

How Oceanography Influences Fishery Biology? - A Case of Distribution Differences in Carnivorous and Planktivorous Fishes along the Coastal Waters of Eastern Arabian Sea

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Abstract

Understanding the link between physical oceanographic events and seasonality in catch composition is a critical component in the accurate assessment of climate change impacts in context of fisheries. This remains elusive owing to the lack of synoptic-level datasets on the relevant oceanographic variables. The advent of satellite remote sensing that can measure oceanographic variables at high spatial and temporal resolution has helped to address this challenge. Prior studies have communicated the puzzling dominance of carnivores (fish groups) in North East Arabian Sea (NEAS) whereas planktivores appear to thrive in South East Arabian Sea (SEAS). The study attempts to address this conundrum by taking cues from the influence of oceanographic forcing upon seasonal trends in catch composition using remotely-sensed oceanographic variables and mean standardized catch. The anoxic conditions associated with intense seasonal upwelling in SEAS waters leads to the reduction in the vertical extent of demersal carnivore habitats. The demersal habitats in NEAS waters have a higher likelihood of entraining oxygen rich (>0.5 ml/L) water column when compared with its southern counterpart especially from August to November. Moreover, NEAS waters cater to the nutritional requirements of juvenile demersal carnivore population as it supports primary production both during summer and winter monsoon months. The perpetual presence of chlorophyll biomass allows for the persistence of a prey base that maximizes the likelihood of demersal adult population being well-fed. The poleward directed West India Coastal Current facilitates the passive drift of juveniles towards productive and oxygen rich habitats in NEAS waters. For demersal/pelagic carnivores that undergo recruitment over a long span of time (> 6 months), NEAS waters provide the best spawning ground capable of meeting their long-term nutritional demands. Pelagic planktivores thrive in SEAS, where seasonal upwelling supported primary production remains the norm, owing to their relatively short recruitment span (< 4 months). Unlike SEAS, NEAS waters are found to provide suitable environment geared towards the successful larval recruitment, sustenance and survival of the demersal carnivore group. This could act as a forcing function in driving the annual catch composition of landing data registered in NEAS waters toward carnivore spectrum.

Keywords : Chlorophyll, Upwelling, Monsoon, Remote sensing, Catch composition, Planktivore, Carnivore, Oceanography

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1 Introduction

Understanding the relationship between oceanographic forcing and its impact on fisheries is essential in accurately gauging the effects of climate change upon marine resources of interest. However, this link has remained largely elusive given the lack of synoptic-level datasets on the oceanographic variables that differentiate diverse ocean sites from each other. Satellite remote sensing has played a pivotal role in addressing this data gap by offering the opportunity to measure and monitor multiple oceanographic variables systematically at desired resolutions (George, 2014). With the advent of remote sensing capabilities, seasonal changes in physical forcing and optical responses of coastal waters can easily be monitored (Ikeda, 1995). For example, the South East Arabian Sea reportedly exhibits a strong seasonality in remote sensing reflectance compared with its North East counterpart (Monolisha *et al.*, 2017). Contrary to this observation, conventional wisdom dictates that strong seasonality in environmental variables is persistent in latitudes outside of the Tropical belt (Hartmann, 1994). Seasonal changes in physical forcing influence the biological behavior (spawning, feeding) of fish. Survival of fish larvae will be enhanced if the spawning coincides with the onset of better food conditions in close proximity both temporally and spatially (Platt *et al.*, 2003). Fishes also exhibit a natural tendency to avoid predators and provide their larvae with best possible resources to improve their chances of recruitment to their adult fishery stock. Such adaptations aim at improving the odds of larval/juvenile/adult sustenance and survival by taking advantage of resources (food, oxygenated water column) that are locally available. The availability/accessibility of such resources are often dictated by seasonal oceanographic forcing (upwelling, direction and magnitude of surface currents).

Tropical waters are often characterized by high species diversity (Lugo, 1988). Greater species diversity of the Tropics compared with higher latitudes (Pianka, 1989) is well reflected in the commercial fisheries of the eastern Arabian Sea. India, being one of the most prominent tropical fishing nations contributes about 3.5 million tons of fish annually. Over a coastline 8129 km, consistent regional differences in catch composition are observed. Such differences may arise from the influence of multiple forcing factors of physical (upwelling, reversal of surface currents, likelihood of shelf water - nutrient enrichment due to tides), chemical (concentration of dissolved oxygen), geological (nature of continental shelf), biological (primary production, spawning adaptations of fish groups) and anthropological (commercial interest) origin. Madhupratap *et al.*, 2001 have communicated the puzzling dominance of carnivores (fish groups) in North East Arabian Sea (NEAS) whereas planktivores appear to thrive in South East Arabian Sea (SEAS). The driving factors responsible for this observed regional difference in catch composition across 15°N latitude have not been investigated hitherto.

We hypothesize that oceanographic forcing has a strong influence in dictating the seasonal trends in catch composition and can even act as a forcing function in introducing the skewness in catch composition towards carnivore spectrum to the North of 15°N latitude along the eastern Arabian Sea. In order to test this hypothesis, the study focuses upon investigating the seasonal influence of oceanographic forcing (upwelling, surface currents, likelihood of shelf water - nutrient enrichment due to tides) within the context of spawning adaptations of fish groups of interest

(Section 2.2.2.2). In order to take cues from the influence of oceanographic forcing upon seasonal trends in catch composition, remotely-sensed oceanographic variables and mean standardized catch (a proxy to represent the abundance of a given marine resource of interest) were employed.

2 Materials and Methods

2.1 Study area

The spatial domain (Figure 1) of this study extends from 8°N to 24°N and 65°E to 78°E covering the entire eastern Arabian Sea. The study site is divided into two sub-domains across the 15°N latitude, namely the zone that falls north of the 15°N latitude, referred to as the North East Arabian Sea (NEAS) and the zone that is located south of 15°N latitude called the South East Arabian Sea (SEAS). For this study, we focus on the coastal waters defined as waters inside 200 m isobaths

FIGURE CAPTIONS

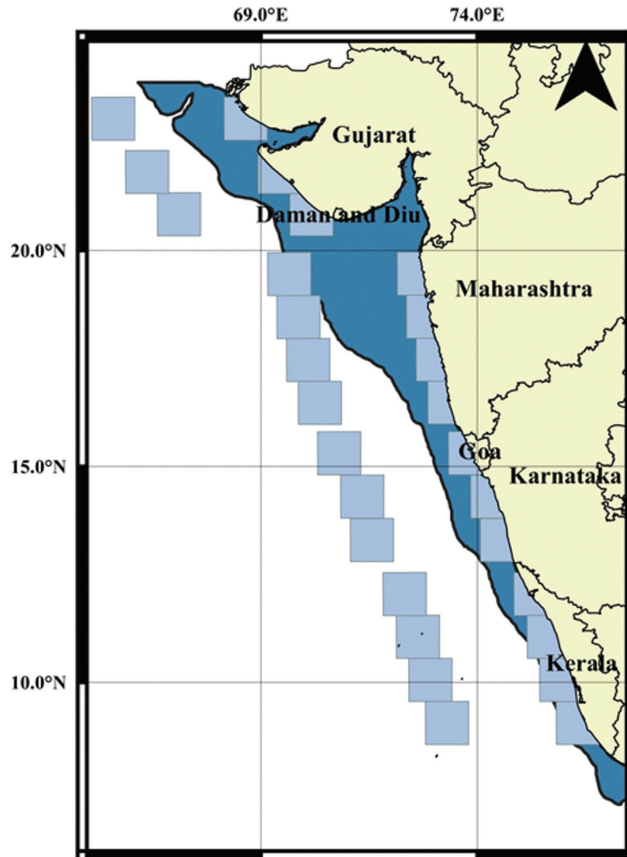


Fig. 1. Study region covering the eastern Arabian Sea. The region (shaded in dark-blue) is enclosed by the coastline on the East and 200 m isobath on the West. The squared-boxes indicate the off-shore and coastal stations considered for deriving Local Temperature Anomaly.

(Figure 1). The marine fish-landing data at monthly intervals for individual States (covering each major marine resource of interest) are mostly derived from the intense fishing that occurs within the Indian Exclusive Economic Zone (EEZ) which extends up to 200 nautical miles from the coast. The 200 m isobath was assigned to ensure adequate spatial overlap between EEZ and highly productive coastal waters (King, 2013) that are likely to serve as spawning sites (for adult fish stock) as well as feeding grounds (for fish larvae, juveniles and adults). The States of Kerala, Karnataka and Goa share their coastline with SEAS whereas Maharashtra and Gujarat coasts lie adjacent to NEAS.

2.2 Datasets used

2.2.1 Physical Datasets

2.2.1.1 Sea-surface wind

The QuikSCAT Level-3 surface wind speed mapped dataset from 2000 to 2009 (NASA, 2012), were obtained at $1^\circ \times 1^\circ$ spatial resolution and monthly resolution from the NASA website <http://dx.doi.org/10.5067/QSSWS-CMIP1>.

2.2.1.2 Sea-surface temperature

The sea surface temperature data, from 2007 to 2016, were derived from NOAA - OI (National Oceanic and Atmospheric Administration - Optimum Interpolation) High Resolution Blended Analysis of daily SST, Version 2 dataset (Reynolds *et al.*, 2007) with a spatial sampling of 0.25° available at <https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html>.

2.2.1.3 Sea-surface height anomaly

The monthly sea surface height anomaly (CMEMS, 2016), having a spatial resolution of 0.25° was derived from Level 4 Global Ocean Gridded Maps REP (Reprocessed) SLA (Sea-level anomaly) from 1993 to 2009 available at http://marine.copernicus.eu/services-portfolio/access-to-products/?option=com_csw&view=details&product_id=SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047.

2.2.1.4 Sea-surface currents

The near sea surface current estimates from 1993 to 2009 were obtained from Level-4 OSCAR (Ocean Surface Current Analysis Real-time) OC (Ocean current) third degree resolution (0.33° spatial resolution) Version 1 dataset (Bonjean and Lagerloef, 2009) at 5-day temporal sampling. The dataset can be accessed from https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg.

2.2.1.5 Vertical Salinity profile and surface density

The vertical salinity profile and surface density was derived from North Indian Ocean Atlas developed for the Indian Exclusive Economic Zone (Chatterjee *et al.*, 2012) restricted to a depth of 1500 m. The dataset can be accessed at http://www.nio.org/index/option/com_nomenu/task/show/tid/2/sid/18/id/229.

2.2.1.6 Bathymetry

The bathymetry dataset was derived from ETOPO1 1 Arc-Minute Global Relief Model dataset at 1 arc-minute spatial resolution (Amante and Eakins 2009). The dataset is available at <http://dx.doi.org/10.7289/V5C8276M>.

