Chapter 8
Primary Productivity Dynamics in the Northern Indian Ocean: An Ecosystem Modeling Perspective

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Abstract Primary productivity is the basic building block of the marine food web, and phytoplankton is the main primary producer in the ocean. The assimilation and fixation of dissolved inorganic carbon and other inorganic nutrients into organic matter by phytoplankton are known as primary production. The oceanic primary production is essential in regulating the ocean carbon cycle. Phytoplankton consumes atmospheric carbon dioxide and subsequently transfers it to the sediment of the deeper ocean in a process called biological pump. Although the Indian Ocean covers less than 5% of the total area of world oceans, its unique geomorphological settings make it a globally significant ecosystem from the perspective of primary productivity and other related biogeochemical processes. The twin basins of the Indian Ocean, namely, the Arabian Sea (AS) and the Bay of Bengal (BoB), are known to have contrasting characteristics regulating primary productivity. The Bay of Bengal is generally considered to be less productive than the Arabian Sea. The drivers controlling the primary productivity in the northern Indian Ocean include

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physical factors like sea surface temperature, sea surface salinity, and upwelling, geochemical factors like nutrients (nitrates, phosphate, and silicate), and biological factors like phytoplankton species composition. There are several crucial physical processes associated with the phytoplankton bloom dynamics and primary production, like vertical and horizontal advection, dynamics of the mixed layer depth, and turbulent diffusion. Productivity measurements and physiological rate parameters of phytoplankton suggest that it is not strongly limited by nutrient supply or irradiance in this region. On the contrary, a reduction in primary productivity has been reported due to increased warming of the tropical Indian Ocean. A major shift in the phytoplankton species composition has also been reported in the Indian Ocean and its two basins. State-of-the-art observations on primary productivity suggest that irrespective of its regulating factors, the primary productivity of the Indian Ocean region can efficiently export carbon to the deeper ocean. The Indian Ocean is one of the most significant regions in the global ocean carbon cycle considering its long-term carbon sequestration process in a changing environment. The availability of observations in the northern Indian Ocean is limited, especially with respect to biogeochemical variables, hindering the explication of the dynamics of the marine system. The ecosystem models prove to be an incredible tool that can reinforce satellite and ship-borne observations to explicate the dynamics of the marine system. The modeling studies on primary productivity that has been carried out on the northern Indian Ocean have resulted in major advances in our understanding. Improved model resolution and better understanding and modeling of the fundamental processes involved in the interactions between the physical and biological states of the ocean can further improve our understanding of primary productivity. Keeping in mind the future climatic projections, the Indian Ocean along with the global ocean needs to be monitored closely on the aspects of physical-biogeochemical interactions.

Keywords Indian Ocean productivity · Satellite chlorophyll-a · Vertically generalized productivity model · Mixed layer depth

1 Introduction

The unique characteristics of the northern Indian Ocean (IO) basin have significant control on the primary productivity (PP) dynamics of the region. One of the prominent features of the region is the northern land boundary extending up to 26° N. The Indian subcontinent divides the northern IO into the Arabian Sea (AS) in the west and the Bay of Bengal (BoB) in the east. Another aspect is the annual monsoons characterized by seasonally reversing surface winds leading to intense rainfall over the northern part of the basin during summer. The circulation pattern driven by the seasonal reversal of monsoonal winds and the distributions of resultant upwelling phenomenon provides the physical forcing that controls the distinct biogeochemical (BGC) variability throughout the region. The convective mixing caused by cool and dry northeasterly winds results in winter blooms of phytoplankton over the northern and central AS during the northeast monsoon (Wiggert et al., 2005; Lévy et al., 2007). However, during the southwest monsoon, a combination of Ekman pumping, horizontal advection, and coastal upwelling result in abundant phytoplankton blooms off the coast of Oman that can propagate more than 500 km away from the coast (Brock & McClain, 1992). Upwelling and entrainment around the Great Whirl give rise to the summer bloom off the coast of Somalia (Schott, 1983; Fischer et al., 1996). In the BoB, the evolution of the cyclonic gyre known as Sri Lanka Dome, recurring annually during the southwest monsoon, is initiated by Ekman pumping (Vinayachandran & Yamagata, 1998). The advection of nutrients upwelled south of the Indian Peninsula to the sea east of Sri Lanka by the intruding Southwest Monsoon Current leads to an enhanced PP at sea east of Sri Lanka (Vinayachandran et al., 2004). In the northern BoB, PP is regulated by the freshwater discharge and also by mesoscale activity (Prasanna Kumar et al., 2004).

In the early stages, the BGC modeling studies of the IO focused mostly on the AS but later it expanded to the whole basin. In an earlier study by Young and Kindle (1994), simple biological formulations were utilized to highlight the significance of horizontal advection of the upwelled water along the Omani coast during the southwest monsoon. This upwelled water supplies nutrients to the open ocean through currents. The first large-scale model for studying coupled ecosystem dynamics of the AS was configured by McCreary Jr et al. (1996) and Fasham et al. (1998). Although the BGC models used in these works were different, both were implemented at relatively a lower horizontal resolution and forced with climatological data. These models also utilized similar mixed layer parameterization, based on Kraus and Turner (1967). Owing to their comparable treatment of the physical processes, the results of the above studies are quite comparable. The studies revealed pronounced phytoplankton blooms during the monsoon season with distinct spatial changes in the bloom dynamics. The classification of the growth response of phytoplankton with respect to physical processes is indicated in these studies. These processes, together with the horizontal advection of nutrient-rich water from the coastal region into the central AS, are the physical drivers of the observed phytoplankton variability. However, the bloom dynamics in these models were simpler and, in several cases inaccurate, compared to observations. Both the models exhibited relatively lower phytoplankton biomass during the monsoon season. Another study by Ryabchenko et al. (1998) discussed similar outcomes based on modeling. But, these studies failed to represent the phytoplankton bloom in the northeastern AS and attributed the reason for this failure to excessive grazing.

