

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

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1. Primary Production¹

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 (CO₂) and water to the high-energy organic carbon compounds used to fuel growth. Free oxygen (O₂) is released during the process. Net primary production (NPP) is GPP less the respiratory release of CO₂ by photosynthetic organisms, i.e., the net photosynthetic fixation of inorganic carbon into autotrophic biomass. NPP supports most life on Earth; it fuels global cycles of carbon, nitrogen, phosphorus and other nutrients and is an important parameter of atmospheric CO₂ and O₂ levels (and, therefore, of anthropogenic climate change).

Global NPP is estimated to be ~105 Pg C yr⁻¹, about half of which is by marine plants (Field et al., 1998; Falkowski and Raven, 1997; Westberry et al., 2008).² Within the euphotic zone of the upper ocean,³ phytoplankton and macrophytes⁴ respectively account for ~94 per cent (~50 ± 28 Pg C yr⁻¹) and ~6 per cent (~3.0 Pg C yr⁻¹) of NPP (Falkowski et al., 2004; Duarte et al., 2005; Carr et al., 2006; Schneider et al., 2008; Chavez et al., 2011; Ma et al., 2014; Rousseaux and Gregg, 2014). All NPP is not equal in terms of its fate. Marine macrophytes play an important role as carbon sinks in the global carbon cycle, provide habitat for a diversity of animal species, and food for marine and terrestrial consumers (Smith, 1981; Twilley et al., 1992; Duarte et al., 2005; Duarte et al., 2010; Heck et al., 2008; Nellemann et al., 2009; McLeod et al., 2011, Fourqurean et al., 2012). Phytoplankton NPP fuels the marine food webs upon which marine fisheries depend (Pauly and Christensen, 1995; Chassot et al., 2010) and the

¹ Microbenthic, epiphytic and symbiotic algae can be locally important in shallow waters and corals, but are not addressed here. Chemosynthetic primary production is addressed elsewhere.

² 1 Pg = 10¹⁵ g

³ Defined here to include the epipelagic (0-200 m) and mesopelagic (200 – -1000 m) zones. The euphotic zone lies within the epipelagic zone.

⁴ Macrophytes include sea grasses, macroalgae, salt marsh plants and mangroves. Phytoplankton are single-celled, photosynthetic prokaryotic and eukaryotic microorganisms growing in the euphotic zone (the layer between the ocean's surface and the depth at which photosynthetically active radiation [PAR] is 1 per cent of surface intensity). Most phytoplankton species are > 1 µm and < 1 mm in equivalent spherical diameter (cf. Ward et al., 2012).

“biological pump” which transports 2-12 Pg C yr⁻¹ of organic carbon to the deep sea (Falkowski et al., 1998; Muller-Karger et al., 2005; Emerson and Hedges, 2008; Doney, 2010; Passow and Carlson, 2012), where it is sequestered from the atmospheric pool of carbon for 200-1500 years (Craig, 1957; Schlitzer et al., 2003; Primeau and Holzer, 2006; Buesseler, et al., 2007).

Changes in the size structure of phytoplankton communities influence the fate of NPP (Malone, 1980; Legendre and Rassoulzadegan, 1996; Pomeroy et al., 2007; Marañón, 2009). In general, small cells (picophytoplankton with equivalent spherical diameters < 2 µm) account for most NPP in subtropical, oligotrophic (< 0.3 mg chlorophyll-a m⁻³), nutrient-poor (nitrate + nitrite < 1 µM), warm (> 20°C) waters. Under these conditions, the flow of organic carbon to harvestable fisheries and the biological pump are relatively small. In contrast, larger cells (microphytoplankton > 20 µm) account for > 90 per cent of NPP in more eutrophic (> 5 mg chlorophyll-a m⁻³), nutrient-rich (nitrate + nitrite >10 µM), cold (< 15°C) waters (Kamykowski, 1987; Agawin et al., 2000; Buitenhuis et al., 2012). Under these conditions, diatoms⁵ account for most NPP during spring blooms at high latitudes and periods of coastal upwelling when NPP is high and nutrients are not limiting (Malone, 1980). The flow of organic carbon to fisheries and the biological pump is higher when larger cells account for most NPP (Laws et al., 2000; Finkel et al., 2010).

1.2 Methods of measuring net primary production (NPP)

1.2.1 Phytoplankton Net Primary Production

Phytoplankton (NPP) has been estimated using a variety of *in situ* and remote sensing methods (Platt and Sathyendranath, 1993; Geider et al., 2001; Marra, 2002; Carr et al., 2006; Vernet and Smith, 2007; Cullen, 2008a; Cloern et al., 2013). Multiplatform (e.g., ships, moorings, drifters, gliders, aircraft, and satellites) sampling strategies that utilize both approaches are needed to effectively detect changes in NPP on ecosystem to global scales (UNESCO-IOC, 2012).

On small spatial and temporal scales (meters-kilometres, hours-days), several techniques have been used including oxygen production and the incorporation of ¹³C and ¹⁴C labelled bicarbonate (Cullen, 2008a). The most widely used and standard method against which other methods are compared or calibrated is based on the incorporation of ¹⁴C-bicarbonate into phytoplankton biomass (Steeman-Nielsen, 1963; Marra, 1995; Marra, 2002; Vernet and Smith, 2007; Cullen, 2008a). On large spatial scales (Large Marine Ecosystems⁶ to the global ocean), the most effective way to detect space-time variability is via satellite-based measurements of water-leaving radiance combined with diagnostic models of depth-integrated NPP as a function of depth-

⁵ Diatom growth accounts for roughly half of marine NPP and therefore for about a quarter of global photosynthetic production (Smetacek, 1999).

