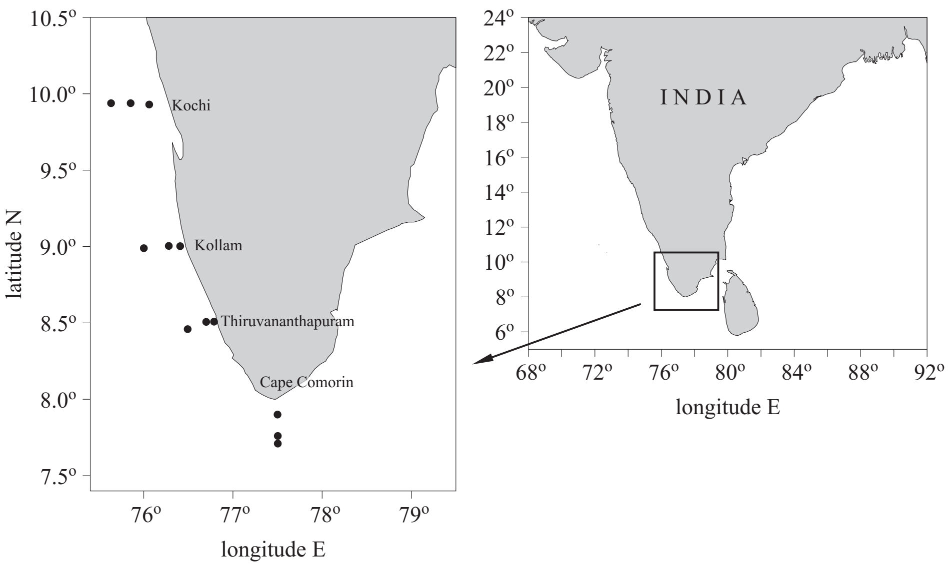

Figure 1. Map showing the study area

rosette system equipped with Niskin bottles, attached to the CTD profiler, was used for the collection of water samples from standard depths (0, 10, 20, 30, 50, 100 and 120 m). Chlorophyll *a* was measured spectrophotometrically using a double-beam Perkin-Elmer UV-Visible spectrophotometer following 90% acetone extraction (Parsons et al. 1984). Major nutrients were analysed using a segmented flow auto-analyser (SKALAR) on board the vessel in accordance with standard procedures (Grasshoff et al. 1983). Phytoplankton samples were collected by filtering ∼ 50 litres of surface water through 20 bolting silk, and the filtrates were preserved in 1–3% neutralized formaldehyde-Lugol's iodine solution. Qualitative and quantitative analysis of phytoplankton samples were carried out using a Sedgewick Rafter counting cell under a Nikon Eclipse microscope following standard identification keys (Tomas 1997).

3. Results and discussion

3.1. Phase 1

During phase 1 (June), upwelling was intense, extending from the coastal waters off peninsular India (8°N, off Cape Comorin) towards the south-west coast up to the nearshore waters at 9°N (off Kollam). In the southernmost regions, off Cape Comorin (8°N), strong upwelling characterized by summer monsoon winds blowing tangentially to the coast occurs early during the onset of summer monsoon. During phase 1, a lower SST (24.8°C) in the inshore waters and a well-marked gradient to offshore (27.03°C) were observed (Figure 2). On moving northward, coastal upwelling at 8.5°N (off Thiruvananthapuram) extended beyond the shelf waters. Coastal SST was 25.36°C, reaching 27.5°C in the mid-shelf waters (100 m depth stations). Upwelling was confined to coastal waters along 9°N (SST 27.2°C). In the regions further offshore as well as northward along 10°N (off Kochi), spring inter-monsoon conditions characterized by weaker winds (wind speed 3.7 m sec $^{-1}$) and higher SSTs (28°C) prevailed. The depth of the 25°C isotherm (D25) lay at 20 m in this area. Surface nitrate concentrations reached a maximum of ∼ 9 μM along the coastal waters off Thiruvananthapuram; along the coastal waters off Cape Comorin, values reached nearly 3 μM, decreasing to nearly 0.01 μM in the non-upwelling northern transects. Elevated surface chlorophyll *a* concentrations were recorded in the regions of intense upwelling. The chlorophyll *a* concentrations peaked in the coastal waters off Thiruvananthapuram (22.7 mg m^{-3}) (Figure 3) followed by the region off Cape Comorin (10 mg m^{-3}). Mean chlorophyll *a* concentrations