Later studies on BGC modeling confirmed the significance of southwest monsoon period nutrient advection in nourishing offshore blooms observed in the ocean color data (Kawamiya, 2001). The first fully coupled biophysical modeling study of the IO was described in Wiggert et al. (2006). Their model successfully captured the basin-wide distinction in phytoplankton abundance during the southwest monsoon. Kone et al. (2009) coupled a 3D primitive equation model to an ecosystem model to understand the biological productivity through BGC cycles of carbon and other key nutrients like phosphate, nitrate, silicate, and iron. Their model reproduced the seasonal phytoplankton bloom well in association with nutrient limitations and highlighted the role of physical processes like turbulent diffusion, horizontal and vertical advection, and mixed layer bloom dynamics.

The main focus of this chapter is delineating the phytoplankton variability in the IO. In the next few sections, a more comprehensive overview of different approaches to estimating PP, modeling PP, and the drivers of PP is elaborated.

2 Different Approaches of Measuring and Estimating Primary Productivity

Primary production is the process of fixation and assimilation of inorganic carbon and other inorganic nutrients into organic matter by autotrophic organisms. PP is defined as "the rate of change of biomass through photosynthesis per unit area (or volume) per unit time." There are two types of primary production: (a) gross productivity, which is "the amount of carbon fixed per unit space per unit time," and (b) net productivity, "the amount of carbon remaining after losses through respiration and decay." Phytoplankton is the main photosynthesizer in the ocean and the base of the marine food web. Hence, measuring in situ phytoplankton PP is a key domain for understanding the marine food web as well as carbon sequestration potential via a biological pump in the ocean. Different approaches have been taken to measure or estimate PP in the IO region. These methods include in situ methods, laboratory measurements, and estimation through remotely sensed data. Stable isotopic and radioisotopic methods are also notable among in situ and laboratory measurements, whereas different kinds of remote sensing and numerical modeling are also widely used for determining the variability of PP on large scales, spatially and temporally. These have been elucidated further in the next subsections.

2.1 Primary Production Measurement and Estimation Methods Implemented in the Indian Ocean Region

PP was mainly studied by in situ and laboratory measurements in the IO region. The concentration of chlorophyll-a (Chl-a) is the primary requirement for the estimation of PP since variations in primary production directly follow the changes in Chl-a concentration (Kulk et al., 2020). Different expedition cruises were conducted for measurement of PP. The concentration of Chl-a was also measured extensively in those cruises (Hanson et al., 2007). For example, during the AS expedition, which was part of the US Joint Global Ocean Flux Studies (US JGOFS), Chl-a and other pigments were measured using both fluorometer and high-performance liquid chromatography (Barber et al., 2001). Along with the measurement of Chl-a as an indispensable part of the PP measurement, the methods for the estimation and enumeration of phytoplankton cell density using the Sedgewick rafter counting chamber were also used, as adopted by Chowdhury et al. (2021) for the IO region. A summary of the studies on PP in the IO, sequentially categorized in the order of time period of data measurement, is listed in Table 8.1.

Radioisotopes for estimating in situ PP were also used during the last few decades. In situ estimation of PP included ^{14}C incubation and clean techniques which was a part of in situ data collection during 1992–1997, as part of the Indian program of Joint Global Ocean Flux Study (JGOFS) (Kumar et al., 2000). A combination of in situ measurements and remotely sensed data as a part of the BoB process studies program was used to analyze the seasonal variability of the upper ocean and associated BGC response (Kumar et al., 2007). They used monthly mean Chl-a pigment concentration data derived from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) global 9 km monthly imagery along with in situ Chl-a and radioactive estimation of PP. Marra and Barber (2005) estimated PP in the AS using surface irradiance (Weller et al., 1998) and in situ observations of Chl-a (Kinkade et al., 2001). They measured productivity from ^{14}C assimilation and used nitrogen-based productivity measurements and heterotrophic processes to explicate changes in the biomass of phytoplankton and productivity in the AS.

Madhupratap et al. (2003) also used the ^{14}C incubation and radioactivity measurement using a scintillation counter, to estimate PP values ranging from 40 to 502 mg C m^{-2} d^{-1} in the BoB, during the summer monsoon, which was lower than that reported in the AS values for the same season. Sarma et al. (2020) computed the total primary production in the BoB, using enriched sodium bicarbonate tracer, following Hama et al. (1983), which involved measurement of particulate organic carbon concentration and the atomic ratio of $^{13}C/^{12}C$. Sherin et al. (2018) measured the isotopic compositions of carbon and nitrogen in suspended matter using an elemental analyzer together with an isotopic ratio mass spectrometer and expressed the results relative to conventional standards for carbon and atmospheric nitrogen. They also grouped pigment biomarkers in the BoB, to understand the influence of different size classes in total phytoplankton biomass following Uitz et al. (2006).

