

## RESEARCH ARTICLE

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### Key Points:

- New production supports ~80% of the primary production and controls ~70% of zooplankton biomass in the Arabian Sea annually
- The regenerated production supports ~50% of primary production of small phytoplankton and ~20% growth of small zooplankton
- The diatom bloom is colimited by nitrate and silicate at the surface, dominated by silicate limitation in the subsurface in Arabian Sea

### Supporting Information:

- Supporting Information S1

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# Understanding the Role of Nutrient Limitation on Plankton Biomass Over Arabian Sea Via 1-D Coupled Biogeochemical Model and Bio-Argo Observations

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**Abstract** Arabian Sea (AS) is known to have seasonal phytoplankton blooms during winter and summer driven by dynamically distinct physical forcing mechanisms and associated nutrient dynamics. A 1-D coupled physical-biogeochemical model based on North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO) with nitrogen and silicon cycles is adapted for the AS environment. The model is implemented to investigate the role of nitrogen (nitrate + ammonium) versus silicate limitation on plankton biomass. The seasonal cycle of plankton biomass is well simulated by the model along bio-Argo (during a period from 2013 to 2016) and ship cruise tracks (for the single year 2009). Further, three sensitivity simulations are conducted by suppressing (1) nitrate availability (representing new production), (2) ammonium availability (representing regenerated production), and (3) silicate availability (for diatom production). The new production represents 80% of the total primary production in the AS and implicitly controls 70% of total zooplankton production annually. The regenerated production augments small phytoplankton (by ~50%; e.g., flagellates) and small zooplankton (by ~20%; e.g., ciliates) growth with negligible effects on large phytoplankton (e.g., diatom) and predatory zooplankton (e.g., copepods). The diatom production remains within the observed range due to silicate limitation which is fundamental in the model for realistic simulation of chlorophyll. Silicate is the primary limiting nutrient in diatom bloom in the subsurface chlorophyll maxima with maximum limitation occurring during the winter season, due to the deeper silicicline as compared to shallower nitricline. At the surface, both nitrogen and silicate co-limit the total production; however, nitrogen is a stronger limiter than silicate from March to June. The study highlights the relative role of silicate versus total nitrogen (nitrate + ammonium) in limiting primary production in the AS.

**Plain Language Summary** An intermediate complexity ecosystem model for ocean known as NEMURO is implemented for the Arabian Sea coupled with a 1-D mixed layer model. The NEMURO model has 13 components of the ecosystem such as two functional groups of phytoplankton, three groups of zooplankton, dissolved and particulate organic matter, and sinking particle fluxes. The model predicts the plankton biomass evolution in the ocean by utilizing the light and nutrients for photosynthetic biomass production, grazing of phytoplankton by zooplankton, the cycling of nutrients via egestion, excretion, mortality, and remineralization. The NEMURO model utilizes silicate as a limiting nutrient for diatom production. Using this model, we have examined the potential role of silicate as a key limiting nutrient in the Arabian Sea productivity. We found that in the surface, both nitrate and silicate are equally limiting biomass production; however, nitrate appears to be a potential limiting nutrient than silicate from March to June. The study highlights the role of silicate versus total nitrogen in establishing the biophysical interactions between lower to upper trophic plankton biomass in the Arabian Sea.

## 1. Introduction

Arabian Sea (AS) is a semienclosed oceanic basin in the north Indian Ocean (IO) and is characterized by two distinct phytoplankton blooms. An intense bloom occurs during the summer monsoon season (i.e., June to September, JJAS) along the continental margins of Somalia and Arabia (Bauer et al., 1991; Brock et al., 1991)

with chlorophyll (Chl-a) filaments extends offshore (Latasa & Bidigare, 1998) and southern tip of west coast of India (Banse, 1987; Bhattathiri et al., 1996; Brock et al., 1991; Smith et al., 1998; Smith & Codispoti, 1980; Wiebinga et al., 1997). Further, a secondary bloom occurs during the northeast monsoon season (i.e., December to January, DJF) in the north and the central AS (Madhupratap et al., 1996; Wiggert et al., 2000, 2002). During the intermonsoon seasons (i.e., fall season from October to November; ON; and spring season from March to May; MAM) stratification induces oligotrophic conditions in the AS resulting a nutrient-depleted surface water, low biological production, and development of subsurface chlorophyll maximum (SCM; Caron & Dennett, 1999; Lévy et al., 2007; Marra et al., 1998; Prasanna Kumar et al., 2000). The contribution of mixed layer dynamics to the timing, magnitude, and persistence of blooms in both the monsoon periods have been well studied in the past (Wiggert et al., 2002, 2005).

In addition to the physical controls on AS productivity (such as upwelling, mixing, eddy-induced transport, etc.), the availability of macro and micronutrients also modulate the seasonality of primary production (Marra & Barber, 2005). Several studies have pointed out the importance of iron limitation in phytoplankton productivity in AS (Moffett et al., 2015; Naqvi et al., 2010; Schoffman et al., 2016). The low iron to nitrogen (Fe/N) ratio in surface waters in the AS during summer monsoon season has a potential to limit the phytoplankton production (Behrenfeld et al., 2009; Koné et al., 2009; Liao et al., 2016; Naqvi et al., 2010; Shigemitsu et al., 2012; Smith, 2001; Wiggert et al., 2006; Wiggert & Murtugudde, 2007).

Several other studies have argued that silicate limitation plays a significant role in phytoplankton (for e.g., diatom) productivity in AS (Burckle, 1989; Koné et al., 2009; Paasche, 1973; Piketh et al., 2000; Wiggert et al., 2006). On the other hand, studies have also reported that nitrogen (nitrate + ammonium) remains a key limiting nutrient north of 10°S in AS especially during the winter bloom (Koné et al., 2009). The modeling study of Wiggert et al. (2006) showed that during intermonsoon seasons strong nitrogen limitation exists at the surface to the north of the equator in AS. Although the interplay between iron, silicon, and nitrogen cycles in phytoplankton productivity of AS has been studied, a complete understanding is still lacking (Piketh et al., 2000; Wiggert et al., 2006).

The upper-ocean silicate concentration in AS is lower compared to the other regions of the global ocean, with the highest concentration observed during the summer monsoon season along with the upwelling centers off Somalia and Oman. A low concentration of silicate throughout the rest of AS during all other seasons are also reported (Wyrski, 1971). The absence of diatom frustules in the surface sediments of the eastern AS points to the nonavailability of silicate in the surface waters there (Burckle, 1989; Young & Kindle, 1994). Further, silicate may be a key limiting nutrient in the northern AS, especially during the winter monsoon season which is inferred from the insignificant contribution of silicate by freshwater runoff (Balachandran et al., 2008; Naqvi et al., 2002). We lack studies regarding the degree to which silicate can act as a limiting nutrient for the basin despite the proven importance of silicate in limiting the growth of diatom groups in the AS by laboratory studies (Paasche, 1973).

However, by analyzing the vertical profiles of nitrate and silicate from World Ocean Atlas (WOA), it is found that at the surface ocean (depth < 60 m), nitrate is almost depleted, and silicate concentration is higher than nitrate, whereas at depths, the situation reverses (c.f. Figure S1). On the basis of this, one might expect nitrogen rather than silicon to be the proximate limiting nutrient and mixing from below would be expected to provide excess nitrogen over silicon. However, nitrate may be getting converted rapidly into ammonium or dissolved nutrients (for which we have far fewer measurements), and so the hydrographic measurements alone may lead us astray. The second point is that the impact of nutrient limitation on large and small phytoplankton biomass is not obvious from the nutrient observations alone. Thus, it makes sense to use a model to investigate this issue with explicit nitrogen and silicon cycles embedded in it to simulate large and small phytoplankton.

In this study, we have three basic aims. (a) We adopt the North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO) model to the environment of AS, (b) we check the role of new and regenerated production in the plankton biomass in AS, and (c) using this model, we examine the role of nitrogen (nitrate + ammonium) and silicate as limiting nutrients for the growth of plankton biomass in the AS. NEMURO was developed for understanding and quantifying the relationship between climate change and ecosystem dynamics by the North Pacific Marine Science Organization (PICES) Model task team (Kishi et al., 2001). The model is used widely for the North Pacific Ecosystem. In this study, we are

implementing an extended version of NEMURO (Yamanaka et al., 2004) in AS. Here, NEMURO is coupled with a turbulence closure 1-D mixed layer model (Ikeda, 1986; Mellor & Yamada, 1982) that explicitly represents the cycling of nitrogen and silicate for calculating primary production.

The rest of the paper is structured as follows. Section 2 describes the model details and methodology. Results are presented in section 3 and Discussions in section 4 followed by Summary and Conclusions in section 5.

## 2. Model, Data, and Methodology

### 2.1. Physical Model

For the physical parameterization of vertical mixing, NEMURO is coupled with a vertical 1-D mixed layer model which has a second-order turbulence closure scheme as in Ikeda (1986), Mellor and Yamada (1982), Valsala et al. (2018), and Singh et al. (2019). The model has 51 vertical layers spanning a domain from the surface to 250 m by a constant resolution of 5 m.

Mellor and Yamada (1982), is a Level 2 second-order closure model based upon the assumption that the local viscous dissipation balances the shear and buoyancy production. The time-dependent momentum, temperature, and salinity equations in the rotating system are given as

$$\frac{\partial U}{\partial t} - fV = \frac{\partial}{\partial z} \left( l q s_m \frac{\partial u}{\partial z} \right) \quad (1a)$$

$$\frac{\partial V}{\partial t} + fU = \frac{\partial}{\partial z} \left( l q s_m \frac{\partial v}{\partial z} \right) \quad (1b)$$

$$\frac{\partial T}{\partial t} = \frac{\partial}{\partial z} \left( l q s_h \frac{\partial T}{\partial z} \right) \quad (1c)$$

$$\frac{\partial S}{\partial t} = \frac{\partial}{\partial z} \left( l q s_h \frac{\partial S}{\partial z} \right) \quad (1d)$$

Where,  $U$  and  $V$  are horizontal velocity components.  $T$  and  $S$  are the mean temperature and salinity, respectively.  $Z$  represents a vertical positive upward coordinate.  $t$  is the time.  $f$  is the Coriolis parameter assumed to be a constant in this study.  $q$  is a parameter related to turbulent kinetic energy (square of  $q$  is twice the turbulent kinetic energy),  $l$  is the mixing length.  $s_h$  and  $s_m$  are stability factors. Details and calculation of all these parameters are taken from Valsala et al. (2018). The three-band parameterization of surface irradiance in the physical model is done according to Morel and Antoine (1994).

### 2.2. Biological Model

The ecosystem model used in this study is based on NEMURO with nitrogen-silicon cycles adapted from Yamanaka et al. (2004) and tuned for the environment of AS. The 13 state variables of NEMURO are as follows. Small phytoplankton (PS; phytoplankton other than diatoms, e.g., flagellates, growth is only limited by nitrogen components) and large phytoplankton (PL; represents diatoms which can make siliceous shells, so their growth can be limited by both nitrogen components and silicate). We neglected other species that use silicate (sponges and radiolarians) in this study because they play a minor role in the silica cycle of the contemporary ocean (Tréguer et al., 1995). Small zooplankton (ZS; e.g., zooflagellates, ciliates, seasonally migrating species) and large zooplankton (ZL; copepods with seasonal vertical migration Aita et al. (2003); ascend in spring to shallower depths and grow there by grazing other plankton, returning to deep water during fall). In the present study, vertical migration is not explicitly considered in our simulations. Predatory zooplankton (ZP; which feed on other plankton) can graze on PL, predate on ZS and ZL, and serve as the basic link between autotrophs and other higher trophic level organisms (e.g., fishes).

The model includes three nutrients, nitrate ( $\text{NO}_3$ ), silicate ( $\text{Si}(\text{OH})_4$ ), and ammonium ( $\text{NH}_4$ ); three types of settling particles, that is, particulate organic matter (POM), opal, and calcium carbonate ( $\text{Ca}(\text{CO}_3)$ ); and a single category of dissolved organic matter (DOM). Both carbon and calcium are abundant in the ocean; therefore, these macronutrients will not limit primary production whereas nitrogen and silicate affect the ecosystem dynamics through nutrient limitation. The present setup of the model does not have an explicit

oxygen cycle and denitrification process associated with it. However, there are literatures which show that the oxycline in the AS can be shallow and varies from 60 to 120 m (Prakash et al., 2012, 2013) whereas observations of nitrite show prominent peaks representing anaerobic respiration and denitrification between 200 and 500 m depths in the AS (Gaye et al., 2013). The literature also says that there are several studies (ecosystem modeling) in the AS which do not have dissolved oxygen cycle and denitrification in it as a limitation of the model (Hood et al., 2003; Koné et al., 2009; McCreary et al., 1996; Swathi et al., 2000, 2010).

Most of the model parameters are based on default values as in Fuji et al. (2002) and Yamanaka et al. (2004) with modification to few parameters in order to calibrate NEMURO to the AS environment (see the bold typeface in Table S1 for details). The model description and equations are in Yamanaka et al. (2004).

### 2.2.1. Equations for Phytoplankton

Both the phytoplankton equations are written in terms of nitrogen (nitrate + ammonium, is the currency of the model). The equations for phytoplankton photosynthesis are given below.

$$PS_{Photosynthesis} = V_{maxS} e^{(k_s T)} \frac{I}{I_{optS}} e^{\left(1 - \frac{I}{I_{optS}}\right)} \left\{ \frac{[NO_3]}{[NO_3] + K_{NO_3S}} e^{(-\psi_s [NH_4])} + \frac{[NH_4]}{[NH_4] + K_{NH_4S}} \right\} [PS] \quad (2a)$$

$$PL_{Photosynthesis} = V_{maxL} e^{(k_L T)} \frac{I}{I_{optL}} e^{\left(1 - \frac{I}{I_{optL}}\right)} \min \left\{ \frac{[NO_3]}{[NO_3] + K_{NO_3L}} e^{(-\psi_L [NH_4])} + \frac{[NH_4]}{[NH_4] + K_{NH_4L}}, \frac{[Si(OH)_4]}{[Si(OH)_4] + K_{SiL}} \right\} [PL] \quad (2b)$$

$$R_{newS} = \frac{\frac{[NO_3]}{[NO_3] + K_{NO_3S}} e^{(-\psi_s [NH_4])}}{\frac{[NO_3]}{[NO_3] + K_{NO_3S}} e^{(-\psi_s [NH_4])} + \frac{[NH_4]}{[NH_4] + K_{NH_4S}}} \quad (2c)$$

$$R_{newL} = \frac{\frac{[NO_3]}{[NO_3] + K_{NO_3L}} e^{(-\psi_L [NH_4])}}{\frac{[NO_3]}{[NO_3] + K_{NO_3L}} e^{(-\psi_L [NH_4])} + \frac{[NH_4]}{[NH_4] + K_{NH_4L}}} \quad (2d)$$

The growth rates are the results of three limitation terms. First is a temperature-dependent term following Eppley (1972). The second describes light limitation, with inhibition both at low and high light level. The third term in each equation describes nutrient limitation. Ammonium in the surface sunlit zone is preferred by both the phytoplankton over nitrate and can suppress the utilization of nitrate for photosynthesis. This is represented in the model by an additive function weighted toward ammonium (equations 2a and 2b) as given by Wroblewski (1977). For diatoms (PL), the nutrient limitation is the minimum of this function and a Michaelis–Menten limitation for silicate. The *f*-ratio associated with this formulation is then given in equations 2c (for PS) and 2d (for PL). The full equation for phytoplankton evolution is then

$$\begin{aligned} \frac{\partial [PS]}{\partial t} = & (PS_{Photosynthesis}) - (PS_{Respiration}) - (PS_{Extracellular\ Excretion}) \\ & - (PS_{Mortality}) - (PS_{Grazing\ by\ ZS}) - (PS_{Grazing\ by\ ZL}) \\ & + Adv(PS) + Diff(PS) \end{aligned} \quad (3a)$$

$$\begin{aligned} \frac{\partial [PL]}{\partial t} = & (PL_{Photosynthesis}) - (PL_{Respiration}) - (PL_{Extracellular\ Excretion}) \\ & - (PL_{Mortality}) - (PL_{Grazing\ by\ ZL}) - (PL_{Grazing\ by\ ZP}) \\ & + Adv(PL) + Diff(PL) \end{aligned} \quad (3b)$$

The first term in equations 3a and 3b represents photosynthesis by PS and PL, all other sink terms in the equations 3a and 3b removing a fraction of phytoplankton population in accordance with respiration, extracellular excretion, mortality, and grazing by zooplankton.