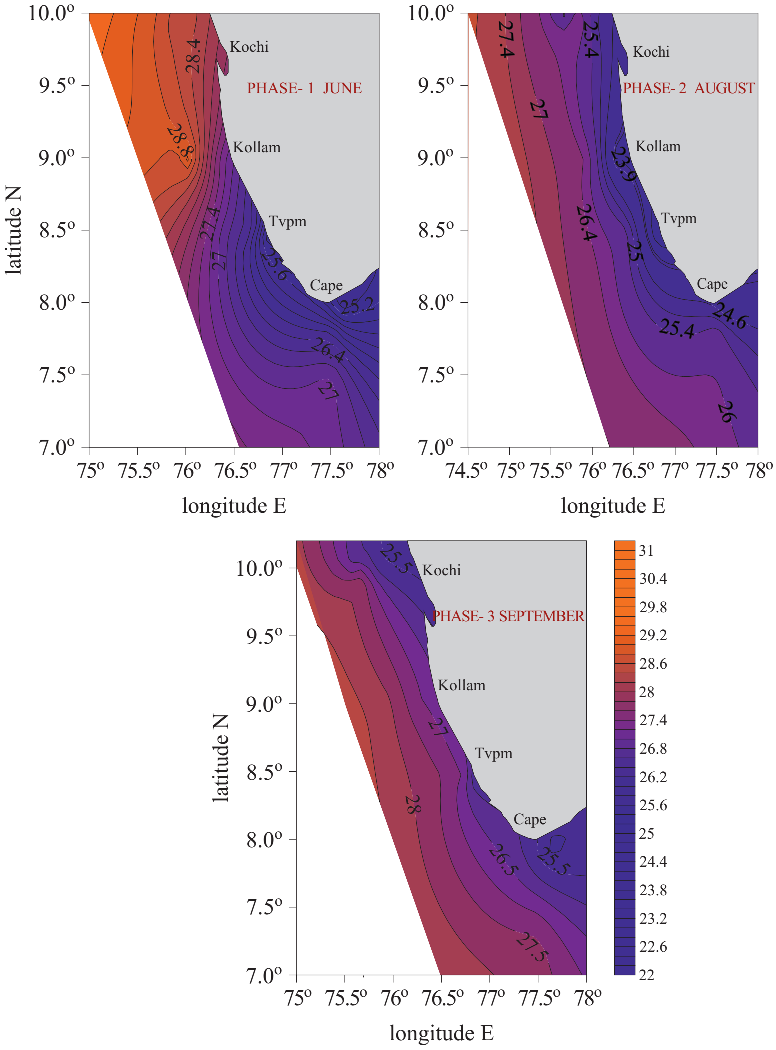

Figure 2. Variations in SST [°C] during different phases of upwelling along the SEAS during the summer monsoon of 2009

were 8 mg m^{-3} in the transect off Cape Comorin and 12.5 mg m^{-3} in the transect off Thiruvananthapuram (Figure 4).

The total phytoplankton cell density along the transect off Cape Comorin was $\sim 20 \times 10^3$ cells L^{-1} and was about twice that value off Thiruvananthapuram ($\sim 40 \times 10^3$ cells L^{-1}). Even though these two transects were subject to significant levels of upwelling, the phytoplankton community exhibited discrepancies. Phytoplankton in the region off Cape Comorin was represented solely by diatoms, while dinoflagellates were absent altogether (Figure 5). *Chaetoceros curvisetus*, a chain-forming

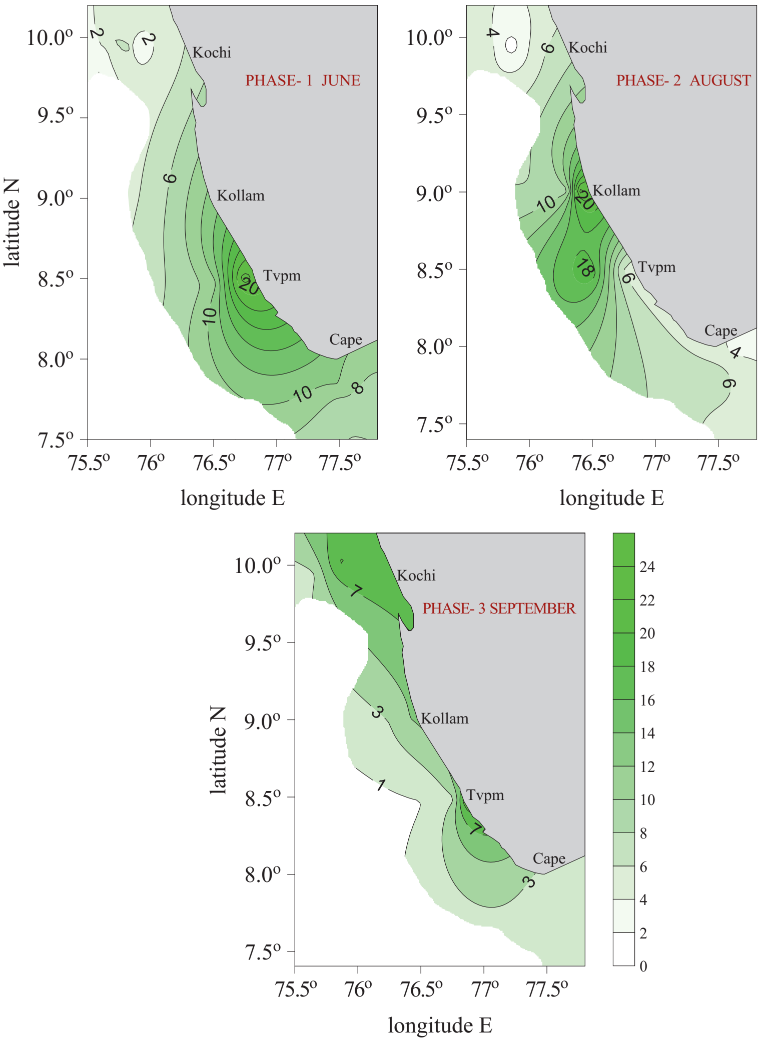

Figure 3. Surface distribution of chlorophyll a [mg m^{-3}] during the different phases of upwelling along the SEAS during the summer monsoon of 2009