Singh and Ramesh (2015) used the ^{15}N tracer technique, to estimate new (based on nitrate uptake) and regenerated production (based on urea and ammonium uptake) (Dugdale & Goering, 1967), in addition to estimation of primary production in the northern IO. This technique computes PP using uptake rates of nitrate, ammonium, and urea, integrated over the photic zone. This technique was first used in the AS during the JGOFS program (Watts et al., 1999; Watts & Owens, 1999). Wei et al. (2019) proposed a fast repetition rate fluorometry-based approach, with the introduction of a non-photochemical quenching proxy, to derive carbon uptake rates in the BoB.

Remotely sensed data based on Moderate Resolution Imaging Spectroradiometer (MODIS) utilizes two global models for the computation of net primary production, (a) vertically generalized productivity model (VGPM) (Behrenfeld & Falkowski, 1997) and (b) mixed layer depth production model (MLPM) (Howard, 1995). Two other available models are the Antoine and Morel absorption-based model (Antoine & Morel, 1996) and Platt and Sathyendranath numerical integration of spectral

Table 8.1 Studies on PP in the IO, sorted by time period of data measurement

Region of study	Range of estimated PP (mg C m^{-2} d^{-1})	Time period for measurement of data	Method adopted for calculation	Reference
AS	163–1782	1992–1997	In situ incubation protocol	Kumar et al. (2000)
AS	1800–3000	1994–1995	^{14}C assimilation	Marra and Barber (2005)
Central AS (65°E)	1032–1476	1995	^{14}C assimilation	Barber et al. (2001)
Northern IO	24–5976	1994–2007	^{15}N tracer technique	Singh and Ramesh (2015)
Coastal eastern IO (21–30°S, 111°E)	110–530	2000	Double integration of photosynthesis through depth and time using trapezoidal method	Hanson et al. (2007)
BoB	400–1400	2001	Light and dark bottle method	Rao et al. (2003)
BoB	40–502	2001	^{14}C incubation	Madhupratap et al. (2003)
BoB	115–513	2002–2003	In situ incubation protocol	Kumar et al. (2007)
BoB	845–1088	2013	Vertically generalized productivity model	Lakshmi et al. (2014)
Southwestern tropical IO	176–268	2014	Vertically generalized productivity model	Tripathy et al. (2020)
BoB		2016 (Nov–Dec)	Fast repetition Fluorometry	Wei et al. (2019)
BoB	60–160	2019 (June)	Enriched sodium bicarbonate tracer	Sarma et al. (2020)

model (Platt & Sathyendranath, 1988). Bhattacharya and Mishra (2005) detailed and compared these models while studying the PP in case 2 waters of northeastern BoB and found that the VGPM gives better results than the MLPM, in their study region.

A study reporting decline in oceanic PP (by 20%) due to increased warming over the tropical IO (Roxy et al., 2016) computed net primary production based on SeaWiFS chlorophyll data, advanced very high-resolution radiometer SST, and photosynthetically active radiation. The above mentioned remotely sensed data were employed by several researchers in a commonly used model (VGPM) for computing PP in the IO (Lakshmi et al., 2014; Tripathy et al., 2020; Roxy et al., 2016; Sarma & Dalabehera, 2019; Rao et al., 2003). The results are detailed in the coming sections.

2.2 Types of Model Estimation of Primary Production

PP models can be classified depending on euphotic depth (Zeu) and wavelength (400–700 nm). The available models are depth-integrated models, wavelength-integrated models, time-integrated models, and wavelength-resolved models. Behrenfeld and Falkowski (1997) proposed the Behrenfeld-Falkowski vertically generalized productivity model in which surface chlorophyll is connected to depth-integrated PP up to the euphotic zone. Along the east coast of India, Lakshmi et al. (2014) estimated the PP using the depth-integrated (euphotic depth) vertically generalized productivity model. The input variables used for the model are remotely sensed concentration of Chl-a, vertically diffused attenuation coefficient, radiation conducive to photosynthesis (PAR), and sea surface temperature. For the BoB region, they have estimated PP ranging between 845 and 1088 mg C m^{-2} d^{-1}, using Megard (1972) method, and 650–857 mg C m^{-2} d^{-1}, using the method proposed by Ryther and Yentsch (1957). The least PP was observed during April, after which it increased from May to July, reaching a maximum of 757 mg C m^{-2} d^{-1}. PP in the BoB decreases from July through November.

For the AS, seasonal estimates of net PP were computed using a biophysical coupled model for different cases of aerosol deposition, by Guieu et al. (2019). They used the Regional Ocean Modeling System model coupled with an ecosystem model, Pelagic Interaction Scheme for Carbon and Ecosystem Studies (PISCES) v2, to signify the role of aerosols in PP over the AS during 1998–2014. In their model simulations without aerosol depositions, the net PP reduced from 498 to 451 mg C m^{-2} d^{-1} from the northeast monsoon (DJFM) to spring inter-monsoon (AM), while a reduction from 554 to 521 mg C m^{-2} d^{-1} was seen during the southwest monsoon (JJAS) and the fall inter-monsoon (ON) seasons, respectively. The model simulations with all aerosol (P, N, Fe, Si) depositions, however, showed relatively higher values, 607 mg C m^{-2} d^{-1} in DJFM, 449 mg C m^{-2} d^{-1} in AM, 855 mg C m^{-2} d^{-1} in JJAS, and 641 mg C m^{-2} d^{-1} in ON.