2.2.1.7 Tidal amplitude

The tidal elevation time-series data for specific stations across 15°N latitude namely (Kandla (23°E, 70.23°N), Bhavnagar (21.8°E, 72.15°N), Mumbai (18.91°E, 72.83°N), Mangalore (12.85°E, 72.83°N), Beypore (11.16°E, 75.8°N) and Cochin (9.96°E, 76.25°N) using Tide and Currents Prediction Tool (Flater, 1998) available at <http://tides.mobilegeographics.com>.

2.2.1.8 Optical classes based on Remote Sensing Reflectance

The dataset containing eight optical classes associated with eastern Arabian Sea were derived from log transformed normalized remote sensing reflectance dataset (Version 2, accessible at ESA CCI Ocean Color website at <http://www.esa-oceancolour-cci.org>.) for six specific wavelengths (412 nm, 443 nm, 490 nm, 510 nm, 555 nm and 670 nm) across 1998-2013 period by employing fuzzy C mean algorithm (Monolisha *et al.*, 2017).

2.2.2 Biological Datasets

2.2.2.1 Sea-surface chlorophyll

The sea-surface chlorophyll-a concentration for the study region was derived from the OC-CCI (Ocean Color Climate Change Initiative) Version 3, Level 3 Mapped data of chlorophyll concentration (OC-CCI, 2015) at 4 km spatial sampling and monthly temporal resolution from 1998 to 2015. The dataset is accessible at ESA CCI Ocean Color website at <http://www.esa-oceancolour-cci.org>.

2.2.2.2 Fisheries data

The marine fish species considered for the study (Table A, Supplementary Material) were broadly categorized into pelagic/demersal and planktivore/carnivore groups based on the vertical extent of habitat and diet preferences of adult fish. Adult fish having vertical habitats below 30 m of depth have been assigned under demersal category. The major marine resources of interest considered for the present study include prawns, pelagic planktivores such as anchovies, mackerel, sardines along with demersal carnivores such as pomfrets, perches and croakers. It is to be noted here that we do not treat these groups to be mutually exclusive as some species can be both planktivore and carnivore whereas most fish species spent their early stages (such as egg, larvae, juvenile) as pelagic entities mostly dependent upon plankton to meet their metabolic requirements. The diet of the adult members of the species categorized as planktivores (Table A, Supplementary Material) mostly comprise of phytoplankton and zooplankton. Apart from plankton (primarily zooplankton), the diet of adult members in species that were labeled as carnivores (Table A, Supplementary Material) also include fish egg/larvae, juveniles and crustaceans. The landing data used for the study pertain to the marine capture fisheries and the list of fishing gears associated with the same is also provided (Table B, Supplementary Material). The marine fish landing dataset for each marine resource of interest coupled with the fishing effort (in terms of the number of units under operation) associated with individual gears were obtained for each State at monthly temporal resolution from Central Marine Fisheries Research Institute database (CMFRI, 2016).

2.3 Methodology used

2.3.1 Upwelling Index

The local temperature anomaly (LTA), a coastal upwelling index, was derived from daily sea surface temperature climatology using Equation (1) by adopting the approach of Wooster *et al.*, (1976), Naidu *et al.*, (1999), Prell and Streeter (1982), Smitha *et al.*, (2008) and Shah *et al.*, (2015) following the justification that the key signature of upwelling-dominated regions is based on temperature difference between regions within the same latitudinal belt (Smitha *et al.*, 2008; Jayaram *et al.*, 2010). The LTA was estimated at the sea surface with a temporal resolution of one day. Upwelling is indicated by positive LTA values.

$$LTA = T_{\text{open ocean}} - T_{\text{coastal waters}} \quad \text{Equation 1}$$

where $T_{\text{open ocean}}$ represents sea surface temperature associated with an off-shore station at a distance of 3° with respect to that recorded at a coastal station (denoted using $T_{\text{coastal waters}}$) within the same latitudinal belt. LTA serves as a proxy to represent oceanographic forcing.

2.3.2 Standardization of marine fish landing data

The marine fish-landing data contains mixed signals underlining the roles played by a myriad of factors (including fishing effort, fishing gear, expertise of the fishermen) and therefore can be considered as a highly biased indicator of abundance for a marine resource of interest. In an attempt to minimize the bias in marine fish landing data due to effort, Catch per Unit Effort was computed using both landing data and effort for each marine resource across multiple fishing gears. The CPUE's were standardized using Multi-Gear Mean Standardization (MGMS) to obtain a dimensionless entity namely Mean Standardized Catch (MSC) which enables us to combine data across multiple gears (Gibson-Reinemer *et al.*, 2016). For a given State, marine resource and sampling time, the standardized CPUE data were combined by adding up the Mean Standardized Catch from individual fishing gears (Hinch *et al.*, 1991, Jackson and Harvey, 1997). The Mean Standardized Catch (MSC) serves as a proxy to represent the abundance of a given marine resource of interest.

2.3.3 Relevance of Datasets Employed

Climatology of variables such as sea surface wind, sea surface height anomaly, sea surface current sea surface chlorophyll and mean standardized catch were prepared by averaging the dataset of individual month across multiple years. The daily climatology of sea surface temperature was used to derive Local Temperature Anomaly. Sea surface wind climatology was used to identify the seasonality in wind magnitude and direction since it acts as an essential forcing function for the initiation and termination of wind-driven upwelling along the eastern Arabian Sea. Local Temperature Anomaly (an upwelling index based on zonal gradient in sea surface temperature across a single latitudinal belt), derived from daily SST climatology targeted the identification of terminal phase (at daily level) of seasonal upwelling within Indian Exclusive Economic Zone when the coastal water column in its entirety is more likely to entertain anoxic conditions. In order to compare the spread and intensity of upwelling in NEAS and SEAS waters, sea surface height anomaly was employed as a useful proxy. The magnitude and direction of sea surface currents was used to gauge the likelihood

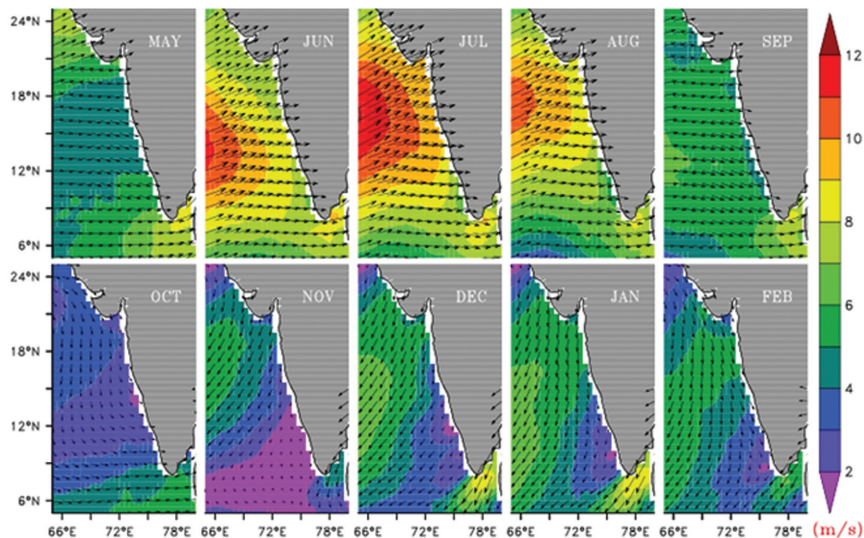


Fig. 2. Climatology of surface wind across eastern Arabian Sea. Panels correspond to months as follows: (A) May, (B) June, (C) July, (D) August, (E) September, (F) October, (G) November, (H) December, (I) January and (J) February.

of fish eggs/larvae transport due to horizontal advection during summer/winter monsoon months. Climatology of vertical salinity profile was used to gain insight with respect to the monthly progression of vertical excursion of sub-surface water during upwelling along the eastern Arabian Sea. The nature of the continental shelf within the Indian Exclusive Economic Zone (EEZ) was characterized using ETOPO 1 bathymetry dataset. Tidal amplitude dataset was used to qualitatively gauge the likelihood of nutrient off-load associated with tidal current amplification (which could potentially enrich the shelf region with nutrients) for NEAS and SEAS waters. The sea surface chlorophyll-*a* climatology was used to study the persistent and seasonal nature of surface chlorophyll along with the regional differences in its concentration observed across 15°N latitude. The seasonality of optical classes in NEAS and SEAS waters was investigated using dataset containing eight optical classes derived from remote sensing reflectance (Monolisha *et al.*, 2017).

We speculate that unlike SEAS, NEAS waters provide suitable environment geared towards the successful larval recruitment, sustenance and survival of the demersal carnivore group. In order to put our hypothesis to test, we investigate the seasonality in oceanographic forcing (upwelling, surface currents) with prime focus upon August-November period (when anoxic conditions due to upwelling is known to persist along the eastern Arabian Sea at least up to 15°N latitude and trawl ban remains lifted) in an attempt to detect its influence in the variation of mean standardized catch for pelagic/demersal planktivore/carnivore fish groups in NEAS as well as SEAS waters that could potentially explain the seasonality and nature of catch composition along the eastern Arabian Sea.

3 Results

The key findings with respect to oceanographic forcing, namely; Upwelling, Sea surface currents, Role of tides in shelf water-nutrient enrichment are provided in this section along with an overview

of the spawning adaptations of fish groups aimed at enhancement of the odds of successful larval recruitment. The section concludes with the impact of upwelling upon catch composition across NEAS and SEAS.

3.1 Oceanographic forcing

3.1.1 Surface current

The climatology for sea surface current is derived from Level-4 OSCAR dataset available at 0.33 degree spatial sampling (Bonjean and Lagerloef, 2009). The sea surface currents are directed equatorward (Figure 3(B)-(D)) during summer monsoon (especially from June to September) with a velocity range mostly within 0.08 and 0.18 m/s and poleward (Figure 3(H)-(I)) during winter monsoon (from November to February) with a velocity range 0.06 and 0.16 m/s. The magnitude of strength (depending on how well-developed current system is) and direction of sea surface currents can play a dominant role in the horizontal transport during the early stages (egg/larvae) of life-history for a given marine resource when it is mostly at the mercy of surface currents which dictate its horizontal advective transport. Hence, sea surface currents can advect (horizontally) the fish egg/larvae from their respective spawning sites and contribute to the eventual aggregation of fish egg/larvae towards or away from their potential feeding grounds, which in turn could affect their survival and recruitment to adult stock.

