Chapter 6. Primary Production, Cycling of Nutrients, Surface Layer and Plankton

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1. Primary Production[1]

1.1 Definition and ecological significance

Gross primary production (GPP) is the rate at which photosynthetic plants and bacteria use sunlight to convert carbon dioxide (CO_2) and water to the high-energy organic carbon compounds used to fuel growth. Free oxygen (O_2

integrated chlorophyll-a concentration (Ψ Chl), photosynthetically active solar radiation, and temperature (Antoine and Morel, 1996; Perry, 1986; Morel and Berthon, 1989; Platt and Sathyendranath, 1993; Behrenfeld and Falkowski, 1997; Sathyendranath, 2000; Gregg et al., 2003; Behrenfeld et al., 2006; Carr et al., 2006; Arrigo et al., 2008; Bissinger et al., 2008; McClain, 2009; Westberry et al., 2008; Cullen et al., 2012; Siegel et al., 2013).

An overview of the latest satellite based models may be found at the Ocean Productivity website.[7] Satellite ocean-colour

Iverson, 1976; Kemp et al., 1986; Duarte, 1989; Kaldy and Dunton, 2000; Duarte and Kirkman, 2001; Plus et al., 2001, Silva et al., 2009).

1.2.3 The Phenology of Phytoplankton Annual Cycles

The timing of seasonal increases in phytoplankton NPP is determined by environmental parameters, including day length, temperature, changes in vertical stratification, and the timing of seasonal sea-ice retreat in polar waters. All but day length are affected by climate change. Thus, phytoplankton phenology provides an important tool for detecting climate-driven decadal variability and secular trends. Phenological metrics to be monitored are the time of bloom initiation, bloom duration and time of maximum amplitude (Siegel et al., 2002; Platt et al., 2009).

1.3 Spatial patterns and temporal trends

Marine NPP varies over a broad spectrum of time scales from tidal, daily and seasonal cycles to low-frequency basin-scale oscillations and multi-decade secular trends (Malone, 1971; Pingree et al., 1975; Steele, 1985; Cloern, 1987; Cloern, 2001; Cloern et al., 2013; Duarte, 1989; Powell, 1989; Malone et al., 1996; Henson and Thomas, 2007; Vantrepotte and Mélin, 2009; Cloern and Jassby, 2010; Bode et al., 2011; Chavez et al., 2011). Our focus here is on low-frequency cycles and multi-decade trends.

1.3.1 Phytoplankton NPP

For the most part, the global pattern of phytoplankton NPP (Figure 1) reflects the pattern of deep-water nutrient inputs to the euphotic zone associated with winter mixing and thermocline erosion at higher latitudes, thermocline shoaling at lower latitudes, and upwelling along the eastern boundaries of the ocean basins and the equator (Wollast, 1998; Pennington et al., 2006; Chavez et al., 2011; Ward et al., 2012).
The global distribution of phytoplankton NPP is also influenced by iron limitation and grazing by microzooplankton in so-called High Nutrient Low Chlorophyll (HNLC) zones which account for ~20 per cent of the global ocean, e.g., oceanic waters of the subarctic north Pacific, subtropical equatorial Pacific, and Southern Ocean (Martin et al., 1994; Landry et al., 1997; Edwards et al., 2004). Nutrient inputs associated with river runoff enhance NPP in coastal waters during the growing season (Seitzinger et al., 2005; Seitzinger et al.,

last 100 years (Gregg et al., 2003; Boyce et al., 2014). A decadal scale decline is consistent with model simulations indicating that both NPP and the biological pump have decreased by ~7 per cent and 8 per cent, respectively, over the last five decades (Laufkötter et al., 2013), trends that are likely to continue through the end of this century (Steinacher et al., 2010).

Given uncertainties concerning global trends, long-term impacts of secular changes in phytoplankton NPP on food security and climate change cannot be assessed at this time with any certainty. Resolving this controversy and predicting future trends will require sustained, multi-decadal observations and modelling of phytoplankton NPP and key environmental parameters (e.g., upper ocean temperature, pCO_2, pH, depth of the aragonite saturation horizon, vertical stratification and nutrient concentrations) o regional and global scales - observations that may have to be sustained for at least another 40-50 years (Henson et al., 2010).