centric diatom dominated the phytoplankton community, contributing ca 60–90% of the total cell density. This species has been previously recorded from upwelling regions (D'Croz et al. 1991, Tilstone et al. 2000) and is considered to be a characteristic species of eutrophic coastal upwelled waters (Pitcher et al. 1991). Accordingly, *Chaetoceros* sp. have high spore production and reseeding rates, which favours their occurrence in the upwelled waters. Moreover, their being suspended in the water column because their non-motile habit with valvular outgrowths (setae) helps them to adapt to the upwelling environment with continuous renewal of surface

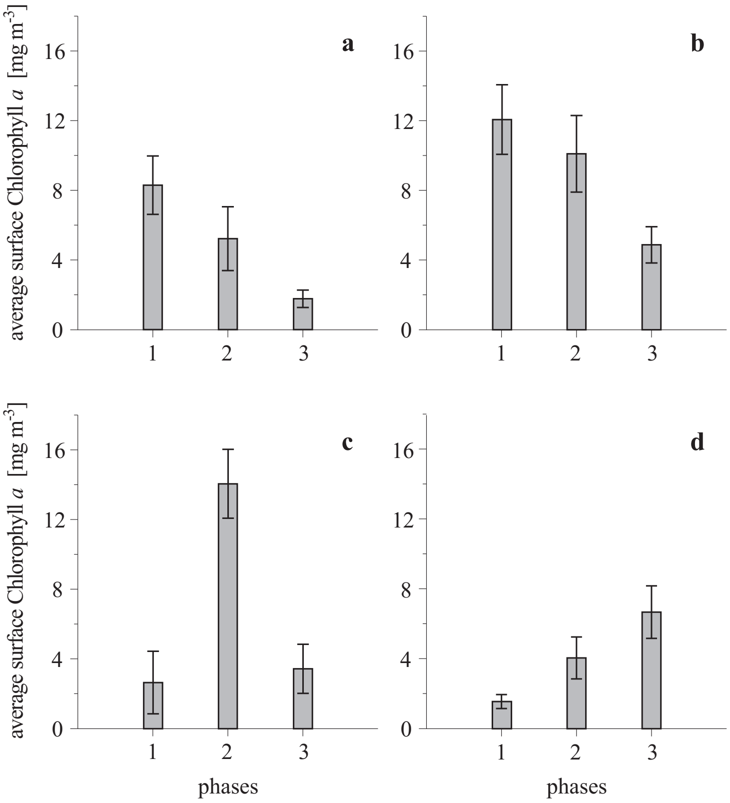

Figure 4. Average surface chlorophyll *a* (mg m^{-3}) distribution along with ± standard deviations around the mean values in all transects of the study area during different phases of upwelling during the summer monsoon of 2009: a) off Cape Comorin, b) off Thiruvananthapuram, c) off Kollam, d) off Kochi

water (Margalef 1978, Margalef et al. 1979). Hence, the region off Cape Comorin with strong winds and the southward drift of upwelled waters favoured turbulence-tolerant species like *Chaetoceros curvisetus. C. lorenzianus*, *C. decipiens*, *Bacteriosira bathyomphala*, *Detonula pumila* and *Skeletonema costatum* were the other phytoplankton species observed in the region during this period (Table 1).

The phytoplankton community along 8.5°N was dominated by diatoms with a few representatives of the dinoflagellates (Figure 5). Diatoms, mainly *Nitzschia seriata*, *Pseudo-nitzschia* sp., *Lauderia* sp. and *Thalassiosira* sp., contributed to the phytoplankton population of the region. *Protoperidinium* sp. (2% of the total cell count) was the major dinoflagellate present. Coastal upwelling progressed only up to the nearshore waters off Kollam (9°N) during phase 1. The region beyond this margin was experiencing extensive blooms of the blue-green algae *Trichodesmium*