⁶ Large marine ecosystems (200,000 km² or larger) are coastal ecosystems characterized by their distinct bathymetry, hydrography, productivity and food webs (Sherman et al., 1993).

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 radiometry (OCR) data have been used to estimate surface chlorophyll-a fields and NPP since the Coastal Zone Color Scanner (CZCS) mission (1978-1986). Uninterrupted OCR measurements began with the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) mission (1997-2010) (Hu et al., 2012). A full accounting of current polar orbiting and geostationary ocean-colour sensors with their capabilities (swath width, spatial resolution, spectral coverage) can be found on the web site of the International Ocean-Colour Coordinating Group.⁸

The skill of model-based estimates of NPP has been improving (O'Reilly et al., 1998; Lee, 2006; Friedrichs et al., 2009; Saba et al., 2010; Saba et al., 2011; Mustapha et al., 2012), but further improvements are needed through more accurate estimates of Ψ Chl. Chlorophyll-a fields can be estimated more accurately by blending data from remote sensing and *in situ* measurements, especially in regions where *in situ* measurements are sparse and in turbid, coastal ecosystems (Conkright and Gregg, 2003; Gregg et al., 2003; Onabid, 2011). An empirical approach has been developed for ocean-colour remote sensing called Empirical Satellite Radiance-In situ Data (ESRID) algorithm (Gregg et al., 2009).

1.2.2 *Macrophyte Net Primary Production*

The NPP of macroalgae, sea grasses, salt marsh plants and mangroves can be estimated by sequentially (e.g., monthly during the growing season) measuring increases in biomass (including leaf litter in salt marshes and mangrove forests) using a combination of *in situ* techniques (e.g., Mann, 1972; Cousens, 1984; Dame and Kenny, 1986; Amarasinghe and Balasubramaniam, 1992; Long et al., 1992; Day et al., 1996; Ross et al., 2001; Curco et al., 2002; Morris, 2007) and satellite-based multispectral imagery (e.g., Gross et al., 1990; Zhang et al., 1997; Kovacs et al., 2001; Gitelson, 2004; Liu et al., 2008; Kovacs et al., 2009; Heumann, 2011; Mishra et al., 2012; Son and Chen, 2013). For remote sensing, accurate *in situ* measurements are critical for validating models used to map these habitats and estimate NPP (Gross et al., 1990; Kovacs et al., 2009; Roelfsema et al., 2009; Mishra et al., 2012; Jia et al., 2013; Trilla et al., 2013). These include shoot- or leaf-tagging techniques, measurements of ¹⁴C incorporation into leaves, and measurements of dissolved O₂ production during the growing season (Bittaker and

⁷ <http://www.science.oregonstate.edu/ocean.productivity/>.

⁸ <http://www.ioccg.org/sensors/current.html>.

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 Phenology⁹ 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).

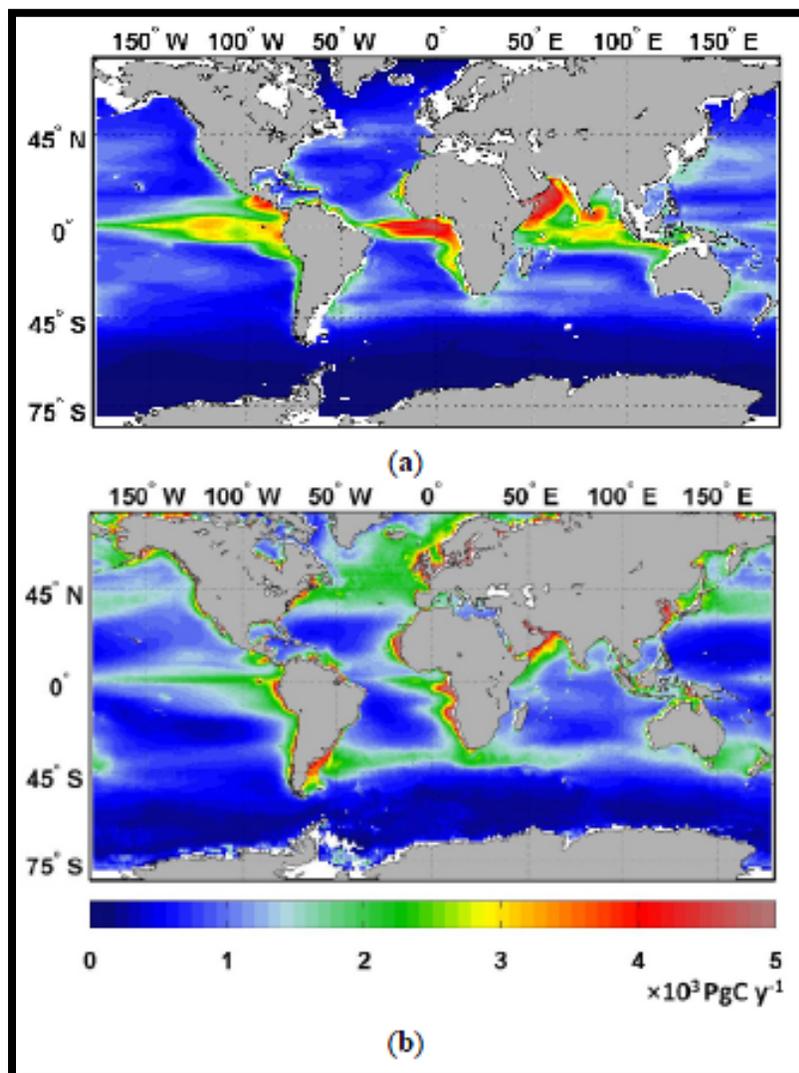
1.3 *Spatial patterns and temporal trends*