Antoine and Morel (1996) introduced an absorption-based model which uses basic variables like irradiation, phytoplanktonic biomass, and the photo-adaptive state of the phytoplankton to determine PP. The use of Chl-a content and photo-

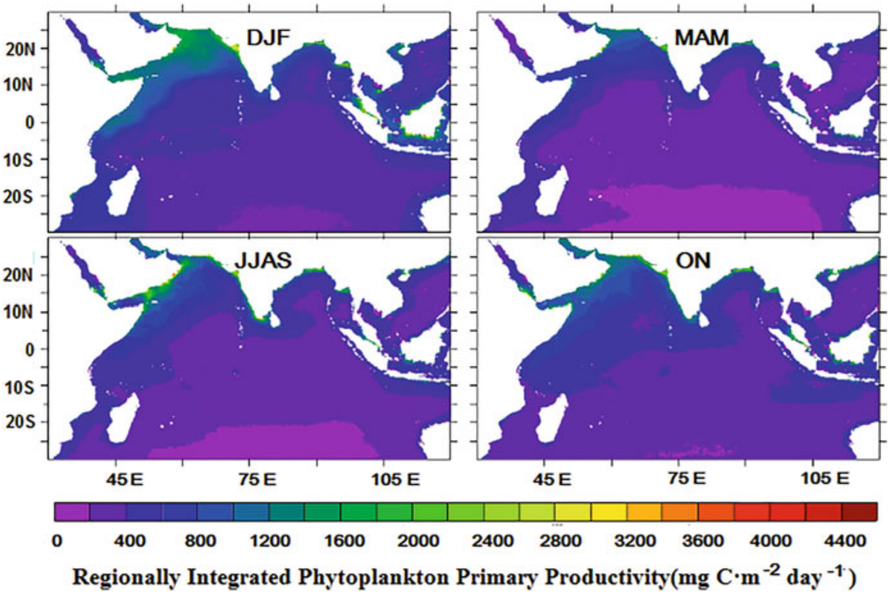

Fig. 8.1 Seasonal variations of PP in the IO. DJF refers to average over the months December, January, and February; MAM refers to March, April, and May; JJAS refers to June, July, August, and September; ON refers to October and November

adoption differentiate this absorption-based model from the depth-integrated model. This model uses column-integrated chlorophyll content, whereas previous models used surface Chl-a. The VGPM is based on an optimal temperature-dependent photo-adoption rate, but the absorption model is based on two basic aspects of the photosynthetic process: the Chl-a-dependent absorption by the photosynthetic apparatus in the phytoplankton and the amount of carbon fixed per mol quanta of absorbed radiation.

Figure 8.1 shows the seasonal variations of PP estimated for the IO region. The estimation is based on a combination of remotely sensed data of Chl-a and light and ship-based measurements on some model parameters. The figure depicts the zones with enhanced biological activity, which is prominent along the northern AS during winter and along the west coast of India during the southwest and northeast monsoons. The monthly data of PP, used to prepare this figure, are available from 1998 to 2010 at 9 km spatial resolution (https://www.oceancolour.org/thredds/catalog/TWAP-PProd/catalog.html; Sathyendranath et al., 2019). PP in this dataset was computed using a spectrally resolved vertical model of light transmission and primary production (Longhurst et al., 1995), using Chl-a, phytoplankton photo-physiology, and surface irradiance. The error estimates for all OC-CCI products are RMSD 0.31 to 0.34, bias −0.006 to −0.04, and R-square 0.73 to 0.81. We have also utilized the same dataset to determine seasonal estimates of PP for regional seas in the IO. These have been detailed in Table 8.2 as regionally integrated values, during 1998–2010.

Table 8.2 Regionally depth-integrated estimates of PP for the IO and its regional seas for different seasons

Seasons	Regionally integrated phytoplankton PP (mg C m^{-2} d^{-1})		
	IO (30°S–30°N, 30°E–120°E)	AS (6°S–30°N, 32°E–78°E)	BoB (5°N–25°N, 80°E–100°E)
DJF	411.0	603.6	488.8
MAM	406.6	588.3	561.7
JJAS	439.9	688.2	546.0
ON	444.4	651.5	526.9

DJF refers to average over the months December, January, and February; MAM refers to March, April, and May; JJAS refers to June, July, August, and September; ON refers to October and November. The error estimates for all OC-CCI products are RMSD (0.31 to 0.34), bias (−0.006 to −0.04), and R-square (0.73 to 0.81)

An extensive review of PP in the BoB is provided in Löscher (2021) with historical values during several seasons. They have also highlighted decreasing rates of primary production in the northern and equatorial IO with a decrease of 9.7% and 17.2% per decade, respectively. This was attributed to a decrease in diatom and chlorophyte primary production, a coinciding increase in cyanobacterial abundance, and decreasing nitrate and silicate concentration. Their estimations based on satellite measurements showed a decrease in PP by 15.4% and 24.8% per decade, for both the BoB and the AS, respectively. They argue that the BoB would be an oceanic basin with a weakened oxygen minimum zone and a marked decrease in primary production unless external inputs of iron, nitrate, and silicate increase.