### 2.2.2. Equations for Zooplankton

$$\frac{\partial[ZS]}{\partial t} = (PS_{\text{Grazing by ZS}}) - (ZS_{\text{Excretion}}) - (ZS_{\text{Egestion}}) - (ZS_{\text{Mortality}}) - (ZS_{\text{Predation by ZL}}) - (ZS_{\text{Predation by ZP}}) + Adv(ZS) + Diff(ZS) \quad (4a)$$

$$\frac{\partial[ZL]}{\partial t} = (PS_{\text{Grazing by ZL}}) + (PL_{\text{Grazing by ZL}}) + (ZS_{\text{Predating by ZL}}) - (ZL_{\text{Excretion}}) - (ZL_{\text{Egestion}}) - (ZL_{\text{Mortality}}) - (ZL_{\text{Predation by ZP}}) + (Ontogenic Migration) + Adv(ZL) + Diff(ZL) \quad (4b)$$

$$\frac{\partial[ZP]}{\partial t} = (PL_{\text{Grazing by ZP}}) + (ZS_{\text{Predating by ZP}}) + (ZL_{\text{Predating by ZP}}) - (ZP_{\text{Excretion}}) - (ZP_{\text{Egestion}}) - (ZP_{\text{Mortality}}) + Adv(ZP) + Diff(ZP) \quad (4c)$$

The source terms for zooplankton are grazing on phytoplankton and predation on other zooplankton. Whereas the sink terms in equations 4a–4c are excretion, egestion, and mortality. The ontogenetic migration of ZL is not included in this study.

### 2.2.3. Equations for Nutrients

$$\begin{aligned} \frac{\partial[NO_3]}{\partial t} = & (Nitrification) - [(PS_{\text{Photosynthesis}}) - (PS_{\text{Respiration}})] \times R_{\text{newS}} \\ & - [(PL_{\text{Photosynthesis}}) - (PL_{\text{Respiration}})] \times R_{\text{newL}} \\ & + Adv(NO_3) + Diff(NO_3) \end{aligned} \quad (5a)$$

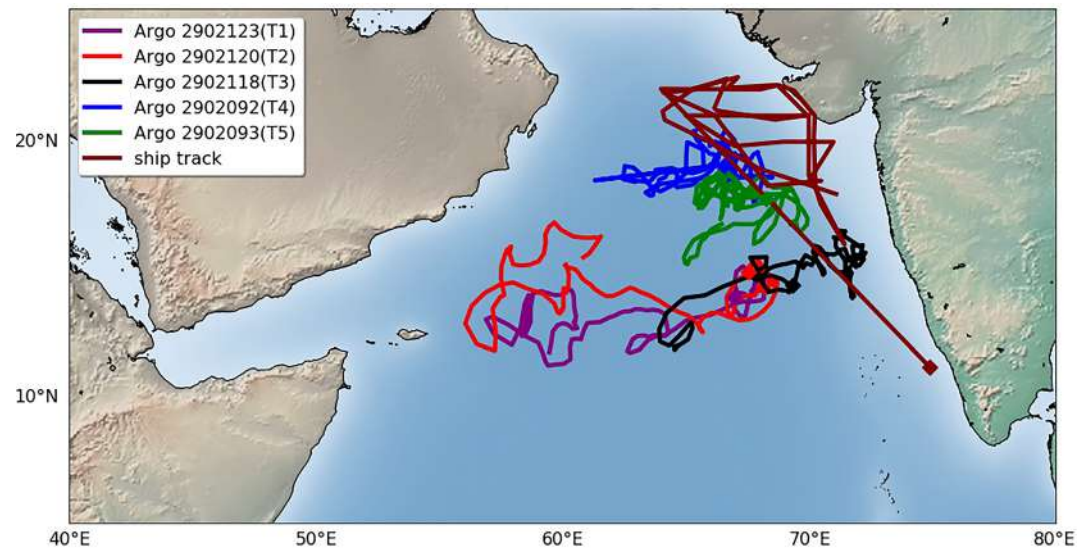
$$\begin{aligned} \frac{\partial[NH_4]}{\partial t} = & (ZS_{\text{Excretion}}) + (ZL_{\text{Excretion}}) + (ZP_{\text{Excretion}}) \\ & + (DOM_{\text{Remineralization}}) + (POM_{\text{Remineralization}}) - (Nitrification) \\ & - [(PS_{\text{Photosynthesis}}) - (PS_{\text{Respiration}})] \times (1 - R_{\text{newS}}) \\ & - [(PL_{\text{Photo}}) - (PL_{\text{Resp}})] \times (1 - R_{\text{newL}}) \\ & + Adv(NH_4) + Diff(NH_4) \end{aligned} \quad (5b)$$

$$\begin{aligned} \frac{\partial[Si(OH)_4]}{\partial t} = & (Opal_{\text{Decomposition}}) - (SiPL_{\text{ShellFormation}}) \\ & + Adv(Si(OH)_4) + Diff(Si(OH)_4) \end{aligned} \quad (5c)$$

The modeled nutrient fluxes are dominated by the growth and loss terms of phytoplankton. A fraction of the sinking biogenic material is allowed to remineralize (as a function of temperature) within each ocean layer.

### 2.2.4. Model Parameters

Most of the parameters of NEMURO are from the default parameter values (Table S1) from Yamanaka et al. (2004). In order to adapt the model to AS, fine tuning is done to the PL maximum photosynthetic rate at 0°C ( $V_{\text{maxL}}$ ), the PS maximum photosynthetic rate at 0°C ( $V_{\text{maxS}}$ ), the light dissipation coefficient for seawater ( $\alpha_1$ ), and the self-shading coefficient ( $\alpha_2$ ). There are studies that suggest that the diatom is the dominant group of phytoplankton in AS during winter monsoon season (Madhupratap et al., 1996; Prasanna Kumar et al., 2001; Prasanna Kumar & Prasad, 1996). In order to attain the dominance of diatom (Egge & Aksnes, 1992; Furnas, 1990) in the model, we kept the maximum growth rate ( $V_{\text{maxL}}$ ) is almost double (i.e.,  $2.0 \text{ d}^{-1}$ ) than that for small phytoplankton (Furnas, 1990; McCreary et al., 1996; Mussap et al., 2016). Diatom is a group for which the size of the species affects growth, photosynthesis and chemical



**Figure 1.** Study region in the Arabian Sea shown by Argo and ship tracks. Violet line (Argo float no: 2902123; T1), red line (Argo float no: 2902120; T2), black line (Argo float no: 2902118; T3), blue line (Argo float no: 2902092; T4), green line (Argo float no: 2902093; T5), brown line (combination of three ship-borne measurements by FORV Sagar Sampada cruises SS-262 from 11 to 25 February 2009, SS-263 from 27 February to 14 March 2009 and SS-264 from 18–30 March 2009). The filled squares represent the starting points of the tracks.

composition (Geiderlo et al., 1986). Montagnes and Franklin (2001) mentioned that the size of diatom decreases with increasing temperature. Therefore, we considered a maximum growth rate of  $2 \text{ d}^{-1}$  (for a small-sized diatom) based on their analysis. The half saturation constant for nitrate ( $K_{\text{NO}_3\text{L}} = 3.0 \mu\text{mol N l}^{-1}$ ) and ammonium ( $K_{\text{NH}_4\text{L}} = 0.3 \mu\text{mol N l}^{-1}$ ) set as a value greater than that of PS ( $V_{\text{maxS}} = 0.3 \text{ d}^{-1}$ ;  $K_{\text{NO}_3\text{S}} = 1.0 \mu\text{mol N l}^{-1}$ ;  $K_{\text{NH}_4\text{S}} = 0.1 \mu\text{mol N l}^{-1}$ ). All other coefficients (photosynthesis, respiration, mortality, etc.) are prescribed to be the same for PS and PL. The carbon to Chl-a ratio is fixed at 50 according to Kawamiya et al. (1995).

### 2.3. Data

The observations of temperature, salinity, and Chl-a are obtained from five Argo floats, Float nos. 2902123, 2902120, 2902118, 2902092, and 2902093 for the period from March 2014 to December 2016. In situ observations were collected onboard three Fishery Oceanographic Research Vessel (FORV) Sagar Sampada cruises, from 11 to 25 February 2009 (SS-262), from 27 February to 14 March 2009 (SS-263), and from 18–30 March 2009 (SS-264) organized by Centre for Marine Living Resources and Ecology (CMLRE), India as part of the Marine Living Resources Programme (MLRP). All the state variables of NEMURO are initialized with constant values ( $1.0 \text{ mol N l}^{-1}$  (PS, PL, ZS, ZL, ZP);  $0.5 \text{ mol l}^{-1}$  ( $\text{NH}_4$ );  $0.1 \text{ mol N l}^{-1}$  (POM, DOM);  $0.1 \text{ mol Si l}^{-1}$  (opal)) except for nitrate and silicate which are taken from WOA (Garcia et al., 2013). Temperature and salinity initial conditions are also provided from WOA (Locarnini et al., 2013; Zweng et al., 2013). All the initial conditions (temperature, salinity, nitrate, and silicate profiles) are taken from the starting point of individual Argo floats as well as the ship for each simulation (i.e., filled squares in Figure 1).

Six hourly air temperature, zonal and meridional components of winds, specific humidity, 12 hourly net surface solar radiation, and precipitation are taken from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-Interim reanalysis product at  $0.75^\circ \times 0.75^\circ$  resolutions as surface boundary conditions. The simulations are done in such a way that the model locations are not fixed; the model moves along the Argo or ship tracks while assimilating all the forcing data along individual tracks. The ocean vertical velocity is taken from Estimating the Circulation and Climate of the Ocean (ECCO) reanalysis data sets. The satellite sea surface temperature (SST) is obtained from the National Oceanic and Atmospheric Administration (NOAA,  $0.25^\circ \times 0.25^\circ$ ). ECCO ( $0.25^\circ \times 0.25^\circ$ ) reanalyzed mixed layer depth that is used

for model validation. The sources of data sets and all the model outputs are provided in the “Data Availability” section.

## 2.4. Methodology

Figure 1 shows the study region. The physical-biogeochemical-coupled model is simulated for “one loop” of 4 years as an initial spin-up with spatially and temporally varying surface forcing parameters sampled along the Argo tracks in real time. We allow the model to spin-up for 4 years along the track since it accumulates the oceanic processes of seasonal to subseasonal scales over 4 years, and the final spun-up state is most suitable model conditions for the initialization of the experimental runs. The output from the “second loop” of 4-year run (from 2013 to 2016 and initialized with the end state of the first run) is utilized to analyze the results. A similar method is used for ship-track simulations too. In order to avoid any strong model drift from the observation, the monthly nitrate and silicate are restored to climatology with a time scale of about 15 days in the surface layers (up to 40 m) and 30 days in the deep layers (below 40 m and up to 250 m). Surface heat fluxes and evaporation are computed using bulk formulas. Simulations are performed from 2013 to 2016 in order to match with available Argo observations and for a single year of 2009 in order to match with the ship observations. Hereafter, “AS” refers only to that part of the AS where the model simulation is performed (i.e., along five Argo tracks and three ship cruises, see Figure 1).