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., 2010). Annual cycles of NPP associated with patterns of nutrient supply and seasonal variations in sunlight tend to increase in amplitude and decrease in duration with increasing latitude. Seasonal increases in NPP generally follow winter mixing when nutrient concentrations are high, the seasonal thermocline sets up, and day length increases. Annual cycles are also more pronounced in coastal waters subject to seasonal upwelling.

⁹ Phenology is the study of the timing and duration of cyclic and seasonal natural phenomena (e.g., spring phytoplankton blooms, seasonal cycles of zooplankton reproduction), especially in relation to climate and plant and animal life cycles.



The boundaries and names shown and the designations used on this map do not imply official endorsement or acceptance by the United Nations.

Figure 1. Climatological map Distribution of annual marine NPP for (a) NASA Ocean Biogeochemical Model and (b) Vertically-Integrated Production Model (VGPM) for the period from September 1998 to 2011 (Rousseaux – August 1999 (Blue < 100 g C m⁻², Green > 110 g C m⁻² and < 400 g C m⁻², Red > 400 g C m⁻²) (Rutgers Institute of Marine and Gregg, 2014). Globally, diatoms accounted for about 50 per cent of NPP while coccolithophores, chlorophytes and cyanobacteria accounted for about 20 per cent, 20 per cent and 10 per cent, respectively. Diatom NPP was highest at high latitudes and in equatorial and eastern boundary upwelling systems. Coastal Sciences, <http://marine.rutgers.edu/opp/>). Coastal ecosystems (red – green) and the permanently stratified subtropical waters of the central gyres (blue) each account for ~30 per cent of the ocean’s NPP, whereas the former accounts for only ~8 per cent of the ocean’s surface area compared to ~60 per cent for the open ocean waters of the subtropics (Geider et al., 2001; Marañón et al., 2003; Muller-Karger et al., 2005).

The global distribution of annual NPP in the ocean can be partitioned into broad provinces with eastern boundary upwelling systems and estuaries exhibiting the highest rates and subtropical central gyres the lowest rates (Figure 1, Table 1).

Table 1. Ranges of phytoplankton mean daily NPP and annual NPP reported for different marine provinces. Estimates are based on *in situ* measurements and models using satellite-based observations of chlorophyll-a fields. Western boundaries of the ocean basins generally feature broad continental shelves and eastern boundaries tend to have narrow shelves with coastal upwelling. (Data sources: Malone et al., 1983; O'Reilly and Busch, 1983; Pennock and Sharp, 1986; Cloern, 1987; Malone, 1991; Barber et al., 1996; Karl et al., 1996; Malone et al., 1996; Pilska et al., 1996; Smith and DeMaster, 1996; Lohrenz et al., 1997; Cloern, 2001; Smith et al., 2001; Steinberg et al., 2001; Marañón et al., 2003; Sakshaug, 2004; PICES, 2004; Teira et al., 2005; Tian et al., 2005; Pennington et al., 2006; Subramanian et al., 2008; Vernet et al., 2008; Bidigare et al., 2009; Sherman and Hempel, 2009; Chavez et al., 2010; 176 Saba et al., 2011; Brown and Arrigo, 2012; Cloern et al., 2013; Lomas et al., 2013).

Province	mg C m ⁻² d ⁻¹	g C m ⁻² yr ⁻¹
Subtropical Central Gyres	20 – 1,040	150 – 170
Western Boundaries	10 – 3,500	200 – 470
Eastern Boundaries	30 – 7,300	460 – 1,250
Equatorial Upwelling	640 – 900	240
Arctic Ocean	3 – 1,100	5 – 400
Southern Ocean	290 – 370	50 – 450
Coastal Seas	100 – 1,400	40 – 600
Estuaries & Coastal Plumes	100 – 8,000	70 – 1,890

Interannual variability and multi-decadal trends in phytoplankton NPP on regional to global scales are primarily driven by: (1) climate change (e.g., basin-scale oscillations and decadal trends, including loss of polar ice cover, upper ocean warming, and changes in the hydrological cycle); (2) land-based, anthropogenic nutrient loading; and (3) pelagic and benthic primary consumers. Global-scale trends in phytoplankton NPP remain controversial (Boyce et al., 2010; Boyce et al., 2014; Mackas, 2011; Rykaczewski and Dunne, 2011; McQuatters-Gollop et al., 2011; Dave and Lozier, 2013; Wernand et al., 2013). Remote sensing (sea-surface temperature and chlorophyll fields), model simulations and marine sediment records suggest that global phytoplankton NPP may have increased over the last century as a consequence of basin-scale climate forcing that promotes episodic and seasonal nutrient enrichment of the euphotic zone through vertical mixing and upwelling (McGregor et al., 2007; Bidigare et al., 2009; Chavez et al., 2011; Zhai et al., 2013). In contrast, global analyses of changes in chlorophyll distribution over time suggest that annual NPP in the global ocean has declined over the

