Environmental Science and Pollution Research (2021) 28:64892–64907
https://doi.org/10.1007/s11356-021-15530-w

RESEARCH ARTICLE

Why the Gulf of Mannar is a marine biological paradise?

Jyothibabu Retnamma[1] · Balachandran Kizhakkepat Kalathil[1] · Jagadeesan Loganathan[2] · Karnan Chinnadurai[1] · Garuda Venkata Madhusudhana Gupta[3] · Kunal Chakraborty[4] · Kali Charan Sahu[5]

Received: 8 December 2020 / Accepted: 16 July 2021 / Published online: 28 July 2021

Abstract

The Gulf of Mannar (GoM), located between India and Sri Lanka, has astonishing faunal richness and diversity. Two oceanographic data sets supplemented with satellite remote sensing observations are discussed here to show the unique ecological setting in the GoM sustaining a rich and diverse fauna. We tested the hypothesis that a specific stretch of a large marine environment behaves differently from the rest of the region due to its peculiar geographical position. Primarily, unlike the adjacent Indian southwestern shelf in the Southeastern Arabian Sea, oxygen deficiency associated with coastal upwelling imparting physiological stress to marine fauna does not occur in the GoM. Secondly, the GoM along the Indian coastline receives an adequate amount of primary (plankton) food from the Arabian Sea and the Bay of Bengal through the advected water associated with the seasonally reversing surface currents. Thirdly, the GoM water has high transparency, aerated sandy seafloor conducive for the growth of diverse corals and much sensitive fauna. All these indicate that an astonishingly rich and diverse aquatic fauna in the GoM is a biological manifestation of a conducive geographical setting and propose that similar other environments worldwide, protected from oxygen deficiency, might also be functioning as a refuge for marine life.

Keywords Upwelling · Oxygen deficiency · Plankton · Gulf of Mannar · Arabian Sea

Introduction

The GoM, along its Indian coastline, has a spread of ~15000 km^2 that extends typically from Tuticorin to Mandapam over a distance of ~ 190 km (Jagadeesan et al. 2013). The northern sector of the GoM (~10500 km^2), the first Marine Biosphere Reserve of India, has a very rich and diverse fauna compared to the adjacent regions (Rao et al. 2008). The 'Kurusadai' Island, one among the 21 small islands situated close to the Indian coastline in the GoM, is traditionally known as 'Marine Biologist's Paradise'. A recent biodiversity record has around 4000 faunal assemblages in the GoM including 1147 species of fishes, 856 species of molluscs, 451 species of tunicates, 262 species of coelenterates of which 117 species of corals, 158 species of arthropods, 153 species of echinoderms and 77 species of sponges (ENVIS 2015; Table 1). The fact that many of these species are listed in the schedules of the Wildlife Protection Act of the Government of India (Table 1) signifies the need to protect this ecologically sensitive region (Rao et al. 2008; ICMAM 2001; ENVIS 2015). The increased human settlement and livelihood activities may disturb the environmental well-being of this region, even though it is a legally declared marine biosphere reserve (Rao et al. 2008). The GoM is one of the largest fish landing centres in India, indicating its potential for rich bioresources (Rao et al. 2008; Supplementary Table 1). Moreover, the GoM is globally known for pearl oyster (*Pinctada fucata*) and molluscan resources with a great reputation for the sacred chank (*Xancus pyrum*). The occurrence of *Ptychodera flava* (living fossil) and *Balanoglossus*, which links invertebrates to the vertebrates, is only reported from this region in India (Rao et al. 2008). A variety of sea cucumbers (*Holothuria scabra*, *H. spinifera* and *Actinopygtablea echinites*), marine turtles

Responsible Editor: V. V.S.S. Sarma

✉ Jyothibabu Retnamma
rjyothibabu@nio.org

1 CSIR-National Institute of Oceanography, Regional Centre, Kochi, India

2 CSIR-National Institute of Oceanography, Regional Centre, Visakhapatnam, India

3 Centre for Marine Living Resources and Ecology (MoES), Kochi, India

4 Indian National Centre for Ocean Information Services (MoES), Hyderabad, India

5 Berhampur University, Odisha, India

Table 1 The faunal diversity of the GoM and the common names of the endangered/threatened groups/species (adapted from ENVIS 2015)

SL.No.	Group	Species Count	Endangered/threatened groups/species
1	Protista	48	-
2	Zooplankton	66	-
3	Porifera	77	All species of Calcarean sponges
4	Coelentrata	262	All species of Black coral, Organ pipe coral, Fire coral and Sea fan
5	Nematoda	3	-
6	Platyhelminthes (Trematoda)	2	-
7	Annelida (Polychaeta)	151	-
8	Bryozoa	37	-
9	Chaetognatha	18	-
10	Arthropoda	158	-
11	Echinodermata	153	All species of Sea cucumber
12	Mollusca	856	King shell, Pink clam shell, Pine apple shell, Clam shell, Glory of India, Spiral chank, Giant clam, Map shell, Spotted shell, Bar shell, Striped shell, Trapezoid shell, Spider shell, Spider conch, Arthritic spider conch, Orange spider conch, Scorpion shell, Millipede conch,White conch, Commercial top shell, Window pan oyster, Turban shell
12	Tunicata - Ascidacea	373	-
14	Tunicata - Thaliacea	78	-
15	Hemichordata	4	-
16	Cephalochordata	2	-
17	Pisces	1147	Whale shark, Pointed sawfish, Spinner shark, Speartoothed shark, Ganges shark, Scaly stingray, Small-toothed sawfish, Green sawfish, White-spotted shovel-noseray, Thorny ray, All species of sea horse and Pipe fish, Giant grouper
18	Reptiles (Turtles)	5	Green turtle, Hawksbill turtle, Leather back turtle, Logger head turtle, Olive ridley turtle
19	Reptiles (Snakes)	13	-
20	Aves	290	-
21	Mammals	7	All species of whales and dolphin, Little Indian Porpoise, Sea Cow

(Green, Hawksbill, Olive ridley, Leatherback and Loggerhead) and whales (10 species including the toothed, baleen, blue, sie, fin and pilot) occur in the GoM (Rao et al. 2008; ICMAM 2001; ENVIS 2015).

The unusually rich and diverse fauna in the GoM is a mystifying feature, which deserves a detailed examination based on its oceanographic characters. During 2010–2011, researchers from the CSIR-National Institute of Oceanography, India, including us have carried out oceanographic observations in the GoM and the adjacent Palk Bay (PB) as a feasibility study to link these water bodies through the Sethusamudram Ship Channel proposed by the Government of India. As an outcome of this study, a series of peer-reviewed publications have emerged detailing the overall oceanographic settings in the GoM, which is summarised in Table 2 (Anjusha et al. 2013; Jagadeesan et al. 2013; Jyothibabu et al. 2014; Madhu et al. 2014; Amrutha and Sanil Kumar 2017). Albeit a large number of studies portraying the rich and diverse fauna in the GoM, a convincing explanation of its oceanographic causes is completely absent (Rao et al. 2008). Since the GoM is an extension of the Southeastern Arabian Sea (SEAS), we differentiated here the oceanographic features of the GoM from the adjacent SEAS. The main objective of this paper is to examine the basic oceanographic properties and ecological characteristics that sustain an unusually rich and diverse fauna in the GoM. To investigate the above, we used the environmental data obtained from our in situ measurements during 2010–2011 in the GoM and during 2018–2019 along the southwest coast of India up to the western boundary of the GoM (Tuticorin). These observations were augmented with satellite remote sensing data and Regional Ocean Model System (ROMS) simulation.

Materials and methods

Online databases (http://giovanni.gsfc.nasa.gov, http://apdrc.soest.hawaii.edu) provided data on sea surface temperature (SST), surface winds, turbidity (reflectance 645nm) and chlorophyll-*a*. Ferret (version 7) was used for generating the monthly composite maps of these parameters. The first in situ

Table 2 Salient seasonal environmental features of the GoM. Abbreviations: GoM—Gulf of Mannar, AS—Arabian Sea, BoB—Bay of Bengal, SWM—Southwest Monsoon, NEM—Northeast Monsoon, SEAS—Southeastern Arabian Sea

Variables	Salient features
Surface currents	Water flow in the GoM is in conjunction with the large scale water circulation between the AS and the BoB (Jagadeesan et al. 2013; Amrutha and Sanil Kumar 2017; Jyothibabu et al. 2014). A strong eastward flow along the Indian shelf during the SWM carry upwelled and plankton-rich waters from the Indian southwestern shelf into the GoM. A much weaker westward flow during the NEM from the BoB through the PB advecting relatively low saline and plankton-rich waters into the GoM.
Wind, Sea surface temperature, Sea surface salinity	Stronger winds prevail in the GoM during the SWM and the NEM (Jagadeesan et al. 2013; Amrutha and Sanil Kumar 2017; Jyothibabu et al. 2014). Surface waters in the GoM are cold during the SWM due to the advected water from the western Indian shelf. The low-saline and cold BoB waters occupy the surface waters along the Indian shelf during the NEM.
Waves	The waves are lower in the GoM as compared to the SEAS regardless of seasons (Amrutha and Sanil Kumar 2017). Swells dominate during the SWM and wind seas during the rest of the period.
Turbidity	Clear waters occur in the GoM throughout the year, while PB acts as a sediment trap during the NEM preventing intrusion of the high suspended sediment into the GoM (Jyothibabu et al. 2014; Anjusha et al. 2013; Madhu et al. 2014).
Nitrate and Dissolved oxygen	Moderate to the high concentration of nitrate occur in the GoM during the SWM and the NEM (Anjusha et al. 2013; Madhu et al. 2014). Dissolved oxygen in the GoM is high throughout the year, and the water column has always > 5 mg/l.
Chlorophyll *a*	Moderate (0.4 mg m^3) to high (1.8 mg m^3) level of phytoplankton stock (chlorophyll-*a*) exists in the GoM throughout the year (Jagadeesan et al. 2013; Jyothibabu et al. 2014; Anjusha et al. 2013; Madhu et al. 2014). A higher concentration of chlorophyll-a is evident in the GoM during SWM and NEM.
Zooplankton	GoM has high zooplankton stock during the SWM and the NEM (Jagadeesan et al. 2013; Anjusha et al. 2013). Upwelling indicator copepod *Timora turbinata* do occur in the GoM during the SWM due to the advected upwelled waters from the Indian southwestern shelf. Similarly, *Paracalanus purvus*, the copepod typical of the low saline BoB waters occur abundantly in the GoM during the NEM, which is an indicator of the advection (though weak) of BoB water into the GoM through the PB.

data from 2010 to 2011 were obtained from 15 locations in the GoM for three seasons [March 2010 (Pre-Monsoon), September 2010 (Southwest Monsoon), and January 2011 (Northeast Monsoon)]. Field sampling for this was conducted on board a trawler along five cross-shore transects in the Indian sector of the GoM (GoM1 to GoM5) (Fig. 1). The second in situ sampling was in September 2018 to verify whether the coastal upwelling process occurs in the GoM. This sampling was carried out onboard *CRV Sagar Purvi* with three sampling locations in each of the five cross-shore transects (SP1 to SP5) from the western proximity of the GoM up to 12°N along the southwest coast of India (Fig. 1). A portable Conductivity Temperature Depth (CTD) profiler (Seacat, Seabird Electronics, USA) recorded the vertical distribution of temperature and salinity. Standard Winkler's method (Grasshoff 1983) was used to estimate the dissolved oxygen concentration from the surface, subsurface, and bottom waters in the first sampling during 2010–2011 and from many prefixed standard depths (1 m, 5 m, 10 m, 20 m, and 40 m) during the second sampling in 2018. We also used the Regional Ocean Modelling System (ROMS) outputs of the vertical distribution of relevant environmental variables for the Southwest Monsoon, obtained from the Indian National Centre for Ocean Information Services (INCOIS), Hyderabad, India (www.incois.gov.in) (Chakraborty et al. 2016, 2018). Vertical sections of four cross-shore transects obtained from ROMS beginning from the southern tip of India (Cape Comorin) towards the GoM were used to comprehend how best the model projection follows the environmental signatures evident in the in situ observations (Chakraborty et al. 2016, 2018).