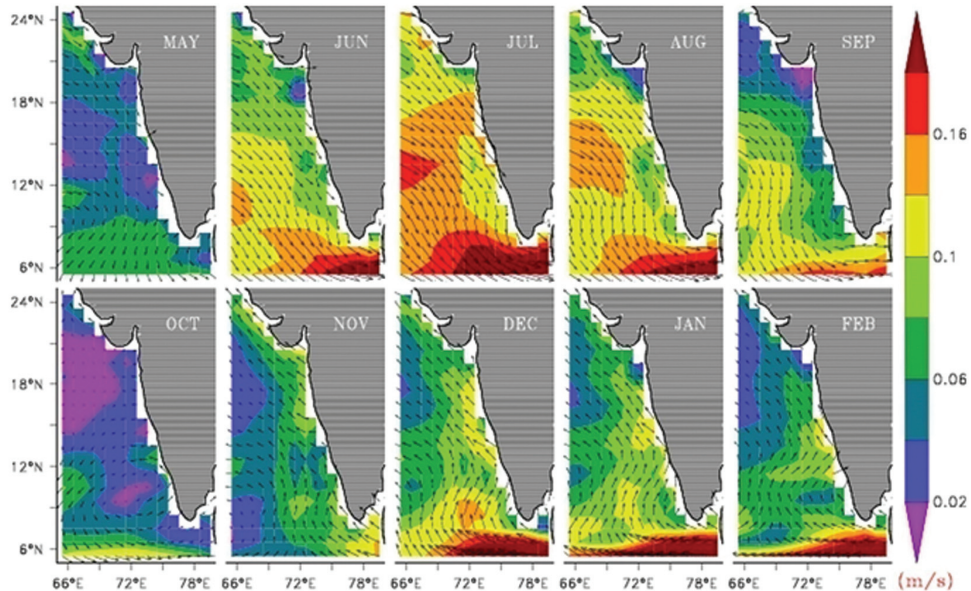


Fig. 3. Climatology of surface currents across eastern Arabian Sea. Panels correspond to months as follows: (A) May, (B) June, (C) July, (D) August, (E) September, (F) October, (G) November, (H) December, (I) January and (J) February

3.1.2 Upwelling/Downwelling in NEAS and SEAS

3.1.2.1 Sea surface wind

The sea surface wind climatology was derived from QuikSCAT Level 3 dataset (NASA, 2012). The eastern Arabian Sea is strongly influenced by the seasonal reversal of monsoon and associated meteorological forcing. During summer monsoon (May-August), winds along this region typically have a velocity range of 5 - 10 m/s along the West coast and are directed from sea towards the land (South West) whereas during winter monsoon (November-January), the wind system reverses its direction and moves from land to sea (North East) with a velocity range of 2 - 6 m/s along the eastern Arabian Sea. Moisture-bearing South West monsoon winds (Figure 2 (C)) exert its influence across the Arabian Sea during July. Dry winds characterizing North East monsoon intensify (Figure 2 (H)) during December over the eastern Arabian Sea. The coastline towards the North of 15°N latitude lies almost perpendicular to the incoming South West monsoon whereas in SEAS, the winds tend to intersect the land mass at shallower angle (when compared with NEAS region). This difference in angle of incidence can fuel the progressive accentuation (towards lower latitudes) of along shore wind component responsible for wind-driven upwelling that dominates SEAS coastal region during Indian summer monsoon period. The increase in strength of along shore wind component especially towards lower latitudes can contribute to the intense upwelling in SEAS waters (when compared with NEAS) which in turn can increase the likelihood of the entire coastal water column to entrain sub-surface waters deficient in oxygen, thereby rendering such habitats inhospitable especially for demersal populations that thrive below the pelagic zone.

3.1.2.2 Sea surface height anomaly

Climatology for sea surface height anomaly, derived from Level 4 Gridded REP (Reprocessed) SLA (Sea-Level Anomaly) Gridded dataset (CMEMS, 2016) was used as a proxy to gauge and compare the intensity and horizontal spread of upwelling episodes in NEAS and SEAS waters. Lowering of mean sea level during summer monsoon (Figure 4(C)-(E)) indicates upwelling (dominant during July, August and September) whereas elevated sea level during winter monsoon (Figure 4(H)-(J)) indicates downwelling (from December to February) along the eastern Arabian Sea. The sea surface height anomaly consistently exhibits its lowest values (between -3 and -15 cm) during June to September close to the SEAS region. Upwelling signals manifested through negative sea surface height anomaly indicates that it is much stronger and more wide-spread in SEAS especially during August. Such prominent upwelling signals are not observed along the NEAS region. The highest values for sea surface height anomaly (>12 cm) are observed during winter monsoon in SEAS coastal waters whereas such prominent downwelling signals are not observed along the NEAS coastal waters. Consistent negative values for sea surface height anomaly indicate the slow emergence of subsurface water associated with anoxic conditions from the ocean depths replacing the surface water transported rapidly offshore under the influence of upwelling, which could render SEAS waters less conducive for demersal population to thrive. Likewise, persistent positive sea surface height anomaly corresponds to the subduction of surface water into the ocean depths and eventual replacement of anoxic, nutrient rich sub-surface water with oxygen-rich, yet nutrient deficient surface water.

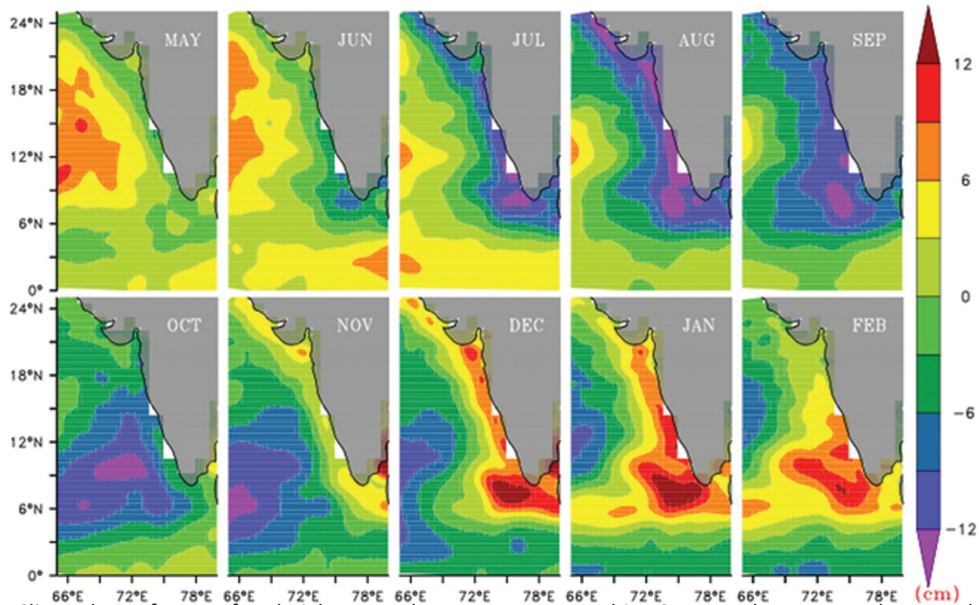


Fig. 4. Climatology of sea surface height anomaly across eastern Arabian Sea. Panels correspond to months as follows: (A) May, (B) June, (C) July, (D) August, (E) September, (F) October, (G) November, (H) December, (I) January and (J) February

3.1.2.3 Vertical excursion of upwelled water

Climatology for vertical salinity profile was obtained from North Indian Ocean Atlas derived by Chatterjee *et al.*, (2012). Upwelling is characterized by the emergence of dense, cold nutrient rich waters from ocean depths to the surface. Along the vertical dimension, such a phenomenon could easily be detected by upward tilt of isopleths whereas the subduction of surface water to the greater ocean depths is manifested by downward tilting isopleths during downwelling.

From Figure 5 panels (C)-(F), it is quite evident that in SEAS during upwelling, the upward tilt of the isopycnals extends from the open ocean to the coastline (66°E to 75°E) where the subsurface water reaches the surface, especially during August and September. This implies that in SEAS, the entire water column adjacent to the coastline has a greater likelihood of entraining nutrient rich waters. This could also indicate that anoxic conditions in coastal water column, a common spawning site for marine resources, could become an established norm in SEAS waters especially towards August – November. Such anoxic conditions (all the way to the surface) when sustained over a span of few months could hamper the survival of marine fish egg/larvae apart from adversely affecting the demersal dwellers whose vertical habitat extent share a larger overlap with anoxic conditions that set in with upwelling.

Downwelling in SEAS (Rao *et al.*, 2009) operates during non-upwelling months (November-February) when, in the absence of upwelling-favorable winds, the surface water gets subducted to the ocean depths as highlighted by downward-tilting isopycnals in Figure 5 (H)-(K) and the water-column (closer to the coastline) slowly replenishes its oxygen concentration.

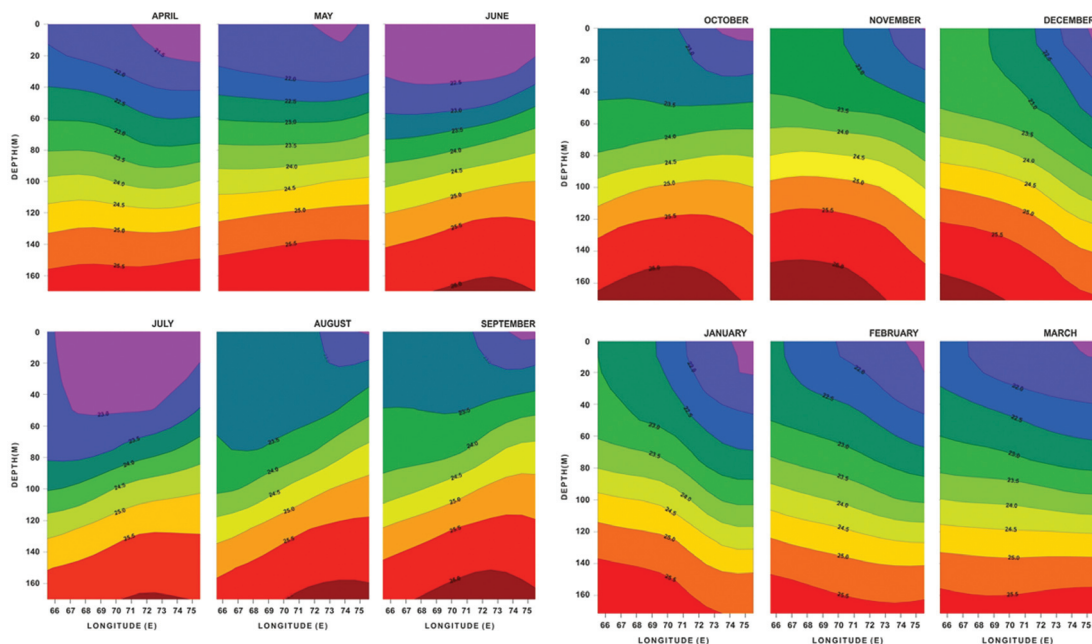


Fig. 5. Isopycnals across eastern Arabian Sea along 8.50N latitude during pre-summer monsoon and South West monsoon period. Panels correspond to months as follows: (A)April, (B)May, (C)June, (D)July, (E)August, (F)September

Fig. 5. Isopycnals across eastern Arabian Sea along 8.50N latitude during post South West monsoon and winter monsoon period. Panels correspond to months as follows: (G)October, (H)November, (I)December, (J)January, (K)February and (L) March.