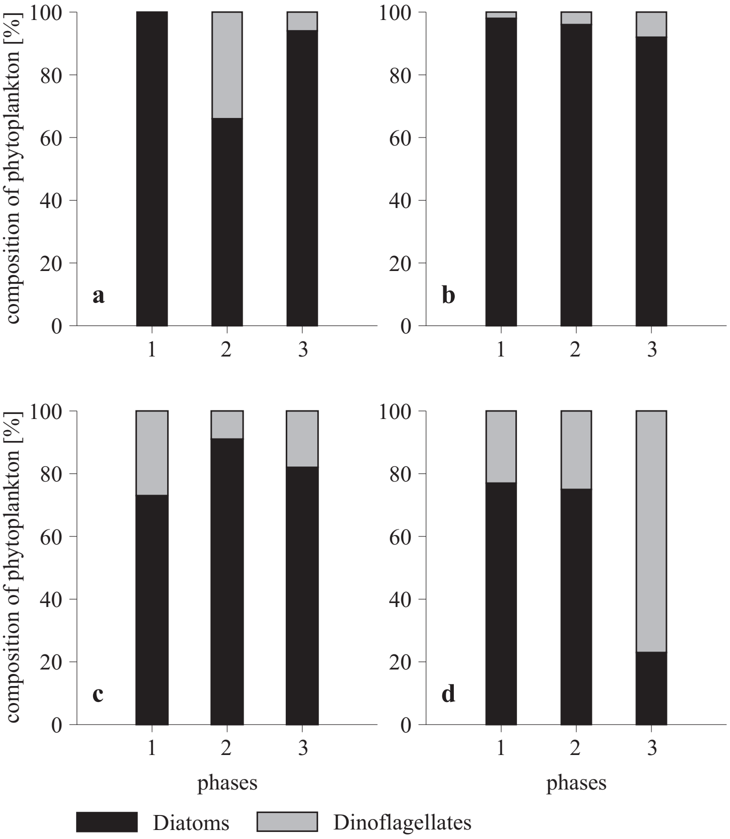

Figure 5. Percentage composition of diatoms and dinoflagellates along the different transects of the SEAS during the summer monsoon of 2009: a) off Cape Comorin, b) off Thiruvananthapuram, c) off Kollam, d) off Kochi

erythraeum, favoured by the pre-monsoon conditions prevailing in the area (Padmakumar et al. 2010a), which continued further northwards (10°N). The surface chlorophyll a level in the region reached 4 mg m^{-3} and the cell density 1×10^6 cell L^{-1} was due mainly to filaments of *T. erythraeum*. The diatom community of the region during this period was represented by *Rhizosolenia* sp., and dinoflagellates by the genera *Protoperidinium* and *Ceratium*, which contributed nearly 25% of the total cell count (Figure 5; Table.1).

3.2. Phase 2

Phase 2 (August) was characterized by coastal upwelling of varying intensity throughout the SEAS. Along 8°N, SST reached 26.7°C with D25 at 10 m. Moving further north, upwelling intensified. In the region off

Table 1. List of phytoplankton identyfied along the SEAS during the summer monsoon of 2009

Region	(8°N) off Cape Comorin			(8.5°N) off Thiruvananthapuram			(9°N) off Kollam			(10°N) off Kochi		
Phases	1	2	3	1	2	3	1	2	3	1	2	3
Class – Bacillariophyceae												
Amphora sp.	−	−	−	−	−	−	−	−	−	−	+	−
Amphiprora sp.	−	−	+	−	−	−	−	−	−	−	−	−
Asterionella japonica	−	−	−	−	−	−	−	−	−	−	−	−
Asterionellopsis glacialis	+	−	−	+	+	+	+	−	−	−	−	−
Asteromphalus sp.	+	+	−	−	−	−	−	−	−	−	−	−
Bacteriastrum hyalinum	−	−	−	−	+	−	−	−	−	−	−	−
Bacteriosira bathyomphala	+	−	−	+	−	−	−	−	−	−	−	−
Bacteriastrum furcatum	+	+	−	+	−	−	−	−	−	−	−	−
Bacteriastrum elongatum	+	−	−	−	−	−	−	−	−	−	−	−
Bellerochea malleus	+	−	+	+	+	+	+	−	+	−	−	−
Cerataulina pelagica	+	+	−	−	−	−	−	−	−	−	−	−
Chaetoceros compressus	−	−	−	−	+	−	−	−	−	−	−	−
Chaetoceros concavicornis	−	−	−	−	+	−	−	−	−	−	−	−
Chaetoceros sp.	+	+	+	+	+	+	+	+	+	+	+	−
Chaetoceros convolutus	−	+	−	−	+	−	−	+	−	−	+	−
Chaetoceros curvisetus	+	+	+	−	+	+	−	+	−	+	−	−
Chaetoceros decipiens	+	+	−	−	−	−	−	−	−	−	−	−
Chaetoceros eibenii	−	−	−	−	−	−	−	+	−	−	−	−
Chaetoceros lorenzianus	+	+	−	−	+	−	−	+	+	−	−	−
Climacodium frauenfeldianum	+	−	+	+	−	−	−	−	−	+	−	−
Coscinodiscus sp.	+	+	+	−	+	+	−	+	−	−	+	+
Coscinodiscus centralis	−	+	−	−	+	−	−	+	−	−	−	−
Coscinodiscus radiatus	−	+	−	−	−	−	−	−	−	−	−	−
Coscinodiscus subtilis	−	+	−	−	−	−	−	−	−	−	−	−
Cylindrotheca closterium	−	+	−	−	+	−	−	−	+	−	−	−
Detonula pumila	+	−	−	−	+	+	+	−	+	−	−	−
Dactyliosolen fragilissimus	−	−	−	−	−	−	+	−	−	−	−	−
Ditylum brightwellii	−	−	−	+	−	−	−	−	−	−	−	−
Eucampia sp.	−	+	−	−	−	−	+	+	−	+	−	−
Eucampia zodiacus	+	−	−	+	+	−	−	+	−	−	−	−
Fragilariopsis sp.	−	−	−	−	−	−	−	+	−	−	−	−
Guinardia striata	+	+	−	+	+	−	−	+	−	−	+	+
Guinardia flaccida	−	−	−	−	−	−	−	−	−	−	−	−
Haslea trompii	−	+	−	−	+	−	−	+	−	−	+	−
Hemiaulus sp.	+	−	−	+	−	+	+	−	−	−	−	−
Hemiaulus hauckii	−	−	−	−	−	−	−	−	−	−	−	−
Hemiaulus sinensis	−	−	−	−	−	−	−	−	−	−	−	−
Hemidiscus cuneiformis	−	+	−	−	−	+	−	−	−	−	−	−
Lauderia sp.	+	−	−	+	−	−	−	−	−	−	−	−
Lithodesmium undulatum	+	−	−	−	−	−	−	−	−	−	−	−
Leptocylindrus danicus	+	+	+	+	+	+	+	−	−	+	−	−
Melosira sulcata	+	−	+	+	−	+	−	+	−	−	−	−