1.3.2 Macrophyte NPP

Marine macrophyte NPP, which is limited to tidal and relatively shallow waters in coastal ecosystems, varies from 10-3,200 g C m^{-2} yr^{-1} (Smith, 1981; Charpy-Roubaoud and Sournia, 1990; Geider et al., 2001; Duarte et al., 2005; Duarte et al., 2010; Fourqurean et al., 2012; Ducklow et al., 2013). In contrast to the uncertainty of decadal to be on the order of 2-4 per cent of river discharge (Beusen et al., 2013). Given this, and challenges of quantifying ground water inputs on ocean basin to global scales (NRC, 2004), this source is not considered herein.

2.1 Nitrogen

The ocean's nitrogen cycle is driven by complex microbial transformations, including N fixation, assimilation, nitrification, anammox and denitrification (Voss et al., 2013) (Figure 2). NPP depends on the supply of reactive N (N_r)[10] to the euphotic zone. Although most dissolved chemical forms of N_r can be assimilated by primary producers, the most abundant chemical form, dissolved nitrogen gas (N_2), can only be assimilated by marine diazotrophs.[11] N_r inputs to the euphotic zone occur via fluxes of nitrate from deep water (vertical mixing and upwelling), marine N_2 fixation, river discharge, and atmospheric deposition.[12] N_r is removed f

zones (OMZs) account for most losses of N from the marine N inventory (Ulloa et al., 2012; Ward, 2013).

Table 2. Summary of estimated sources and sinks (Tg N yr^{-1}) in the global marine nitrogen budget (Data sources: Codispoti et al., 2001; Gruber and Sarmiento, 2002; Karl et al., 2002; Galloway et al., 2004; Mahaffey et al., 2005; Seitzinger et al., 2005; Boyer et al., 2006; Moore et al., 2006; Deutsch et al., 2007; Duce et al., 2008; DeVries et al., 2012; Grosskopf et al., 2012; Luo et al., 2012; Naqvi, 2012)

Sources	N fixation	60-200
	Rivers	35-80
	Atmosphere	38-96
	TOTAL	133-376
Sinks	Denitrification & anammox	120-450
	Sedimentation	25

sustained a balanced N budget (Landolfi et al., 2013). If the coupling is close as argued above, the budget may not be in steady state. In this scenario, increases in vertical stratification of the upper ocean and expansion of OMZs associated with ocean warming (Keeling et al., 2010) could lead to closer spatial coupling of N_2 fixation and denitrification, a net loss of N from the marine N_r inventory, and declines in NPP and CO_2 sequestration during this century.

2.2 Phosphorus

Phosphorus (P) is an essential nutrient utilized by all organisms for energy transport and growth. The primary inputs of P occur via river discharge and atmospheric deposition (Table 3). Biologically active P (BAP) in natural waters usually occurs as phosphate (PO_4^{3-}), which may be in dissolved inorganic forms (including orthophosphates and polyphosphates) or organic forms (organically bound phosphates). Natural inputs of BAP begin with chemical weathering of rocks followed by complex biogeochemical interactions, whose time scales are much longer than anthropogenic P inputs (Benitez-Nelson, 2000). Primary anthropogenic sources of BAP are industrial fertilizer, sewage and animal wastes.

The Marine Phosphorus Budget. River discharge of P into the coastal ocean accounts for most P input to the ocean (Table 3). However, most riverine P is sequestered in continental shelf sediments (Paytan and McLaughlin, 2007) so that only ~25 per cent of the riverine input enters the NPP-driven marine P cycle. Estimates of BAP reaching the open ocean from rivers range from a few tenths to perhaps 1 Tg P yr^{-1} (Seitzinger et al., 2005; Meybeck, 1982; Sharpies et al., 2013). Mahowald et al., (2008) estimated that atmospheric inputs of BAP are ~0.1 Tg P yr^{-1}. Together these inputs would support ~1 per cent of NPP annually. Thus, like N_r, virtually all NPP is supported by BAP recycled within the ocean on a global scale.

Table 3. Summary of estimated sources and sinks (Tg P yr^{-1}) in the global marine phosphorus budget. (Data sources: Filippelli and Delaney, 1996; Howarth et al., 1996; Benitez-Nelson, 2000; Compton et al., 2000; Ruttenberg, 2004; Seitzinger et al., 2005; Paytan and McLaughlin, 2007; Mahowald et al., 2008; Harrison et al., 2010; Krishnamurthy et al., 2010.)

very soluble, and most of it is found downwind of desert and arid regions. Only ~1 Tg P yr^{-1} of BAP appears to enter the oceans via atmospheric deposition (Mahowald et al., 2008). Although a small term in the P budget (Table 3), atmospheric deposition appears to be the main external source of BAP in the oligotrophic waters of the subtropical gyres and the Mediterranean Sea (Paytan and McLaughlin, 2007; Krishnamurthy et al., 2010).