Univariate ANOVA identified the significance of the spatial difference in hydrographical parameters between transects sampled during 2018 (SP1–SP5). Before the ANOVA test, the homogeneity and distribution of the environmental variables were analysed using XL Stat PRO software. Tukey's HSD post hoc test was performed for pairwise data comparisons. The distribution of the ecological variables was analyzed in XL stat Pro. ANOVA was analyzed in PASTUiO software Version 4.02. Principle component analysis (PCA) was also performed to visualize the spatial differences in the distribution of relevant environmental variables. Correlation matrix-based scaling was used in PCA Biplots, having the first two principal components. The dissolved oxygen values were overlaid (dotted line) on the Biplots to indicate the spatial variation. PCA was performed using CANOCA 4.5 software.

Results and discussion

Environmental setting

Winds

The surface winds in the study domain are weak during March-April (Pre-Monsoon) (Fig. 2). Strong westerly/north-

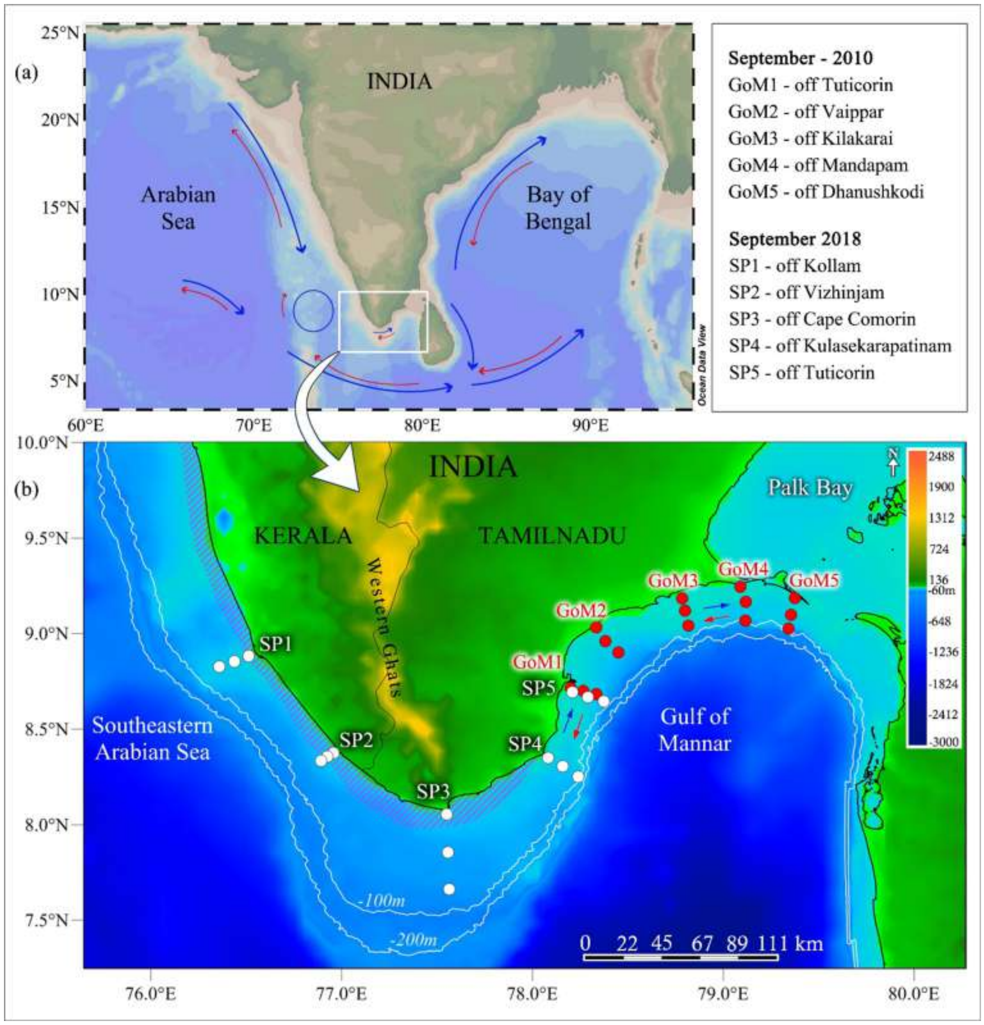

Fig. 1 (**a**) Study domain showing the GoM and the SEAS. (b) Sampling transects in the study domain. Five cross-shore transects (red filled circles, GoM1 to GoM5) sampled in the GoM during the 2010–2011 period and five cross-shore transects (white filled circle, SP1 to SP5) in the Indian shelf waters along the southwest coast of India up to the western boundary of the GoM sampled in 2018. The zone of coastal upwelling along the southwest coast of India is shown as hatched oblique blue lines close to the coastline in panel (**b**). The seasonally reversing ocean surface currents in the GoM is represented in both panels (**a**) and (**b**); blue arrows represent the Southwest Monsoon (June–September) while the red the Northeast Monsoon (November–February)

westerly winds (>6m S^{-1}) blows along the southwest coast of India from mid-May to September (Southwest Monsoon) due to the orographic influence of the western ghats (Harishkumar and Anand 2016). Instead, well organised south-westerly winds blow over the GoM during the Southwest Monsoon. The wind speed enhances by May, peaks in June and remains steady till September. By October, winds weaken and by November change its direction to north-easterly, which peaks during December–January and then subsides by February. The surface wind in the GoM is always forceful than its adjacent regions. One most possible reason could be the wind tunnelling effect by the orography of the vast Western Ghats Mountain ranges situated along the southwest coast of India and Knuckles Mountain ranges in south-central Sri Lanka (Fig. 2).

SST and turbidity

The distribution of SST in the SEAS and the GoM has some characteristic behaviour (Fig. 3). The warmest SST in the study domain exists during the Pre-Monsoon, which is the first solar heating period in the region (Shenoi et al. 2005; Kurian and Vinayachandran 2007). Following it, relatively cold water appears along the southwest coast of India and the GoM by June, and this cold SST situation prevails till October. It is also evident that much cooler SST (25–26°C) prevails along the southwest coast of India compared to the GoM (~27°C) during the Southwest Monsoon (May to September). Also, the cooler water patch persists for a longer duration in the southern tip of the southwest coast of India as it lasts from May to October, probably a cause of extended periods of upwelling there by local winds (Harishkumar and Anand 2016). The upwelling signatures appear first at the southern tip of the Indian subcontinent (Rao et al. 2008) and later advances northward along with the coastally trapped Kelvin wave (McCreary et al. 1993; Shankar and Shetye 1997). Though the cold water along the southwest coast of India disappears by October, relatively cold water reappears in the GoM by November. It lasts up to February (Northeast Monsoon), as a continuity of the cold-water mass in the Bay of Bengal, intruded through the PB (Rao et al. 2011; Jyothibabu et al. 2014). Satellite reflectance at 645nm is