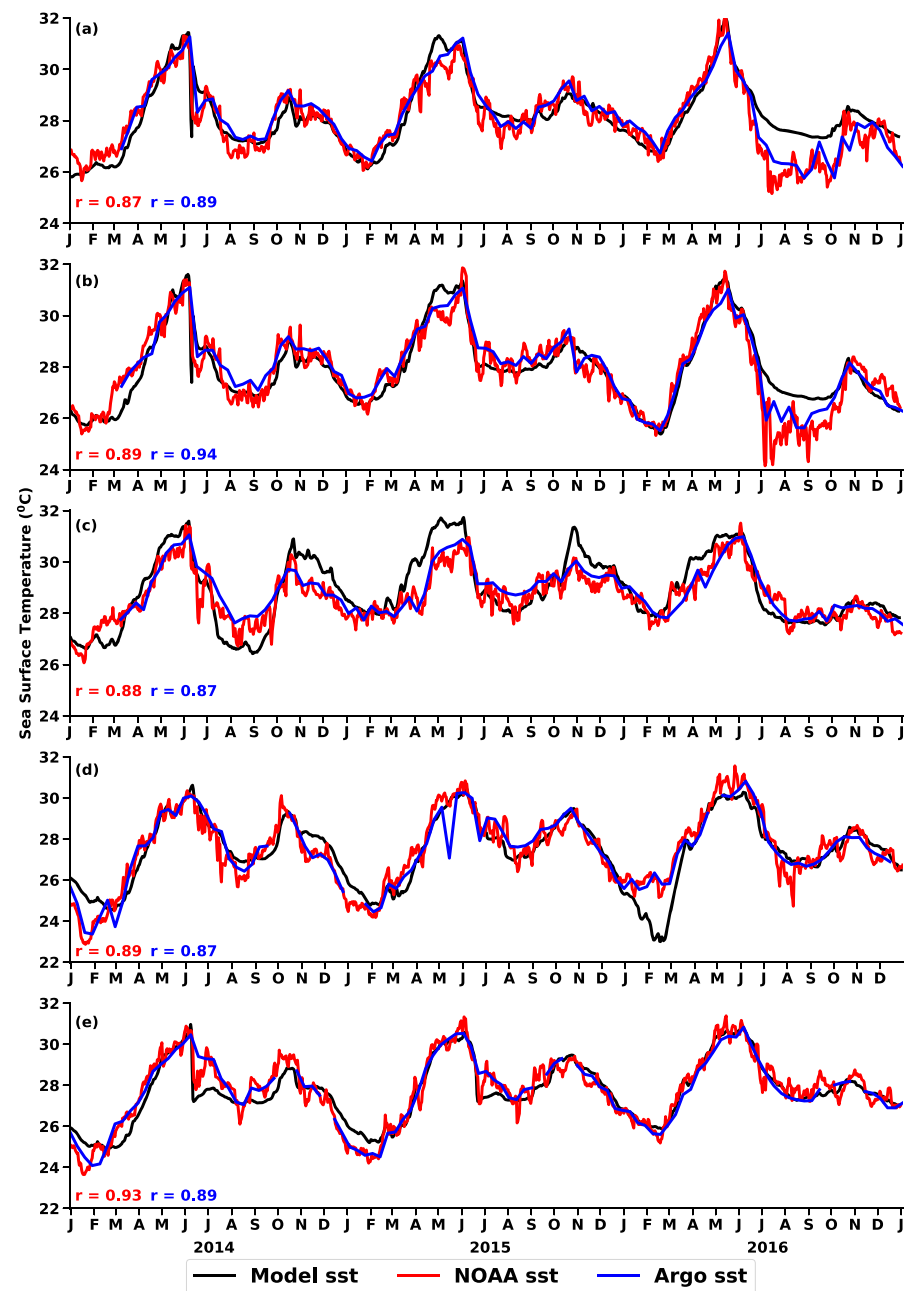
In order to identify the role of nutrient limitations on plankton biomass, we conducted a couple of sensitivity studies. Case I assumes that the primary production is driven by only nitrogen in terms of ammonium (i.e., regenerated production). It is achieved by switching off the new production in the model (i.e., the new production term  $\frac{[NO_3]}{[NO_3] + K_{NO_3L}} e^{(-\psi_L [NH_4])}$  is set to zero) in equations 2a and 2b. Case II assumes that the primary production is only supported by nitrogen in terms of nitrate (i.e., new production). This is achieved by switching off the regenerated production (i.e.,  $\frac{[NH_4]}{[NH_4] + K_{NH_4L}}$  is set to zero) in equations 2a and 2b. Case III assumes that silicate is not limiting the production of PL, which is achieved by removing the silicate limitation term ( $\frac{[Si(OH)_4]}{[Si(OH)_4] + K_{SiL}}$ ) from PL photosynthesis and avoid the minimum condition in equation 2b.

## 3. Results

### 3.1. Validation of Mixed Layer Model With Observations

The model simulated Sea Surface Temperature (SST) is in good agreement with observed SST (the satellite and Argo derived temperature) along all the Argo tracks as examined in Figure 2. The high correlation between model and observations along the tracks of five Argos corroborates the capacity of the model to reproduce the upper ocean physics even given the limits of a 1-D model (such as lack of horizontal advection, eddies, etc). SST reaches a seasonal maximum of 31°C during JJAS and a minimum of around 24°C in the DJF season. The intraseasonal signals (i.e., the variability of SST within each year) are not well captured in the model. Considering the fact that the seasonal SST and mixed layer dynamics of central AS are primarily controlled by 1-D air-sea fluxes than horizontal dynamics, the usage of the 1-D model in this study is justifiable (Montégut et al., 2007; Murtugudde & Busalacchi, 1999).

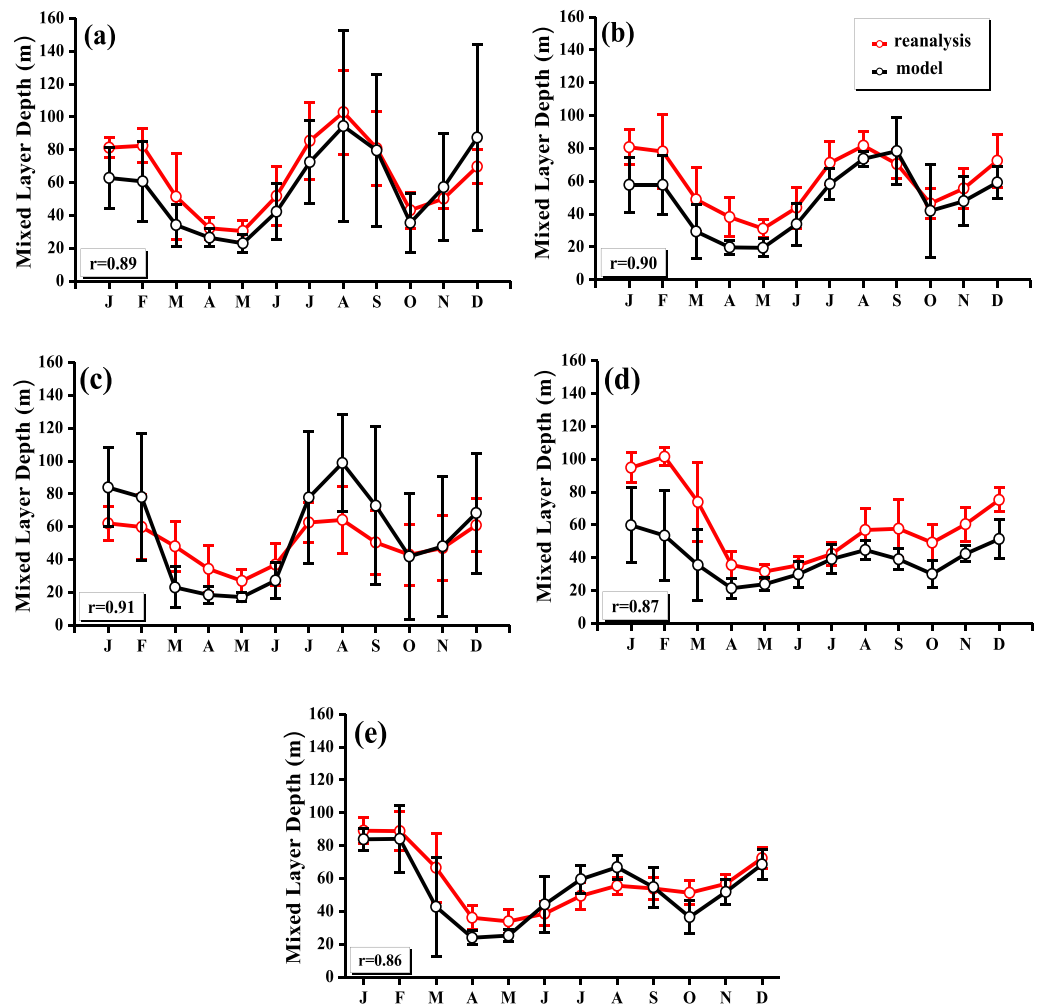
The model captures observed MLD variability of the central AS (Figure 3) when compared with ECCO reanalysis MLD along the Argo tracks, indicating that the model reproduced the mixing and mixed layer depth reasonably well. The model is able to capture the deepening of MLD along Argo track T1 and T2 during both winter (with a slight underestimation of MLD) and summer season. The MLD is shallow (~20–30 m) in both of the intermonsoon season. The bias in MLD is comparatively high along T3 and T4. The model was able to capture the seasonality of MLD along T3 and T4 as well, but there is an ~25 m bias that exists in the winter along T4. The model well reproduced the cycle of MLD along T5. Since the model is capable of reproducing the seasonal cycle of MLD, it is possible to use the model nutrient and biological cycles for the further analysis.



**Figure 2.** Comparison of model-simulated daily SST (black line) with satellite SST (red line) and Argo temperature (at 10 m depth; blue line) from 2014 to 2016 along (a) T1, (b) T2, (c) T3, (d) T4, and (e) T5. Units are in degree Celsius. "r" in red, blue represents the correlation coefficients between model and satellite SST, Argo temperature, respectively.

### 3.2. Dependence of Half-Saturation Constant for Silicate ( $K_{\text{sil}}$ ) in PL Growth

Fixing a calibrated value for  $K_{\text{sil}}$  is very important for a study of silicate limitation on diatom bloom. The diatom silicate uptake kinematics varies greatly from place to place (Kristiansen et al., 2000), and there is no specific value available for  $K_{\text{sil}}$  in northern AS.  $K_{\text{sil}}$  represents a measure of the ability of diatom to take up silicate at low external concentrations, and it regulates when the diatom growth is limited by silicate. Conway et al. (1976), Jacques (1983) reported that the  $K_{\text{sil}}$  value for silicate uptake by diatom in the culture environment varies from 0.3 to 22  $\mu\text{mol Si l}^{-1}$ .

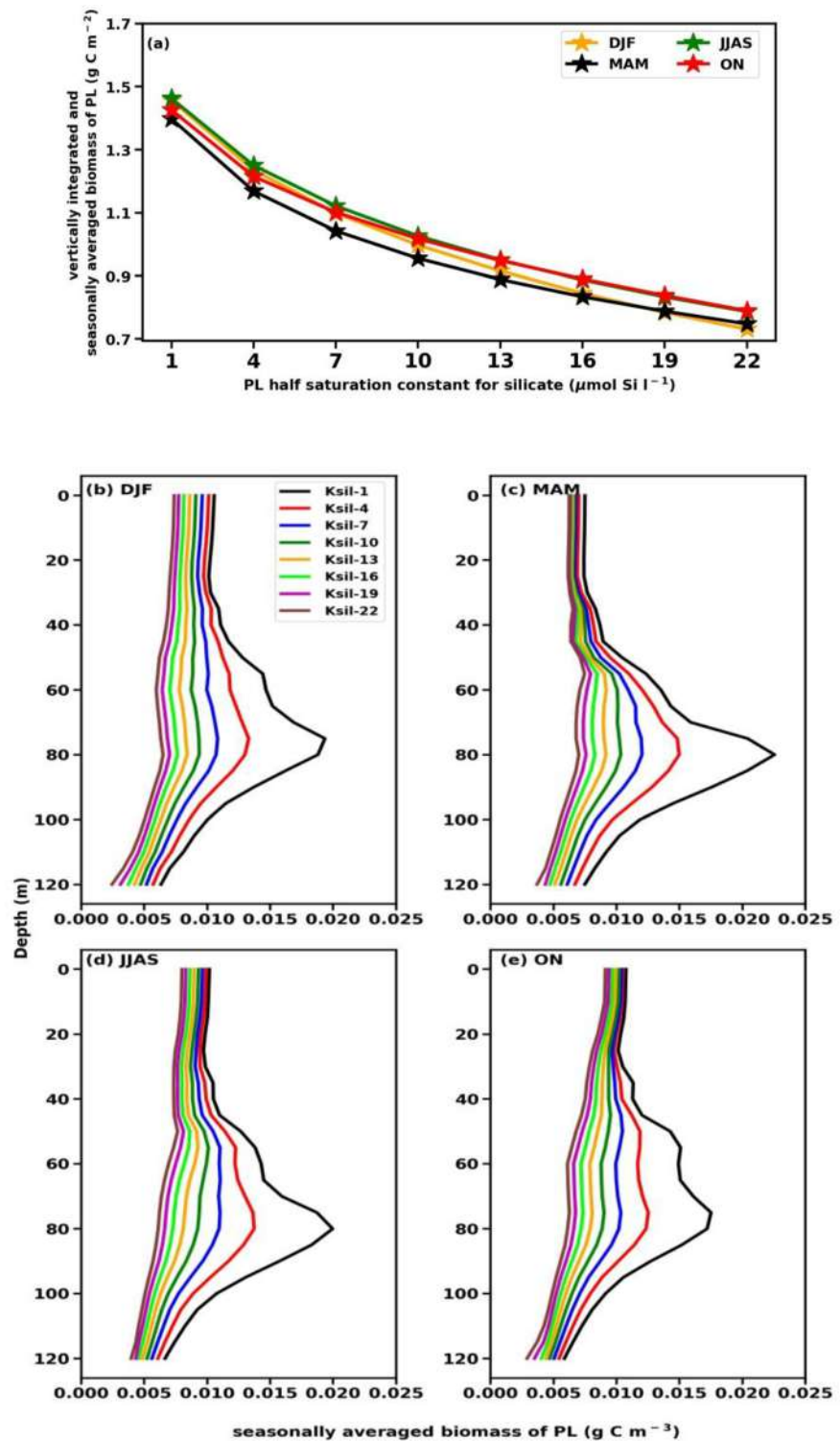


**Figure 3.** Seasonal variation of model-simulated MLD (black line) with reanalysis MLD (ECCO; red line) shown as climatology computed from 2013 to 2016 along (a) T1, (b) T2, (c) T3, (d) T4, and (e) T5. Units are in meters. Error bars show the standard deviations of daily model outputs of individual months over these years.  $r$  represents the correlation coefficient between model and observations.

In order to identify the sensitivity of PL primary production on  $K_{sil}$ , we did a sensitivity analysis with varying  $K_{sil}$  (from 1 to 22  $\mu\text{mol Si l}^{-1}$  with interval of 3) and found out that there is a weak inverse relation between  $K_{sil}$  and PL biomass (Figure 4; PL biomass shown as averaged over all five Argo, see also Text S1 for unit conversions). When  $K_{sil}$  increases from 1 to 22 ( $\mu\text{mol Si l}^{-1}$ ), the PL biomass drops by approximately a factor of two ( $\sim 1.4$  to  $\sim 0.7 \text{ g C m}^{-2}$ ). The PL biomass reduction is high when  $K_{sil}$  changes from 1 to 10 ( $\sim 0.5 \text{ g C m}^{-2}$ ) after that PL biomass has a very slow reduction ( $\sim 0.2 \text{ g C m}^{-2}$ ). We also analyzed the vertical structure of PL with varying  $K_{sil}$  values. The inverse relation between PL biomass and  $K_{sil}$  is strong in the region of SCM and that too for extreme lower values of  $K_{sil}$  (Figures 4b–4e in all the seasons). For higher  $K_{sil}$  values ( $> 10 \mu\text{mol Si l}^{-1}$ ), the SCM does not exist in the model. This indicates that the silicate concentration at SCM depths is less than  $K_{sil}$  and results in no SCM formation. In our study, we adopt  $K_{sil}$  as  $6 \mu\text{mol Si l}^{-1}$  which is the same value in Yamanaka et al. (2004). Any higher value of  $K_{sil}$  will destroy the basic profile of PL which is expected to have a SCM at the intermediate depths.