Table 1. List of phytoplankton identyfied along the SEAS during the summer monsoon of 2009 (*continued*)

Region	(8°N) off Cape Comorin			(8.5°N) off Thiruvananthapuram			(9°N) off Kollam			(10°N) off Kochi		
Phases	1	2	3	1	2	3	1	2	3	1	2	3
Meuniera sp.	−	+	−	−	−	−	−	−	−	−	−	−
Navicula sp.	+	+	+	+	+	+	+	+	+	−	+	+
Navicula delicatula	−	−	−	−	+	−	−	−	−	−	−	−
Navicula granii	−	−	−	−	+	−	−	−	−	−	−	−
Nitzschia sp.	−	−	+	+	−	−	−	−	+	−	−	+
Nitzschia seriata	−	−	−	+	+	−	−	−	−	−	−	−
Odontella sp.	−	−	−	+	−	−	+	−	−	−	−	−
Odontella aurita	−	+	−	−	−	−	−	+	−	−	−	−
Odontella mobiliensis	−	+	−	+	+	+	−	+	−	−	+	−
Odontella sinensis	+	−	+	−	−	+	−	+	−	−	−	−
Odontella longicricis	−	−	−	−	−	−	−	+	−	−	−	−
Planktoniella sol	+	+	+	+	−	−	−	+	−	+	−	−
Pleurosigma directum	−	−	−	+	−	−	−	−	−	−	−	−
Pleurosigma normanii	−	+	−	−	+	−	−	+	−	−	−	−
Pleurosigma sp.	−	+	+	+	+	−	−	−	−	−	+	+
Podosira sp.	−	−	−	+	−	−	−	−	−	+	−	−
Pseudo-nitzschia sp.	−	+	+	−	+	+	−	+	+	−	+	−
Pseudo-nitzschia multiseries	−	−	−	−	−	−	−	+	+	−	−	−
Pseudo-nitzschia multistriata	−	−	−	−	+	−	−	−	−	−	−	−
Pseudo-nitzschia seriata	+	−	−	+	−	−	+	−	−	−	−	−
Rhizosolenia sp.	+	+	+	+	+	+	+	+	+	+	−	+
Rhizosolenia hebetata	−	+	−	−	−	−	−	+	−	−	+	+
Rhizosolenia imbricata	−	+	−	−	+	−	−	−	−	−	−	+
Rhizosolenia styliformis	−	+	−	−	+	−	−	+	−	−	−	−
Schroderella delicatula	−	−	−	+	−	−	+	+	−	+	−	−
Skeletonema costatum	+	+	−	+	+	+	+	+	−	−	+	+
Streptotheca tamesis	−	−	+	+	−	+	+	+	−	−	−	−
Stephanopyxis sp.	+	−	+	+	−	−	−	−	−	−	−	−
Thalassionema frauenfeldii	−	+	−	−	−	+	−	−	−	−	−	−
Thalassionema nitzschioides	+	+	−	+	+	+	+	+	+	−	+	−
Thalassiosira sp.	−	+	+	+	+	+	+	+	+	−	+	+
Thalassiothrix sp.	−	−	−	−	+	−	−	−	−	−	+	−
Thalassiothrix longissima	−	−	−	−	−	+	−	+	−	−	−	−
Class – Dinophyceae												
Alexandrium sp.	−	−	−	−	−	−	−	+	−	−	−	−
Ceratium sp.	−	−	+	−	+	−	+	−	−	+	−	−
C. dense	−	−	−	−	−	−	−	−	−	+	−	−
C. dens	−	−	−	−	−	−	−	−	−	−	−	+
C. furca	−	+	+	+	+	+	+	+	+	−	+	+
C. fusus	−	+	+	−	+	−	+	+	+	+	+	+
C. gibberum	−	−	−	−	−	+	−	−	−	−	−	−
C. horridum	−	−	−	−	+	+	−	−	−	−	−	+
C. gibberum	−	−	−	−	−	+	−	−	−	−	−	−