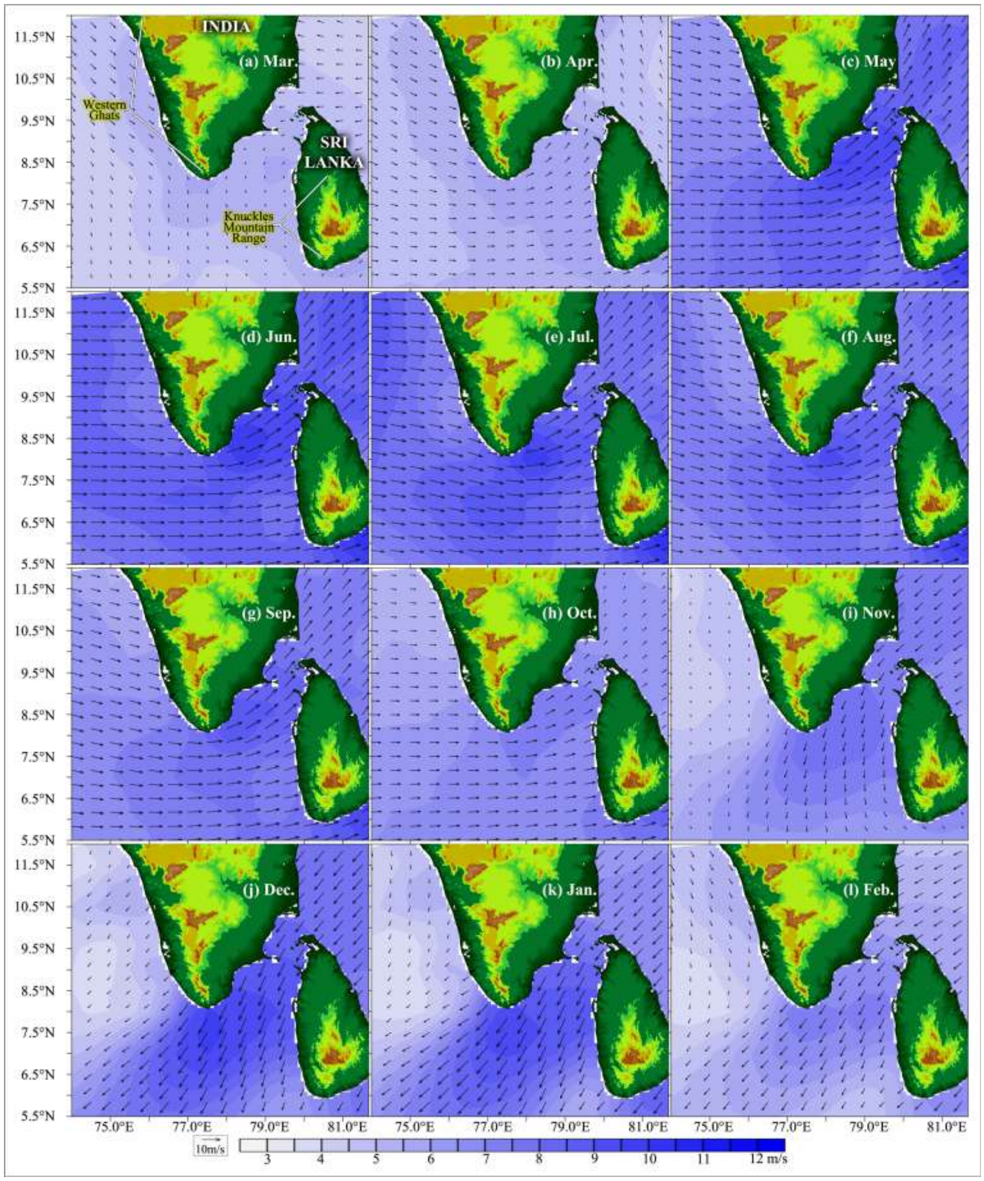

Fig. 2 Wind velocity (m s^{-1}) in the study domain and its variations associated with the seasonal evolution from the Pre-Monsoon (Mar.) to the Northeast Monsoon (Feb.). Strong winds are a characteristic feature of the GoM during the SWM (Jun.–Sep.) and NEM (Nov.–Feb.) periods

considered a good index of turbidity in coastal waters (Dogliottia et al. 2015). The monthly distribution of turbidity (satellite reflectance at 645nm) in the study domain showed clearer waters in the GoM compared to the adjacent regions (Fig. 4). The PB showed significantly high turbidity levels during the most time of the year due to the intrusion of coastal Bay of Bengal water and tidal resuspension of bottom sediments (Rao et al. 2011; Jagadeesan et al. 2013; Jyothibabu et al. 2014). As a result of enhanced land and river runoff associated with the heavy monsoonal rainfall, increased turbidity levels are quite usual along the southwest coast of India during the Southwest Monsoon (Jyothibabu et al. 2010; Karnan et al. 2017). This feature was evident in the present analyses as increased turbidity levels were clear along the southwest coast of India during the peak Southwest Monsoon period (Fig. 4).

Chlorophyll-*a*

Pre-Monsoon (March–May) and Northeast Monsoon (November–February) are low productive periods in the SEAS along the southwest coast of India (Fig. 5). This situation is caused by surface layer stratification through solar heating during the Pre-Monsoon and the intrusion of low saline oceanic Bay of Bengal waters during the Northeast Monsoon (Jyothibabu et al. 2010). Both these cause meagre nutrient availability in the upper euphotic column creating low phytoplankton biomass (chlorophyll-*a*) concentration (Jyothibabu et al. 2010). The scenario changes by late May/June due to the coastal upwelling, as the chlorophyll-*a* biomass increases rapidly along the entire southwest coast of India by June and persists up to October, whereas the GoM continues to sustain moderate to high chlorophyll-*a* (0.4–

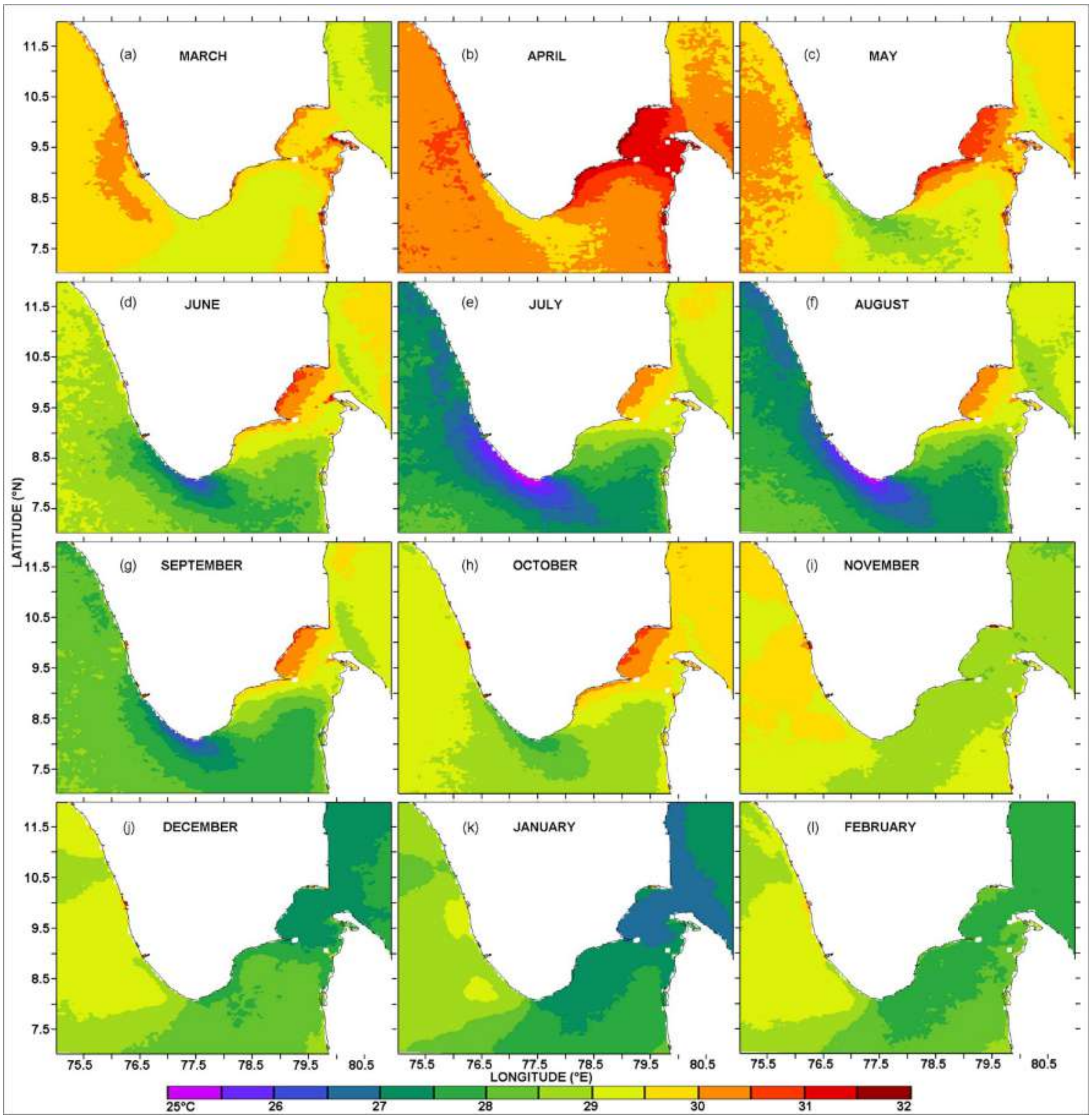

Fig. 3 SST (°C) distribution in the study domain showing its monthly variations associated with the seasonal evolution from the Pre-Monsoon (March–May) to the Northeast Monsoon (November–February) period. Relatively cool SST in the GoM was observed during the SWM due to the advected surface waters from the Indian south-western shelf and during the NEM due to the Bay of Bengal water intrusion

1.8 mg m^3) throughout the year (Fig. 5; Table 2). Enhancement of chlorophyll-*a* in the GoM starts by late May, just after the Pre-Monsoon, and it peaks during July–August and then declines by September–October. During the Northeast Monsoon, though the chlorophyll-*a* concentration decreases in the offshore waters in the GoM, its moderate concentration persists in the shelf waters along the Indian coastline as a continuity of the water masses intruded from the Bay of Bengal through the PB.

The contrast of GoM from the southwestern shelf of India

The environmental variables collected during the first in situ sampling during 2010–2011 (Table 2) shows that the hydrography of the GoM was very similar to the waters in the SEAS along the southwest coast of India (Table 2; Anjusha et al. 2013; Jagadeesan et al. 2013; Jyothibabu et al. 2014; Madhu et al. 2014; Amrutha and Sanil Kumar 2017). At the same time, the vertical distribution of temperature and dissolved oxygen in the GoM during the Southwest Monsoon displayed two significant features, which were strikingly different from the southwest coast of India during the same period. The water column in the GoM during the Southwest Monsoon was warm (>26°C) and without any significant vertical temperature gradients (Fig. 6), unlike that on the southwest coast of India due to coastal upwelling. Also found in this data is high oxygen concentration throughout the water column (>4.2 mg L^{-1}) negating the possibility of coastal