Burial in continental shelf and deep-sea sediments is the primary sink, with most riverine input being removed from the marine P cycle by rapid sedimentation of particulate inorganic (non-reactive mineral lattices) P in coastal waters (Paytan and McLaughlin, 2007). Burial in deep-sea sediments occurs after transformations from dissolved to particulate forms in the water column. Of the riverine input, ~85 per cent is buried in continental shelf sediments (Slomp, 2011). Assuming that inputs from river discharge and atmospheric deposition are, respectively ~15 Tg P yr^{-1} and 1 Tg P yr^{-1}, and that 11 Tg P yr^{-1} and 5 Tg P yr^{-1}, respectively are buried in shelf and open-ocean sediments, the P budget appears to be roughly balanced on the scale of P turnover times in the ocean (~1500 years, Paytan and McLaughlin, 2007).

3. Variability and Resilience of Marine Ecosystems

3.1 Phytoplankton species diversity and resilience

Biodiversity enhances resilience by increasing the range of possible responses to perturbations and the likelihood that species will functionally compensate for one another following disturbance (functional redundancy) (McCann, 2000; Walker et al., 2004; Hooper et al., 2005; Haddad et al., 2011; Appeltans et al., 2012; Cleland, 2011). Annually averaged phytoplankton species diversity of the upper ocean tends to be lowest in polar and subpolar waters, where fast-growing (opportunistic) species account for most NPP, and highest in tropical and subtropical waters, where small phytoplankton (< 10 µm) account for most NPP (Barton et al., 2010). Phytoplankton species diversity is also a unimodal function of phytoplankton NPP, supported by large phytoplankton (> 20 µm). As such, they are critical links in nutrient cycles and the transfer of NPP to higher trophic levels of metazoan consumers. They fuel the biological pump and they limit excessive increases in NPP (e.g., Corten and Linley, 2003; Greene and Pershing, 2004; Steinberg et al., 2012). Microbial food webs dominate the biological cycles of C, N and P in the upper ocean and feed into metazoan food webs involving zooplankton, planktivorous fish, and their predators (Pomeroy et al., 2007; Moloney et al., 2011; Ward et al., 2012). Zooplankton in microbial food webs are typically dominated by heterotrophic and mixotrophic flagellates and ciliates. Metazoan food webs dominate the flow of energy and nutrients to harvestable fish stocks and to the deep sea (carbon sequestration). Zooplankton in metazoan food webs are typically dominated by crustaceans (e.g., copepods, krill and shrimp) and are part of relatively short, efficient, and nutritionally rich food webs supporting large numbers of planktivorous and piscivorous fish, seabirds, and marine mammals (Richardson, 2008; Barnes et al., 2010; Barnes et al., 2011).

Microbial food webs support less zooplankton biomass than do metazoan food webs, and a recent analysis suggests that zooplankton/phytoplankton ratios range from a low of ~0.1 in the oligotrophic subtropical gyres to a high of ~10 in upwelling systems and subpolar regions (Ward et al., 2012). Such a gradient is consistent with a shift from "bottom-up", nutrient-limited NPP in the oligotrophic gyres, where microflagellates are the primary consumers of NPP (Calbet, 2008), to "top-down", grazing control of NPP by zooplankton in more productive high-latitude and upwelling ecosystems, where planktonic crustaceans are the primary grazers of NPP (Ward et al., 2012). Thus, zooplankton grazing on phytoplankton is an important parameter of spatial patterns and temporal trends in NPP, particularly at high latitudes and in coastal upwelling systems (section 6.1.4).