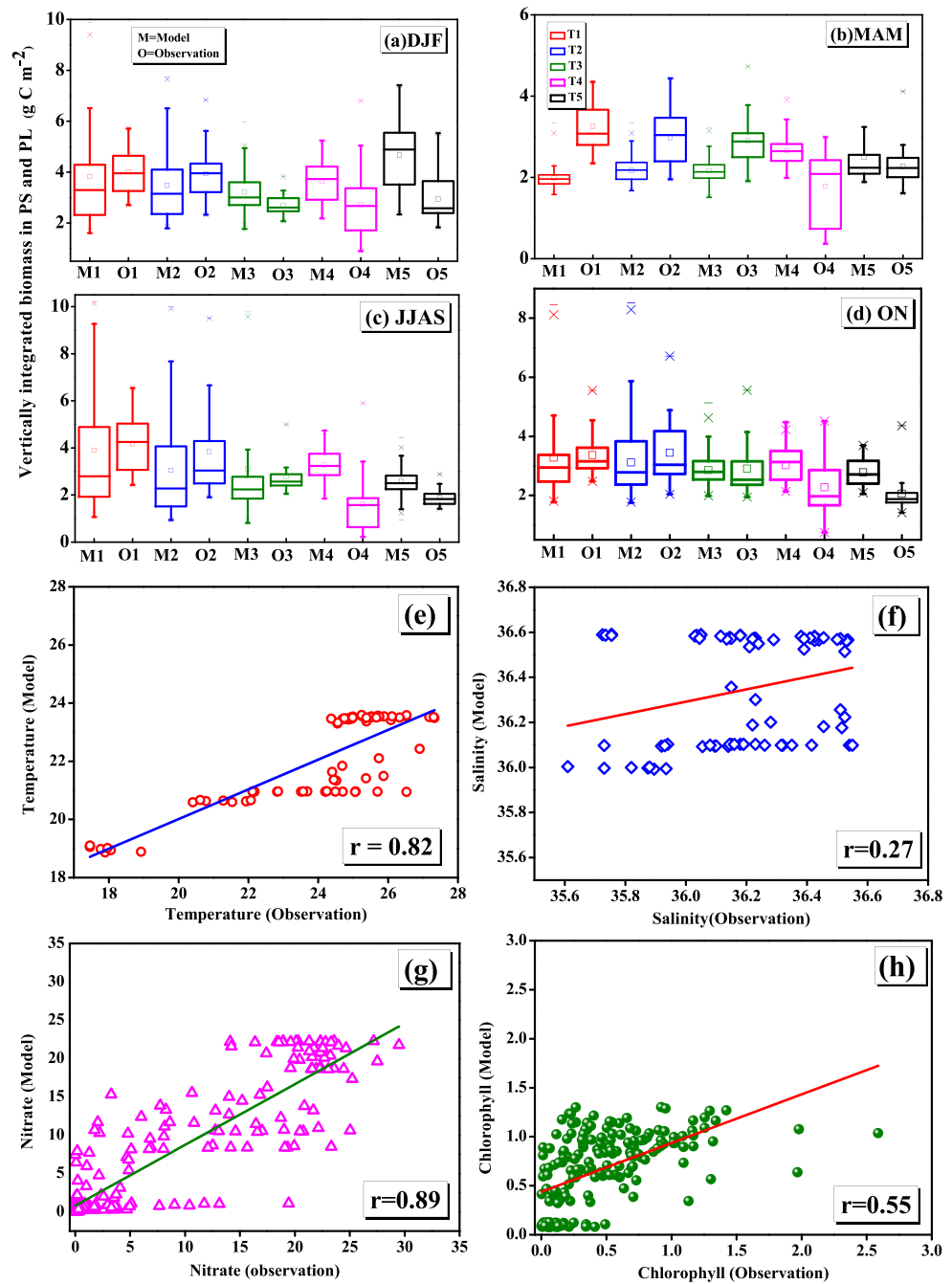
### 3.3. Validation of NEMURO With Bio-Argo, Ship Observations

Figures 5a–5d show the Whisker box plot (for four seasons) of the vertically integrated (0–120 m) biomass of phytoplankton (PS + PL) from the model and observations (see Text S1 for unit conversion). In all the seasons, the range of model estimations is close to the observations. During DJF, the spread of both model and



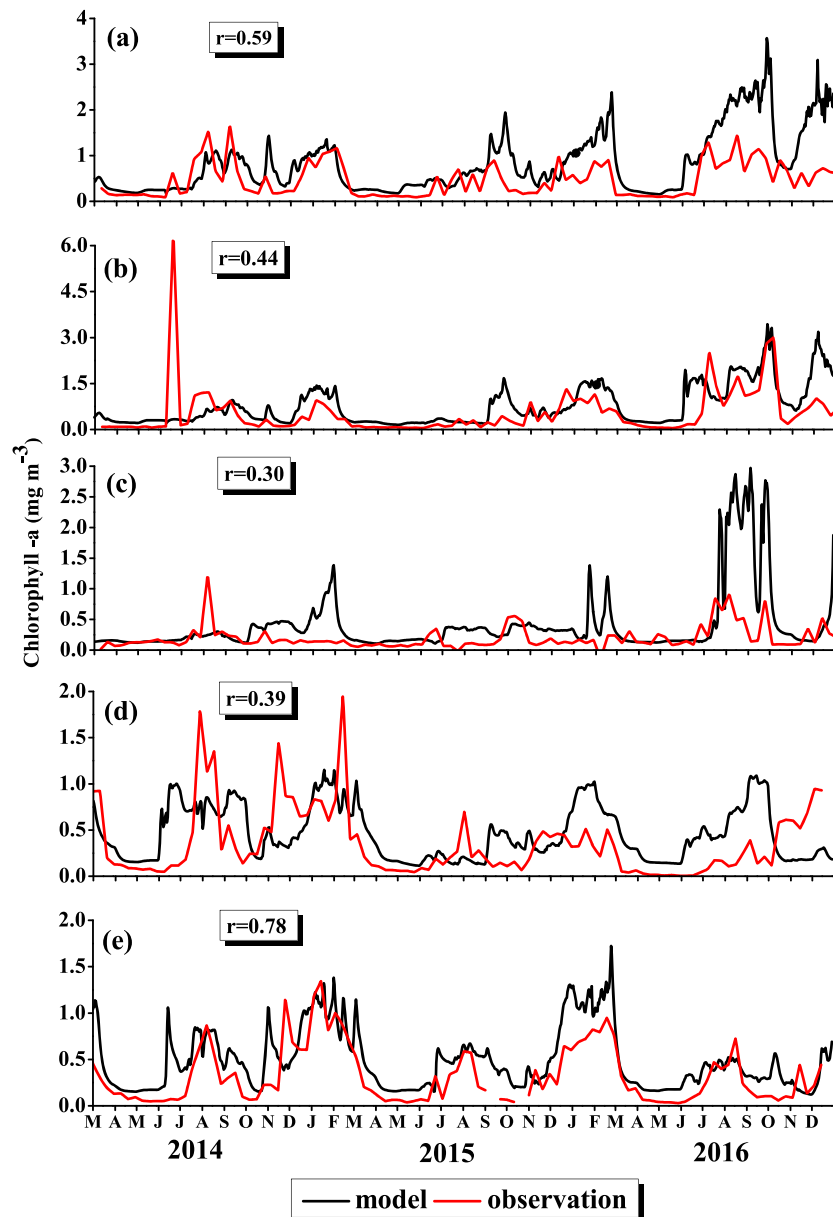
**Figure 4.** The relation between (a) vertically (1–120 m) integrated biomass in PL (g C m<sup>-2</sup>) and  $K_{sil}$  (μmol Si l<sup>-1</sup>). (b–e) represents the vertical profile of PL biomass (g C m<sup>-3</sup>) for varying  $K_{sil}$  (μmol Si l<sup>-1</sup>) values for different seasons DJF, MAM, JJAS, and ON, respectively.

observed data are almost the same. The observation shows that mean biomass for DJF is approximately between 3 and 4 g C m<sup>-2</sup>. The average biomass in the model is also within the range of observations. During intermonsoon seasons (MAM and ON), also the model and observations are in good agreement.



**Figure 5.** Comparison of model-simulated vertically (0–120 m) integrated biomass ( $\text{g C m}^{-2}$ ) with that obtained from all five Argo tracks during the period of (a) DJF, (b) MAM, (c) JJAS, and (d) ON. M1–M5 and O1–O5 represent model simulations and observations along T1–T5. The small square box and the line in the center of the box represent the mean and median of the data. Scatter compares the model simulated (e) temperature ( $^{\circ}\text{C}$ ), (f) salinity, (g) nitrate ( $\mu\text{mol N l}^{-1}$ ), and (h) Chl-a ( $\text{mg m}^{-3}$ ) for the upper 120 m with those obtained from the ship observations. “ $r$ ” represents the correlation coefficient between the model and observations.

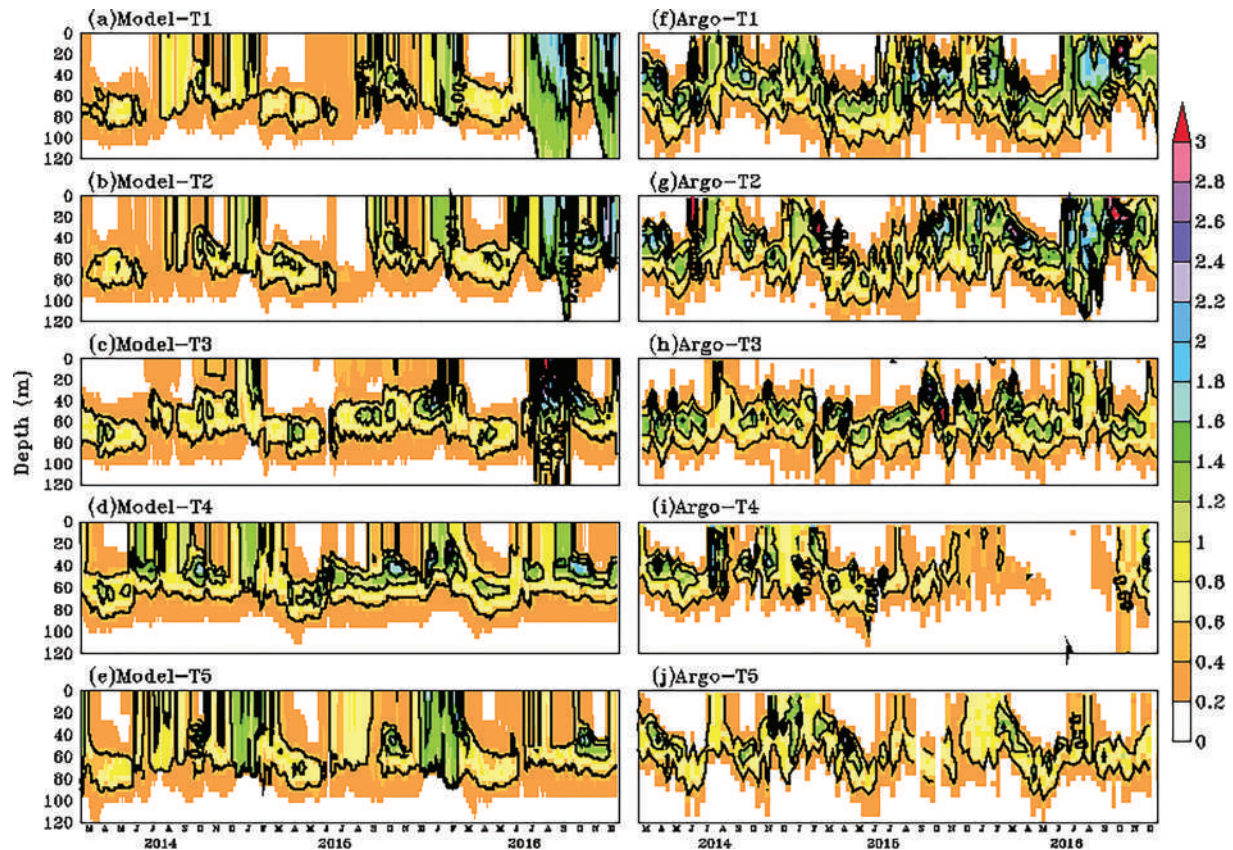
Vertically integrated biomass is relatively less in this season ( $\sim 3 \text{ g C m}^{-2}$ ). But the model reproduces the mean biomass close to  $2 \text{ g C m}^{-2}$  along T1, T2, and T3. The interquartile range (IQR) for the model is lower than the IQR for the observations along all the tracks except T5; the model simulations are not having much variance around the mean. During JJAS, the model and observations are consistent except along T4 (model overestimates).



**Figure 6.** Comparison of model-simulated daily surface Chl-a (black line; at 5 m depth) with that of Argo observation (red line, at 5 m) from 2014 to 2016 along (a) T1, (b) T2, (c) T3, (d) T4, and (e) T5. Units are  $\text{mg m}^{-3}$ . “ $r$ ” represents the correlation coefficient between model and observation.

Figures 5e–5h shows the scatter of model variables and observations along the ship track. The correlation coefficient between model-simulated temperature, nitrate, and Chl-a with that from the ship cruise are significant, whereas a weak correlation is present in the comparison of salinity along the ship track with the model. Figure S3 shows the detailed comparison of model variables with that from ship observations. The model successfully reproduces the temperature (Figures S3a and S3b) and salinity (Figures S3c and S3d) profile along ship tracks. The model failed to reproduce the temporal variability in temperature (i.e., warming of the surface ocean from mid-February to late February; Figures S3a and S3b) and salinity (Figure 5f, Figures S3c and S3d). It can be explained by the absence of thermocline undulations (limitation of a 1-D framework) associated with ocean dynamics, eddies and lateral advections, and so forth. The model temperature at the surface remains  $2^{\circ}\text{C}$  colder than the observation in late February.

The model captures both winter and summer blooms observed at the surface during the simulation period (Figure 6). The model simulated surface Chl-a is consistent with the observed Chl-a from Argo as evident



**Figure 7.** Vertical profiles of model-simulated Chl-a (a–e) compared with corresponding bio-Argo observations (f–j) for the period 2014 to 2016 along T1, T2, T3, T4, and T5. Units are in  $\text{mg m}^{-3}$ .