3.1.2.4 Surface density

The surface density was derived from North Indian Ocean Atlas developed by Chatterjee *et al.*, (2012). The NEAS region is characterized by the presence of denser water (Figure 6) throughout the year when compared with its SEAS counterpart. The surface density difference between NEAS and SEAS is observed to be minimum during upwelling months (June - September). This could be attributed to the strong upwelling in SEAS which in turn results in the vertical intrusion of dense water from the ocean depth to the sea surface. Since upwelling signals are not as strong in NEAS (when compared with SEAS), the duration of increase in surface density values remains short (June -August), whereas the higher surface density values in SEAS is sustained for longer (April - September) during upwelling months.

For non-upwelling months (November-February), the difference in surface density values between NEAS and SEAS waters is accentuated. This could be attributed to two factors namely:

- 1) The influx of low-salinity water from Bay of Bengal into eastern Arabian Sea by Winter Monsoon Current (WMC) which bifurcates close to Lakshadweep High and flows as West India Coastal Current along the West coast of India (Wyrtki, 1971; Bruce *et al.*, 1994; Han, 1999; Shenoi *et al.*, 1999; Shankar and Shetye, 1999; Han and McCreary 2001; Han *et al.*, 2001; Howden and Murtugudde, 2001; Shankar *et al.*, 2002).

- 2) Intense downwelling in SEAS (due to Kelvin wave as reported by Rao *et al.*, 2009) can result in the subduction of surface water which in turn gradually replaces the nutrient-rich waters that had flooded the shelf region during upwelling

Subduction of high salinity surface water during winter monsoon in the northern Arabian Sea also contributes to the high surface density values observed in NEAS adjacent to the mixed layer (Morrison, 1997; Schott and Fischer, 2000). Latitudes, particularly 16°N and 20°N (Figure 6) consistently register high sigma-t values (>22.4 kg/m³) in comparison coastal stations (8°N and 11°N) in SEAS thereby suggesting that denser surface waters characterize the coastal waters to the North of 15°N latitude.

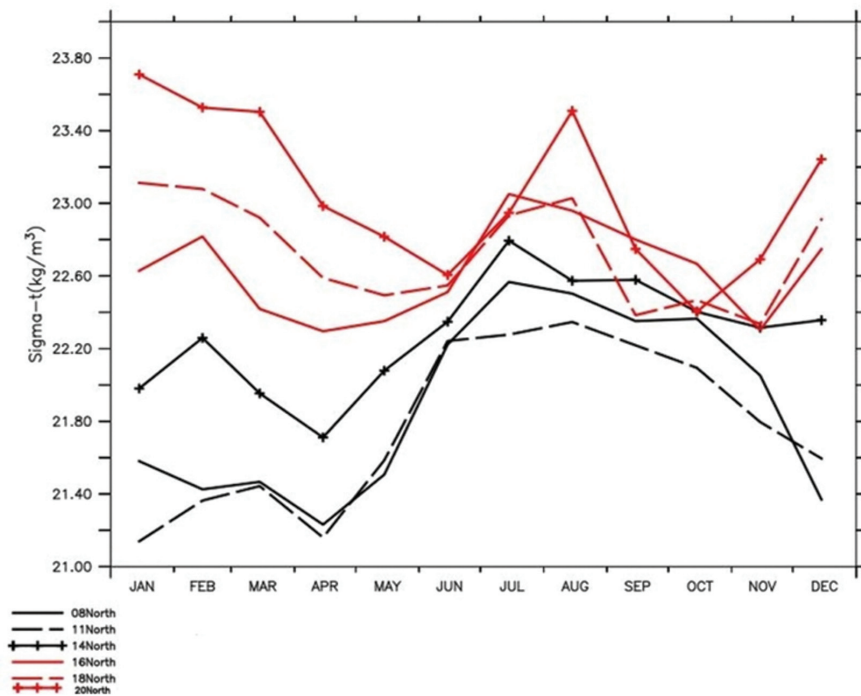


Fig 6. Seasonality of sea surface water density across multiple latitudes (8°N, 11°N, 14°N, 16°N, 18°N and 20°N latitude). Red and black color denotes stations located in NEAS and SEAS respectively.

The surface density acts as a critical factor in determining the vertical positioning of marine fish egg (Sundby and Kristiansen, 2015) since adult marine fishes can alter the buoyancy of the eggs (May, 1974) in response to the environmental density variations to optimize the chance that their eggs/larvae remain adjacent to surface coastal waters that are more likely to be productive (with lower predation pressure) enough to sustain their metabolic requirements during the critical phase of larval development in order to facilitate higher likelihood of recruitment of the juveniles to adult stock.

3.1.2.5 Sea surface chlorophyll

The sea surface chlorophyll dataset was obtained from OC-CCI (Ocean Color Climate Change Initiative) chlorophyll-a concentration (Version 3) dataset (OC-CC1, 2015). High values of chlorophyll biomass (Figure 8 (C)-(E)) are observed along the eastern Arabian Sea during peak (when monsoon winds attain their maximum magnitude) months (June - September) of summer monsoon owing to the intense upwelling characterizing the eastern Arabian Sea coast. However, despite the absence of upwelling-favorable winds over NEAS waters during winter monsoon, we observe high chlorophyll biomass values particularly in northern Arabian Sea (Figure 8 (G)-(J)) due to the influx of iron-rich aerosols transported by the dry North East monsoon winds from Indian sub-continental desert regions (Kumar., 2010) and the winter convective mixing (Madhupratap *et al.*, 1996; Kumar and Prasad, 1996) in coastal waters.

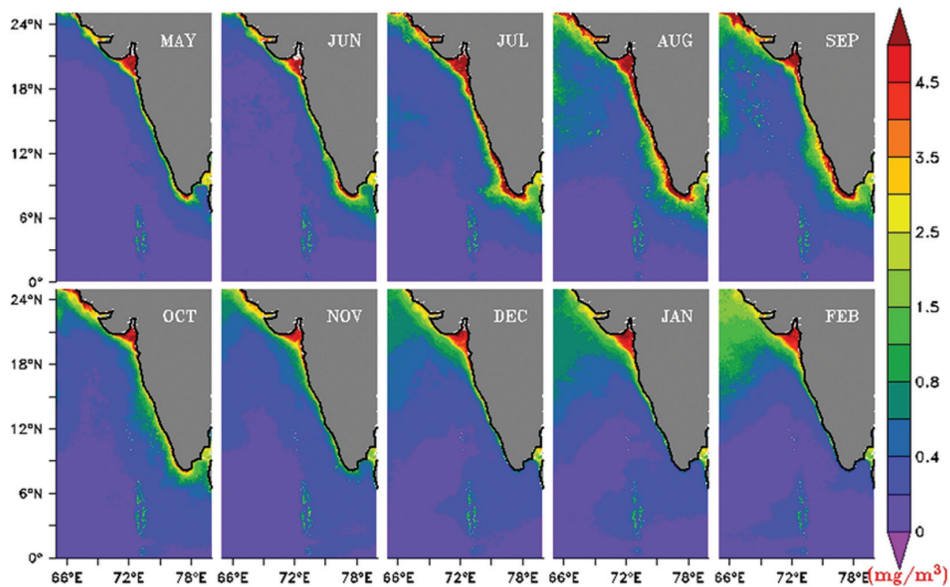


Fig. 8. Climatology of sea-surface chlorophyll for eastern Arabian Sea. Panels correspond to the months as follows: (A) May, (B) June, (C) July, (D) August, (E) September, (F) October, (G) November, (H) December, (I) January and (J) February

The peak (approximately 4.75 mg/m^3 for 9°N latitude) in surface chlorophyll-a values recorded in SEAS waters (Figure 9) spans across all the summer monsoon months (May - September) whereas for NEAS waters, the spike (approximately 7.5 mg/m^3 for 21°N latitude) in surface chlorophyll-a lasts for a shorter duration (June - August). Such an observation indicates that SEAS holds more favorable conditions for phytoplankton for a longer duration than NEAS especially during upwelling months. However, it should also be noted that NEAS waters (21°N latitude) consistently registers a higher surface chlorophyll value with respect to SEAS (9°N latitude) throughout the course of an entire year. This difference in surface chlorophyll-a between NEAS and SEAS waters could be attributed to the crucial role played by winter convective mixing along with nutrient-enrichment of

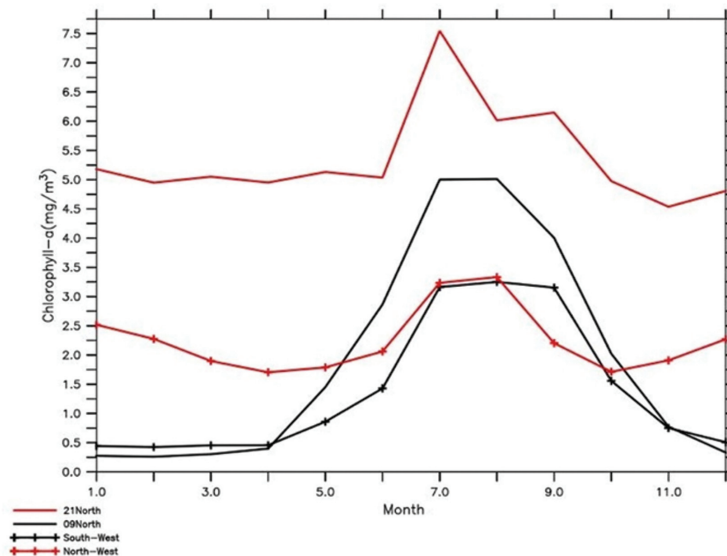


Fig. 9. Seasonality of chlorophyll across multiple latitudes (90N and 210N latitude) in eastern Arabian Sea. . Red and black color denotes stations located in NEAS and SEAS respectively. X-axis labels correspond to months as follows: 1)January, 2)February, 3)March, 4)April, 5)May, 6)June, 7)July, 8)August, 9)September, 10)October, 11)November and 12)December

NEAS surface waters by deposition of iron-rich aerosols associated with dry North East monsoon winds. In the absence of upwelling-favorable winds during winter monsoon, SEAS surface waters remain nutrient-poor and are not capable of maintaining high chlorophyll concentrations (as observed during upwelling months). In NEAS, during non-upwelling months, winter convective mixing and fertilization of surface waters under the influence of iron-rich aerosols collectively sustain higher surface chlorophyll-a values (1.75 - 2.5 mg/m³) when compared with SEAS waters which remain nutrient-poor during the same period. Therefore, NEAS is capable of ensuring the critical nutrient-supply required for phytoplankton to flourish during upwelling (May - October) as well as non-upwelling months (November - February). Here we speculate that the primary production observed though out the year in NEAS waters could potentially act as a strong foundation that could consistently sustain planktivore group which in turn could serve as prey base to support a thriving carnivore community.