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, pCO₂, pH, depth of the aragonite saturation horizon, vertical stratification and nutrient concentrations) on 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 30-1,200 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 trends in phytoplankton NPP, decadal declines in the spatial extent and biomass of macrophytes (a proxy for NPP) over the last 50-100 years are relatively well documented. Macrophyte habitats are being lost and modified (e.g., fragmented) at alarming rates (Duke et al., 2007; Valiela et al., 2009; Waycott et al., 2009; Wernberg et al., 2011), i.e., 2 per cent for macrophytes as a group, with total areal losses to date of 29 per cent for seagrasses, 50 per cent for salt marshes and 35 per cent for mangrove forests (Valiela et al., 2001; Hassan et al., 2005; Orth et al., 2006; Waycott et al., 2009; Fourqurean et al., 2012). As a whole, the world is losing its macrophyte ecosystems in coastal waters four times faster than its rain forests (Duarte et al., 2008), and the rate of loss is accelerating (Waycott et al., 2009).

2. Nutrient Cycles

Nitrogen (N) and phosphorus (P) are major nutrients required for the growth of all organisms, and NPP is the primary engine that drives the cycles of N and P in the oceans. The cycles of C, N, P and O₂ are coupled in the marine environment (Gruber, 2008). As discussed in section 6.1.3, the global pattern of phytoplankton NPP reflects the pattern of dissolved inorganic N and P inputs to the euphotic zone from the deep ocean (Figure 1). Superimposed on this pattern are nutrient inputs associated with N fixation, atmospheric deposition, river discharge and submarine ground water discharge. In regard to the latter, ground water discharge may be a significant source of N locally in some parts of Southeast Asia, North and Central America, and Europe, but on the scale of ocean basins and the global ocean, ground water discharge of N has been estimated

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 dinitrogen 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 from the marine N inventory through denitrification and anammox¹³ with subsequent efflux of N_2 and N_2O to the atmosphere (Thamdrup et al., 2006; Capone, 2008; Naqvi et al., 2008; Ward et al., 2009; Ward, 2013). Although there is no agreement concerning the oxygen threshold that defines the geographic extent of denitrification and anammox (Paulmier and Ruiz-Pino, 2009), these processes are limited to suboxic waters with very low oxygen concentrations (< 22 μM).

¹⁰ Reactive or fixed N forms include dissolved inorganic nitrate, nitrite, ammonium and organic N compounds, such as urea and free amino acids.

¹¹ Prokaryotic, free-living and symbiotic bacteria, cyanobacteria and archaea.

¹² River discharge and atmospheric deposition include nitrate from fossil fuel burning and fixed N in synthetic fertilizer produced by the Haber-Bosch process for industrial nitrogen fixation.

¹³ Anaerobic ammonium oxidation.

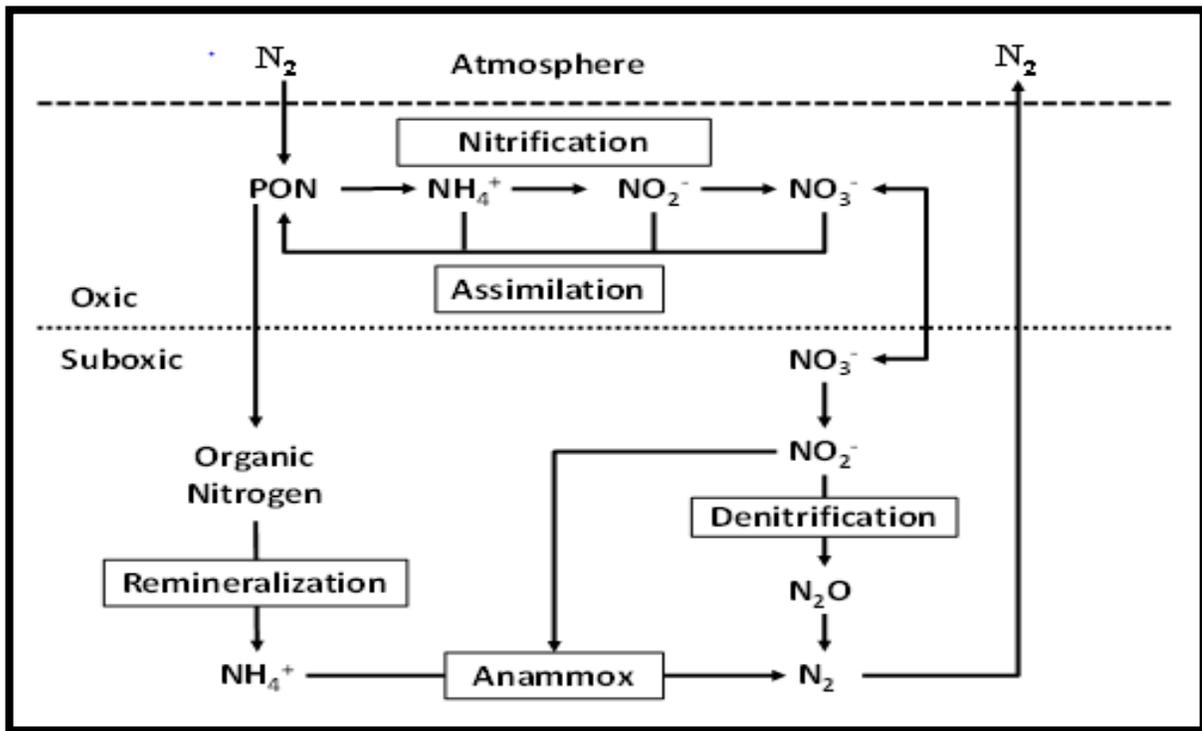


Figure 2. The biological nitrogen cycle showing the main inorganic forms in which nitrogen occurs in the ocean (PON-pariculate organic nitrogen) (adapted from Ward, 2012).