3.2.1 NPP and Fisheries

Fish production depends to a large extent on NPP but the relationship between NPP and fish landings is complex. For instance, Large Marine Ecosystems (LMEs) of the coastal ocean account for ~30 per cent of marine phytoplankton NPP and ~80 per cent of marine fish landings globally (Sherman and Hempel, 2009). They are also "proving grounds" for the development of ecosystem-based approaches (EBAs) to fisheries management (McLeod and Leslie, 2009; Sherman and Hempel, 2009; Malone et al., 2014b-

Ware and Thomson, 2005; Frank et al., 2006; Chassot et al., 2007; Sherman and Hempel, 2009; Blanchard et al., 2012). However, the NPP required to support annual fish landings (PPR) varies among LMEs, e.g., fi

3.2.3 Coastal Eutrophication and "Dead Zones"

Excess phytoplankton NPP in coastal ecosystems can lead to accumulations of phytoplankton biomass and eutrophication. Anthropogenic N and P loading to estuarine and coastal marine ecosystems has more than doubled in the last 100 years (Seitzinger et al., 2010; Howarth et al., 2012),[17] leading to a global spread of coastal eutrophication and associated increases in the number of oxygen-depleted "dead zones" (Duarte, 1995; Malone et al., 1999; Diaz and Rosenberg, 2008; Kemp et al., 2009), loss of sea grass beds (Dennison et al., 1993; Kemp et al., 2004; Schmidt et al., 2012), and increases in the occurrence of toxic phytoplankton blooms (see below). Current global trends in coastal eutrophication and the occurrence of "dead zones" and toxic algal events indicate that phytoplankton NPP is increasing in many coastal ecosystems, a trend that is also likely to exacerbate future impacts of over-fishing, sea-level rise, and coastal development on ecosystem services (Dayton et al., 2005; Koch et al., 2009; Waycott et al., 2009).

3.2.4 Oxygen minimum zones (OMZs)

OMZs, which occur at midwater depths (200–1000 m) in association with eastern boundary upwelling systems, are expanding globally as the solubility of dissolved O_2 decreases and vertical stratification increases due to upper ocean warming (Chan et al., 2008; Capotondi et al., 2012; Bijma et al., 2013). Currently, the total surface area of OMZs is estimated to be ~30 x 10^6 km^2 (~8 per cent of the ocean's surface area) with a volume of ~10 x 10^6 km^3 (~0.1 per cent of the ocean's volume). It is expected that the spatial extent of OMZs will continue to increase (Oschlies et al., 2008), a trend that is likely to affect nutrient cycles and fisheries—especially when combined with the spread of coastal dead zones associated with coastal eutrophication.

3.2.5 Toxic Algal Blooms

Toxin-producing algae are a diverse group of phytoplankton species with only two characteristics in common: (1) they harm people and ecosystems; and (2) their initiation, development and dissipation are governed by species-specific population

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production by phytoplankton and cyanobacteria (Häder et al., 2007; Villar-Argaiz et al., 2009; Ha et al., 2012), changes in the structure and function of plankton communities (Ferreyra et al., 2006; Häder et al., 2007; Fricke et al., 2011; Guidi et al., 2011; Santos et al., 2012a; Ha et al., 2014), and alterations of the N cycle (Goes et al., 1995; Jiang and Qiu, 2011). The ozone layer in the Earth's stratosphere blocks most UV-B from reaching the ocean's surface. Consequently, stratospheric ozone depletion since the 1970s has been a concern, especially over the South Pole, where a so-called ozone hole has developed.[21] However, the average size of the ozone hole declined by ~2 per cent between 2006 and 2013 and appears to have stabilized, with variation from year to year driven by changing meteorological conditions.[22] It has even been predicted that there will be a gradual recovery of ozone concentrations by ~2050 (Taalas et al., 2000). Given these observations and variations in the depths to which UV-B penetrates in the ocean (~1-10 m), a consensus on the magnitude of the ozone-depletion effect on NPP and nutrient cycling has yet to be reached.

4. Socioeconomic importance

Marine NPP supports a broad range of ecosystem services valued by society and

2006/2007; Braatz et al., 2007; Koch et al., 2009;

atmospheric deposition over most of the ocean is estimatmh e/3f the deathede phytoplankton NPP. Amplitude decreased by 1–2 per cent over most of the ocean, except in the Arctic, where an increase of 1 per cent by 2100 is projected. These results are supported by the response of phytoplankton and zooplankton to global climate change projections carried out with the IPSL Earth System Model (Chust et al., 2014). Projected upper ocean warming by the turn of the century led to reductions in phytoplankton and zooplankton biomass of 6 per cent and 11 per cent, respectively. Simulations suggest such declines are the predominant response over nearly 50 per cent of the ocean and prevail in the tropical and subtropical oceans while increasing trends prevail in the Arctic and Antarctic oceans. These results suggest that the capacity of the oceans to regulate climate through the biological carbon pump may decrease over the course of this century. The model runs also indicate that, on average, a 30–40 year time series of observations will be needed to validate model results.