3.1.3 Tidal current amplification

The tidal amplitude data was obtained using an online tool used for prediction of tidal amplitudes and currents (Flater, 1998). Apart from upwelling, significant nutrient off-load has also been attributed to tidal currents. The occurrence of viable coral reefs associated with waters characterized by low nutrient content has been attributed to the nutrient off-load associated with tidal currents (Thompson and Golding, 1981). Presence of island chains separating continental shelf from open sea can further accentuate the net transfer of nutrient load to the continental shelf waters through tidal current amplification (Maxwell 1968) owing to the limited tidal wave access. Narrow channels

between the islands further strengthen the tidal currents thereby initiating intense mixing on the continental shelf. Periodic nutrient off-load to the continental shelf region by tidal floods can cause substantial nutrient enrichment of surface waters even in the absence of wind-driven upwelling. However, the nutrient off-load associated with such mechanisms might relatively be less in comparison with that of upwelling, yet sufficient enough in lending a supporting role (in addition to surface fertilization of coastal waters by iron-rich aerosols) to the essential nutrient supply required for the sustenance of primary production in NEAS coastal waters, especially during winter monsoon months.

Moreover, the continental shelf area is wider in NEAS in comparison with SEAS. The tidal amplitudes exhibit a strong variation across 15°N latitude. The maximum values for tidal elevation for the sites located towards North of 15°N latitude (NEAS) namely Kandla, Bhavnagar and Bombay (Figure 7) vary mostly between 4 – 10 m whereas for sites situated to the South of 15°N latitude (SEAS) namely Cochin, Mangalore and Beypore, the maximum values for tidal amplitude vary between 1 - 2 m. The NEAS waters with high tidal amplitudes, wide continental shelf characterized by the presence of islands (especially Gujarat coastline) has higher likelihood of surface water nutrient-enrichment through tidal current amplification in comparison with SEAS waters characterized by low tidal amplitudes and narrow shelf. Here we speculate that such mechanisms that enrich shelf waters can contribute to support primary production in the absence of upwelling-favorable winds (during October - February) especially in NEAS waters.

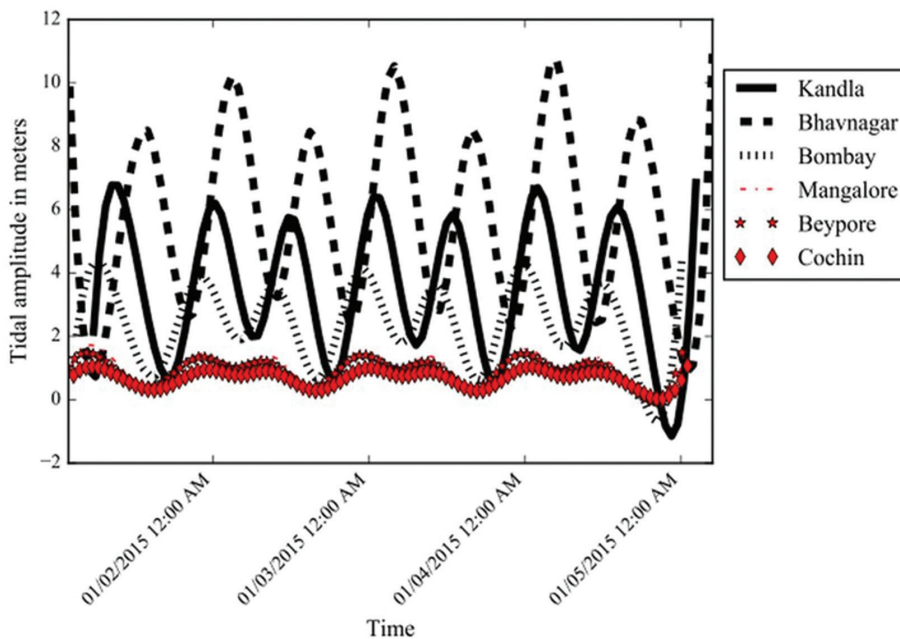


Fig. 7. Variation of tidal amplitude across the eastern Arabian Sea. Tidal stations located to the North and South of 15°N latitude are highlighted using black and red color respectively.

3.2 Optical Classes derived from Remote Sensing Reflectance

The dataset containing eight optical classes for eastern Arabian coastal waters was derived from OC-CCI (Ocean Color Climate Change Initiative) remote sensing reflectance dataset (Version 2) for 1998-2013 period using fuzzy C mean algorithm (Monolisha *et al.*, 2017). A strong seasonality (Figure 10) in the optical classes derived from remote-sensing reflectance was observed for SEAS waters (South of 15°N latitude) whereas no such seasonal signal was detectable from NEAS. This could be attributed to the primary production supported by intense seasonal upwelling during summer monsoon in SEAS waters whereas for NEAS, we observe that the primary production is well supported throughout the year even in the absence of upwelling favorable winds (Figure 8 (F)-(J)).

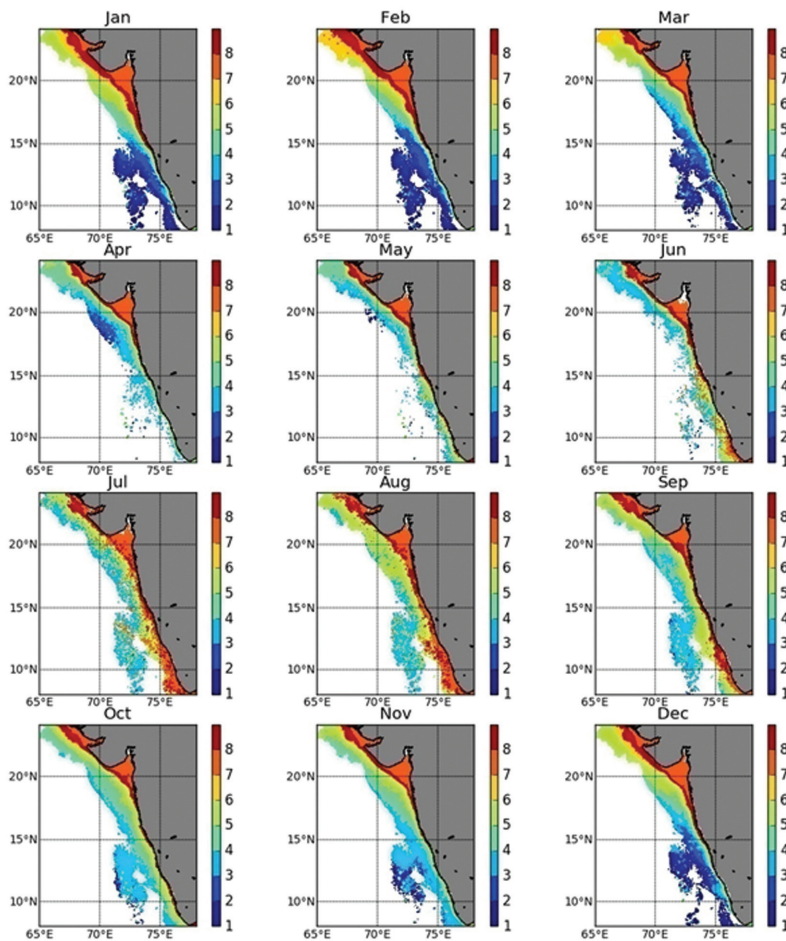


Figure 10. Seasonal variation in optical classes derived from remote sensing reflectance along the entire eastern Arabian Sea. Panels correspond to months as follows: (A)January, (B)February, (C)March, (D)April, (E)May, (F)June, (G)July, (H)August, (I)September, (J)October, (K)November and (L)December

3.3 Spawning behavior and recruitment

The temporal extent of spawning season for key species within each group was compiled from scientific literature. The term breeding has been used interchangeably with spawning although the former involves a chain of events in connection with pre-spawning and spawning phases (Qasim, 1973). Breeding season subsumes the time of peak maturity and spawning period in a population. Likelihood for recruitment of newly produced broods to adult stock is enhanced when spawning overlaps (both spatially and temporally) with favorable (availability of food resources, safety from predators) of newly hatched larvae. The spawning behavior of representative species belonging to the major pelagic planktivore and demersal carnivore groups is highlighted in Table 1. Species representing individual groups were chosen based on their commercial importance. A common thread with respect to spawning behavior that we can note from Table 1 is that spawning period for the pelagic and demersal marine resources overlaps with the summer monsoon months (May - September) which in turn coincides with upwelling along the eastern Arabian Sea. This could be attributed to the fish-larvae favorable conditions (availability of food) that persist in close proximity to the coast throughout the entire Arabian Sea during summer monsoon. Although primary production is a critical factor for successful larval recruitment, it is not a sufficient condition (Bakun *et al.*, 1998). In an effort to increase the likelihood of successful recruitment of larvae to adult stock, the spawning fish population tend to minimize larval mortality (due to food scarcity, predation pressure, anoxic conditions) by selectively breeding in sites or adapting their egg buoyancy in response to environmental fluctuations where larvae-favorable conditions (availability of food, minimum predation pressure and oxygen rich environment) tend to persist (for example adjacent to the coastal surface waters) at least until they transition from the critical larval phase when their survival is most susceptible to availability of food resources in the near vicinity (both spatially and temporally), accessibility to oxygen-rich environment and predation pressure.

Table 1. Species-wise spawning season

Group Name	Species name	Breeding season	Cited in
Oil sardine	<i>Sardinella longiceps</i>	June - September	Dhulkhed, 1964
Mackerel	<i>Rastrelliger kanagurta</i>	June - July	Radhakrishnan, 1962
Anchovies	<i>Encrasicholina devisi</i>	July-September, October/ November - June	Luther, 1979
Perches	<i>Nemipterus japonicus</i>	June - August	Murthy et al., 1992
Croakers	<i>Otolithes ruber</i>	July - October	Devadoss, 1969
Pomfrets	<i>Pampus argenteus</i>	April - June	Gopalan, 1967

3.4 Influence of oceanographic forcing in fish catch seasonality

The monthly climatology for individual marine resource of interest was derived from Mean Standardized Catch for individual States and their seasonality was investigated within the context of coastal upwelling using Local Temperature Anomaly derived from daily sea surface temperature climatology. The prime focus of this analysis revolves around months (highlighted using green color in Figure 11, Figure 12 and Figure 13) that characterize the terminal upwelling phase (August-September) along with early onset of winter monsoon months (October- November) along eastern

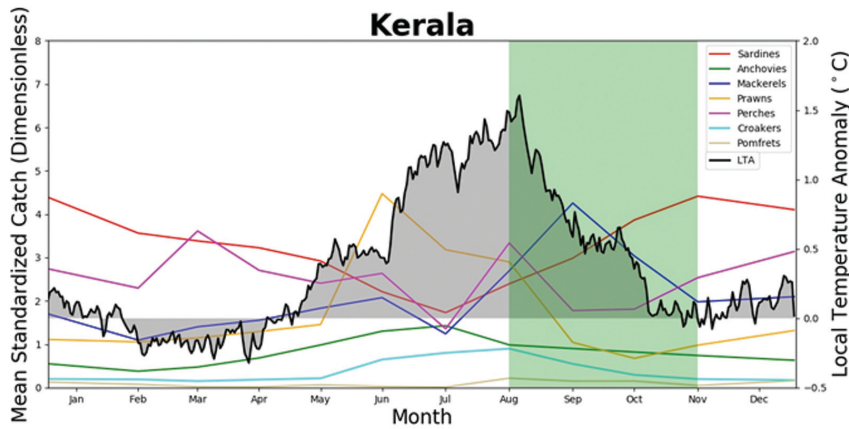


Fig. 11. Monthly Mean Standardized Catch (highlighted by colored solid lines) for the State of Kerala overlaid upon daily Local Temperature Anomaly (coastal upwelling index, highlighted by grey region bordered with solid black line). The region highlighted in green coincide with the terminal phase of upwelling in eastern Arabian Sea along with the onset of winter monsoon season. The Y-axis on left-hand side represents Mean Standardized Catch whereas the one on the right hand side indicate strength of upwelling in degree Celsius. The X-axis correspond to time in months.