Variations in the ocean's inventory of N_r have driven changes in marine NPP and atmospheric CO_2 throughout the Earth's geological history (Falkowski, 1997; Gruber, 2004; Arrigo, 2005). Marine N_2 fixation provides a source of "new" N and NPP that fuel marine food webs and the biological pump. Thus, the rate of N_2 fixation can affect atmospheric levels of CO_2 on time-scales of decades (variability in upper ocean nutrient cycles) to millennia (changes in the N_r inventory of the deep sea). This makes the balance between the conversion of N_2 to biomass (N_2 fixation) and the production of N_2 (reduction of nitrate and nitrite by denitrification and anammox) particularly important processes in the N cycle that govern the marine inventory of N_r and sustain life in the oceans (Karl et al., 2002; Ward et al., 2007; Gruber, 2008; Ward, 2012).

2.1.1 The Marine Nitrogen Budget

Estimates of global sources and sinks of N_r vary widely (Table 2). Marine biological N_2 fixation accounts for ~50 per cent of N_2 fixation globally (Ward, 2012). Most marine N_2 fixation occurs in the euphotic zone of warm ($> 20^\circ C$), oligotrophic waters between $30^\circ N$ and $30^\circ S$ (Karl et al., 2002; Mahaffey et al., 2005; Stal, 2009; Sohm et al., 2011). Denitrification and anammox in benthic sediments and mid-water oxygen minimum

zones (OMZs) account for most losses of N from the marine N_r 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
	N_2O loss	4-7
	TOTAL	149-482

Assuming a C:N:P ratio of 106:16:1 (the Redfield Ratio, Redfield et al., 1963), the quantity of N_r needed to support NPP globally is $\sim 8800\ Tg\ N\ yr^{-1}$. Given current estimates, inputs of N_r from river discharge and atmospheric deposition support 2-4 per cent of NPP annually, i.e., most NPP is supported by recycled nitrate from deep waters (cf. Okin et al., 2011).

Although the N_2O flux is a small term in the marine N budget (Table 2), it is a significant input to the global atmospheric N_2O pool. Given a total input of $17.7\ Tg\ N\ yr^{-1}$ (Freing et al., 2012), marine sources may account for 20-40 per cent of N_2O inputs to the atmosphere. As N_2O is 200-300 times more effective than CO_2 as a greenhouse gas, increases in N_2O from the ocean may contribute to both global warming and the destruction of stratospheric ozone. We note that although global estimates for anammox have yet to be made, this anaerobic process may be responsible for most N_2 production in some oxygen minimum zones (OMZs) (Strous et al., 2006; Hamersley et al., 2007; Lama et al., 2009; Koeve and Kähler, 2010; Ulloa et al., 2012).

The accounting in Table 2 suggests that total sinks may exceed total sources, but the difference is not significant. Many scientists believe that biological N_2 fixation is underestimated or the combined rates of denitrification and anammox are overestimated (Capone, 2008). On average, the Redfield Ratio approximates the C:N:P ratio of phytoplankton biomass, and the distribution of deviations from the Redfield Ratio (Martiny et al., 2013) suggests that: sources exceed sinks in the subtropical gyres; sources and sinks are roughly equal in upwelling systems (including their OMZs); and sources tend to be less than sinks at high latitudes. This pattern is consistent with the

known distribution of marine diazotrophs and the observation that most marine N₂ fixation occurs in warm, oligotrophic waters between 30° N and 30° S (Mahaffey et al., 2005; Stal, 2009; Sohm et al., 2011). However, given the wide and overlapping ranges of current estimates of N_r sources and sinks (Table 2), the extent to which the two are in steady state remains controversial.

Atmospheric deposition of iron to the oceans via airborne dust may ultimately control the rate of N₂ fixation in the global ocean and may account for the relatively high rate of N₂ fixation in the subtropical central gyres (Karl et al., 2002). Fe II is required for photosynthetic and respiratory electron transport, nitrate and nitrite reduction, and N₂ fixation. The large dust plume that extends from North Africa over the subtropical North Atlantic Ocean dominates the global dust field (Stier et al., 2005). Consequently, iron deposition is particularly high in this region (Mahowald et al., 2005) where it may increase phytoplankton NPP by stimulating N₂ fixation (Mahowald et al., 2005; Krishnamurthy et al., 2009; Okin et al., 2011). Model simulations indicate that the distribution and rate of N₂ fixation may also be influenced by non-Redfield uptake of N and P by non-N₂ fixing phytoplankton (Mills and Arrigo, 2010). In these simulations, N₂ fixation in ecosystems dominated by phytoplankton with N:P ratios < Redfield is lower than expected when estimated rates are based on Redfield stoichiometry. In contrast, in systems dominated by phytoplankton with N:P ratios > Redfield, N₂ fixation is higher than expected based on Redfield stoichiometry.