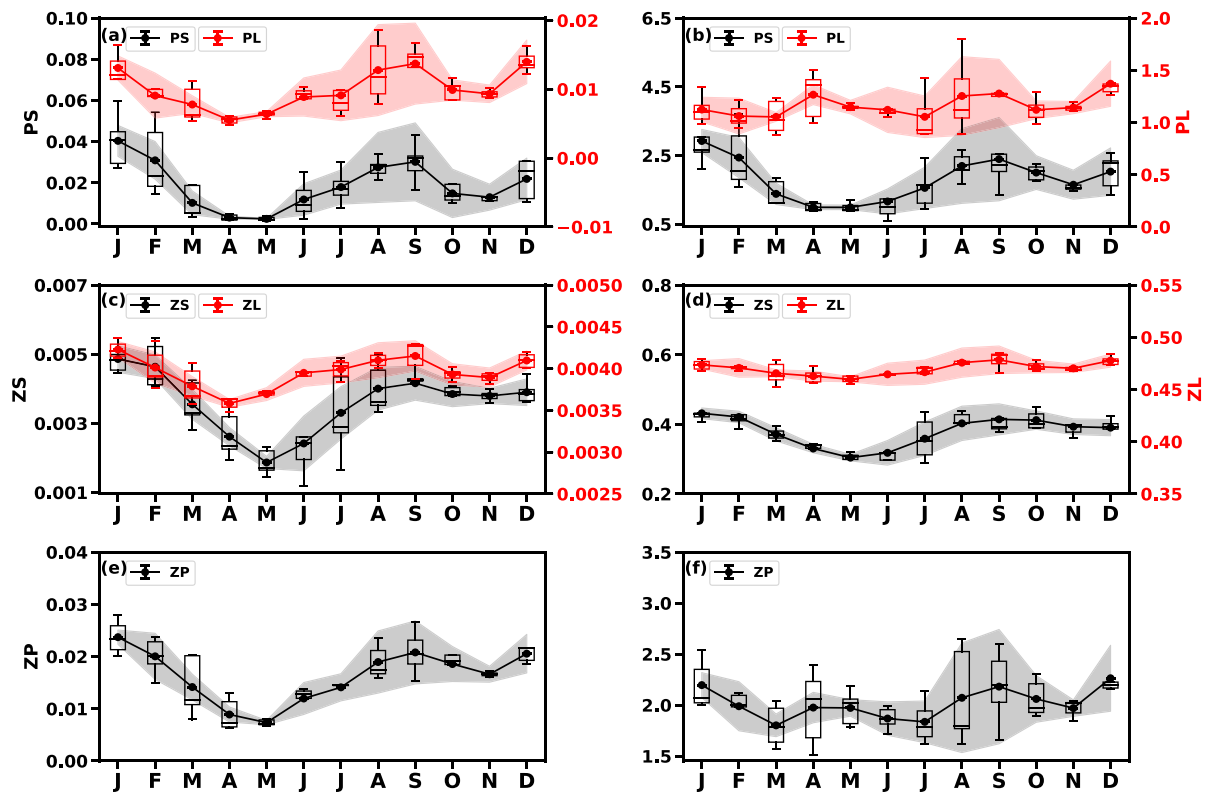
from the correlation analysis. The model reproduces the weak production during the intermonsoon seasons ( $<0.4 \text{ mg m}^{-3}$ ), which is a characteristic of AS (Prasanna Kumar et al., 2000).

The coupled NEMURO and mixed layer model capture the observed seasonal Chl-a bloom along all the Argo tracks from the surface to 120 m (Figure 7). The model successfully reproduces the vertical distribution of Chl-a with a persistent occurrence of SCM ( $\sim 1.0 \text{ mg m}^{-3}$ ) throughout the year (Matondkar et al., 2006), at a depth range of 40–80 m. The model is able to capture the specific Chl-a bloom events such as during JJAS and DJF of 2016 along the tracks T1 and T2. Thus, Figures 2–3 and 5–7 summarize the validation of the model with respect to observations in reproducing the seasonality of physical and biological variables over AS.

### 3.4. The Seasonal Cycle of Plankton Biomass

The seasonal cycle represents the model-simulated seasonal variations shown as climatology computed from 2013 to 2016. Here we note that a climatological cycle based on averaging all Argos may average out the potential large spatial variability, as the floats traveled over great distances in the AS (see Figure 1). Therefore, all the climatological plots are supplemented with intertrack deviations as Whisker box for each month over and above the temporal uncertainty.

In the surface, the magnitude of PS is greater than that of PL throughout the year (Figure 8a). Both PS and PL have two blooms in a year (winter bloom–DJF and summer bloom–JJAS) and low biomass during both the intermonsoon seasons. The seasonal amplitude of PS is also greater than that of PL at the surface. The magnitude of ZP is an order of magnitude greater than that of ZS and ZL (Figures 8c and 8e). The ZS and ZP follow the seasonal pattern of PS and PL, whereas the magnitude of ZL is almost constant throughout the year. The vertically integrated biomass (Figure 8b) of PS and PL also have large seasonal variations; the former is larger than that of PL. Both the biomasses (at the surface and vertically integrated) have maximum values



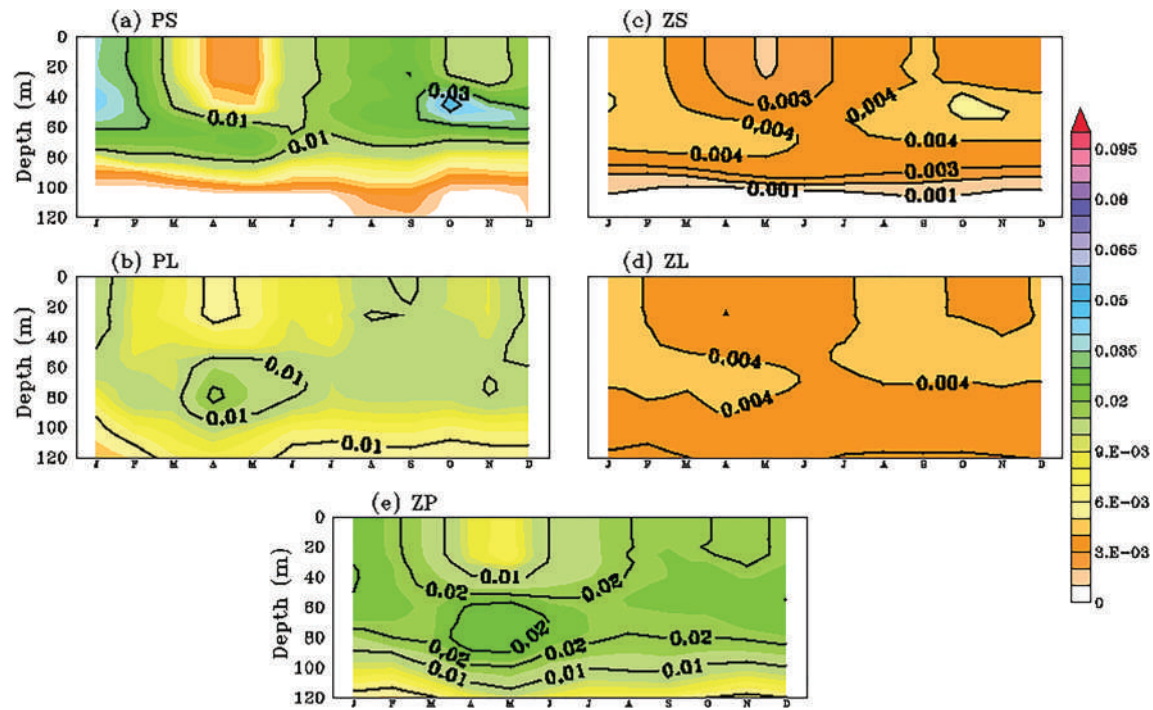
**Figure 8.** The model-simulated seasonal variation of biomass in plankton shown as climatology computed from 2013 to 2016 (a) PS and PL at the surface, (b) PS and PL vertically (0–120 m) integrated, (c) ZS and ZL at the surface, (d) ZS and ZL vertically integrated (0–120 m), (e) ZP at the surface, and (f) Z vertically integrated (0–120 m). Units are  $\text{g C m}^{-3}$  and  $\text{g C m}^{-2}$  for surface and vertically integrated plankton, respectively. Shaded regions show the standard deviation of daily data of individual months from 2013 to 2016. The box Whisker plot shows the inter track deviations arise due to averaging of variables along different Argo tracks. Closed circles, line in the box represents the mean and median of inter track data, respectively.

during JJAS and DJF for the case of PS. By contrast for the case of PL, the surface bloom occurs during DJF and JJAS while the vertically integrated bloom shows a peak during MAM. The vertically integrated biomass in ZS follows the pattern of vertically integrated biomass of PS, whereas ZP follows that of PL (Figures 8d and 8f). There is no appreciable seasonality present for vertically integrated ZL (Figure 8d).

The intertrack deviations highlight the differences in the model variables along different Argo tracks (see Whisker boxes in figures). It is noteworthy that the intertrack deviations are well captured within the temporal uncertainty representing daily-to-subseasonal variability. Therefore averaging different Argo although they have traveled in large distances apart is not a caveat in constructing a consolidated seasonal cycle. For clarity, the seasonal cycles constructed for individual Argo are supplemented in Figure S4.

The intertrack deviations are maximum during DJF for PS at the surface as well as for the case for vertically integrated PS. The PS bloom occurs during December and January along T1, T2, and T3 (Figures S4a, S4e, and S4i) whereas, the bloom peaks in January and February along T4 and T5 (Figures S4m and S4q). In the case of PL, the intertrack deviation is high during March and August (both for the surface and for the vertically integrated PL). Both PS and PL, the summer bloom is weak along T5 compared to other tracks. There are no intertrack deviations present for ZL (Figures 8c and 8d) whereas ZS at the surface shows large differences in July which arises due to the differences in ZS magnitude along different Argo tracks (Figures S4c, S4g, S4k, S4o, and S4s). The concentration of ZP (vertically integrated) peaks during August along T1 to T3 whereas it is low along T4 and T5 which causes a high intertrack deviation in ZP during August.

PS (at SCM depths  $\sim 0.06 \text{ g C m}^{-3}$ ) and PL (at SCM depths  $\sim 0.01 \text{ g C m}^{-3}$ ) have distinct patterns (Figures 9a and 9b). PL has a higher vertical spread (almost down to 120 m) than PS. The magnitude of PS-SCM is



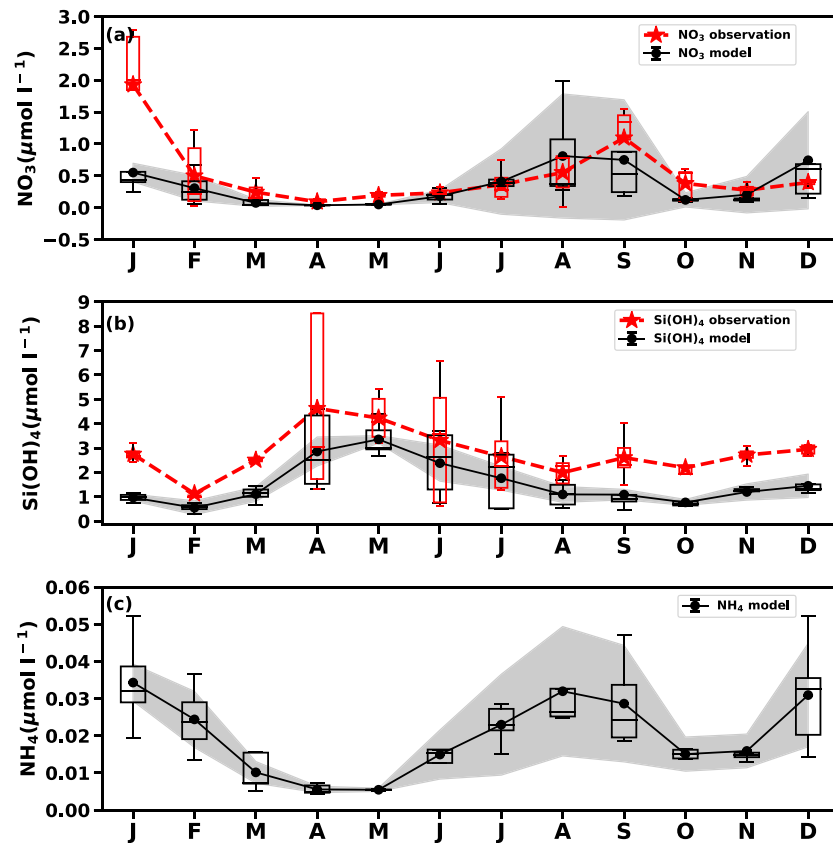
**Figure 9.** Model simulated seasonal variability in the vertical profile of plankton averaged over all the five Argo, (a) PS, (b) PL, (c) ZS, (d) ZL, and (e) ZP. Units are  $\text{g C m}^{-3}$ .

slightly higher than PL-SCM, and both are around 40–80 m. The zooplankton community also has an almost similar vertical profile as phytoplankton (Figures 9c–9e). The concentration of ZP is greater than that of ZS and ZL. There is a well-developed patch of ZP found along with the SCM in the water column. The weak concentrations of ZS and ZL can be due to the predation by ZP. The maximum concentration of ZS and ZL are around 60–80 m in the water column. The grazing of ZS on PS, ZL on PS and PL, predation of ZP on ZS, ZL, and PL can be explained by the coexistence of zooplankton community with the phytoplankton community. The fine details of intertrack deviations in the plankton biomass along different Argo tracks are given in Figure S5.

### 3.5. The Seasonal Cycle of Nutrients

The model simulated seasonal cycle of nutrients is in agreement with that of observations (Figures 10a and 10b) partially due to the fact that the nutrients are restored to climatology. Here the WOA nitrate and silicate are also sampled along the Argo tracks. The model reproduces surface nitrate concentration peaks during DJF (the model underestimated the nitrate at the surface during January) and JJAS. The silicate concentration in AS increases during MAM, and a secondary peak occurs from August to October. The model is able to capture this seasonality in silicate but with a slight underestimation in the magnitude throughout the year. The model that simulated ammonium concentration at the surface (Figure 10c) shows that the seasonal cycle of ammonium is the same as that of nitrate in the surface ocean with two peaks in concentration one during DJF and another during JJAS.

The model reproduces the intertrack deviations during February, August, and September in nitrate at the surface (in comparison with intertrack deviations of nitrate from WOA sampled along each Argo track; Figure 10a). Both observations and the model suggest that the nitrate concentration is comparatively higher along T4 and T5 during January (Figure S6; even though these differences are very negligible). There is a negligible intertrack deviation occurring during August to October in the observation of nitrate at the surface; however, the model overestimates this especially due to higher nitrates simulated along T1 and T3 (Figure 10a and Figure S6). During the intermonsoon season, there are very negligible intertrack deviations present for surface nitrate both in the observation and model (Figure 10a).