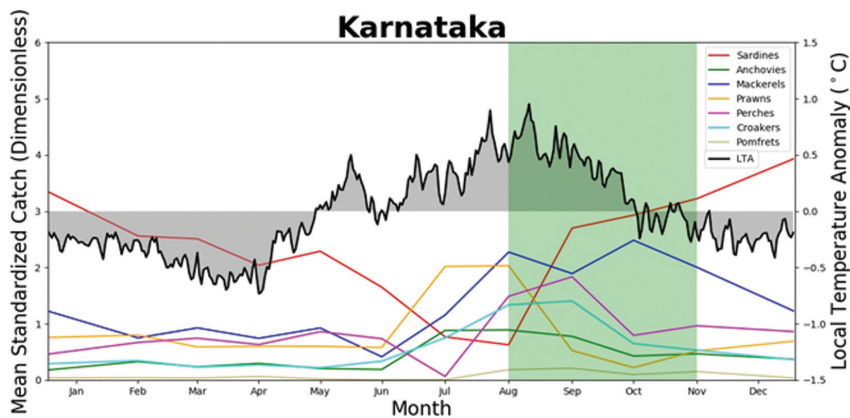


Fig. 12. Monthly Mean Standardized Catch (highlighted by colored solid lines) for the State of Karnataka overlaid upon daily Local Temperature Anomaly (coastal upwelling index, highlighted by grey region bordered with solid black line). The region highlighted in green coincide with the terminal phase of upwelling in eastern Arabian Sea along with the onset of winter monsoon season. The Y-axis on left-hand side represents Mean Standardized Catch whereas the one on the right hand side indicate strength of upwelling in degree Celsius. The X-axis correspond to time in months

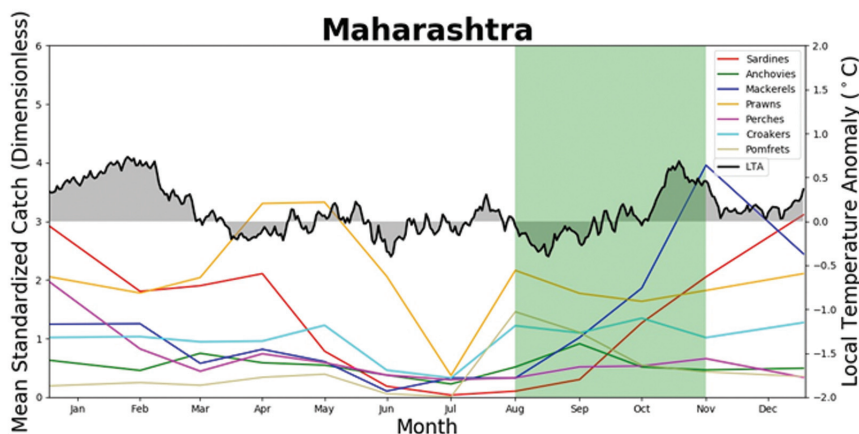


Fig. 13. Monthly Mean Standardized Catch (highlighted by colored solid lines) for the State of Maharashtra overlaid upon daily Local Temperature Anomaly (coastal upwelling index, highlighted by grey region bordered with solid black line). The region highlighted in green coincide with the terminal phase of upwelling in eastern Arabian Sea along with the onset of winter monsoon season. The Y-axis on left-hand side represents Mean Standardized Catch whereas the one on the right hand side indicate strength of upwelling in degree Celsius. The X-axis correspond to time in months.

Arabian Sea since this time frame has the maximum likelihood of entraining anoxic conditions in the entirety of the coastal water column (spanning across pelagic and demersal habitats) along the eastern Arabian Sea (Naqvi *et al.*, 2009). For Kerala and Karnataka, the demersal groups such as prawns, perches and croakers reveal a consistent decreasing trend during August-November period (Figure 11 and Figure 12) whereas pelagic entities (for example sardines) reveal an increasing trend for the same period. It is striking to note that such a strong declining trend was not observed for demersal entities in NEAS waters (Figure 13) whereas an increasing trend (similar to that of Kerala and Karnataka) was observed for pelagic planktivore groups (sardines and mackerels) for the State of Maharashtra. The intrusion of oxygen-deficient subsurface water during upwelling have detrimental impacts in store for demersal carnivores and prawns (Banse, 1959, Naqvi *et al.*, 2009) that inhabit SEAS waters where the likelihood of vertical habitat reduction for such groups due to upwelling is very high with respect to NEAS waters. However, pelagic groups appear to be relatively less affected (when compared with demersal population) in both SEAS and NEAS waters. The upwelling signals being visible at the surface (Figure 13) in NEAS waters only towards October-November appear to suggest delayed overlap of anoxic conditions associated with upwelled waters with demersal habitat beyond 15°N latitude. The early onset of upwelling signals at the surface level in SEAS waters as revealed by Local Temperature Anomaly also appear to suggest that the demersal habitats in SEAS waters remain anoxic for a longer duration (August-October) when compared with NEAS waters. The upwelled waters, in NEAS, reach a depth of 30 m (Shah *et al.*, 2015) close to November when anoxic conditions tend to subside with the reversal of West India Coastal Current (Naqvi *et al.*, 2009).

4 Discussion

The section synthesizes the key findings of the study by attempting to isolate the underlying oceanographic factors responsible for the observed regional difference in annual catch composition along the eastern Arabian Sea across 15°N latitude (Madhuratap *et al.*, 2001).

4.1 Upwelling in SEAS

In SEAS, the month of May marks the arrival of South West monsoon wind which persists until the end of September. Upwelling in eastern Arabian Sea has been attributed to both remotely-forced baroclinic adjustment and along-shore component of wind stress field accentuated during South West monsoon period (Wyrтки, 1973; Shetye *et al.*, 1985; Shetye and Shenoi, 1988; Gopalakrishna *et al.*, 2008; Jayaram *et al.*, 2010). Geostrophic upward tilt of density contours is initiated during April even before wind-driven upwelling sets in (Longhurst, 2010). The anti-cyclonic gyre conceived by the South West monsoon also lends additional support to the shoreward tilting up of isopleths in Arabian Sea (McCreary *et al.*, 1993). Once the equatorward wind stress field intensifies, Ekman pumping becomes a norm along the eastern Arabian Sea during summer monsoon. It should be noted here that wind stress required to initiate upwelling is relatively less with respect to what higher latitudes demand. During pre-upwelling period, the off-shore component of equatorward flow is weak with nutrient-poor surface waters. Although, the mixed layer remains shallow, subsurface waters with low oxygen content initiates its progress to the shelf. With the onset of Ekman upwelling, nutrient content of surface water increases and an environment with extremely low (< 0.5 ml/L) oxygen concentration is established in the shelf waters beneath the thermocline (Longhurst, 2010). Intense upwelling in SEAS could also dislodge nutrients trapped in mud banks (found exclusively in SEAS) associated with coastal waters contributing to further enrichment. Vertical intrusion of oxygen-deficient subsurface waters onto the shelf region is another norm that exists in eastern Arabian Sea during upwelling (Wooster *et al.*, 1967) along with the spread of shoreward tilting up of thermoclines towards higher latitudes (NEAS). Equatorward WICC is also reported to be stronger in SEAS than NEAS (Shankar *et al.*, 2002). Therefore, during summer monsoon nutrient-enrichment of surface waters is more intense in SEAS (compared with NEAS waters) as a suite of forcing factors working in unison to bring sub-pycnocline water to the surface.

4.2 Effect of upwelling upon primary production

Assuming that sea surface height anomaly serves as a proxy for intensity of upwelling/downwelling, we observe that upwelling is stronger and spread across a larger area in SEAS, whereas it is restricted over a smaller area within the NEAS during the summer monsoon period. Similar behavior is observed during winter monsoon period, where downwelling is observed to be less dominant (lower in magnitude and highly localized) for latitudes north of 15°N. The South West monsoon winds play a pivotal role in initiating the Ekman pumping mechanism which allows the cool nutrient rich waters (Figure 5 (C)–(F)) from the depths to reach closer to the surface. Upwelling is the primary factor responsible for enhanced biological production in the SEAS waters. However, it is interesting to observe that the NEAS is capable of sustaining a higher chlorophyll biomass (close to 7 mg m⁻³) even during the winter-monsoon period where the wind system reverses its direction (with respect to the summer monsoon period). The progressively (longitude-wise)

downward tilting isopycnals (Figure 5(C)-(F)) indicate downwelling along the eastern Arabian Sea suggesting that there might be factors (winter convective mixing, surface fertilization of coastal waters by iron-rich aerosols) other than Ekman pumping responsible for sustaining high chlorophyll biomass in NEAS. Although the North East monsoon winds are not conducive to upwelling along the eastern Arabian Sea, higher chlorophyll biomass values in the NEAS can be attributed to the winter convective mixing (with a net heat loss of approximately 30 Wm^{-2} and freshwater loss of approximately 125 mm per month during winter due to evaporative cooling as reported by Madhupratap *et al.*, (1996)) and the influence of iron-rich aerosols brought by the dry winter monsoon winds (Kumar *et al.*, (2010)) from the sub-continental desert region. The iron rich dust aerosols (observed to increase the Aerosol Optical Thickness from 0.19 to 0.24 during September as reported by Kumar *et al.*, (2010)) also tend to fertilize the NEAS waters from the surface thereby enhancing the biological production during winter monsoon period. The tilting up of isopycnals underlines the importance of the strong mixing responsible for entraining nutrients that fuel the seasonal spike in chlorophyll biomass in SEAS.

4.3 Nutrient-enrichment and primary production in NEAS

Weak dry winds (North East directed) dominate over Arabian Sea during winter monsoon (November - February). Downwelling of surface waters near the coast is triggered by the cyclonic circulation (with WICC directed poleward) that persists in the Arabian Sea during this period. Seasonal convective mixing initiated due to winter cooling of NEAS waters was observed to be dominant especially towards North of 18°N latitude (Banse, 1968; Banse, 1984; Kumar and Prasad, 1996). Enrichment of NEAS surface waters due to the influx of iron-rich aerosols transported by North East monsoon winds from inland desert (Kumar *et al.*, 2010) reinforces enrichment of NEAS waters during non-upwelling months. Therefore, NEAS is capable of supporting higher chlorophyll biomass whereas nutrient-poor surface waters in SEAS remains relatively barren during winter monsoon period (Figure 5 (E)-(F)).