2.1.2 Time-Space Coupling of N₂ Fixation and Denitrification/Anammox

Early measurements of N₂ fixation and the geographic distribution of *in situ* deviations from the Redfield Ratio suggest that the dominant sites of N₂ fixation and denitrification are geographically separated and coupled on the time scales of ocean circulation (Capone et al., 2008 and references therein). In this scenario, the ocean oscillates between being a net source and a net sink of N_r on time scales of hundreds to thousands of years (Naqvi, 2012). However, there is also evidence that N₂ fixation is closely coupled with denitrification/anammox in upwelling-OMZ systems¹⁴, i.e., rates of N₂ fixation are high downstream from OMZs where denitrification/anammox is high (Deutsch et al., 2007). Their findings indicate that N₂ fixation and denitrification are in steady state on a global scale. Results from 3-D inverse modelling (DeVries et al., 2013) and observations that the marine N_r inventory has been relatively stable over the last several thousand years (Gruber, 2004; Altabet, 2007) support the hypothesis that rates of N₂ fixation and denitrification/anammox are closely coupled in time and space.

At the same time, global biogeochemical modelling suggests that the negative feedbacks stabilizing the N_r inventory cannot persist in an ocean where N₂ fixation and denitrification/anammox are closely coupled, i.e., spatial separation, rather than spatial proximity, promoted negative feedbacks that stabilized the marine N inventory and

¹⁴ Oxygen minimum zones (OMZs) are oxygen-deficient layers in the ocean's water column (Paulmier and Ruiz-Pino, 2009).

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 N₂ fixation and denitrification, a net loss of N from the marine N_r inventory, and declines in NPP and CO₂ 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 (PO₄⁻³), 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 ~0.1 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.)

Sources	River discharge	10.79 – 31.00
	Atmospheric deposition	0.54 – 1.05
	TOTAL	11.33 – 32.05
Sinks	Open ocean sedimentation	1.30 – 10.57

The primary source of P in the atmosphere is mineral dust, accounting for approximately 80 per cent of atmospheric P. Other important sources include biogenic particles, biomass burning, fossil-fuel combustion, and biofuels. The P in mineral particles is not

very soluble, and most of it is found downwind of desert and arid regions. Only $\sim 0.1 \text{ Tg P yr}^{-1}$ 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, 60-85 per cent is buried in continental shelf sediments (Slomp, 2011). Assuming that inputs from river discharge and atmospheric deposition are, respectively, $\sim 15 \text{ Tg P yr}^{-1}$ 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 ($< 10 \mu\text{m}$) account for most NPP (Barton et al., 2010). Phytoplankton species diversity is also a unimodal function of phytoplankton NPP, with maximum diversity at intermediate levels of NPP and minimum diversity associated with blooms of diatoms, dinoflagellates, *Phaeocystis* sp., and coccolithophores (Irigoien et al., 2004). This suggests that pelagic marine food webs may be most resilient to climate and anthropogenic forcings at intermediate levels of annual phytoplankton NPP.

3.2 *Events, phenomena and processes of special interest*

Zooplankton grazing: Zooplankton populations play key roles in both microbial food webs¹⁵ supported by small phytoplankton ($< 10 \mu\text{m}$) and metazoan food webs¹⁶

¹⁵ The microbial food web (or microbial loop) consists of small phytoplankton (mean spherical diameter $< 10 \mu\text{m}$), heterotrophic bacteria, archaea and protozoa (flagellates and ciliates).

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). EBAs are guided in part by the recognition that the flow of energy and nutrients from NPP through marine food webs ultimately limits annual fish landings (Pauly and Christensen, 1995; Pikitch et al., 2004).

Both mean annual and maximum fish landings have been shown to be related to NPP on regional scales, with increases in potential landings at high latitudes (> 30 per cent) and decreases at low latitudes (up to 40 per cent) (Pauly and Christensen, 1995; Ware, 2000;

¹⁶ The so-called “classical” food web is dominated by larger phytoplankton, metazoan zooplankton and nekton.

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., fisheries relying on NPP at the Eastern Boundary Upwelling Systems require substantially higher levels of NPP than elsewhere (Chassot et al., 2010). Variations in PPR/NPP are related to a number of factors, including the relative importance of microbial and metazoan food webs and differences in the efficiencies of growth and transfer efficiencies among trophic levels. The level of exploitation (PPR/NPP) increased by over 10 per cent from 2000 to 2004, and the NPP appropriated by current global fisheries is 17-112 per cent higher than that appropriated by sustainable fisheries. Temporal and spatial variations in PPR/NPP call into question the usefulness of global NPP *per se* as a predictor of global fish landings (Friedland et al., 2012). Friedland et al. (2012) found that NPP is a poor predictor of fish landings across 52 LMEs, with most variability in fish landings across LMEs accounted for by chlorophyll-a concentration, the fraction of NPP exported to deep water, and the ratio of secondary production to NPP. Given these considerations and uncertainties concerning the effects of climate change on fluxes of nutrients to the euphotic zone, it is not surprising that there is considerable uncertainty associated with projections of how changes in NPP will affect fish landings over the next few decades.