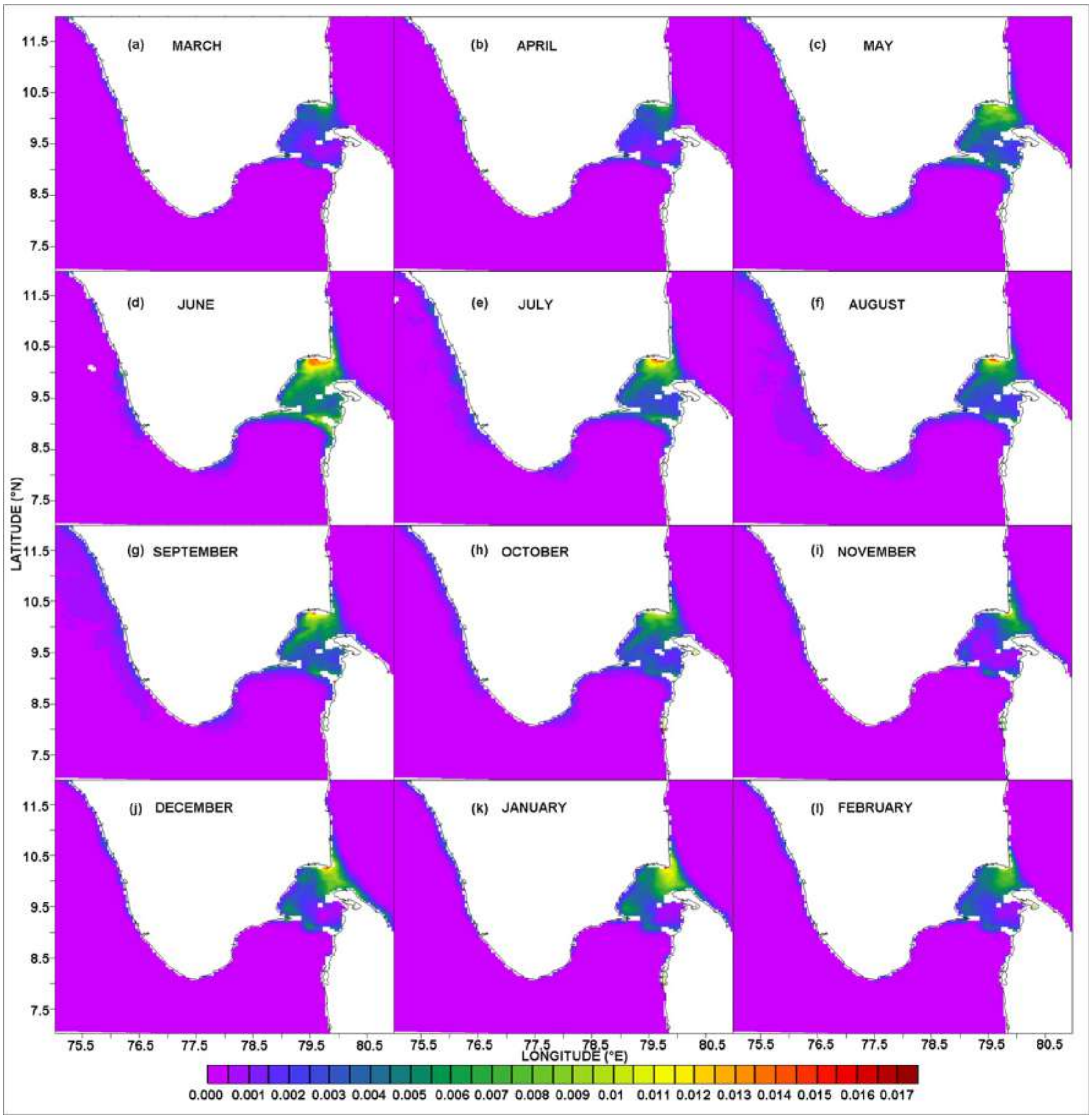

Fig. 4 Monthly satellite reflectance at 645nm (a measure of turbidity) showing high transparency of the water column in the study domain compared to the adjacent regions especially the Palk Bay

upwelling in the GoM (Fig. 7). We confirmed the robustness of this feature based on a few earlier records on the environmental variables from this region (Jayaraman 1954; Bindu and Muniyandi 2005). The upwelling along the southwest coast of India during the Southwest Monsoon (Harishkumar and Anand 2016; Ramasastry and Myrland 1959; Shetye et al. 1994) and its implications on the biological resources are well known (Banse 1959, 1968; Naqvi et al. 2006; Gupta et al. 2016; Jagadeesan et al. 2017; Karnan et al. 2017; Jyothibabu et al. 2018). During the Southwest Monsoon, westerly/northwesterly winds close to the coastline induces upwelling along the west coast of India (Harishkumar and Anand 2016; Shetye et al. 1994; Naqvi et al. 2006), which lowers the SST by 4–5°C (Banse 1959; Naqvi et al. 2006). During this process, the cold (23°C) and low oxygenated (~2 mg L^{-1}) deep oceanic waters (from 75 to 150 m) are elevated to the surface waters along the entire west coast of India (Banse 1959; Naqvi et al. 2006; Gupta et al. 2016; Karnan et al. 2017; Jyothibabu et al. 2018). Both local winds and remote forcing facilitate coastal upwelling along the extensive southwest coast of India (Kurian and Vinayachandran 2007; Gupta et al. 2016; Jyothibabu et al. 2018).

The vertical distribution of temperature and dissolved oxygen at different depth zones (10m, 25m, and 40m) in the shelf waters along the southwest coast of India up to the western proximity of the GoM (Tuticorin) clearly shows coastal upwelling signatures in terms of the surfacing of cold and low-oxygenated deep water (Fig. 8). The

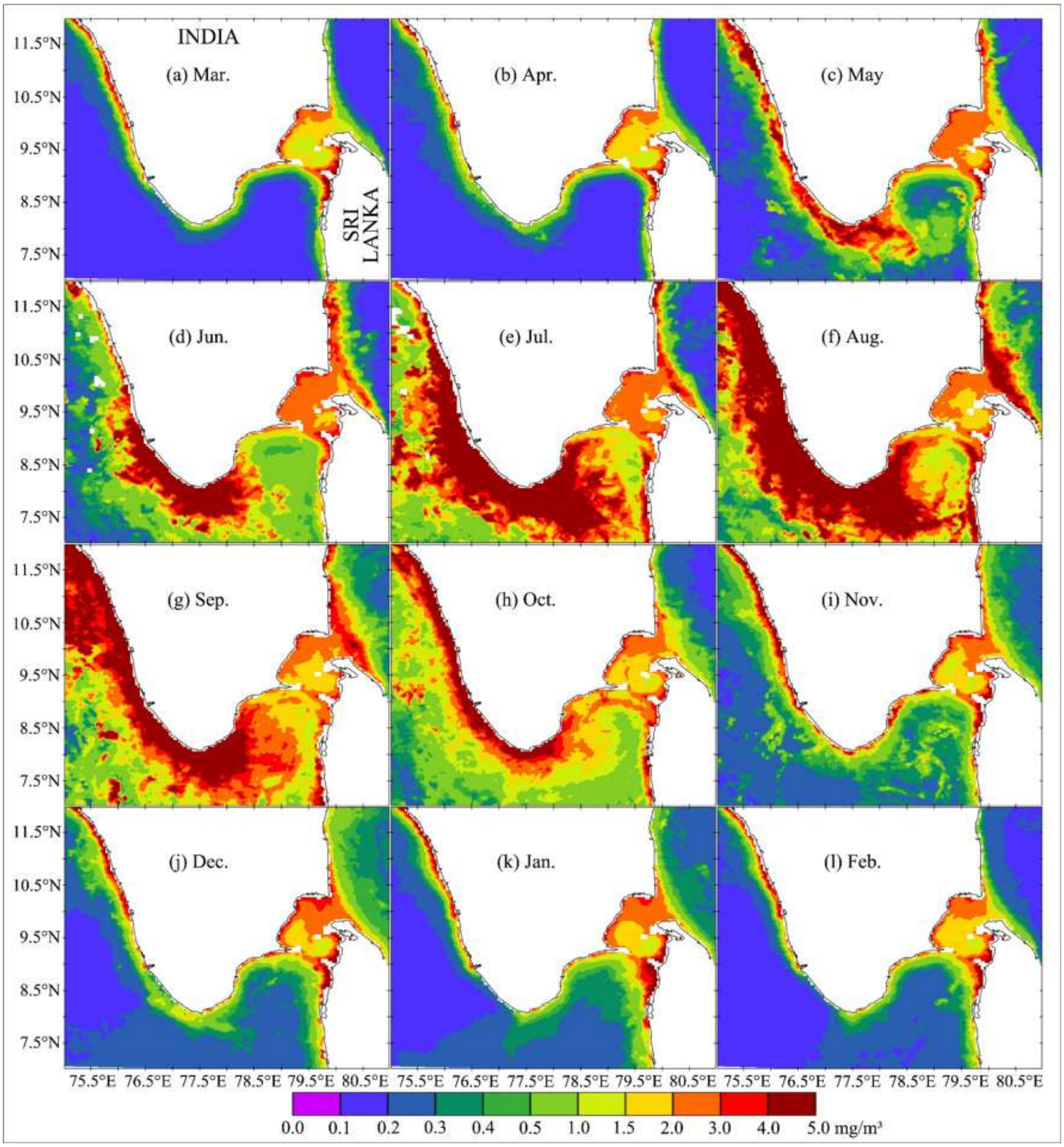

Fig. 5 Chlorophyll-*a* (mg m^{-3}) distribution in the study domain and its monthly variations associated with the seasonal evolution from the Pre-Monsoon to the Northeast Monsoon period. The presence of moderate to the high concentration of chlorophyll-*a* occurs in the GoM most of the year

most striking feature here in the present context is the spatial extent of the cold and low oxygenated water in the three depth zones. Along with the 10 m depth, upwelling signatures were evident up to Vizhinjam (SP2), but in 25m and 40m, it was apparent up to Kulasekharapatnam (SP4). ANOVA results confirmed the significant spatial differences in the levels of temperature and dissolved oxygen between the northern (SP1 & SP2) and southern (SP4 & SP5) sections ($P<0.05$; Supplementary Table 1). PCA showed that transects in the western proximity of the GoM (SP4 and SP5) were significantly warmer and more oxygenated compared to those in the north along the southwest coast of India (SP1 and SP2) (Fig. 9). All the in situ data showed that upwelling along the Indian southwest coast does not extend towards the GoM. This feature is also consistent in the vertical sections of temperature and dissolved oxygen in ROMS, showing that the coastal upwelling prevails only up to the southern Indian tip (Cape Comorin) and does not extend into the GoM (Fig. 10). This vital feature we reaffirmed in a historical oceanographic survey data sets published, as the upwelling signatures of the southwest coast of India phase-out by