Regardless of the direction of global trends in NPP, climate change may be causing shifts in phytoplankton community size spectra toward smaller cells which, if confirmed, will have profound effects on the fate of NPP and nutrient cycling during this century (Polovina and Woodworth, 2012). The size spectrum of phytoplankton communities in the upper ocean's euphotic zone largely determines the trophic organization of pelagic ecosystems and, therefore, the efficiency with which NPP is channelled to higher trophic levels, is exported to the deep ocean, or is metabolized in the upper ocean ([illegible]

trend. Should these trends continue, additional loss of ice during Arctic spring could boost NPP more than three-fold above 1998-2 year for some species and being delayed for others (Edwards and Richardson, 2004, section 6.3.2). In the North Pacific, there is a strong correlation between sea-surface temperature in the spring and the latitude at which subtropical species reach In the seasonal peak in abundance[26]. Water temperature also influences the annual cycle of Neocalanus plumchrus biomass in including the following: (1) decreases in the degree of aragonite saturation makes it harder for calcifying organisms (e.g., coccolithophores, foraminifera, and pteropods) to precipitate their mineral structures; (2) decreases in pH alters the bioavailability of essential algal nutrients such as iron and zinc; and (3) increases in CO_2 decrease the energy requirements for photosynthetic organisms to synthesize biomass. Such biological effec and Cazenave, 2010). Macrophyte

"Great Southern Coccolithophore Belt" of the Southern Ocean[28] and at high latitudes in the NE Atlantic (Barnard et al., 2004; Balch et al., 2011; Sadeghi et al., 2012). If the abundance of these functional groups decline in these regions, likely impacts will be to reduce the capacity of the oceans to take up CO_2, export carbon to the deep sea, and support fisheries (Cooley et al., 2009).

6. Information needs

As shown above, anthropogenic nutrient-loading of coastal waters and climate change pressures on marine ecosystems (ocean warming and acidification, sea-level rise) are driving changes in NPP and nutrient cycles that are trn affect the provision of ecosystem services and, therefore, sustainable development. However, although changes in macrophyte NPP and their impacts are relatively well documented (and must continue to be), a consensus on the magnitude of changes and even the direction of change in phytoplankton NPP and upper ocean nutrient cycles has yet to be reached.

Documenting spatial patterns and temporal trends in NPP and nutrient cycles (and their causes and socioeconomic consequences) will rely heavily on the accuracy and frequency with which changes in NPP and nutrient cycling can be detected over a broad range of scales (cf. deYoung et al., 2004; UNESCO, 2012; Mathis and Feely, 2013). Given the importance of marine NPP and the species diversity of primary producers to sustaining ecosystem services, rapid detection of changes in time-space patterns of marine NPP and in the diversity of primary producers that contribute to NPP is an important dimension of the Regular Process[29] for global reporting and assessment of the state of the marine environment, including socioeconomic aspects

Data requirements for the Regular Process have been used to help guide the development of the Global Ocean Observing System and an implementation strategy for

6.1 Net primary production

Sustained observations of chlorophyll, irradiance and temperature fields are required for model-based estimates of phytoplankton NPP (see section 6.1.2). An integrated approach using long term data streams from both remote sensing and frequent in situ observations is needed to capture the dynamics of marine phytoplankton NPP and to detect decadal trends. Remote sensing provides a cost-effective means to observe physical and biological variables synoptically in time and space with sufficient resolution to elucidate linkages between climate-driven changes in the NPP of ecosystems and the dynamic relationship between phytoplankton NPP and the provision of ecosystem services (Platt et al., 2008; Forget et al., [illegible])-4()-4()-4or ds engeN

Quantifying inputs of N and P to coastal ecosystems and the open ocean requires a network of coordinated and sustained observations on local to global scales. For atmospheric deposition, monitoring should focus on regions that have intense deposition plumes downwind of major population centres in West Africa, East Asia, Europe, India, North and South America (section 6.2.1 and Schulz et al., 2012). This is a major goal of the SOLAS programme.

Altabet, M.

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