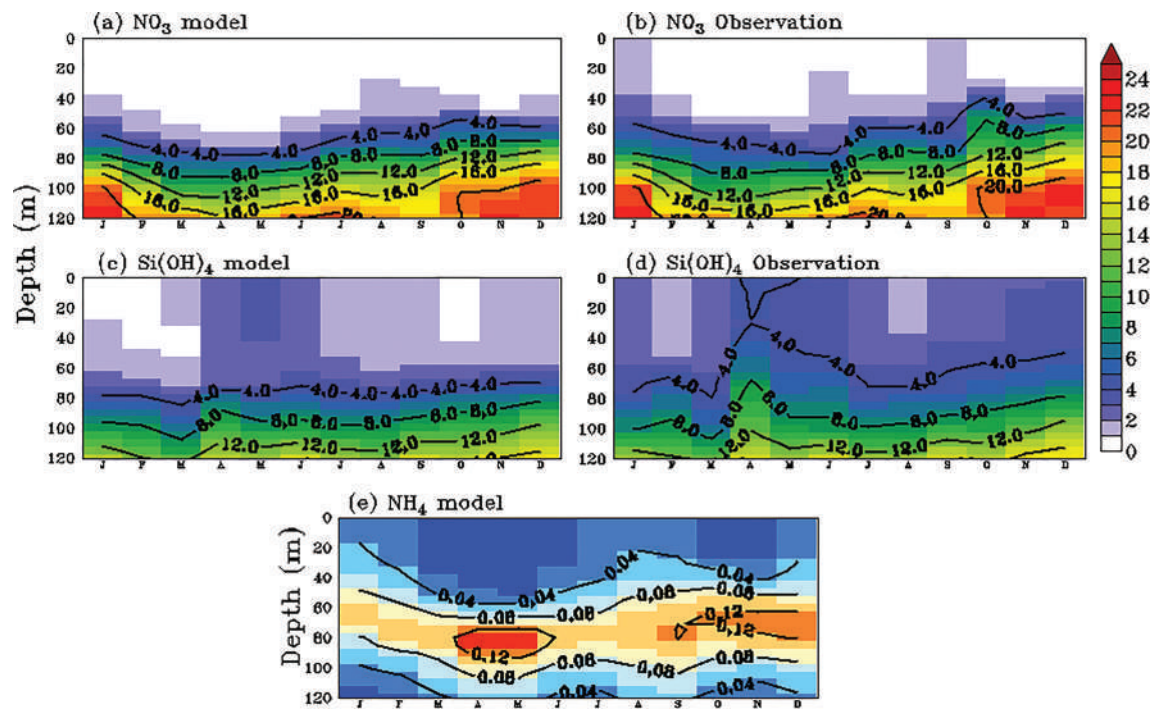


**Figure 10.** Comparison of model-simulated seasonal variation of surface nutrients shown as climatology computed from 2013 to 2016 with that from WOA (a) nitrate, (b) silicate, and (c) ammonium (model only). Shaded regions show the standard deviation of daily data of individual months from 2013 to 2016. The box Whisker plot shows the inter track deviations arise due to averaging of variables along different Argo tracks. Closed symbols, line in the box represents the mean and median of inter track data, respectively. Units are  $\mu\text{mol l}^{-1}$ .

Silicate at the surface (both in the model and observation) shows high intertrack deviations of  $\sim 7 \mu\text{mol l}^{-1}$  from April to August (Figure 10b). These intertrack deviations arise due to the differences in season at which silicate peaks at the surface along different Argo tracks. Along T1 and T3, the silicate concentration remains  $\sim 1$  to  $3 \mu\text{mol l}^{-1}$  during MAM. Whereas the surface silicate concentration is at its peak ( $\sim 9 \mu\text{mol l}^{-1}$ ,  $\sim 5 \mu\text{mol l}^{-1}$  in observation, model, respectively) during MAM along T4 and T5 (i.e., the Argo's which are in the eastern AS, Figure S6). The silicate concentration peaks ( $\sim 5 \mu\text{mol l}^{-1}$ ,  $\sim 3 \mu\text{mol l}^{-1}$  in observation, model, respectively) from May to July along T1 and T2, whereas it remains low along T4 and T5. The silicate concentration oscillates between 1 and  $5 \mu\text{mol l}^{-1}$  both in observation and model along T3 (Figure S6). The detailed analysis of nutrients along different Argo tracks in the AS indicates that the silicate shows more regional differences than nitrate in AS. Therefore, the mean silicate limitation concluded from this study encapsulates the possible spread in this conclusion due to combining all the five Argo tracks and evaluating their differences.

The vertical profiles of model-simulated nitrate (Figure 11a) and silicate (Figure 11c) compared with that from WOA observations indicate that the model is successful in capturing the vertical profile of nutrients for the AS faithfully. The model simulated ammonium vertical profile is in agreement with the observed ammonium (Rush et al., 2012) concentration range for AS. The maximum concentration of ammonium is around 80 m (Figure 11e) located at a shallower depth compared to the relatively “sparse” observations available. The patch of maximum ammonium concentration is collocated with the SCM positions of PS and PL, which is consistent with the results of Sarma and Aswanikumar (1991).

The nutrient profile comparison along all the five Argo tracks is given in Figure S7. There is no appreciable difference present for nitrate along the different Argo tracks except along T1 where the nitrate concentration



**Figure 11.** Vertical profiles of model-simulated seasonal variation of nutrients shown as climatology computed from 2013 to 2016 with that from WOA. (a) Nitrate ( $\text{NO}_3$  model), (b) nitrate ( $\text{NO}_3$  observation), (c) silicate ( $\text{Si}(\text{OH})_4$  model), (d) silicate ( $\text{Si}(\text{OH})_4$  observation), and (e) ammonium ( $\text{NH}_4$  model). Units are  $\mu\text{mol l}^{-1}$ .

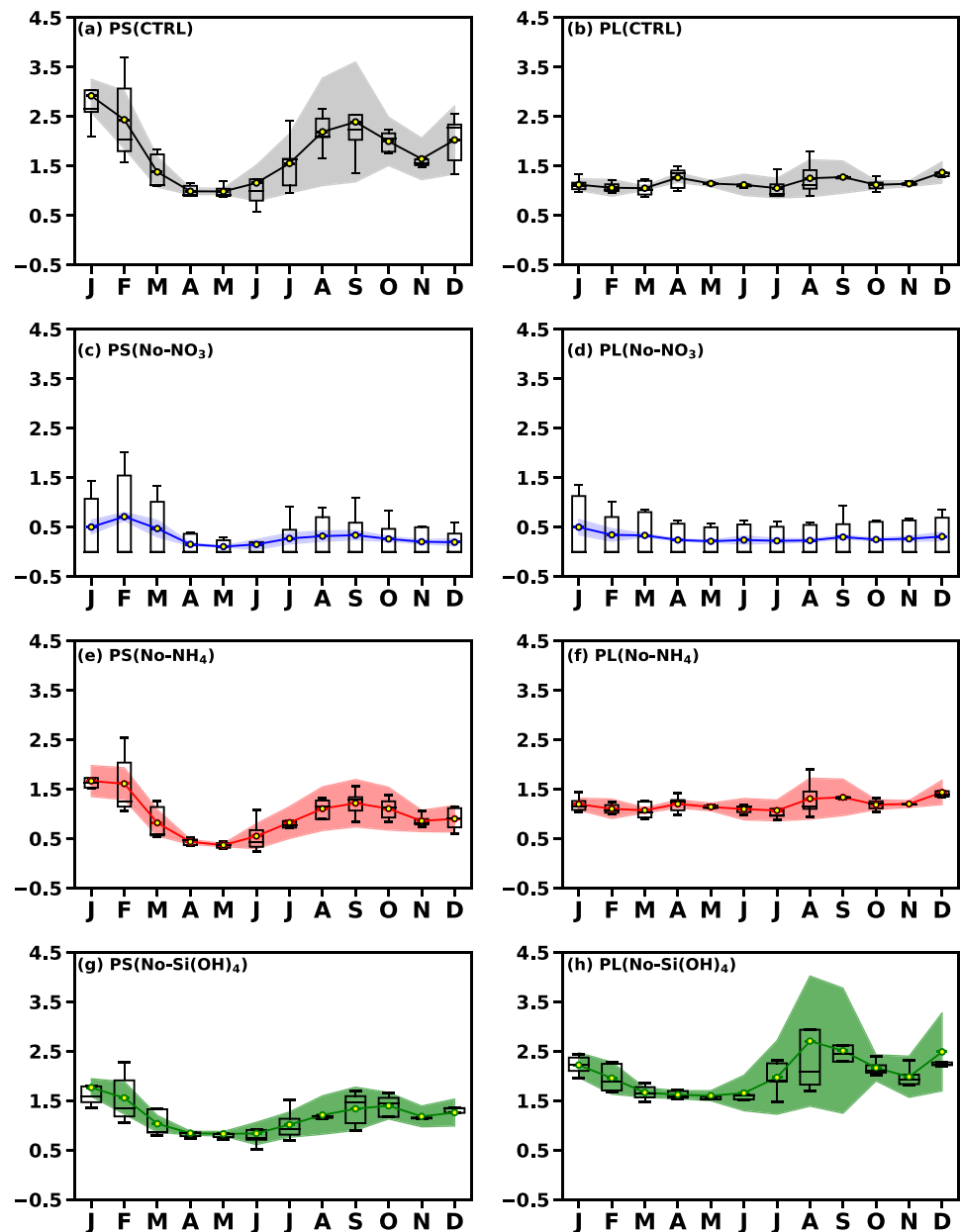
at the upper ocean (0–40 m) are higher than other tracks (Figure S7a–S7e). The model is successful in the reproduction of the nitrate, silicate in the upper 120 m (Figures S7a–S7j, Figures S7k–S7t, respectively). The silicate concentration at the surface ocean (0–60 m) shows differences along different Argo tracks (Figures S7k–S7o). The silicate concentration is higher in the surface ocean during MAM along T4 and T5 whereas the silicate peaks from May to July along T1 and T2. Along T3, the silicate in the upper ocean remains high from April to July. There is a difference in silicate profile from the west (along T1 and T2) to the east (along T4 and T5) AS. These differences can contribute to differences in the community of plankton and the pattern of nutrient limitation present.

### 3.6. The Role of Nutrient Limitations in the Seasonality of Plankton Biomass

In order to delineate the role of nitrate, ammonium, and silicate limitations in AS primary production, we have conducted sensitivity experiments as detailed in section 2.4. Case I examines the role of regenerated production ( $\text{NO}-\text{NO}_3$ ) on PS and PL primary production by assuming no new production. Case II examines the role of new production on both PS and PL primary production by assuming no regenerated production ( $\text{NO}-\text{NH}_4$ ). Case III examines how the primary production changes if silicate is not a limiting nutrient for PL ( $\text{NO}-\text{Si}$ ).

In Case I (i.e.,  $\text{NO}-\text{NO}_3$ ) the vertically integrated biomass of PS drastically decreases (by ~80%) throughout the year due to the unavailability of nitrate for the production (Figures 12a and 12c solid line). The seasonality of PS is also lost albeit with a weak bloom during DJF and JJAS driven by ammonium (refer Figure 11e also). In Case II (i.e.,  $\text{NO}-\text{NH}_4$ ), however, PS maintains its seasonality with an approximate reduction of 45% from the CTRL throughout the year (Table 1, Figures 12a and 12e). The importance of new production over regenerated production in the seasonality of PS productivity is highlighted in Table 1.

The intertrack deviations of PS in CTRL (Figure 12a) are higher (about  $\sim 2 \text{ g C m}^{-2}$ ) in February. The magnitude of PS is higher along T4 and T5 than other tracks during February (Figures S8g and S8i). In Case I (only with regenerated production), the intertrack deviations are high in PS during winter months especially caused by T4 and T5 which occupied the eastern AS (Figure 12c, Figures S8g and S8i). In the absence of new production, the PS magnitude completely depleted to zero along T1, T2, and T3 (for those Argos traveled to



**Figure 12.** The model simulated vertically integrated biomass (a) PS (b) PL shown as climatology computed from 2013 to 2016. shaded regions show the standard deviation of daily data of individual months from 2013 to 2016. The box whisker plot shows the inter track deviations arise due to averaging of variables along different Argo tracks. Closed symbols, line in the box represents the mean and median of inter track data respectively. Units are  $\text{g C m}^{-2}$ . CTRL, NO- $\text{NO}_3$ , NO- $\text{NH}_4$ , NO- $\text{Si(OH)}_4$  represents control run, Case I, Case II, and Case III, respectively.

central-western AS; Figures S8a, S8c, and S8e). This indicates that the primary production of PS along these three tracks is completely dependent on new production. In Case II (only with new production), the intertrack deviation is rather weak for PS (Figure 12e).

In Case I, throughout the year, the production of PL decreases by more than 65% (Table 1, to an amount of  $\sim 0.25 \text{ g C m}^{-2}$ ) from CTRL, there is no seasonal bloom in PL unlike PS in Case I. In Case II, there is not much deviation in PL biomass from CTRL. In Case III (i.e., NO-Si) the magnitude and seasonality of PL is higher than that in CTRL as expected. Interestingly, a strong bloom during JJAS and a secondary bloom during DJF are simulated in Case III indicating that silicate is limiting the seasonality of PL in CTRL. Moreover, the

**Table 1**

Percentage Change in Plankton Biomass (w. r. t. CTRL Run) in Each Sensitivity Analysis During the Four Seasons. Positive (Negative) Values Indicates an Increase (Decrease) in the Biomass From CTRL Run

| Sensitivity analysis        | Plankton biomass | The response of plankton biomass w. r. t. nutrient limitation (in %) |     |      |     |
|-----------------------------|------------------|----------------------------------------------------------------------|-----|------|-----|
|                             |                  | DJF                                                                  | MAM | JJAS | ON  |
| Case I: NO-NO <sub>3</sub>  | PS               | -81                                                                  | -78 | -85  | -87 |
|                             | PL               | -68                                                                  | -77 | -79  | -77 |
|                             | ZS               | -68                                                                  | -63 | -71  | -72 |
|                             | ZL               | -71                                                                  | -70 | -73  | -74 |
|                             | ZP               | -68                                                                  | -73 | -79  | -76 |
| Case II: NO-NH <sub>4</sub> | PS               | -43                                                                  | -52 | -49  | -46 |
|                             | PL               | 5                                                                    | -1  | 2    | 5   |
|                             | ZS               | -18                                                                  | -16 | -25  | -18 |
|                             | ZL               | -1                                                                   | -2  | -1   | -1  |
|                             | ZP               | 1                                                                    | -1  | -1   | 3   |
| Case III: NO-Si             | PS               | -38                                                                  | -19 | -40  | -29 |
|                             | PL               | 87                                                                   | 41  | 88   | 83  |
|                             | ZS               | -14                                                                  | -6  | -12  | -10 |
|                             | ZL               | -1                                                                   | -1  | -1   | -1  |
|                             | ZP               | 74                                                                   | 51  | 72   | 78  |

increase in PL is at the expense of nutrients available to PS causing a net reduction in PS (Case III; Figure 12g).

The intertrack deviations of PL are rather weak in CTRL (Figure 12b). The PL concentration depleted to zero along T1, T2, and T3 (indicative of complete dependency on new production) of PL like PS in Case I (Figures S8b, S8d, and S8f) but not in T4 and T5. As a result, there are moderate inter-track deviation can be seen in Figure 12d implying heterogeneity in the regenerated production among these Argo tracks. In Cases II and III, the intertrack deviation is high during August (Figures 12f and 12h). Those Argo traveled central to west AS (i.e., T1, T2, and T3), the silicate severely limits the PL from July to September (Case III, Figures S8b, S8d, and S8f).

In all three cases, the magnitude and seasonality of ZS decrease relative to CTRL (Figures 13a, 13d, 13g and 13j). In Case I, there is more than 60% decrease in ZS throughout the year as compared to the much lower sensitivity (~20% reduction) in Case II and Case III (~10% reduction only). ZS thus exactly follows the pattern of PS (prey for ZS) in all the cases with much more reduction in Case I (Figures 12c and 13d).