2.3 Significance of Model Estimation of Primary Production

Changes in ocean primary production control the concentration of atmospheric CO_2 and thereby regulate the global climate. The rising interest in studying the influence of the ocean in controlling the global climate system has pivoted modeling studies for determining PP. Mathematical models of primary production range from simple functions of Chl-a concentration at surface to complex bio-optical models. Global projections make it essential that model inputs are limited to datasets that can be remotely measured or easily calculated from surface measurements. Ecosystem models implemented in climate research show high variations in simulating trends in primary production. In the latest IPCC report, it was shown that some models presented no significant trends in forecast values while others projected negative trends. Froelicher et al. (2015) were able to report uncertainties in marine PP trends estimated using these ecosystem models. Some of these uncertainties were attributed to incomplete knowledge of the fundamental processes. In this context, it is important to understand the fundamental processes better and to improve existing models for better prediction of future climate.

Ecosystem modeling is an essential scientific pathway to explicate the dynamics of the marine system and predict its evolution at both short and long timescales. There has been much work done in recent years to simulate BGC processes prevalent in the northern IO using different suites of models ranging from simple 1D process and location-specific models to highly complex basin-scale models such as Tracers of Phytoplankton with Allometric Zooplankton (TOPAZ) (McCreary Jr et al., 1996, 2001, 2013; Swathi et al., 2000; Hood et al., 2003; Vinayachandran et al., 2005; Sharada et al., 2008; Resplandy et al., 2012). Regional models were also developed to study the BGC processes regulating the productivity of the IO (Chakraborty et al., 2016, 2018, 2019a).

Several observational studies showed that nutrient enrichment in coastal and open ocean waters triggers the phytoplankton bloom in the AS (Madhupratap, 1999; Banse & English, 2000; Wiggert et al., 2005). Previous research on phytoplankton dynamics in this region envisaged dominance of phytoplankton bloom in the order of diatoms, cyanobacteria, and dinoflagellates (Sawant & Madhupratap, 1996). The ecosystem models prove to be an incredible tool that can reinforce and back satellite and ship-borne observations to provide assessment of PP at greater spatial and temporal timescales for the IO as well as the global ocean. The modeling studies can aid in revealing the role of PP in regulating the carbon cycle of the ocean and atmosphere. The identification of potential fishing zones of the ocean can also be easily done using the outputs of high-resolution coupled ocean-ecosystem models (Chakraborty et al., 2019b).

3 Modeling Primary Production

The carbon cycle in any oceanic ecosystem is known to depend strongly on physical dynamics in that ecosystem. One such example is the process of vertical mixing which can increase phytoplankton growth by bringing in nutrients from the subsurface into the surface, or contrariwise it can decrease photosynthetic activity by carrying down nutrients and phytoplankton away from the photic zone. Whether vertical mixing can enhance the quantity of the marine biota depends on a delicate balance of competing circumstances like nutrient and light availability. The relation between changes in the upper ocean ecosystem and the mixed layer depth (MLD) has been studied previously on the basis of numerical modeling (e.g., Venrick et al., 1987; Polovina et al., 1995). Processes within the MLD have a great influence in controlling PP, and thus, these processes should be replicated in numerical models for better estimation. Hence, most of the model studies that investigate the BGC dynamics include the coupling of carbon and nutrient cycles with these physical mechanisms. Bacastow and Maier-Reimer (1990) developed a coupled ocean-ecosystem general circulation model which reproduced the deep layer distribution of tracers and, for the first time, tried to resolve the global ocean carbon cycle from a modeling perspective. However, this simplified model could not resolve the oceanic processes in MLD responsible for enhanced biological activities. In the subsequent modeling studies, several improvements were incorporated (e.g., Bacastow & Maier-Reimer, 1991; Najjar et al., 1992; Anderson & Sarmiento, 1995; Yamanaka & Tajika, 1996). In particular, Fasham (1993) and Sarmiento et al. (1993) integrated ecological components such as phytoplankton and zooplankton concentration into an ocean general circulation model as explicit state variables. This was done under the assumption that planktonic variables are controlled by vertical mixing and, therefore, the MLD and ecosystem relation could be improved.

The development of phytoplankton PP models and the fundamental synonymy between nearly all the models developed since the 1960s is well documented in Behrenfeld and Falkowski (1997). All of these models used a single formulation equating depth-integrated primary production ($\mathrm{PP_{eu}}$ [mg C $\mathrm{m^{-2}}$ $\mathrm{d^{-1}}$]) to surface phytoplankton biomass ($\mathrm{Chl_{sat}}$ [mg Chl $\mathrm{m^{-3}}$]), a photo-adaptive variable ($P^{\mathrm{b}}_{\mathrm{opt}}$ [mg C (mg Chl)$^{-1}$ $\mathrm{h^{-1}}$]), euphotic depth (Z_{eu} [m]), an irradiance-dependent function ($f(E_{\mathrm{par}})$), and day length (DL [h $\mathrm{d^{-1}}$]):

$$\mathrm{PP_{eu}} = \mathrm{Chl_{sat}} Z_{\mathrm{eu}} f\left(E_{\mathrm{par}}\right) \mathrm{DL}\ P^{\mathrm{b}}_{\mathrm{opt}} \tag{8.1}$$

where $\mathrm{PP_{eu}}$ is the daily carbon fixation integrated from the surface to the euphotic depth (Z_{eu}) and $P^{\mathrm{b}}_{\mathrm{opt}}$ is the maximum chlorophyll-specific carbon fixation rate observed in a water column measured under variable irradiance during incubations lasting several hours.