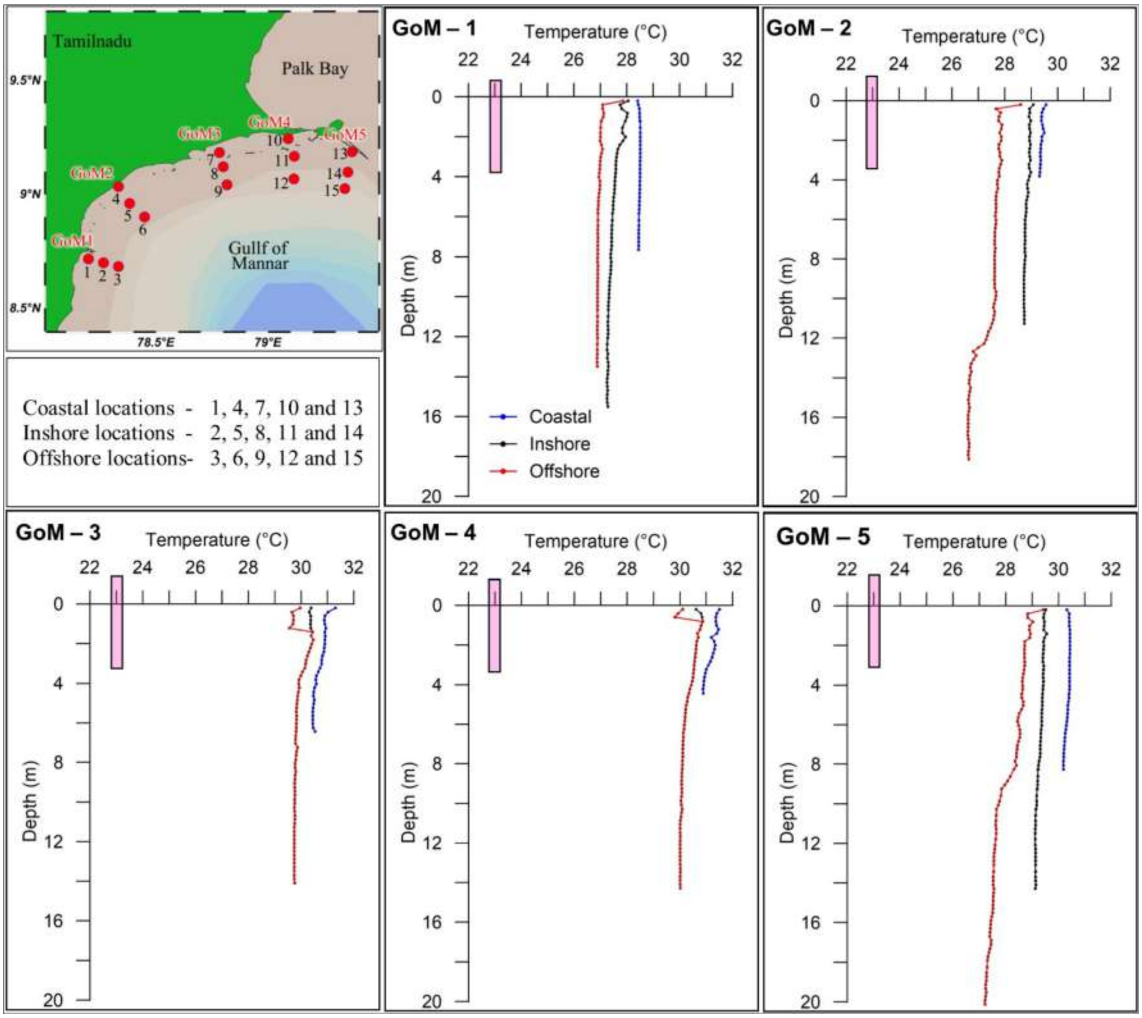

Fig. 6 The vertical distribution of temperature in five cross-shore transects along the Indian shelf in the GoM during the Southwest Monsoon (September 2010). The upwelling temperature (<23°C) is indicated on the x-axis as a pink bar to show the significantly warmer water that prevails in the GoM during the Southwest Monsoon

reaching the western proximity of the GoM (Tuticorin) region (Johannessen et al. 1981) (Supplementary Figure 1 & 2). The reason for the absence of coastal upwelling in the GoM could be the alignment of its coastline differently from the Indian southwest coastline. Thus, the wind and remote forces, which cause upwelling along the adjacent southwest coast of India might not be favouring upwelling in the GoM as observed in the case of the western and eastern shores of Sri Lanka (Vinayachandran et al. 2004).

Why the GoM is a marine biological paradise?

The Indian continental shelf of the GoM is significantly narrow (< 20 km cross-shore expand) (Rao et al. 2008; Jagadeesan et al. 2013). Being a tropical region, the GoM has a warm climate with less change in sea surface temperature over seasons (26.5 to 30.3°C). The sea surface salinity in the GoM varies seasonally (32–35.4), but remains high due to its continuity to the SEAS and the lack of any significant rivers in the vicinity (Jagadeesan et al. 2013; Anjusha et al. 2013). The GoM gets partially renewed during the Southwest Monsoon associated with the large scale ocean circulation around India and Sri Lanka (Jagadeesan et al. 2013; Anjusha et al. 2013). The surface currents in the GoM during the Southwest Monsoon enable the flow of high saline Arabian Sea waters into the PB. The surface currents reverse during the Northeast Monsoon (November–February) and bring the coastal low saline Bay of Bengal waters into the GoM (Table 2). This circulation pattern enables (a) GoM to receive a high amount of plankton stock from the SEAS during the Southwest Monsoon and from the Bay of Bengal during the Northeast Monsoon (Jagadeesan et al. 2013; Anjusha et al. 2013; Jyothibabu et al. 2014) and, (b) PB to efficiently trap the suspended sediments coming from the Bay of Bengal during the Northeast Monsoon (Anjusha et al. 2013; Jyothibabu

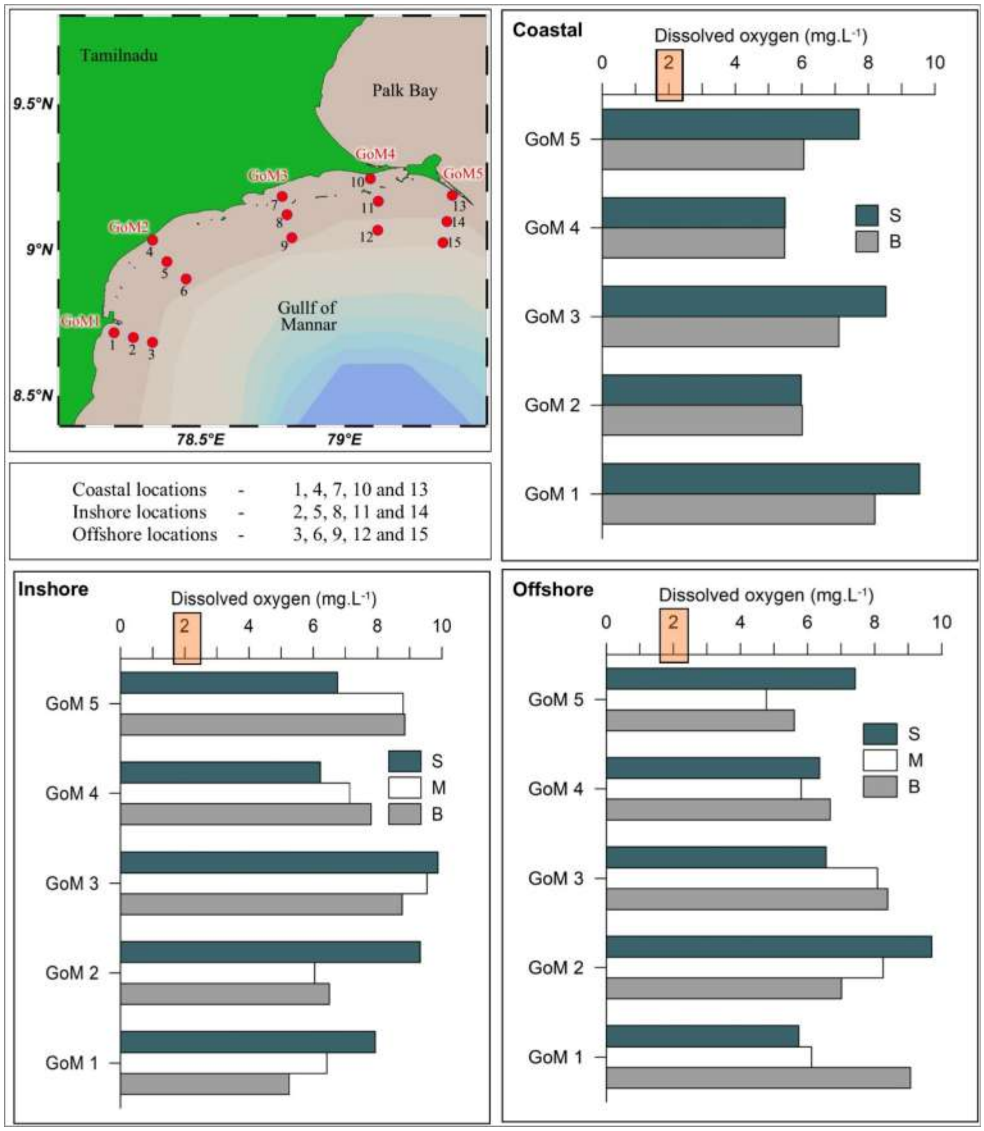

Fig. 7 The vertical distribution of dissolved oxygen in five cross-shore transects along the Indian shelf in the GoM during the Southwest Monsoon (September 2010). The oxygen concentration in the (S) surface, (M) middle, and (B) bottom depths in each sampling location are presented. The hypoxic levels (<2mg L^{-1}) is indicated on the x-axis as a pink bar to show the significantly oxygenated water that prevails in the GoM during the Southwest Monsoon

et al. 2014). As a result, the bottom sediment in the GoM is mostly sandy and well-aerated, which is conducive for the life of diverse corals and sensitive fauna (Rao et al. 2008; Parameswaran et al. 2018).

The nearshore characteristics of the Indian southwestern shelf and the GoM evidenced the oceanographic mechanisms that make the GoM evolve into a biological resource reserve. Primarily, during the Southwest Monsoon, the entire western shelf waters of India are under the influence of the coastal upwelling and the incursion of the oxygen-deficient waters (Naqvi et al. 2006; Gupta et al. 2016; Karnan et al. 2017). This situation has a profound influence on organisms living in the nearshore region along the southwest coast of India (Banse 1959, 1968; Regunathan et al. 1981; Parameswaran et al. 2018; Pandiyarajan et al. 2021). In contrast, the adjacent GoM is devoid of any such negative impacts of low oxygenated waters on fauna. The benthic habitats in the shelf waters are the feeding grounds for most of the demersal finfishes and shellfishes and provide a link between the water column and fisheries (Banse 1959; Regunathan et al. 1981; Pihl et al. 1991, 1992; Rabalais et al. 2001). Mobile consumers of benthic macro-invertebrates usually emigrate/escape from areas where dissolved oxygen concentrations reach hypoxic levels (Banse 1959; Pihl et al. 1991, 1992; Pihl 1994). Demersal finfishes and shellfishes disappear seasonally from the outer shelf of the southwest coast of India and often aggregate in oxygenated estuarine waters (Banse 1959; Seitz et al. 2003). If low-oxygen conditions are relatively mild, some of these demersal consumers may remain in the vicinity for a short period, exploiting stunned benthic prey, which is not customarily available (Santos and Simon 1980; Powers et al. 2001; Diaz and Rosenberg 2008). As dissolved oxygen concentrations rise after the hypoxic event, mobile demersal consumers generally return to their original habitat. While higher consumers