In Case I, ZL decreases by more than 70% through most of the year. ZL can graze on both PS and PL and predate on ZS, the net effect of which will decide the magnitude of ZL. In Case I, the reduction in both PS and PL

has reflected a reduction in ZL as well. In Case II, ZL is not sensitive to the decrease in PS and ZS. However, the grazing of ZL on PL, which itself is not changed in this case, maintains ZL biomass (Figures 12f and 13h). ZL is unaffected in Case III because of the abundance of PL (Figures 12h and 13k).

The seasonality of ZP (e.g., Euphausiids) follows that of PL in all cases (Figures 12 and 13). In Case I, the magnitude of ZP drops by ~70% throughout the year due to the corresponding reduction in PL biomass. ZP is not sensitive in Case II which is similar to that of PL. Whereas in Case III, the ZP increases more than 50% in all the seasons which is consistent with the increase in PL. In all of the above sensitivity runs, the looping of phytoplankton and small zooplankton (such as zooflagellates and ciliates) through intermediate size zooplankton (such as copepods) appears to be important for maintaining the flow of nutrients from autotrophs to heterotrophs in the model.

The intertrack deviations are less for all the zooplankton groups in CTRL, Case II and Case III (Figures 13a–13c, 13g–13i, and 13j–13l). Whereas for Case I in which the new production is switched off, the zooplankton were completely depleted in consistent with the absence of PS and PL for tracks T1 to T3. However, for T4 and T5, the regenerated production of PS and PL supported some formation of zooplankton.

We present the seasonal change in vertically integrated biomass of PS, PL, ZS, ZL, and ZP for all the three cases (Figure 14 and Table 1). All the plankton decrease by more than 70% (an average from all the five Argo simulations) in Case I throughout the year. However, only PS (reduction of ~40%) and ZS (reduction of ~20%) show sensitivity to regenerated production as revealed in Case II. In Case III with no silicate limitation for PL growth, in all the seasons except MAM, there is almost an 80% increase in PL with corresponding changes largely manifest in ZP (see Figure S10 for individual Argo).

### 3.6.1. The Relative Role of Silica Versus Total Nitrogen in Limiting Diatoms Growth

In order to examine how the nutrient limitation plays a role in PS and PL growth, we examine the total limitation factors  $N$  (representing  $\frac{[NO_3]}{[NO_3] + K_{NO_3S}} e^{(-\psi_s[NH_4])}$ ),  $A$  (representing  $\frac{[NH_4]}{[NH_4] + K_{NH_4S}}$ ) and  $S$  (representing

$\frac{[Si(OH)_4]}{[Si(OH)_4] + K_{SiL}}$ ) in equation 2b for nitrate, ammonium, and silicate growth limitations, respectively. In

Figure 15, zero to one represents a complete limitation to no limitation. Nitrate and silicate are strongly limiting from the surface to a depth of 40 m albeit with slightly less limitation from silicate from March to June. The modeled and observed silicate concentrations from March to June are maximum relative to other

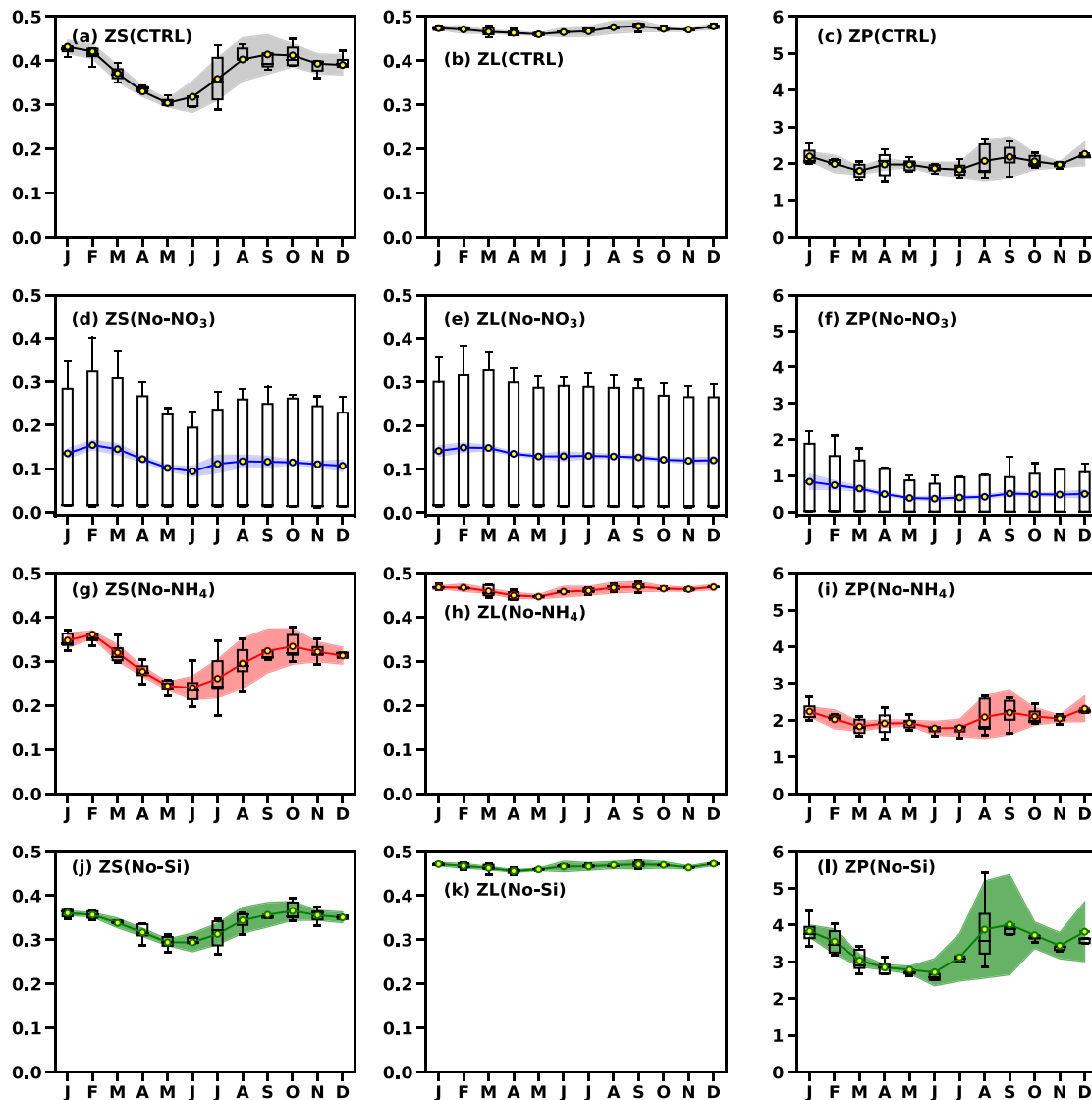
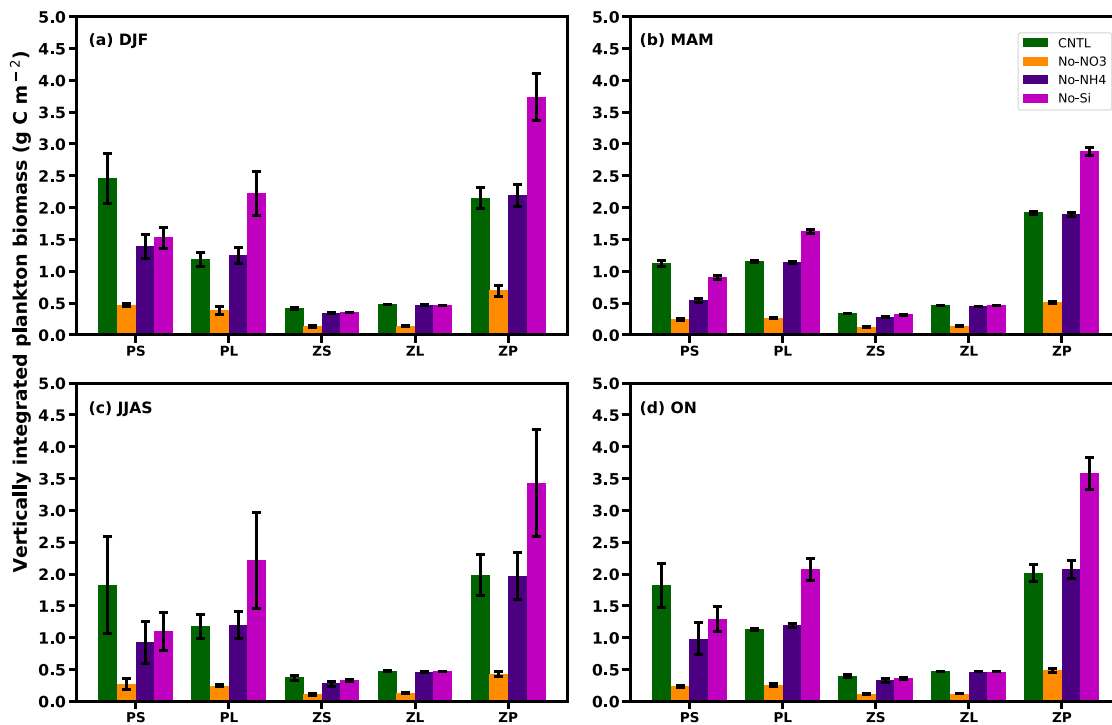


Figure 13. Same as Figure 12, but for zooplankton.

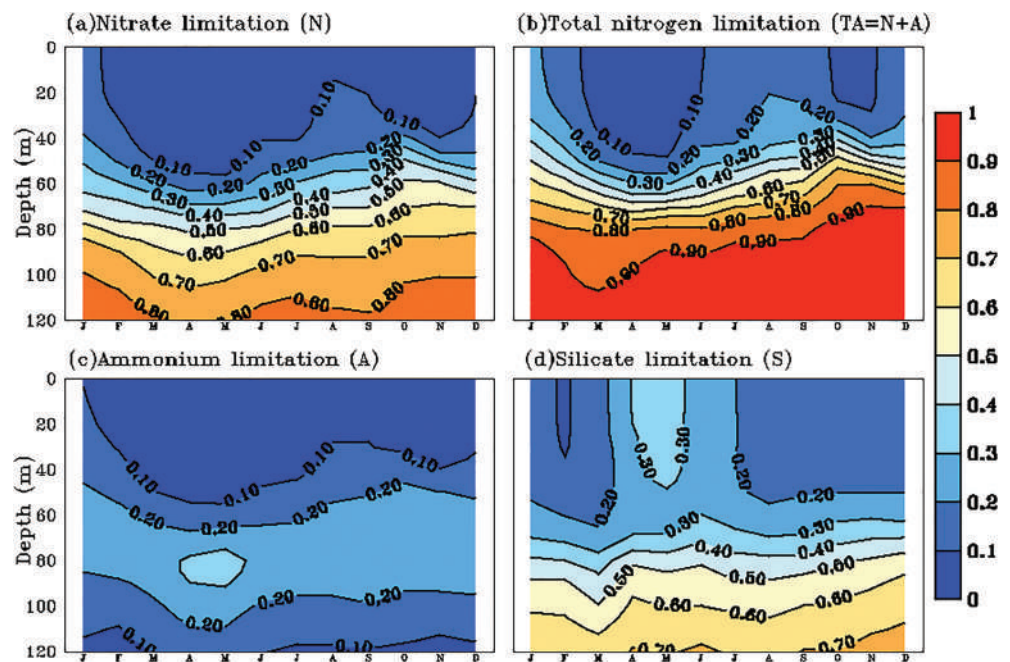
seasons. Ammonium limitation occurs throughout the water column with some exception at the SCM level where ammonium is generated through decomposition, egestion, and excretion processes. However, the combined nutrient limitation depth is confined to well above 45 m in the central AS. This is consistent with the depth of community compensation depth (where primary production balances the community respiration) in central AS as reported in Sreeush et al. (2018). There are no notable differences in nutrient limitation terms when we consider the individual Argo's (Figure S11). Along all the Argo tracks, the ammonium limitation is low at the SCM depths. Low silicate limitation exists during April and May along T4 and T5 whereas along T1, T2, and T3, the low silicate limitation extends from May to July.

The difference between  $N + A$  and  $S$  shows the dominant limiting nutrients in central AS (Figure 16). Positive values indicate a higher limitation potential of silicate with respect to nitrate and ammonium. Similarly, negative values indicate the opposite. Zero corresponds to equal limitation by both nitrogen (nitrate + ammonium) and silicate. Throughout the year, from the surface to 20 m (except during March to June), both nitrogen and silicate limit production by equal amounts. Throughout the SCM region, silicate severely limits primary production as compared to nitrate. From March to June and from the surface to 40 m,

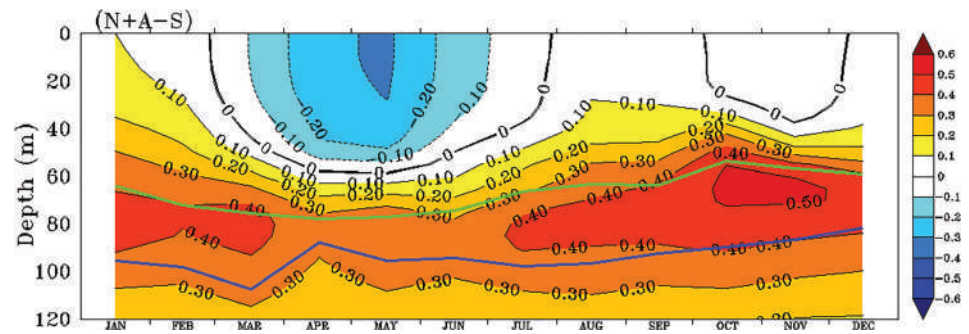


**Figure 14.** Seasonally averaged and depth-integrated (0–120 m) plankton biomass during (a) DJF, (b) MAM, (c) JJAS, and (d) ON in all the three sensitivity cases. Error bar shows the standard deviation of daily data during each season from 2013 to 2016. Units are  $\text{g C m}^{-2}$ .

nitrate has a larger potential to limit primary production in the central AS. There is an interplay of opposite phasing between silicate and nitrogen limitations at the surface throughout the year (Figures 16 and 17, Figures S12, S13, and S14 for intertrack deviations, respectively). Figures 11c and 11d are indicative of the



**Figure 15.** Seasonality of vertical distribution of growth limitation factors for PL shown as climatology computed from 2013 to 2016. (a) and (c) nitrate limitation ( $N$ ) and ammonium limitation ( $A$ ), (b) Total nitrogen limitation ( $TA = N + A$ ), (d) silicate limitation ( $S$ ). Zero represents complete limitation, and one represents no limitation.



**Figure 16.** Seasonality of differences between nitrogen and silicate limitation factors for PL shown as climatology calculated from 2013 to 2016 (plus regions represent silicate limitation, and the negative regions represent nitrogen limitation). The thick black line represents 0 (i.e.,  $N + A = S$ ). The green and blue lines represent nitricline and silicicline, respectively.