The modeling of PP for different sectors of the world ocean advanced in the last three to four decades. A summary of the sequential development of models used for the evaluation of PP has been depicted in Fig. 8.2. Earlier, there have been few attempts to model the nutrient and plankton dynamics of the upper ocean. The models then concentrated more on the interaction of phytoplankton and zooplankton only (Fasham et al., 1990). The models described in Pace et al. (1984), Fasham et al. (1985), Moloney et al. (1986), and Parsons and Kessler (1987) integrated all the components of the ecosystem and the flows of materials between these components. The background for a plankton dynamics model incorporating bacteria, protozoans, and dissolved organic matter was provided in Williams (1981). The results from such a model incorporating a large number of groups of organisms were described in Pace et al. (1984).

A realistic model based on plankton and nutrient dynamics of the mixed layer incorporating the major plankton groups (phytoplankton, zooplankton, and bacteria) and the major forms of nitrogen was first described in Fasham et al. (1990). This model tested several hypotheses prevalent for marine biota about food web structure and plankton dynamics and eased the configuration of sub-models which could resolve ocean circulation and biogeochemistry over basin-scale (Sarmiento et al., 1990). The main intention of the authors of Fasham et al. (1990) was to utilize this method to model the plankton dynamics and nutrient cycle over seasonal scales in the global ocean so that greater insight can be attained about the significance of

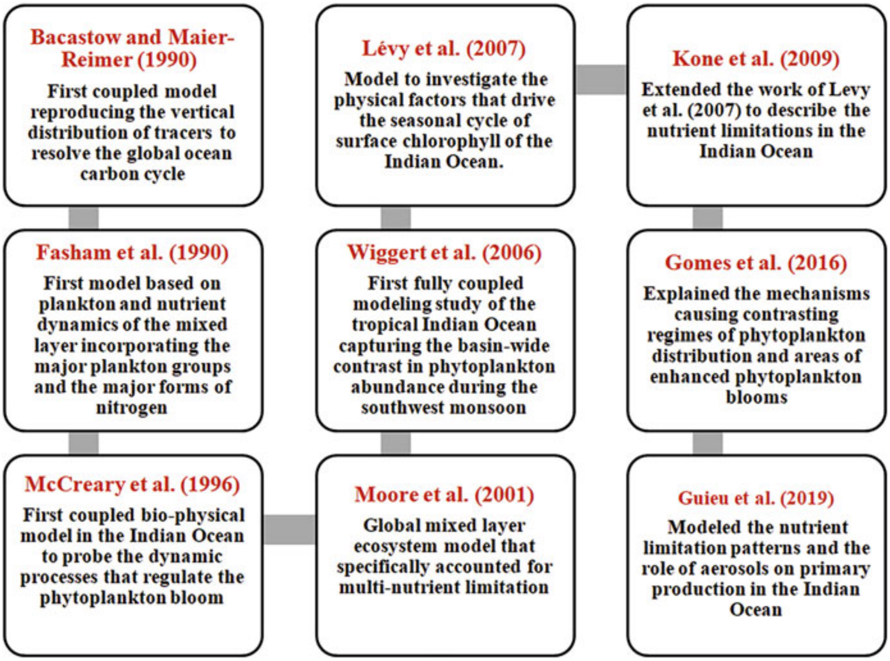

Fig. 8.2 Flowchart on development of models for estimation of PP

marine biology in controlling atmospheric CO_2. Consequentially, a global mixed layer ecosystem model that specifically accounted for multi-nutrient limitation (nitrogen, phosphorus, silica, and iron), diatoms, picoplankton, nitrogen fixation, and calcification was represented in Moore et al. (2001).

One of the earlier works on ecosystem modeling of the IO was chronicled in McCreary Jr et al. (1996), where the authors mainly focused on the biological productivity of the AS. The authors delineated the setup of a coupled biophysical model to probe the dynamic processes that regulate the biological processes and their annual cycles in the AS. They majorly concluded that three types of phytoplankton bloom develop in response to the physical processes like upwelling, entrainment, and detrainment in the AS. The phytoplankton bloom during the upwelling is strong and long-lasting, persisting as long as the upwelling occurs. Mostly, upwelling events in the AS take place during the southwest monsoon off Somalia, Oman, and India. This is in response to alongshore coastal winds. Near the mouth of the Gulf of Aden, bloom is mediated through Ekman pumping. The phytoplankton bloom due to detrainment is intense. However, these are brief events that develop due to abrupt thinning of the mixed layer. Contrary to the before-mentioned phytoplankton bloom events, the entrainment blooms are identified to be weak as entrainment leads to steady thickening of the mixed layer.

A coupled ocean-ecosystem model had been developed by Wiggert et al. (2006) to study the BGC processes over the IO basin. The ecosystem component used in this work has nine functional groups with size classified phytoplankton, zooplankton, and detritus and nutrients like nitrate, ammonium, and iron. The authors projected that the model successfully captured the basin-wide disparity in phytoplankton abundance during the southwest monsoon. The model also exhibited that the circulation pattern of the Somali Current and the spring Wyrtki jet has resulted in a remarkable influence on ecosystem dynamics of the southern BoB during the southwest monsoon.