Table 1. List of phytoplankton identyfied along the SEAS during the summer monsoon of 2009 (*continued*)

Region	(8°N) off Cape Comorin			(8.5°N) off Thiruvananthapuram			(9°N) off Kollam			(10°N) off Kochi		
Phases	1	2	3	1	2	3	1	2	3	1	2	3
C. horridum	−	−	−	−	+	+	−	−	−	−	−	+
C. inflatum	−	−	+	−	−	−	−	−	−	−	−	+
C . macroceros	−	−	−	−	−	+	−	+	−	+	−	−
C. pulchellum	−	−	−	+	−	−	−	−	−	−	−	−
C. pentagonum	−	−	−	−	−	+	−	−	−	−	−	−
C. symmetricum	−	−	+	+	+	−	+	+	+	−	−	+
C. trichoceros	−	−	−	−	−	−	−	−	−	+	−	+
C. tripos	−	+	−	−	+	+	−	−	+	−	+	+
C. vulture	−	−	−	−	−	−	−	+	−	−	−	−
Dinophysis acuminata	−	−	−	+	+	+	−	+	−	−	+	−
D. caudata	−	−	+	−	+	−	−	+	+	−	+	+
Dissodinium lunula	−	−	−	+	−	−	−	−	−	−	−	−
Gonyaulax digitale	−	−	−	−	−	−	−	+	−	−	−	−
Gonyaulax polygramma	−	+	−	−	−	−	−	−	−	−	−	−
Gonyaulax sp.	−	−	−	+	+	+	+	−	−	−	−	−
Gymnodinium sp.	−	+	−	−	−	−	+	−	−	−	−	−
Noctiluca scintillans	−	+	+	−	+	−	−	+	−	−	+	−
Ornithocercus sp.	−	−	+	−	−	+	−	+	−	−	−	+
Phalacroma sp.	−	−	−	−	+	−	−	−	−	−	+	−
Prorocentrum sp.	−	−	+	−	−	−	+	−	−	−	−	+
P. gracile	−	−	−	−	−	−	−	+	−	−	+	−
P. lima	−	−	−	−	−	−	−	−	−	−	+	−
P. micans	−	−	+	+	−	−	+	−	+	+	−	+
Protoperidinium sp.	+	+	+	+	+	+	+	+	+	+	+	+
P. oblongum	−	+	−	−	−	−	−	−	−	−	−	+
P. oceanicum	−	−	−	−	+	−	+	+	−	−	−	+
P. leonis	−	−	−	−	−	−	−	−	−	+	−	−
Pyrophacus steinii	−	−	−	−	+	−	−	−	−	+	−	−
Pyrocystis sp.	−	+	+	−	−	+	−	−	−	−	−	−
Pyrocystis robusta	−	−	−	−	−	−	−	−	−	−	+	−
Zygabikodinium lenticulatum	−	−	+	−	−	+	−	−	−	+	+	−
Blue-green algae (Cyanobacteria)												
Trichodesmium erythraeum	+	−	+	−	−	−	+	+	−	+	−	−
Cyanobacterial filaments	−	−	−	−	−	+	−	−	+	−	−	−
Class: Prymnesiophyceae												
Phaeocystis globosa	−	+	−	−	−	+	−	−	−	−	−	−
Flagellates												
Chattonella marina	−	−	−	−	−	−	−	−	−	−	−	+
Dictyocha sp.	−	−	−	+	−	−	+	−	−	−	−	−
Dictyocha octanaria	−	−	+	−	−	−	−	−	−	−	−	−
Mesocena hexagona	−	+	+	−	+	−	−	−	−	−	−	−
Octactis octonaria	−	+	−	−	+	−	−	+	−	−	−	−

Thiruvananthapuram (8.5°N) and Kollam (9°N) coastal waters had lower SSTs of 23.4°C and 23.8°C respectively (Figure 2). Along 10°N SST rose to 25.23°C with D25 at 5 m. The region is reported to have a higher nutrient concentration during the period (5 μM surface nitrate in the coastal waters) throughout the study area (Habeebrehman 2008). With the northward progression of upwelling, surface chlorophyll *a* concentrations also increased in these regions. In the region off Cape Comorin the concentrations of chlorophyll *a* were lower (av. 5 mg m^{-3}) during phase 2 than in phase 1 (av. 8 mg m^{-3}) (Figure 4). The total phytoplankton cell density was found to be 8×10^3 cells L^{-1} with *Chaetoceros* sp. as the dominant group. Upwelling in the waters off the southern tip of the peninsula is thought to be influenced by strong westerly winds blowing tangentially to the coast, with strong offshore Ekman mass transport from May to October peaking during August (Smitha et al. 2008). Phytoplankton groups able to thrive in disturbed waters flourish in an environment where upwelled waters are actively renewed (Margalef 1978, Estrada & Blasco 1985). Chain-forming diatoms, such *as Chaetoceros* sp., *Thalassiosira* sp., *Cerataulina* sp., *Leptocylindrus danicus* etc., were the major groups present, and these diatoms can flourish in turbulent and cold, nutrient-rich upwelled waters (Falkowski & Woodhead 1992). In addition to the major group of Bacillariophyta (diatoms), certain dinoflagellates, mainly *Noctiluca scintillans* and *Ceratium* sp., were also present, contributing nearly 30% to the total cell density (Figure 5; Table 1).