Tidal amplitude for latitudes north of 15°N latitude fluctuates in the range of 6 to 10 m whereas for the SEAS it falls within 1 to 2 m. We speculate that the shallow continental shelf, coupled with higher tidal elevation, facilitate the frequent nutrient-enrichment of shelf waters through the periodic nutrient off-load associated with amplified tidal currents (Thompson and Golding, 1981) in NEAS, which in turn offers additional support (apart from winter convective mixing, surface water fertilization due to iron-rich aerosols) to the sustenance of higher chlorophyll biomass (with respect to SEAS during winter monsoon months) even in the absence of favorable external wind forcing. However, for SEAS, with narrow continental shelf and lower tidal elevation, the odds are against such forms of nutrient enrichment and therefore sustenance of primary production can only become a reality with the support of strong external wind-forcing (such as summer monsoon wind system) that could initiate the vertical crawl of nutrient rich subsurface waters through Ekman pumping.

4.4 Reproductive habitat ecology

The likelihood of successful recruitment of juveniles to adult fish stock improves with the increased overlap of algal bloom across time and space with spawning season and breeding grounds respectively, where their metabolic demands can be met (Platt *et al.*, 2003). Although primary

production directly constitutes a critical component for the development and sustenance of coastal pelagic fish population, it is not considered a sufficient condition. The critical processes that work together to address the requirements of juvenile population include enrichment (such as upwelling, mixing), concentration processes (convergence, frontal formation) and processes that support retention (of critical resources such as food) or passive drift towards favorable habitats (Bakun *et al.*, 1998). Enrichment processes serve the metabolic requirements of juvenile populations. Concentration processes ensure that the juveniles have access to food resources in their immediate neighborhood thereby providing improved feeding conditions (Bakun, 1996). Passive larval drift stage is common across multiple marine life-forms. Processes that favor drift (towards larvae-friendly habitats) tend to minimize immense wastage of reproductive resources through massive loss of potential recruits in their early life-stages. Adapting the egg buoyancy in response to environmental fluctuations is another strategy adopted by fish groups to ensure that their eggs remain suspended adjacent to surface waters characterized by availability/accessibility to better food conditions (when compared with deeper waters). Therefore, fish populations tend to strategically spawn in certain locations at particular seasons to minimize early losses (Parrish, 1981).

4.4.1 Role of surface currents in fish recruitment

The summer and winter monsoon current form a subset of the West India Coastal Current (WICC) system characterizing near-surface circulation (limited to uppermost few hundred meters) of seasonally reversing nature (Shetye, 1998). Among many pioneering advances (Potemra *et al.*, 1991; Yu *et al.*, 1991; Shankar *et al.*, 1996; Vinayachandran *et al.*, 1996) aimed at improving the understanding of large-scale seasonal currents in North Indian Ocean, the one that stands out in successfully identifying the driving elements (free and forced long waves set off by the monsoon winds) of WICC is McCreary *et al.*, (1993). The first appearance of southward flowing WICC along West coast was reported for the month of March, followed by its peak prominence (with respect to magnitude) during July and the waning phase concludes by October (Cutler and Swallow, 1984; Shetye and Shenoi, 1988). The equatorward WICC, which is least prominent off the North West coast, slightly gains strength in the middle (closer to 15°N latitude) and evolves into a major current system off South West coast of India (Shetye, 1998). However, the poleward-directed WICC, which is better developed than its equator-ward counterpart (Shetye, 1998), becomes dominant current system from December to March (Shankar *et al.*, 2002) and temporally overlaps with the winter monsoon period (Schott and McCreary, 2001). Although the association of life-history of marine resources (especially during the egg/larval stage) with surface current patterns could be labeled as intricate (Sinclair, 1988), in this section, we attempt to elucidate (qualitatively), the role of surface current in egg/larval drift along with its implications for fisheries recruitment. During the initial stages of the lifecycle, the movement of fish larvae is dictated largely by ocean currents. The sea surface current (WICC), directed towards the equator (Figure 3(B)-(D)) during South West monsoon period is responsible for the advection and accumulation of the pelagic eggs/larvae closer to the waters adjacent to the southern States such as Karnataka and Kerala, which serve as the feeding ground for larvae since SEAS waters register a high chlorophyll biomass value during South West monsoon period. NEAS manages to sustain primary production in its coastal waters during winter-

monsoon months when SEAS waters remain largely unproductive. The equatorward wing of WICC is observed to be prominent in SEAS domain whereas it is hardly perceptible in NEAS (Shankar *et al.*, 2002). Therefore, we conclude that the eggs of pelagic/demersal fish population, occupying NEAS habitats, whose spawning season overlaps with upwelling months undergo very little horizontal drift (due to equatorward WICC) thereby allowing its juveniles to have close proximity to productive feeding grounds having surface waters with relatively rich oxygen concentration when compared with SEAS waters (since sub-surface waters reach a depth of 30 m in NEAS waters as reported by Shah *et al.*, (2015)), which is critical in ensuring successful recruitment of juveniles to adult fish stock. During North East monsoon period, the sea surface currents (of WICC) are directed poleward along the eastern Arabian Sea (Figure 3(H)-(I)). The demersal eggs/larvae suspended closer to surface drift passively with the surface currents and accumulate in the waters closer to northern Maharashtra and Gujarat which in turn act as the feeding ground for fish larvae as NEAS waters are characterized by high chlorophyll biomass during winter monsoon unlike their south eastern counterpart. During summer monsoon months (when pelagic planktivores usually spawn), the surface currents are directed equator-ward which ensures a similar drift of fish eggs/larvae towards habitats with better feeding conditions. Such strategies developed by fish population aid the survival and recruitment of their respective larvae into adult stock.

4.4.2 Role of density in fish recruitment

NEAS waters registers a higher surface density (with respect to SEAS waters) throughout the course of the entire year and this difference in surface density is accentuated especially during winter monsoon period (Figure 6). This could either be attributed to the influx of low-salinity water by pole-ward flowing West India Coastal Current (owing to the close proximity of SEAS waters to the incoming freshwater transport distributed along the eastern Arabian Sea by WICC) or the intense downwelling (Rao *et al.*, 2009) of surface waters in SEAS which in turn replaces the dense waters that had flooded the shelf during upwelling. Salinity has been reported as a key factor determining the buoyancy in marine fish eggs, which in turn dictates their vertical distribution (in water column) and dispersal under the influence of currents (Sundby and Kristiansen, 2015). In the context of fisheries, buoyancy adaptations have been known to exist as a strategy to improve the odds of survival of fish larvae. Proximity of fish eggs/larvae with respect to surface waters ensures low-level threats from predators with better access to food resources (primary production) that thrive in nutrient-rich surface waters (through upwelling/winter-convective mixing/surface fertilization) in presence of sunlight. Salinity has been reported to have a profound effect upon egg buoyancy as well. Even within the same species (*Bairdiellaichistia*) for Sciaenids, eggs fertilized in less dense water were observed to be more buoyant than the ones found in more saline environment (May, 1974). The more buoyant pelagic eggs naturally rise to the surface in the SEAS water with lower surface density whereas the denser demersal eggs remain suspended within the water column adjacent to the surface in saline NEAS waters. Moreover, the spawning season of most of the species coincides with the summer monsoon period (Table 1). Higher accessibility to food resources closer to spawning grounds ensures sustenance and survival during the critical period of larval development and increases the chances for subsequent recruitment to fish-stock.

4.5 Favorable habitat for demersal resources

For eastern Arabian Sea, the visibility of upwelling signals at the surface (during May and September) is limited up to 16°N latitude (Shah *et al.*, 2015). During summer monsoon months, the vertical limit observed for upwelled water in NEAS is 10 m whereas sub-pycnocline waters were able to reach the surface in SEAS territory (Shah *et al.*, 2015). Since weak upwelling signals (at the surface level) persist in NEAS, vertical excursion of oxygen poor sub-pycnocline waters is limited. Therefore, upwelling in NEAS fails to replace completely the oxygen rich surface waters in the shelf region with oxygen deficient subsurface waters. Although anoxic conditions might prevail in NEAS during summer monsoon, such inhospitable conditions are less extreme and lasts for a shorter span of time when compared with SEAS waters. Therefore, NEAS offers column waters with tolerable oxygen levels (compared with SEAS) for the demersal dwellers to survive especially during upwelling months. Hence, the demersal group (prawns, perches and croakers) are able to thrive in the partially oxygenated water column (close to 30 m depth from the sea surface) associated with NEAS waters along with the pelagic entities (sardines, mackerel) especially during terminal phase of upwelling (August to September) or initial phase of winter monsoon (October to November) as highlighted by Figure 13. The inhibition of surface divergence with the cross-shore driven surface mass transport overpowering the Ekman pumping mechanism in NEAS has been documented as well (Muraleedharan and Kumar, 1996, Shah *et al.*, 2015). Since upwelling intensity observed in NEAS is not as strong (with respect to SEAS) at the surface level, the weak off-shore transport associated with the same (coupled with strong cross-shore driven surface mass transport) could contribute in retaining the primary production within its coastal waters. During non-upwelling months (November to February), NEAS waters remain nutrient rich (due to winter convective mixing and nutrient enrichment of surface waters by iron-rich aerosols), thereby providing ideal conditions to sustain primary production (unlike SEAS). Downwelling in NEAS during winter monsoon ensures concentration of primary production within its coastal waters. The poleward directed WICC facilitates the passive drift of juveniles towards productive and oxygen rich habitats. For demersal/pelagic carnivores that undergo recruitment (from juvenile stage) over a long span of time (> 6 months), NEAS waters provide the best spawning grounds, capable of meeting their long-term nutritional demands. Therefore, NEAS waters adhere to all the requirements essential for a habitat to sustain and support the needs of juvenile fish populations during both upwelling and non-upwelling months.

Apart from reporting that carnivores dominate NEAS waters (Madhupratap *et al.*, 2001), the study also observed higher catch contribution of prawns and carnivorous cephalopods beyond 15°N latitude. Epipelagic crustaceans such as *Acetes*, which could potentially be considered as a contender that contributes to the strong prey base in NEAS for the predator community to thrive upon, have been known to contribute heavily to the marine landings reported from Maharashtra and Gujarat. The perpetual presence of chlorophyll biomass allows for the persistence of a prey base that maximizes the likelihood of demersal adult population being well-fed. The spawning grounds for the groups considered for present study overlap with the coastal waters that satisfy the pre-requisites (availability of food, oxygenated water column) which can increase the odds of survival and sustenance of juvenile populations (King, 2013). Therefore, NEAS waters are capable of meeting

the requirements of pelagic/demersal planktivore/carnivore groups (both adults and juveniles) during upwelling and non-upwelling months.