Lévy et al. (2007) used the outputs from a physical ocean general circulation model to investigate the physical factors that drive the seasonal cycle of surface chlorophyll of the IO. They showed that OGCMs precisely assemble, both spatially and temporally, the bloom along with dynamical factors like the surface currents, the vertical velocity, and the mixed layer depth that most likely modulate productivity. They finally concluded that the physical control on the ocean biology may differ greatly over a short spatial extent. In an extended work of Lévy et al. (2007), Kone et al. (2009) analyzed the major physical and BGC coupled processes in the ocean using a biophysical model. The analysis presented by the authors manifested that at the onset of the bloom periods, the limiting nutrient over most of the IO was nitrogen. However, along the eastern part of the BoB, the ecosystem inclined toward silicate limitation. Their analysis also highlighted the fact that a variety of physical processes (mixed layer depth dynamics, advection in both the horizontal and the vertical, and turbulent diffusion) influence these bloom dynamics. Similar to this, Gomes et al. (2016) used a coupled biophysical ocean model to explain the dynamics behind increased phytoplankton blooms, observed first in remotely sensed datasets, in the oligotrophic regions of the BoB. The model results precisely indicated the contrasting regimes of phytoplankton distribution in the northern and the southern parts of the BoB and the effect of major IO dipole events on the ocean biology of the region.

In another modeling study of BGC processes of the BoB, Chakraborty et al. (2019a) used a coupled biophysical model configured using Regional Ocean Modeling System (ROMS) to study the upper ocean BGC variability of the BoB. The authors culminated that the physical state variables (temperature and salinity), the BGC state variables (nitrate, Chl-a, and dissolved oxygen), barrier layer thickness, and the mixed layer depth have strong seasonal and interannual variability. The variability is primarily controlled by the advection of water mass, local wind stress, and river runoff. Guieu et al. (2019) used ROMS coupled with BGC model, PISCES v2, to study the nutrient limitation patterns and the role of aerosols on primary production. Their study states that PP over the AS would be reduced by half if atmospheric iron inputs through dust deposition during the summer monsoon are absent. Most of the nitrogen fixation over the AS is supported by this atmospheric deposition of iron, while only a negligible fraction of the primary production is fixed by dinitrogen components.

4 Drivers of Primary Productivity in the Indian Ocean Region from Modeling Perspective

In the northern IO, low primary production in the BoB in comparison to the AS is a characteristic feature that is well-known (Prasanna Kumar et al., 2002). Previous studies concluded that low primary production in the BoB on annual timescales results from strong stratification due to freshwater river discharge and direct precipitation onto the sea, which impoverish nutrients in surface layers (Vinayachandran et al., 2002; Madhupratap et al., 2003; Gauns et al., 2005). On the other hand, higher PP in the AS is seen mainly due to the availability of high nutrient concentration in the upper ocean layers associated with wind-driven mixing during winter and coastal upwelling during summer (Schott, 1983; Anderson & Prell, 1992; Madhupratap et al., 1996; Gardner et al., 1999; Kumar et al., 2001; Wiggert et al., 2005). The seasonal and interannual changes in PP in the AS and the BoB result primarily due to changes in nutrient availability in the euphoric zone which in turn is controlled by salinity stratification in the water column. The extent of stratification is controlled by the balance between local evaporation-precipitation, freshwater discharge, wind-driven mixing, and upwelling-related dynamics (Lévy et al., 2001; Vinayachandran et al., 2002; Rao et al., 2011; van de Poll et al., 2013).

Over the global oceans, PP is controlled by many factors. The most commonly known drivers of PP are nutrients, irradiance, and temperature (Watts et al., 1999; Marra et al., 2007; Singh & Ramesh, 2015). A self-explanatory schematic showing the general drivers of PP is depicted in Fig. 8.3. In the IO, the monsoonal winds, circulation patterns, mesoscale features like eddies, and the ocean topography play an important role in controlling PP (Brock et al., 1993; Kumar et al., 2000; Barber et al., 2001; Wiggert et al., 2002; Kantha, 2004; Sherin et al., 2018; Sarma et al., 2020). Growth rates, grazing, and water column stability also cause PP variability in the water column (Sharada & Yajnik, 1997; Goericke, 2002; Wei et al., 2019). High nutrients in the photic zone and optimum irradiance within the spectrum of photosynthetically active radiation (wavelength between 400 and 700 nm) are known conditions that promote higher productivity. However, the interesting factor to note is the collective effect these variables have, along with temperature and salinity, in controlling PP, as seen in the case of the BoB and the AS. Even though productivity, in general, is limited in the BoB, new production is found to be high here, leading to a higher f-ratio (ratio of new production to primary production) in the BoB in contrast to the AS. This is due to sustained N_2 fixation by diazotrophs and eddy-mediated upwelling of nutrients from the below stratified waters (Singh & Ramesh, 2015; Da Silva et al., 2017; Zhou et al., 2020).