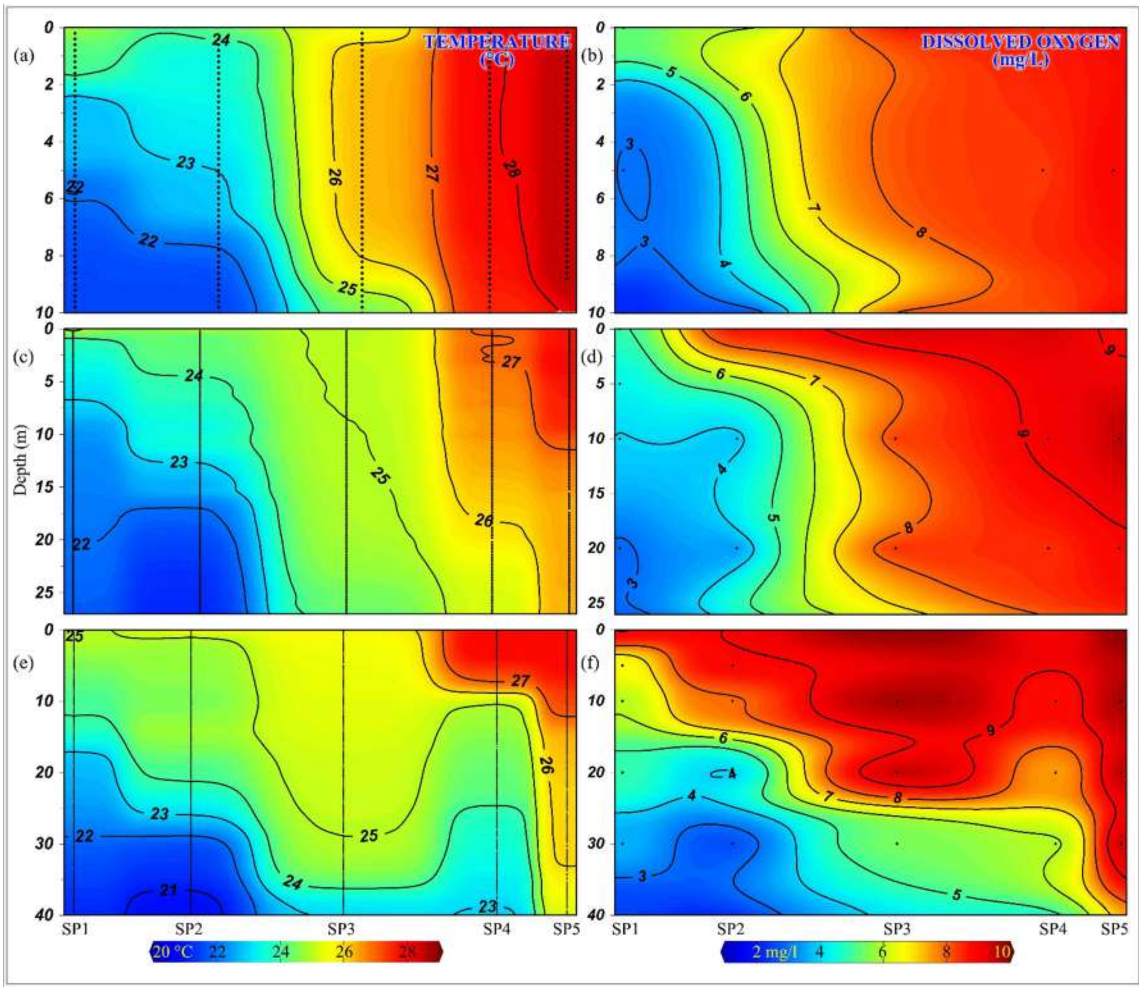

Fig. 8 Vertical distribution of temperature (°C) and dissolved oxygen (mg L^{-1}) in the nearshore waters along the southwest coast of India up to the western boundary of the GoM (Tuticorin). Panels represent (**a** & **b**) 10m, (**c** & **d**) 25m and (**e** & **f**) 40m depth during the Southwest Monsoon (September 2018). SP1 to SP5 are as indicated in Fig. 1

may benefit from easy access to stressed prey in some areas, the large spatial and temporal extent of seasonal hypoxia is likely to limit higher trophic—level transfer via the inhibition of macrobenthic production (Officer et al. 1984; De Léo and Pires-Vanin 2006; Chan et al. 2008; Rodrigues and Pires-Vanin 2012).

Oxygen deficiency is the primary cause of the dead zones in the world ocean (Officer et al. 1984; Diaz and Rosenberg 2008; Chan et al. 2008; Altieri et al. 2017). Dissolved oxygen is the prime physiological driver of respiration, photosynthesis, and calcification of coral communities (Altieri et al. 2017; Nelson and Alteir 2019). Crustaceans and echinoderms are typically more sensitive to hypoxia, and at <2 mg L^{-1} dissolved oxygen, crustacean dies within 119 h of exposure, is the reason for piles of dead crabs and lobsters a common feature in hypoxic zones (Santos and Simon 1980; Powers et al. 2001; Seitz et al. 2003; Diaz and Rosenberg 2008). Naturally, the lack of seasonal hypoxia in the GoM avoids the seasonal wipe out of sensitive fauna there, facilitating increased faunal richness and diversifications, which is advantageous especially to the native sessile and sedentary organisms having longer life span. Sedentary organisms like molluscs, echinoderms, and clams may undertake seasonal migration from the Indian southwestern shelf to the GoM as a response to escape from low oxygenation during the Southwest Monsoon (Banse 1959; Parameswaran et al. 2018; Pandiyarajan et al. 2021). So here we propose that the hypoxia avoidance migration of the mobile fauna from the nearby southwestern Indian shelf may also be contributing to the precious resource potential of arthropods, molluscs, bivalves and echinoderms inhabiting in the GoM (Rao et al. 2008). Thus GoM may also be acting as a refuge for marine fauna while oxygen-deficient waters spread over the Indian southwestern shelf (Fig. 11).

Availability of primary (plankton) food is another essential requirement in sustaining a rich and diverse fauna in any aquatic ecosystem. In the GoM, this gets possible chiefly through the seasonal surface circulation along the Indian shelf

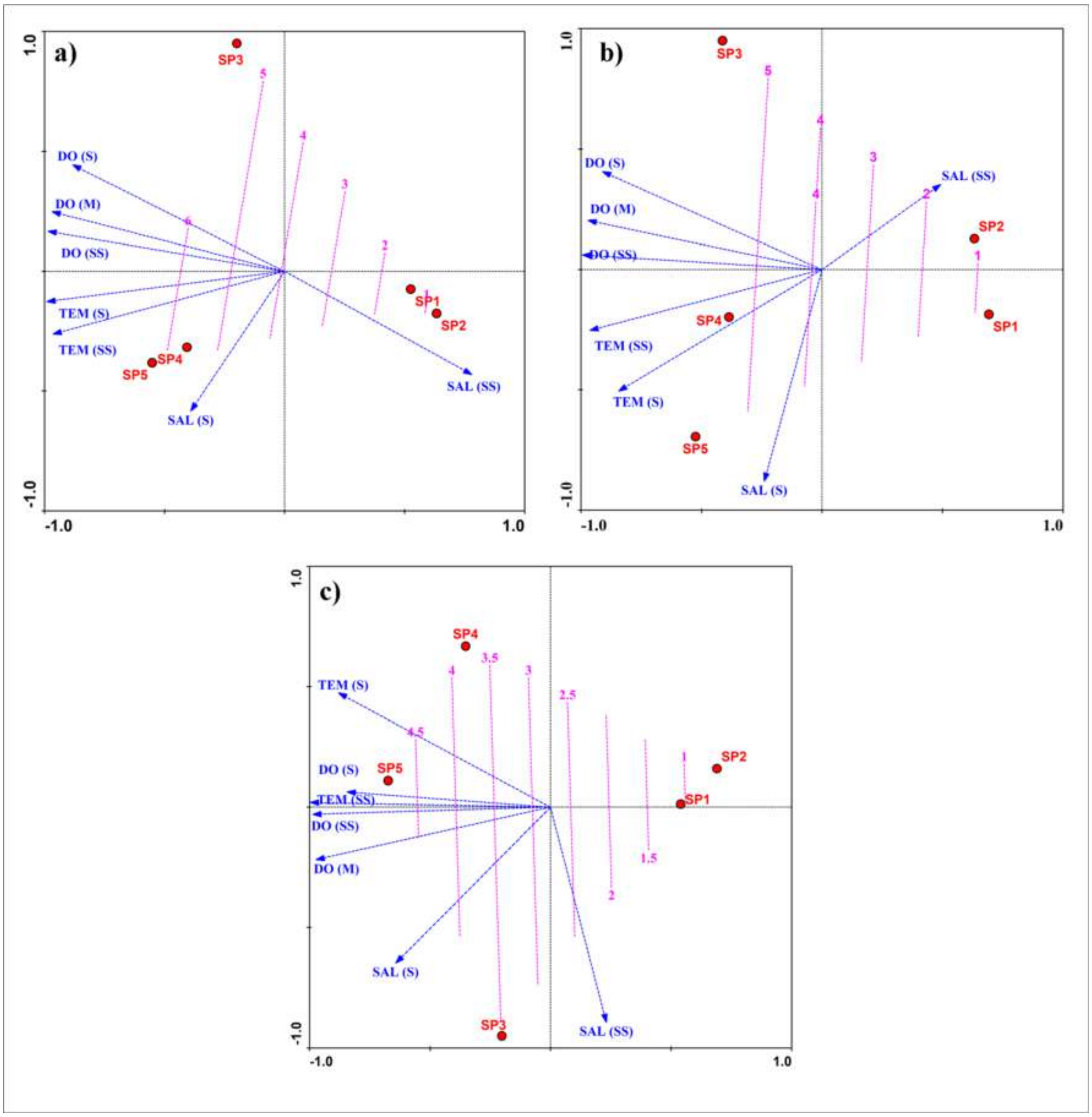

Fig. 9 Principal component analysis (first two axes—PC1 and PC2) biplot representing the hydrographical variables (blue dotted lines) and their relatedness in (**a**) 10m, (**b**) 25m, and (**c**) 40m depths of SP1 to SP5 transects. The attribution plot (GLM model) of the dissolved oxygen values (pink dotted lines) were overlaid on the PCA 2D plot. The attribution model represents the variations of dissolved oxygen concentration between various transects. PCA plots show that the hydrographical conditions in SP1 and SP2 have a significant difference between SP4 and SP5. The SP4 and SP5 in the vicinity of the GoM had relatively warm and oxygenated waters compared to SP1 and SP2. Abbreviations: SAL—salinity; TEM—temperature; DO—dissolved oxygen. S—surface; SS—subsurface; M—Middle (5m in 10m location; 10m in 25m location; 20m in 40m location)

waters. The GoM receives the positive effect of upwelling (as plankton-rich advected surface waters) during the Southwest Monsoon from the southwest coast of India. Relatively low saline (plankton-rich) coastal waters from the Bay of Bengal complement the plankton availability in the GoM during the Northeast Monsoon. Thus, an adequate amount of plankton stock (primary food) occurs in the GoM almost throughout the year. All these positive factors facilitate an advantageous ecological setting in the GoM with very minimal seasonal variations in major environmental parameters (temperature, salinity, dissolved oxygen, and plankton stock). This condition helps to sustain high species diversity through k-selection and build up their population sizes to the maximum of the carrying capacity of the environment. We demonstrate the GoM as a naturally evolved invaluable resource reserve in the region, especially during the upwelling time (Southwest Monsoon) when seasonal wipe out of sensitive fauna occurs along the southwestern Indian shelf in the SEAS.