Further north in the study area, intense upwelling was observed during this period. Chlorophyll *a* concentrations were considerably higher, reaching 19.5 mg m^{-3} in shelf waters off Thiruvananthapuram (8.5°N) and nearly 25 mg m^{-3} in the coastal waters off Kollam (9°N), but only 5 mg m^{-3} off Kochi (Figure 3). Dominated by diatoms, the phytoplankton cell density reached 35×10^3 cells L^{-1} in the waters off Thiruvananthapuram (8.5°N). The phytoplankton cell density was dominated by chain-forming centric diatoms that replaced the pennate genus, *Nitzschia* sp. of phase 1. *Chaetoceros curvisetus*, *C. lorenzianus*, *Chaetoceros* spp., *Thalassiosira* sp., and *Thalassionema nitzschioides* were the dominant groups present (Table 1). Dinoflagellates contributed nearly 4% to the total phytoplankton cell density, with *Dinophysis caudata*, *D. acuminata*, *Ceratium* spp. and *Noctiluca scintillans* being the major ones (Figure 5). As a result of the intense upwelling and lower SST during phase 2 in the waters off Kollam (9°N), increased phytoplankton abundance (Chl *a* $\sim$ 25 mg m^{-3}) with a total cell density of 54×10^3 cells L^{-1} was observed. The diatom community was represented mainly by *Chaetoceros* spp. and *Thalassiosira* sp. Dinoflagellates were also present in a significant proportion, with *Protoperidinium* spp., *Dinophysis caudata*, *D. acuminata*, *Noctiluca scintillans*, *Ceratium furca*, *C. fusus*, *C. tripos* etc. in the community.

According to Blasco et al. (1980), who studied the upwelling regions of north-west Africa, functional groups of phytoplankton include dinoflagellates along with the diatom assemblage. During our investigation, as mentioned earlier, several dinoflagellate genera were found together with the diatom assemblage during intense upwelling conditions. *Ceratium* spp. was the dominant dinoflagellate, of which *Ceratium furca* was a frequently occurring species in both inshore and shelf waters. The abundance of *C. furca* in the dinoflagellate assemblage has been reported previously from Arabian Sea coastal waters (Mendon 2002). Similarly, Alkawri & Ramaiah (2010) identified *C. furca* as the dominant dinoflagellate in coastal waters off Goa. The species is said to be common in high nutrient conditions but can survive well where nutrient levels are low (Baek et al. 2008). Moreover, they are able to escape the grazing pressure of zooplankton due to their heavy theca (Neilson 1991). In the coastal waters off Kochi (10°N), *Skeletonema costatum* and *Thalassiosira* sp. were the dominant diatoms; besides these, certain solitary pennate diatoms like *Amphora* sp. and *Navicula* sp. were also present in significant cell densities in the region (Table 1). The proportion of dinoflagellates was distinctly higher in the region, biased by the enhanced cell density of *Noctiluca scintillans* (60×10^2 cells L^{-1}). Even though a considerable density of *Noctiluca* cells was present, a bloom as intense as that of the previous year (Padmakumar et al. 2010b) was not observed during the present study.

3.3. Phase 3

During phase 3 (September), moderate upwelling with lower SSTs (24.77°C and 25.66°C) was observed in the regions off Cape Comorin (8°N) and off Thiruvananthapuram (8.5°N) respectively. The intensity of upwelling decreased northwards with comparatively higher SSTs along 9°N (26.89°C and D25 at 23 m) and 10°N (25.5°C with D25 at 8 m) (Figure 2). This period is considered to be the waning phase of the summer monsoon upwelling in the SEAS (Smitha et al. 2008, Habeebrehman et al. 2008). Nitrate concentrations in surface waters were higher in the waters off Thiruvananthapuram (> 11 μM), which decreased northwards (1.7 μM). Surface chlorophyll *a* concentrations in the waters off Cape Comorin reached 2.2 mg m^{-3} with an average of 1.7 mg m^{-3} (Figure 4). The phytoplankton cell density was lower in the area during this phase (6×10^3 cells L^{-1}). Diatoms dominated the phytoplankton community (94%) and were represented by *Chaetoceros* spp., *Leptocylindrus danicus*, *Navicula* sp., *Odontella* spp. etc. (Table 1). The dinoflagellates present were

Ceratium spp., *Dinophysis* sp., *Protoperidinium* sp. and *Prorocentrum* sp. Likewise, in the region off Thiruvananthapuram surface chlorophyll *a* concentrations were nearly 11 mg m^{-3} with a total phytoplankton cell density of 10×10^3 cells L^{-1}, and maximum concentrations were confined to nearshore waters (coastal regions of 30 m station depth). The phytoplankton composition was dominated by diatoms like *Chaetoceros* sp. and *Thalassiosira* sp. with a higher proportion of dinoflagellates compared to the previous two phases. Dinoflagellates were represented by *Ceratium* spp., *Protoperidinium* sp. and *Dinophysis caudata*. Meanwhile, there was a greater abundance of the prymnesiophyte *Phaeocystis* sp. in inshore waters (5×10^2 cells L^{-1}).