3.2.2 *NPP Fisheries and zooplankton*

Zooplankton is a critical link between NPP and fish production (Cushing, 1990; Richardson, 2008). Efficient transfer of phytoplankton NPP to higher trophic levels ultimately depends on the relative importance of microbial and metazoan food webs and the coherence between the timing of phytoplankton blooms (initiation, amplitude, duration) and the reproductive cycles of zooplankton and planktivorous fish (Cushing, 1990; Platt et al., 2003; Koeller et al., 2009; Jansen et al., 2012). Energy transfer to higher trophic levels via microbial food webs is less efficient than for metazoan food webs (e.g., Barnes et al., 2010; Barnes et al., 2011; Suikkanen et al., 2013). Coherence in time and space is especially important in higher-latitude ecosystems (Sherman et al., 1984; Edwards and Richardson, 2004; Richardson, 2008; Ohashia et al., 2013), where seasonal variations in NPP are most pronounced and successful fish recruitment is most dependent on synchronized production across trophic levels (Cushing, 1990; Beaugrand et al., 2003). The phenological response to ocean warming differs among functional groups of plankton, resulting in predator-prey mismatches that may influence PPR/NPP in marine ecosystems. For example, phytoplankton blooms in the North Atlantic begin earlier south of 40°N (autumn – winter) and in spring north of 40°N (Siegel et al., 2002; Ueyama and Monger, 2005; Vargas et al., 2009). Likewise, a 44-year time series (1958-2002) revealed progressively earlier peaks in abundance of dinoflagellates (23 days), diatoms (22 days) and copepods (10 days) under stratified summer conditions in the North Sea (Edwards and Richardson, 2004). Such differential responses in phytoplankton and zooplankton phenology lead to mismatches between successive trophic levels and, therefore, a decline in PPR/NPP, i.e., a decrease in carrying capacity for harvestable fish stocks.

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 O₂ 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 $\sim 30 \times 10^6$ km² (~ 8 per cent of the ocean’s surface area) with a volume of $\sim 10 \times 10^6$ km³ (~ 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 dynamics and oceanographic conditions (Cullen, 2008b). Negative impacts of algal toxins include illness and death in humans who consume contaminated fish and shellfish or are exposed to toxins via direct contact (swimming, inhaling noxious aerosols); mass mortalities of wild and farmed fish, marine mammals and birds; and declines in the capacity of ecosystems to support goods and services (Cullen, 2008b; Walsh et al., 2008). Impacts associated with toxic algal blooms are global and appear to be increasing in severity and extent in coastal ecosystems as a consequence of anthropogenic nutrients, introductions of non-native toxic species with ballast water from ships, and climate-driven increases in water temperature and vertical stratification of the upper ocean (Glibert et al., 2005; Glibert and Bouwman, 2012; Cullen, 2008b; Franks, 2008; Malone, 2008; Hallegraeff, 2010; Moore et al., 2008; Babin et al., 2008).

¹⁷ Primarily due to the rapid rise in fertilizer use in agriculture, production of manure from farm animals, domestic sewage, and atmospheric deposition associated with fossil-fuel combustion.

3.2.6 Nanoparticles

Nanoparticles have dimensions of 1-100 nm and are produced both naturally and anthropogenically. Of concern here are anthropogenic nanoparticles, such as titanium dioxide (TiO₂)¹⁸ and nanoplastics¹⁹. Nanoparticulate TiO₂ is highly photoactive and generates reactive oxygen species (ROS) when exposed to ultraviolet radiation (UV). Consequently, TiO₂ has been used for antibacterial applications, such as wastewater treatment. It also has the potential to affect NPP. For example, it has been found that ambient levels of UV from the sun can cause TiO₂ nanoparticles suspended in seawater to kill phytoplankton, perhaps through the generation of ROS (Miller et al., 2012). Recent work has also highlighted the potential environmental impacts of microplastics (cf. Depledge et al., 2013; Wright et al., 2013). Experimental evidence suggests that nanoplastics may reduce grazing pressure on phytoplankton and perturb nutrient cycles. For example, Wegner et al., (2012) found that mussels (*Mytilus edulis*) exposed to nanoplastics consume less phytoplankton and grow slower than mussels that have not been exposed. In addition, microplastics contain persistent organic pollutants, and both mathematical models and experimental data have demonstrated the transfer of pollutants from plastic to organisms (Teuten et al., 2009).

Understanding the ecotoxicology of anthropogenic nanoparticles in the marine environment is an important challenge, but as of this writing there is no clear consensus on environmental impacts *in situ* (cf. Handy et al., 2008). We know so little about the persistence and physical behaviour of anthropogenic nanoparticles *in situ* that extrapolating experimental results, such as those given above, to the natural marine environment would be premature. We urgently need to develop the means to reliably and routinely monitor nanoparticles of anthropogenic origin and their impacts on production and fate of phytoplankton biomass. A first step towards risk assessment would be to establish and set limits based on their intrinsic toxicity to phytoplankton and the consumers of plankton biomass. The provision of such information is part of the mission of Working Group 40 of the Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection (GESAMP). WG 40 was established to assess the sources, fate and effects of micro-plastics in the marine environment globally.²⁰

3.2.7 Ultraviolet Radiation and the Ozone Layer

The Sun emits ultraviolet radiation (UV, 400-700 nanometers), with UV-B (280-315 nm) having a wide range of potentially harmful effects, including inhibition of primary

¹⁸ The world production of nanoparticulate TiO₂ is an order of magnitude greater than the next most widely produced nanomaterial, ZnO. About 70 per cent of all pigments use TiO₂, and it is a common ingredient in products such as sunscreen and food colouring. Titanium dioxide is therefore likely to enter estuaries and oceans, for example, from industrial discharge.

¹⁹ Plastic nanoparticles are released when plastic debris decomposes in seawater. Nanoparticles are also released from cosmetics and from clothes in the wash, and enter sewage systems where they are discharged into the sea.

²⁰ <http://www.gesamp.org/work-programme/workgroups/working-group-40>.