In conclusion, the present study shows that the astonishingly rich and diverse fauna of the GoM is a biological manifestation

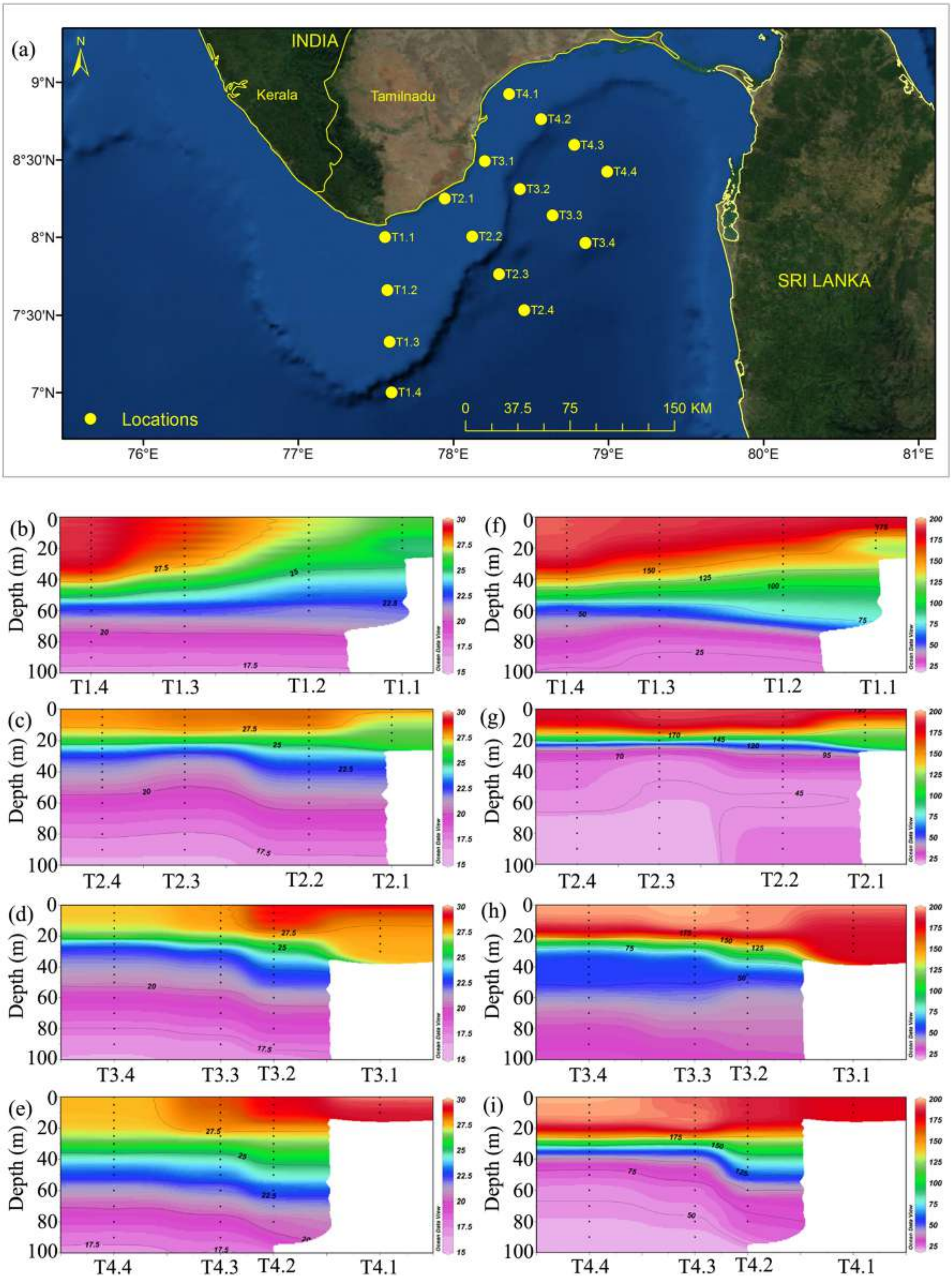

Fig. 10 (**a**) Four cross-shore transects (T1–T4) selected in the GoM for ROMS projections. The vertical structure of (**b**-**e**) temperature (°C) and (f-i) dissolved oxygen (mg L^{-1}) during the SWM (July). It is evident that the model projections closely follow the trend in the *in-situ* data presented in Fig. 4 and supplementary materials 6 & 7. Upwelling signatures were apparent in Cape Comorin transect (T1), whereas such features were absent in the rest of the transects (T2–T4) located in the GoM

of a conducive environment facilitated by its sheltered geographical position between India and Sri Lanka. The GoM has always been a sensitive geographical area for researchers and ecological conservationists, which led to the declaration of 21 islands and surrounding areas as a Marine Biosphere Reserve in 1989 by the Government of India (ENVIS 2015).

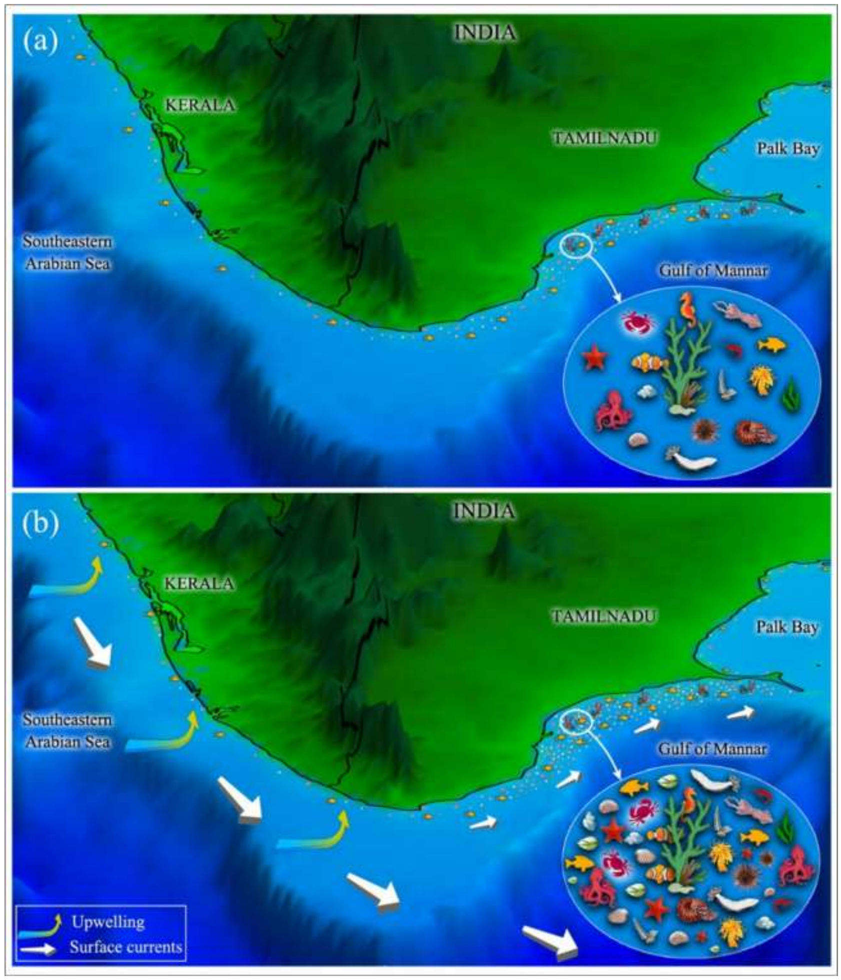

Fig. 11 Schematic of the seasonal scenario of faunal diversity and richness in the GoM during (**a**) non-upwelling and (**b**) upwelling periods. The geographically sheltered environment in the GoM provides conducive environmental conditions to support high faunal richness and diversity compared to its adjacent region. The hypoxia avoidance mechanism of fauna from the Indian southwestern shelf during the upwelling period cause their high concentration in the GoM

The present study, based on a detailed analyses of oceanographic data, satellite imageries and ROM simulation, explains that the abundant bio-resources of the GoM is enabled through its unique geographical setting. Since this is the result of a prolonged natural evolution, it is very important to protect the GoM from all kinds of environmental degradation for the conservation of its astonishing marine life.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11356-021-15530-w.

Acknowledgements The authors thank the Directors of the CSIR-National Institute of Oceanography (Dr Satish R Shetye, Dr S.W.A. Naqvi, and Prof. Sunil Kumar Singh) for the facility and encouragement. Part of the sampling for this study was carried out with the Marine Ecosystem Dynamics of the Eastern Arabian Sea (MEDAS) funded by the Ministry of Earth Sciences (MoES). We thank Dr M. Sudhakar, the former Director, Centre for Marine Living Resources and Ecology (CMLRE), Kochi, and Dr M.V. Ramanamurty, Director, National Centre for Coastal Research (NCCR), Chennai, for their enthusiastic support of the MEDAS program. The Director ICAR-CMFRI is sincerely acknowledged for providing fish landing data of the GoM. We thank all the field participants in the GoM during 2010–2011 and also along the southwest coast of India in 2018. The authors thank Mr Rajasekhar and Mr Sundar, vessel Management Cell, National Institute of Ocean Technology (NIOT), Chennai, as well as the Captain and crew of CRV Sagar Purvi cruise in September 2018 to complete the field measurements under a hostile sea environment. This is CSIR-NIO, CMLRE and INCOIS contributions 6780, 139 and 427, respectively.

Author contribution Jyothibabu Retnamma: conceptualization, methodology, writing-original draft, supervision, project administration, funding acquisition; Balachandran Kizhakkepat Kalathil: conceptualization, writing-original draft, data curation, writing-review & editing; Jagadeesan Loganathan: conceptualization, methodology, resources, data curation; Karnan Chinnadurai: visualization, methodology; Garuda Venkata Madhusudhana Gupta: conceptualization, data curation; Kunal Chakraborty: methodology, data curation & editing: Kali Charan Sahu: conceptualization, methodology, writing-review & editing.

Funding This study was financially supported by the Ministry of Earth Sciences, New Delhi through National Centre for Coastal Research Chennai.

Data availability The data sets used and/or analyzed during the current study are available from the corresponding author on reasonable request through the Director, CSIR-National Institute of Oceanography, India.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable

Competing interests The authors declare no competing interests.