After intense upwelling during phase 2, the region off Kollam was more or less in a relaxation stage with higher SSTs and lower chlorophyll *a* concentrations (3.5 mg m^{-3}) than during phase 2 (25 mg m^{-3}). The phytoplankton community also exhibited variation, with a higher cell density of dinoflagellates, represented mainly by *Dinophysis caudata*, *D, acuminata*, *Ceratium furca*, *C. fusus*, *C. tripos* etc. Diatoms were represented only by *Pseudo-nitzschia* sp., and *Rhizosolenia* sp. Both inshore and shelf waters off Kochi were inhabited by a noxious bloom of the marine raphidophyte *Chattonella marina* during phase 3 (Padmakumar et al. 2011). The ambient SST (25.56°C) favoured these blooms; its occurrence is known to be governed by temperature (Nakamura & Watanabe 1983). The cell abundance of *Chattonella marina* reached 1.59×10^7 cells L^{-1}. Mean surface chlorophyll *a* concentrations were 10 mg m^{-3}. Other phytoplankton present in the area include diatoms like *Skeletonema costatum*, *Coscinodiscus* sp., *Thalassiosira* sp., *Nitzschia* sp., *Guinardia* sp., *Rhizosolenia* spp., *Pseudo-nitzschia* spp., and dinoflagellates, mainly *Ceratium furca*, *C. fusus*, *C. symmetricum*, *C. trichoceros*, *Dinophysis caudata*, *D. acuminata*, *Ornithocercus* sp., *Prorocentrum* sp. etc. In the diatom-dinoflagellate assemblage dinoflagellates made up nearly 70% of the cell count (Figure 5). The region was characterized by an elevated abundance of dinoflagellates compared to other southern regions during both phase 2 and phase 3. Upwelling in the region weakened in time, producing a stable water column, which favours the existence of dinoflagellates (Padmakumar et al. 2011). In addition, terrigenous input in the region associated with riverine influx could have contributed to the increasing dinoflagellate trend (Anderson et al. 2002). Dinoflagellates are known to increase in coastal waters with considerable terrigenous input. Anthropogenic sources of nutrients, including domestic waste and industrial runoff, are known to affect coastal marine ecosystems (Spatharis et al. 2007). The Cochin backwaters adjoining the inshore waters off Kochi are affected by massive eutrophication as a result of rapid urbanization (Gopalan et al. 1983, Madhu et al. 2007). The coastal waters off Kochi receive a significant portion of the organic matter loadings from the estuary (Parulekar 1973, Menon et al. 2000, Nair 2002). This input could be a reason for the greater dinoflagellate assemblage in the region.

4. Conclusion

The spatio-temporal variability observed in the process of upwelling along the SEAS is due to differential forcing mechanisms. These variations significantly influence the phytoplankton biomass as well as the community structure. Temporal variations in the phytoplankton composition were observed along each transect. Upwelling was in an initial phase, reaching only as far as inshore waters along 9°N from the southern tip of India during June (phase 1). The process strengthened with varying intensity throughout the SEAS during August (phase 2), thereafter waning during September (phase 3). Chlorophyll *a* concentrations peaked during phase 2, mainly in the 8.5°N and 9°N regions. *Chaetoceros curvisetus* is the major phytoplankton species in the highly turbulent, upwelled waters of the SEAS. *Thalassiosira* sp., *Thalassionema nitzschioides*, *Pseudo-nitzschia* sp., *Leptocylindrus danicus* and *Lauderia* sp. were other major diatoms present in the upwelled waters. Active upwelling was observed along the Cape Comorin transect (8°N) throughout the study period with frequent renewal of upwelled waters. The chain-forming diatom *Chaetoceros curvisetus* was the major phytoplankton species in the area. Along the Thiruvananthapuram transect (8.5°N) purely wind-driven upwelling with a succession of phytoplankton occurring in tune with upwelling variability was observed. Off Kollam (9°N) and off Kochi (10°N) the transects were characterized by a phytoplankton composition different from that in the south, with an increased abundance of dinoflagellates compared to the southern transects. *Ceratium* spp., mainly *Ceratium furca*, *C. fusus*, *C. symmetricum*, and *Dinophysis caudata*, *D. acuminata*, *Protoperidinium* spp. etc., were the major dinoflagellate species in these regions. Since phytoplankton form the basis of production in upwelling coastal ecosystems, information on their distribution and abundance is of vital importance.

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