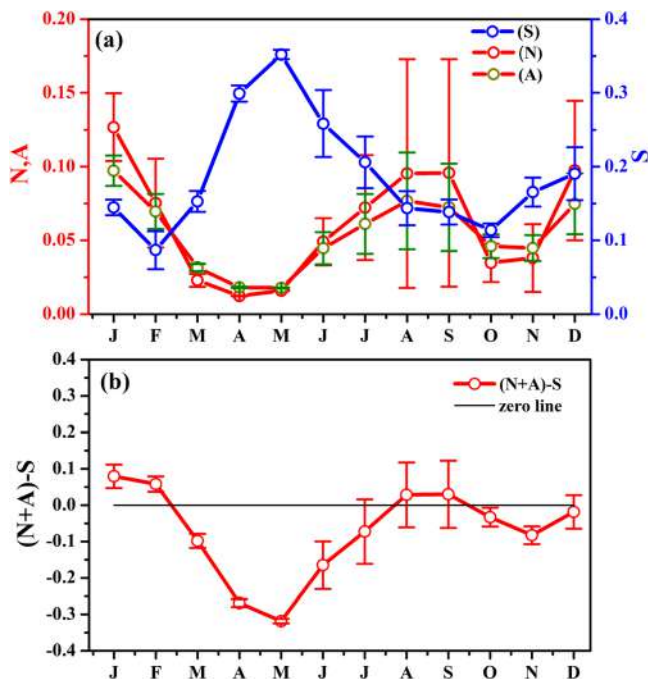
presence of supply of silicate at the surface during March to June which is also seen in the WOA observations.

Central AS is severely limited by silicate throughout the year from a depth range of 40 to 80 m albeit with less severity during April to June. It is interesting to note that below this depth (at ~100 m), silicate concentration increases (also refer Figures 11c and 11d). However, the supply of this into the core SCM zone is a delicate process involving deepening of the mixed layer and other entrainment processes which control diatom production. The duration of dominance of nitrogen limitation over silicate is longer (March to July) along T1, T2, and T3 (Figures S12a to S12c), whereas it is shortened to April and May in the remaining tracks. It is noteworthy that in T3 (T4), there is some dominance of nitrogen limitation over silicate in September and December (November) and is seen very close to the surface ocean.

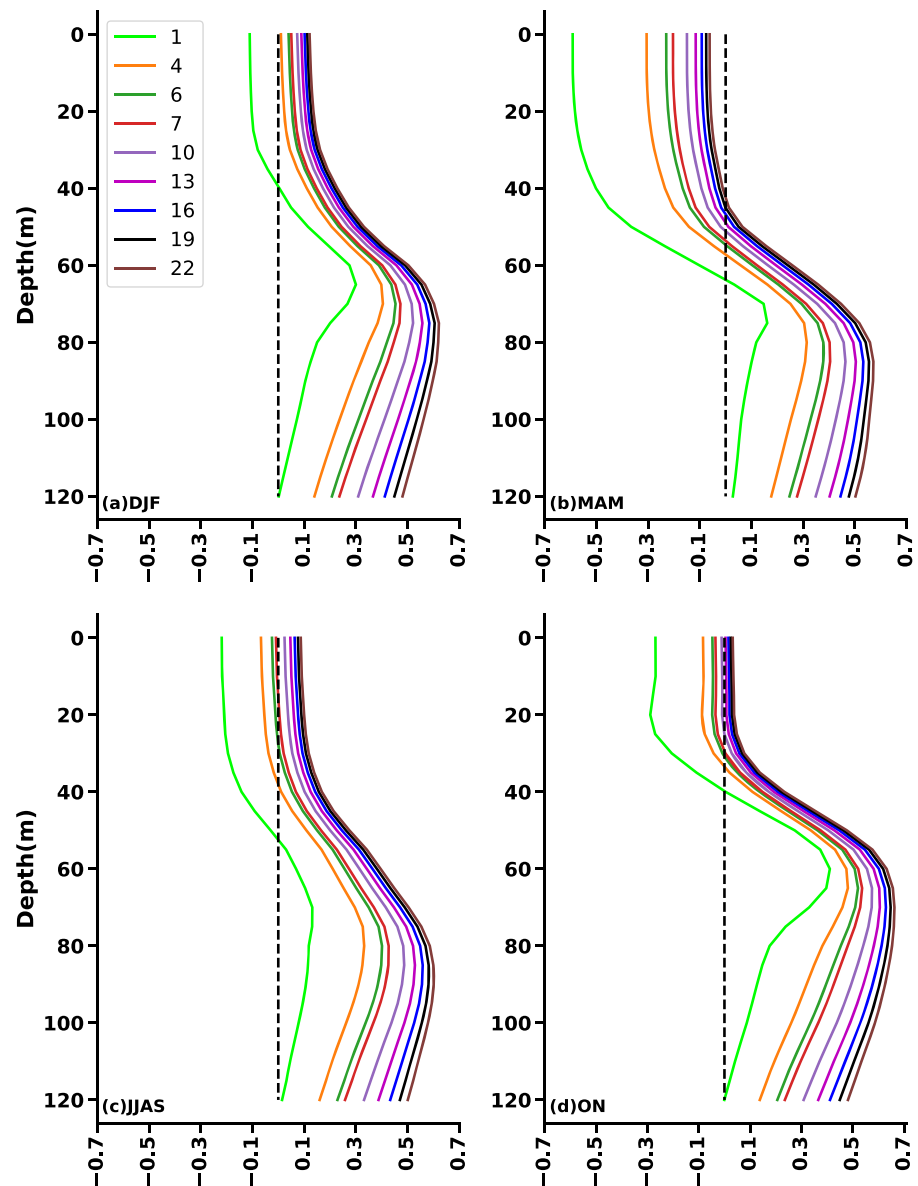
We have evaluated whether our conclusions (such as dominance of nitrogen limitation over silicate in the upper ~40 m of the ocean during March to June and dominance of silicate limitation over nitrogen at SCM depths throughout the year) arise due to our choice of  $K_{\text{sil}}$  according to Yamanaka et al. (2004). Figure 18 compares the vertical profile of  $N + A - S$  for various  $K_{\text{sil}}$  values and for various seasons. It is clear that the upper 40 m of the ocean and during March to May, none of the  $K_{\text{sil}}$  values results in positive  $N + A - S$  indicating that the dominance of nitrogen limitation over silicate is not sensitive to the choice of  $K_{\text{sil}}$  in the model. Similarly, at SCM depths, the silicate limitation over nitrogen is also not sensitive to the choice of  $K_{\text{sil}}$ .

#### 4. Discussion

Our efforts in adapting NEMURO to the AS and coupling it with a 1-D mixed layer module have yielded remarkably realistic simulations of the ecosystem response compared to observations. The absence of SST intra-seasonal variability in the present model can be attributed to the absence of thermocline undulations associated with ocean dynamics, eddies, lateral advection, and so forth, which are not captured in the 1-D framework. Along all Argo tracks simulated here, MLD peaks during JJAS (wind-induced mixing) and DJF (convective mixing). During the intermonsoon periods MLD shoals (20–30 m) due to the relatively weaker winds and increased insolation. The model MLD variability for the central AS is in agreement with Bhaskar et al. (2007) with maximum depth (70 m) during JJAS (due to wind stirring) and DJF (60 m, due to strong convective mixing). The strong mixing (wind-induced



**Figure 17.** (a) Seasonality of differences in  $N$ ,  $A$ , and  $S$  at the surface (b) differences between limitation ( $N + A - S$ ) factors for PL at the surface shown as climatology calculated from 2013 to 2016. Error bar shows the standard deviation of daily data of individual months from 2013 to 2016.



**Figure 18.** Seasonally averaged vertical profiles of  $N + A - S$  factors for PL for different values of  $K_{sil}$ . (a) for DJF, (b) for MAM, (c) for JJAS, and (d) for ON.

and convective) and the nutrient enrichment to the surface ocean are responsible for summer and winter blooms over the AS (Banse, 1987), respectively.

The model reproduces SCM quite successfully as compared to Argo observations. The seasonal cycle of SCM is associated with the mixing processes in AS. During JJAS and DJF, high mixing allows enrichment of nutrients to the upper ocean which enhances production in the surface waters and leads to a spread of SCM in the water column (Piontkovski et al., 2017). SCM is noticed within the depth of maximum ammonium concentration which indicates that regenerated production has a role in SCM formation which is consistent with observational evidence from Sarma and Aswanikumar (1991) and is found particularly important for two Argos in the eastern AS. A well-developed patch of SCM in the intermonsoon is highlighted due to the weak production at the surface due to nutrient limitation.

In the detailed analysis of plankton groups, we found that the magnitude of PS in the surface is higher than that of PL. It can be due to the potential silicate limitation and high grazing pressure on PL by zooplankton

(Roman et al., 2000). The weaker surface bloom of PL during March to June is due to strong nitrogen limitation on diatoms at the surface while the stronger vertically integrated bloom of PL during March to June is due to the availability of silicate at depths. The higher magnitude of PS than PL at SCM depths can be due to the upper growth limitation by zooplankton (ZP) grazing and silicate limitation on PL (Piketh et al., 2000; Roman et al., 2000; Wiggert et al., 2006). The higher magnitude of ZP compared to ZS and ZL can be due to the high grazing pressure on PL. ZS can graze only on PS (size dependent grazing), and ZP can graze on PL. As a result, the seasonality of ZS (ZP) depends on PS (PL). The maximum concentration of ZP at subsurface is due to the abundance of prey.

The subsurface maximum concentration of ammonium in the water column is due to the remineralization and excretion from zooplankton communities which are concentrated more at the subsurface around 40–80 m due to availability of prey. Compared to nitrate, the ammonium concentration at the depths of SCM is weaker. However, this weak concentration of ammonium can support the primary production in the sunlit zone of the ocean because the assimilation of ammonium requires less energy during photosynthesis than that required for nitrate assimilation (MacIsaac, 1978; MacIsaac & Dugdale, 1972).

In the model, the half saturation coefficient for both nitrate and ammonium for PL is three times greater than that of PS as in Yamanaka et al. (2004). This indicates that PS can acquire resources rapidly even at its lower concentration of nutrients than PL (Mulder & Hendriks, 2014). Sigman and Hain (2012) point out that PS (PL) appears to have an important role in regenerated (new) production. It can be explained by the choice of half saturation coefficients of nutrients for PS and PL and preference of phytoplankton for ammonium over nitrate (Wroblewski, 1977). The lower value of half saturation coefficient of ammonium for PS allows it to depend on ammonium along with nitrate for its photosynthesis; that is, both new and regenerated productions have a significant role in PS production (i.e., reduced PS in Cases I & II). On the other hand, PL depends on new production alone because it demands higher concentrations of ammonium in the water column (i.e., reduction of PL in Case I and no reduction of PL in Case II).

Observational evidence from the central AS shows a higher concentration of PS as compared to PL (Balachandran et al., 2008; Naqvi et al., 2002; Paasche, 1973) indicating the importance of silicate limitation. The silicate limitation can reproduce the observed concentration differences between PS and PL in the model (Balachandran et al., 2008; Naqvi et al., 2002; Paasche, 1973). It is worth mentioning that the model does not consider any external sources of silicate. The wind-borne dust can be an important source of silicate especially when westerly winds from the deserts are prominent over the AS during May to June. Moreover, the mixing over the AS is minimum during the MAM, and thereby, the entrainment of total nitrate to surface waters is limited leading to a severe limitation in production by nitrate than silicate. As the mixing progresses from MAM to JJAS and also during DJF when the convective mixing is prevalent, both the total nitrogen and silicate equally limit the production. Model studies (Koné et al., 2009; Wiggert et al., 2006) have shown that strong nitrogen limitation north of the equator over the entire IO and a reduction in the nutrient limitation during JJAS does occur. The stronger limitation of silicate compared to nitrate during DJF in the model results are consistent with the study of Naqvi et al. (2002).

## 5. Summary and Conclusions

A 1-D ecosystem model based on Yamanaka et al. (2004) with 13 state variables having silicon and nitrogen cycling is coupled with the 1-D mixed layer model of Mellor and Yamada (1982) and utilized for studying the role of silicate limitation in diatom blooms in the central AS. Model simulations are performed along five bio-Argo tracks (from 2013 to 2016) available from the central AS and along ship cruise tracks (for the year 2009) for the northern AS. AS is known to have seasonal phytoplankton blooms during winter and summer months driven by distinctive physical forcing mechanisms and subsequent nutrient dynamics. The model successfully reproduces the physical properties of the mixed layer when compared to satellite-derived observations and Argo as well as ship-borne observations with very reliable seasonality in the simulated ocean MLD and nutrient entrainment. Further, the model is used to investigate the role of nutrient limitation (nitrate, ammonium, and silicate) on primary production. Throughout the season, new production appears to support 80% of the primary production in the AS and implicitly controls the 70% production of the zooplankton biomass. Regenerated production supplements 50% for flagellates and other small phytoplankton with very little contribution to diatom blooms. Diatom production in the model is maintained close to the

observed values due to the silicate cycling in the model. Silicate is the primary limiting nutrient in the diatom bloom in the SCM with maximum limitation occurring during the winter season due to the deeper silicicline and a shallower nitricline. At the surface, both nitrate and silicate equally contribute to limiting the biomass. Nitrate appears to be a more dominant limiter as compared to silicate from March to June. Considering the relatively small riverine input of silicate to the AS, the seasonal upwelling in the western AS is ultimately an important source of silicate. Therefore, diatom bloom depends on this nutrient input which characterizes AS into two prominent zones; (a) western AS (west of 65°E) consist of a dominant diatom bloom and (b) eastern AS (to the east of 65°E) comprising a dominant flagellates bloom. In this context, a model with silicate cycling is essential to study the primary production of the AS. Interannual variability of these processes should yield further insights which will be reported elsewhere.

#### Data Availability Statement

The bio-Argo observations are available at <http://www.ifremer.fr/co-argoFloats/float?detail=true&ptfCode=6900451&lang=en>, and ship observations are available from the Centre for Marine Living Resources and Ecology (CMLRE). Atmospheric forcing was downloaded from the European Centre for Medium-range Weather Forecasts (ECMWF; <https://apps.ecmwf.int/datasets/data/interim-full-daily/lev-type=sfc/>). Ocean vertical velocity and mixed layer depth are downloaded from Estimating the Circulation and Climate of the Ocean (ECCO; <http://apdr.csoest.hawaii.edu/las/v6/constrain?var=4993> <http://apdr.csoest.hawaii.edu/las/v6/constrain?var=4981>).

Temperature, salinity, and nutrients data sets are available from World Ocean Atlas (<https://www.nodc.noaa.gov/OC5/woa13/woa13data.html>).

Sea surface temperature are downloaded from National Oceanic and Atmospheric Administration (NOAA) (<https://www.esrl.noaa.gov/psd/data/gridded/tables/sst.html>). All model outputs and observations used for analysis are uploaded ([https://zenodo.org/record/3339274#.XTAI\\_p9fg8o](https://zenodo.org/record/3339274#.XTAI_p9fg8o)).

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