The variability of PP was found to be related more to phytoplankton absorption than to Chl-a variation, such that productivity normalized to absorption remains relatively invariant over the world oceans (Marra et al., 2007). Seasonal variability of PP in the IO is driven by the monsoonal circulation. Despite low iron and dust flux, high nutrient flux during the monsoons gives rise to high productivity than the inter-

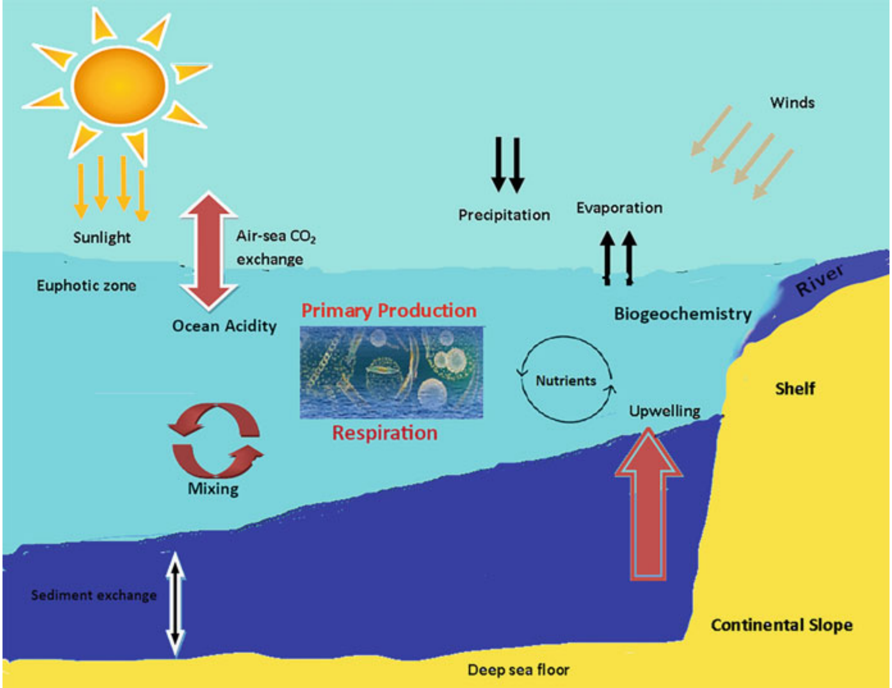

Fig. 8.3 Schematic showing the drivers of PP in the ocean

monsoons in the AS (Brock et al., 1993; Kumar et al., 2000; Barber et al., 2001). Dynamic processes governing circulation and mixing in the upper ocean computed from the mixed layer depth model in a given region were found to have a huge impact on modeling productivity patterns in that region (Kantha, 2004). However, it has been reported that depth-integrated models of PP estimation provide better results than mixed layer depth models of PP estimation (Bhattacharya & Mishra, 2005). Sharada and Yajnik (1997) have modeled the effects of grazing preference of prey densities on the behavior of the ecosystem and shown correlations of PP with Chl-a and sediment fluxes. Wei et al. (2019) applied fast repetition rate fluorometry to an independent field model-derived productivity in the BoB and found that in natural assemblages, light and depth responses to PP are less crucial than the numbers and structure of the phytoplankton communities in the region.

Studies on productivity in the Seychelles-Chagos Thermocline Ridge in the western IO showed how the interactions of currents with the ocean bathymetry may change nutrient supplies to the water column altering PP in the upper ocean. The Seychelles-Chagos Thermocline Ridge acts as a boundary along which the South Equatorial Current is diverted that prevents nutrient enrichment to the east making the western part a region for phytoplankton bloom all the year round

(Dilmahamod, 2014). In the IO region of the Southern Ocean where fronts give rise to characteristic vertical structures in the upper ocean, a pronounced variability in the hydrographic variables can be observed due to variations in the water column stability. The formation of deep chlorophyll maxima in these regions greatly affects rates of PP, making them regions of carbon sequestration and a sink for atmospheric CO_2 (Tripathy et al., 2015).

5 Summary and Future Directions

The availability of observations in the northern IO is limited, especially in terms of BGC variables. This hinders the understanding of the BGC response to physical forcing across the water column at various seasonal and interannual timescales. Improvements in coupled ocean-ecosystem models to accurately simulate the BGC dynamics of the northern IO can overcome these limitations. The modeling studies on PP that has been carried out on both the basins of the northern IO and their subsequent synthesis have resulted in major progress in our understanding. Further, we need to have a better understanding of the spatiotemporal variability of PP of the AS and the BoB. The biophysical models developed to date have successfully described the complex phytoplankton bloom dynamics of the IO along with the seasonal and interannual variability of PP. Improved model resolution and better understanding and modeling of the fundamental processes involved in the interactions between the physical and biological states of the ocean can further improve our understanding of PP.

To have a better understanding of the oceanic variability at wide spatiotemporal scales, it is necessary to have sustained observations spanning over a longer timescale. The lower temporal resolution of in situ and remotely sensed observations has resulted in a hindrance to the time series analysis. The spatial coverage of satellite data is often limited owing to cloud cover. Nevertheless, numerical models overcome these shortcomings, and thus model simulated outputs are extremely useful to assess the long-term changes of the physical and BGC state of the ocean. The influence of nutrients and light in regulating the distribution of phytoplankton, which in turn controls grazing and carbon fluxes to deeper ocean, can be assessed by using the model simulated outputs. There are few studies on the size-fractionated productivity in the BoB and AS region. In the future, size-based studies on phytoplankton can be further emphasized using outputs from high-resolution ecosystem models. The IO is the fastest heating ocean, besides the Arctic Ocean, and in recent investigations, it has been found that the marine productivity of the western IO has decreased by 20% over the past six decades (Roxy et al., 2016). Keeping in mind the future climatic projections, the IO along with the global ocean needs to be monitored closely on the aspects of physical-biological interactions.

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