References

Altieri AH, Harrison SB, Seemaan J, Collin R, Diaz RJ, Knowlton N (2017) Tropical dead zones and mass mortalities on coral reefs. PNAS 114:3665

Amrutha MM, Sanil Kumar V (2017) Observation on the dominance of swells over wind-seas in the coastal waters of Gulf of Mannar, India. Ocean Sci 13:703–717

Anjusha A, Jyothibabu R, Jagadeesan L, Mohan AP, Sudheesh K, Krishna K, Ullas N, Deepak MP (2013) Trophic efficiency of plankton food webs, Observations from the Gulf of Mannar and the Palk Bay, Southeast Coast of India. J Mar Syst 115 -116:40–61

Banse K (1959) On the upwelling and bottom trawling off the southwest coast of India. J Mar Biol Assoc India 1:33–49

Banse K (1968) Hydrography of the Arabian Sea shelf of India and Pakistan and effects on demersal fishes. Deep-Sea Res I 15:45–79

Bindu S, Muniyandi K (2005) Hydrographic parameters off the Gulf of Mannar and Palk Bay during an year of abnormal rainfall. J Mar Biol Assoc India 47(2):198–200

Chakraborty K, Guptab A, Lotliker AA, Tilstonec G (2016) Evaluation of model-simulated and MODIS-Aqua retrieved sea surface chlorophyll in the eastern Arabian Sea. Estuar Coast Shelf Sci 181:61–69

Chakraborty KK, Valsala V, Gupta GVM, Sarma VVSS (2018) Dominant biological control over upwelling on pCO2 in sea east of Sri Lanka. J Geophys Res Biogeosci. https://doi.org/10.1029/2018JG004446

Chan M, Barth JA, Lubechenco J, Kirincich A, Weeks H, Pterson WT, Menge BA (2008) Emergence of anoxia in the California Current Large Marine Ecosystems. Science 319:920

De Léo FC, Pires-Vanin AMS (2006) Benthic megafauna communities under the influence of the South Atlantic Central Water intrusion onto the Brazilian SE shelf: A comparison between an upwelling and a non-upwelling ecosystem. J Mar Syst 60:268–284

Diaz RJ, Rosenberg R (2008) Spreading Dead Zones and Consequences for Marine Ecosystems. Science 321:926–929

Dogliottia AI, Ruddick KG, Nechad B, Doxaranc D, Knaeps E (2015) Single algorithm to retrieve turbidity from remotely-sensed data in all coastal and estuarine waters. Remote Sens Environ 156:157

ENVIS (2015) Database on Gulf of Mannar Biosphere Reserve, Environmental Information System (ENVIS) Centre, Department of Environment, Government of Tamil Nadu, Chennai, India, p 74. http://tnenvis.nic.in/writereaddata/DATABASE%20ON%20GULF%20OF%20MANNAR%20FINAL%20.pdf

Grasshoff K (1983) In: Grasshoff K, Ehrhardt M, Kremling K (eds) Methods of Seawater Analysis. Verlag Chemie, Weinheim, p 419

Gupta GVM, Sudheesh V, Sudharma KV, Saravanane N, Dhanya V, Dhanya KR, Lakshmi G, Sudhakar M, Naqvi SWA (2016) Evolution to decay of upwelling and associated biogeochemistry over the southeastern Arabian Sea shelf. J Geophys Res Biogeosci 121:159–175

Harishkumar PV, Anand P (2016) Coastal upwelling of the southwest coast of India: Observations and simulations. Int J Digit Earth 9: 1256–1274

ICMAM (2001) Resource Information System for Gulf of Mannar (India). Integrated Coastal and Marine Area Management Project Directorate (ICMAM), Chennai, India Department of Ocean Development, Govt. of India. p 294. https://www.nccr.gov.in/sites/default/files/GulfofMannar.PDF

Jagadeesan L, Jyothibabu R, Anjusha A, Mohan AP, Madhu NV, Muraleedharan KR, Sudheesh K (2013) Ocean currents structuring the mesozooplankton in the Gulf of Mannar and the Palk Bay, southeast coast of India. Prog Oceanogr 110:27–48

Jagadeesan L, Jyothibabu R, Arunpandi N, Karnan C, Balachandran KK (2017) The dominance of coastal upwelling over Mud Bank in shaping the mesozooplankton along the southwest coast of India during the Southwest Monsoon. Prog Oceanogr 156:252–275

Jayaraman R (1954) Seasonal variations in salinity, dissolved oxygen and nutrient salts in the inshore waters of the Gulf of Mannar and Palk Bay near Mandapam (S. India). Indian J Fish 1(1&2):345–364

Johannessen OM, Subaraju G, Blindheim J (1981) Seasonal variations of the oceanographic conditions off the Southwest coast of India during 1971 - 1975. FiskDir.SKR.Ser.HavUnders 18: 247–261.

Jyothibabu R, Madhu NV, Habeebrehman H, Jayalakshmy KV, Nair KKC, Achuthankutty CT (2010) Re-evaluation of 'paradox of mesozooplankton' in the eastern Arabian Sea based on ship and satellite observations. J Mar Syst 81:235–251

Jyothibabu R, Madhu NV, Jagadeesan L, Anjusha A, Mohan AP, Ullas N, Sudheesh K, Karnan C (2014) Why do satellite imageries show exceptionally high chlorophyll in the Gulf of Mannar and the Palk Bay during the Northeast Monsoon? Environ. Environ Monit Assess 186:7781–7792

Jyothibabu R, Balachandran KK, Jagadeesan L, Karnan C, Arunpandi N, Naqvi SWA, Pandiyarajan RS (2018) Mud Banks along the Southwest Coast of India are not too muddy for plankton. Sci Rep 8(1):2544

Karnan C, Jyothibabu R, Arunpandi N, Jagadeesan L, Muraleedharan KR, Pratihari AK, Balachandran KK, Naqvi SWA (2017) Discriminating the biophysical impacts of coastal upwelling and mud banks along the southwest coast of India. J Mar Syst 172:24–42

Kurian J, Vinayachandran PN (2007) Mechanisms of formation of the Arabian Sea mini warm pool in a high-resolution Ocean General Circulation Model. J Geophys Res 112:C05009

Madhu NV, Ullas N, Ashwini R, Meenu P, Rehitha TV, Lallu KR (2014) Charecterization of phytoplankton pigments and functional community structure in the Gulf of Mannar and Palk Bay using HPLC-CHEMTAX analysis. Cont Shelf Res 80:79–90

McCreary JP, Kundu PK, Molinari RL (1993) A Numerical Investigation of Dynamics, Thermodynamics and Mixed-layer Processes in the Indian Ocean. Prog Oceanogr 31(3):181–244

Naqvi SWA, Naik H, Jayakumar DA, Shailaja MS, Narvekar PV (2006) Seasonal Oxygen deficiency over the western continental shelf of India Past and Present Water Column Anoxia, vol 64. Springer Netherlands, pp 195–224

Nelson HR, Alteir AH (2019) Oxygen: the universal currency on coral reefs. Coral Reefs 38:177–198

Officer CB, Briggs RB, Taft JL, Cronin LE, Tyler MA, Boyton WR (1984) Chesapeake Bay anoxia. Origin, development and significance. Science 6 223(4631):22–27

Pandiyarajan RS, Jyothibabu R, Arunpandi N, Parthasarathi S (2021) Seasonality of macrobenthic assemblages and the biotic environmental quality of the largest monsoonal estuary along the west coast of India. Environ Sci Pollut Res. https://doi.org/10.1007/s11356-021-13144-w

Parameswaran UV, Jaleel AKU, Sanjeevan VN, Gopal A, Sudhakar M (2018) Diversity and distribution of echinoderms in the South Eastern Arabian Sea shelf under the influence of seasonal hypoxia. Prog Oceanogr 165:189–204

Pihl L (1994) Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. Can J Fish Aquat Sci 51: 321–336

Pihl L, Baden SP, Diaz RJ (1991) Effects of periodic hypoxia on distribution of demersal fish and crustaceans. Mar Biol 108:349–360

Pihl L, Baden SP, Diaz RJ, Schaffner LC (1992) Hypoxia-induced structural changes in the diet of bottom-feeding fish and crustacea. Mar Biol 112:349–361

Powers SP, Harper DE Jr, Rabalais NN (2001) The effect of large scale hypoxia/anoxia on the supply and settlement of benthic invertebrate larvae. In: Rabalais NN, Turner RE (eds) Coastal hypoxia: consequences for living resources, Coastal and Estuarine Studies, vol 58. American Geophysical Union, Washington, pp 165–184

Rabalais NN, Harper DE Jr, Turner RE (2001) Responses of nekton and demersal and benthic fauna to decreasing oxygen concentrations. In: Rabalais NN, Turner RE (eds) Coastal hypoxia: consequences for living resources, Coastal and Estuarine Studies, vol 58. American Geophysical Union, Washington, pp 115–128

Ramasastry AA, Myrland P (1959) Distribution of temperature, salinity and density in the Arabian Sea along the South Malabar Coast (South India) during the post-monsoon season. Indian J Fish 6: 223–255

Rao SDV, Srinivasa Rao K, Iyer CSP, Chittibabu P (2008) Possible ecological consequences from the Sethu Samudram canal project India. Mar Pollut Bull 56:172–186

Rao RR, Gireeshkumar MS, Ravichandran M, Gopalakrishna VV, Thadathil P (2011) Do cold low saline waters pass through the Indo Sri Lankan channel during winter? Int J Remote Sens 32(22): 327383–327398

Regunathan A, Mathew KJ, Kurup NS, Murty AVS (1981) Monsoon fishery and Mud Banks of Kerala coast. Bull Cent Mar Fish Res Inst India 30:37–41

Rodrigues CW, Pires-Vanin AMS (2012) Spatio-temporal and functional structure of the amphipod communities off Santos, Southwestern Atlantic. Braz J Oceanogr 60:421–439. https://doi.org/10.1590/S1679-87592012000300013

Santos SL, Simon JL (1980) Marine soft-bottom community establishment following annual defaunation: larval or adult recruitment? Mar Ecol Prog Ser 2:235–241

Seitz RD, Marshall LS, Hines AH, Clark KL (2003) Effects of hypoxia on predator-prey dynamics of the blue crab *Callinectes sapidus* and the Baltic clam *Macoma balthica* in Chesapeake Bay. Mar Ecol Prog Ser 257:179–188

Shankar D, Shetye S (1997) On the Dynamics of the Lakshadweep High and Low in the Southeastern Arabian Sea. J Geophys Res 102: 12551–12562

Shenoi SC, Shankar D, Gopalakrishna VV, Durand F (2005) Role of the ocean in the genesis and annihilation of the core of the warm pool in the Southeastern Arabian Sea. Mausam 56:147–160

Shetye SR, Gouveia AD, Shenoi SSC (1994) Circulation and water masses of the Arabian Sea. Proc Indian Acad Sci Earth Planet Sci 103:107–123

Vinayachandran PN, Chauhan P, Mohan M, Nayak S (2004) Biological responses of the seas around Sri Lanka to summer Monsoon. Geophys Res Lett 31:L01302