Since upwelling brings subsurface waters from the Arabian Sea oxygen minimum zone, the demersal dwellers of SEAS (especially during August and September when upwelled waters reach the surface) are known either to suffer from mass mortality against the shore or to vacate the mid-shelf depths where vertical column gets progressively filled with oxygen-deficient subsurface waters owing to strong upwelling (Banse, 1959). It has also been observed that demersal fishes (*Cynoglossus spp.*) tend to migrate away from the shores at the onset of summer monsoon only to return once its intensity has subsided (George, 1958). The onset of South West monsoon heralded the departure of juveniles of prawn (*Parapeneopsis styliifera*) towards the end of May (Menon, 1953). They were soon accompanied by older individuals (only to return in October) of the population such that a decrease in their landing off the Malabar coast was reported from July onwards. In SEAS, the sub-pycnocline oxygen deficient waters were observed to replace the oxygen-rich surface waters of the shelf whereas the upwelled waters were only able to climb up to 30m depth in NEAS waters during summer monsoon months (Shah *et al.*, 2015). The study also reported upwelling signals of greater amplitude at deeper ocean layers when compared with those observed at the surface. The propagation velocity (towards higher latitudes) for upwelling signals also revealed a similar difference between the surface and subsurface waters. Towards the North of 15°N, tilting up of isotherms was observed from August which persisted till November (Shah *et al.*, 2015). Owing to more intense upwelling signals that persist in SEAS for a longer span of time (when compared with NEAS), the oxygen-rich surface waters are slowly replaced by low-oxygen containing subsurface waters along the shelf. Especially towards the terminal phase of summer monsoon, the demersal dwellers in SEAS tend to experience an abrupt decline in oxygen levels associated with their habitats. Although some species might be able to thrive in such hostile environments near the coastal waters, most of the demersal dwellers would tend to migrate towards habitats (either open seas or higher latitudes) that favor their survival. This is further supported by the sharp decline in mean standardized catch especially for demersal groups (prawns, perches and croakers) in SEAS waters (Figure 11 and Figure 12) from August to November when fishing ban remains lifted within the Indian Exclusive Economic Zone. Similar depletion of exploitable stocks of demersal fishes and prawns (manifested through decreasing trend in landing data) within the shelf waters along the West coast of India and Pakistan was reported by Banse, (1968). The situation is observed to improve once subsurface waters with low oxygen concentration retreat from the shelf.

4.6 Favorable habitat for pelagic resources

Upwelling of nutrient (inorganic) rich subsurface waters can fuel diatom-dominated algal blooms (Subrahmanyam, 1959; Subrahmanyam and Sarma, 1965) along with the support offered by nutrients released from sediments that become re-suspended in the water column due to strong onshore swell during summer monsoon (Banse, 1959). Therefore, such upwelling events that result in diatom-based algal blooms could provide ideal conditions for pelagic planktivores to thrive. The pelagic planktivores (sardines and mackerels) registered a higher catch contribution with respect to demersal groups in both SEAS and NEAS from August to November (Figure 11, Figure 12 and Figure 13) implying that their habitat had significantly smaller spatial and temporal overlap with the anoxic

conditions when compared with demersal habitats. However, demersal dwellers tend to live in water column that is not as oxygen rich when compared with pelagic habitats. Hence, the sustained presence of oxygen-deficient water in the shelf (during upwelling in SEAS) forces the demersal dwellers to migrate towards hospitable waters. When such conditions overlap with spawning period of a marine resource, it may trigger large-scale mortality of eggs, resulting in acute wastage of reproductive resources (North and Houde, 2004) immediately followed by recruitment failure that gets reflected in landing data. The detrimental effects of low oxygen (< 0.2 ml/L) has been already observed for the coastal waters of Goa for croakers where the prompt establishment of seasonal sub-surface oxygen deficient environment (Naqvi *et al.*, 2009) post their spawning period initiated the large-scale egg/larval mortality (North and Houde, 2004) and motivated the adults to find more hospitable waters (as indicated by the decrease in their landing data especially in the year 2001) thereby indicating that such a phenomenon is prominent in the SEAS region approximately up to 15°N latitude (Hegde *et al.*, 2016).

During non-upwelling months, SEAS waters remain nutrient-poor and incapable of sustaining primary production at a scale that could support the development of juvenile fish populations. Even when SEAS waters become nutrient-rich and sustain primary production during summer monsoon months, the strong vertical mixing/off-shore surface mass transport could possibly act contrary to the concentration/retention processes. The off-shore surface mass transport is observed to be more dominant for SEAS (Shah *et al.*, 2015) when compared with NEAS especially during summer monsoon months. The strong off-shore transport associated with wind-driven upwelling also provides the possibility to advect surface chlorophyll to the open ocean (Banse, 1959). Off-shore transport associated with wind-driven upwelling is limited to SEAS *i.e.* 8°N - 15°N latitude belt (Smitha *et al.*, 2008; Muraleedharan and Kumar 1996; Shah *et al.*, 2015). Therefore, the likelihood of such advection of biota due to off-shore surface mass transport is higher in SEAS (with respect NEAS surface waters). The strong vertical mixing associated with upwelling in SEAS could result in the potential removal of chlorophyll biomass from surface waters to deeper layers with restricted access to sunlight. In the absence of retention/concentration processes associated with SEAS upwelling, fish-larvae are left with a short span of time (< 4 months) to undergo its recruitment to adult fish-stock. Pelagic planktivores (for example Sardines) which can do so, thrive in such waters (George, *et al.*, 2012). The dominance of zero-year class in the sardine landing data (Balan, 1984; Raja, 1969; Longhurst and Wooster, 1990) is another evidence that corroborates the former statement.

SEAS is well capable of sustaining the pelagic groups (both planktivore and carnivore) during summer monsoon months. However, demersal dwellers (juveniles/adults) appear to thrive in NEAS waters since habitats located to the North of 15°N latitude has a higher likelihood of entraining surface/column waters with bearable oxygen levels (> 0.5 ml/L) apart from being productive enough to sustain the metabolic demands of juveniles and adults. The establishment of conducive environment for demersal carnivore group (juveniles/adults) in NEAS waters could contribute to the skewness of catch composition towards carnivore spectrum towards North of 15°N latitude.

5 Concluding remarks

We believe that oceanographic forcing (summarized in Table 2) has a strong bearing on seasonality in catch composition. In this study, we have attempted to explore the putative link by

identifying the key characteristics of coastal waters of Arabian Sea that render them suitable to meet the demands of fish population (both juveniles and adults). Although skewness in catch composition (towards carnivore spectrum) across 15°N latitude was reported earlier (Madhupratap *et al.*, 2001), the driving factors responsible for such unique catch composition have not been investigated hitherto. The study concludes that anoxic conditions associated with intense seasonal upwelling in SEAS waters leads to the reduction in the vertical extent of demersal carnivore habitats. NEAS waters cater to the nutritional requirements of juvenile demersal carnivore population as it supports primary production both during summer and winter monsoon months (Madhupratap *et al.*, 1996 ; Kumar *et al.*, 2010). The perpetual presence of chlorophyll biomass allows for the persistence of a prey base that maximizes the likelihood of demersal adult population being well-fed. The poleward directed West India Coastal Current facilitates the passive drift of juveniles towards productive and oxygen rich habitats in NEAS waters. For demersal/pelagic carnivores that undergo recruitment over a long span of time (> 6 months), NEAS waters provide the best spawning ground capable of meeting their long-term nutritional demands. Pelagic planktivores thrive in SEAS, where seasonal upwelling supported primary production remains the norm, owing to their relatively short recruitment span (< 4 months). Unlike SEAS, NEAS waters are found to provide suitable environment geared towards the successful larval recruitment, sustenance and survival of the demersal carnivore group (King, 2013). This could act as a forcing function in driving the annual catch composition of landing data registered in NEAS waters toward carnivore spectrum.

Table 2. Oceanographic forcing and biological field characterizing North East Arabian Sea (NEAS) and (South East Arabian Sea) SEAS

Oceanographic forcing/ Biological field	NEAS	SEAS	Remarks
Surface density	Higher	Lower	Allows the eggs of pelagic and demersal fish to remain suspended closer to surface
Surface Currents	Poleward during Winter monsoon	Equator-ward during summer monsoon	Causes drift /aggregation of fish eggs/larvae nearer to habitats with better feeding conditions
Upwelling intensity (based on Sea surface height anomaly, Isopycnals)	Low and highly localized	High and more widespread	Upwelling based biological production dominates SEAS during summer monsoon. Anoxic conditions prevail in the SEAS water column during upwelling months whereas NEAS entertains oxygen-rich water column at least up to a depth of 30 m from the surface.
Surface wind	North-eastward aerosol laden dry winds during winter monsoon	South-westward moisture laden wind during summer monsoon	Contributes to primary production in NEAS/ SEAS during winter/summer monsoon months
Likelihood for Tidal current amplification	High	Low	Contributes to nutrient enrichment of shelf waters in NEAS.
Continental shelf	Wide	Narrow	Improves the likelihood for nutrient-enrichment of shelf waters through tidal forcing

Off-shore surface mass transport	Weak during summer monsoon	Strong during summer monsoon	Serves as a concentration process by containing the primary production within coastal waters
Chlorophyll biomass	Sustained primary production throughout the year	High primary production observed during summer monsoon	Breeding season of fish groups overlaps with summer monsoon when eastern Arabian Sea surface water is productive enough to meet the demands of juveniles

Regional differences in abundance of pelagic carnivores can also contribute to the bias in catch composition across 15°N latitude. However, since the vertical extent of their habitats share very little overlap with the anoxic conditions associated with upwelling, such conditions are assumed to have very little impact upon their landing. Hence, such groups have not been considered for the current study. Moreover, the landing data could contain marine resource caught from open seas. Although the study used landing data standardized across multiple fishing gears in an attempt to remove the biases in data introduced due to the differences in effort/fishing gears employed, market demand (which is not taken into account in the current study) could also be another key player that sways the catch composition in favor of a given marine resource of preference at a given point in time and space. A strong decrease in landings can also occur due to overexploitation of marine resources. Such drawbacks need to be carefully considered and the bias they introduce in the landing data needs to be addressed by future endeavors.

Within the exclusive economic zone (up to 200 nautical miles from coast), maximum fishing is undertaken. The territorial waters (up to 12 nautical miles from the coast) come under the jurisdiction of the respective maritime States. As per the State Marine Fisheries Regulation Act formulated based on the guidelines recommended by Central Ministry, trawling remains banned from June 14th (mid-night) to July 31st during South West monsoon period, which coincides with the breeding season for commercially important species. However, the breeding season for certain fish populations occur during winter monsoon, when the season remains open for mechanized fishing. The study suggests that trawling ban should also be enforced during winter monsoon, which might benefit carnivore species as well as the fishing community in the long term. However, the breeding behavior and distribution pattern of commercially important species are not uniform in general. There is a need for ecosystem based management where regulations associated with marine protected areas (where fishing is prohibited), and seasons during which trawling ban is enforced locally, ought to be formulated based on indicators that reflect the health of the ecosystem.

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