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 required for sustainable development (Millennium Ecosystem Assessment, 2005; Worm et al., 2006; Conservation International, 2008; Perrings et al., 2010; Schlitzer et al., 2012; Malone et al., 2014b; Chapter 3 in this assessment). These include:

- (1) food security through the production of harvestable fish, shellfish and macroalgae (Sherman and Hempel, 2009; Chassot et al., 2010; Barbier et al., 2011);
- (2) climate regulation through carbon sequestration (Twilley et al., 1992; Cebrian, 2002; Schlitzer et al., 2003; Duarte et al., 2005; Bouillon et al., 2008; Mitsch and Gosselink, 2008; Schneider et al., 2008; Subramaniam et al., 2008; Laffoley and Grimsditch, 2009; Nellemann et al., 2009; Chavez et al., 2011; Crooks et al., 2011; Henson et al., 2012);
- (3) maintenance of water quality through nutrient recycling and water filtration (Falkowski et al., 1998; Geider et al., 2001; Dayton et al., 2005; Howarth et al., 2011);
- (4) protection from coastal erosion and flooding through the growth of macrophyte habitats (Danielsen et al., 2005; UNEP-WCMC, 2006; Davidson and Malone,

²¹ Ozone can be destroyed by reactions with by-products of man-made chemicals, such as chlorine from chlorofluorocarbons (CFCs). Increases in the concentrations of these chemicals have led to ozone depletion.

²² <http://www.nasa.gov/content/>.

2006/2007; Braatz et al., 2007; Koch et al., 2009; Titus et al., 2009; Barbier et al., 2011), and

- (5) development of biofuels and discovery of pharmaceuticals through the maintenance of biodiversity (Chynoweth et al., 2001; Orhan et al., 2006; Han et al., 2006; Yusuf, 2007; Negreanu-Pîrjol et al., 2011; Vonthron-Sénécheau et al., 2011; Pereira et al., 2012; Sharma et al., 2012).

On a global scale, the value of these services in coastal marine and estuarine ecosystems has been estimated to be > 25 trillion United States dollars annually, making the coastal zone among the most economically valuable regions on Earth (Costanza et al., 1997; Martínez et al., 2007). The global loss of macrophyte ecosystems threatens the ocean's capacity to sequester carbon from the atmosphere (climate control), support biodiversity (Part V of this Assessment) and living marine resources (Part IV of this Assessment), maintain water quality, and protect against coastal erosion and flooding (Boesch and Turner, 1984; Dennison et al., 1993; Duarte, 1995; CENR, 2003; Scavia and Bricker, 2006; Davidson and Malone, 2006/07; Diaz and Rosenberg, 2008; MacKenzie and Dionne, 2008; Nellemann et al., 2009). Estimates of the value of these services by Koch et al., (2009) and Barbier et al., (2011) suggest that the socioeconomic impact of the degradation of marine macrophyte ecosystems is on the order of billions of US dollars per year.

5. Anthropogenic Impacts on Upper Ocean Plankton and Nutrient Cycles

5.1 Nitrogen loading

The rate of industrial Nitrogen gas (N₂) fixation increased rapidly during the 20th century and is now about equal to the rate of biological N₂ fixation, resulting in a two- to threefold increase in the global inventory of Reactive nitrogen (N_r) (Galloway et al., 2004; Howarth, 2008), a trend that has accelerated the global N cycle (Gruber and Galloway 2008). Today, anthropogenic N_r inputs to surface waters via atmospheric deposition and river discharge are now roughly equivalent to marine N₂ fixation (Table 2) and are expected to exceed marine N₂ fixation in the near future as a result of increases in emissions from combustion of fossil fuels and use of synthetic fertilizers. This trend is expected to continue (Duce et al., 2008; Seitzinger et al., 2010).

Atmospheric deposition of anthropogenic N_r increased by an order of magnitude during the 20th century to ~54 Tg N y⁻¹ (80 per cent of total deposition), an amount that could increase NPP by ~0.06 per cent. Estimates of anthropogenic emissions for 2030 indicate a 4-fold increase in total atmospheric N_r deposition to the ocean and an 11-fold increase in AAN deposition (Duce et al., 2008). However, Lamarque et al., (2013) suggest that oxidized N_r may decrease later this century because of increased control of the emission of oxidized N compounds. At the same time, the geographic distribution of atmospheric deposition has also changed (Suntharalingam et al., 2012). In the late 1800s,

atmospheric deposition over most of the ocean is estimated to have been $< 50 \text{ mg N m}^{-2} \text{ y}^{-1}$. By 2000, deposition over large ocean areas exceeded $200 \text{ mg N m}^{-2} \text{ y}^{-1}$ with intense deposition plumes ($> 700 \text{ mg N m}^{-2} \text{ y}^{-1}$) extending downwind from Asia, India, North and South America, Europe and West Africa. Predictions for 2030 indicate similar patterns, but with higher deposition rates extending farther offshore into the oligotrophic, subtropical central gyres. Likewise, marine N_2O production has increased compared to pre-industrial times downwind of continental population centres (in coastal and inland seas by 15-30 per cent, in oligotrophic regions of the North Atlantic and Pacific by 5-20 per cent, and in the northern Indian Ocean by up to 50 per cent). These regional patterns reflect a combination of high N_r deposition and enhanced N_2O production in suboxic zones.

The major pathway of anthropogenic N_r loading to the oceans is river runoff. Anthropogenic N_r input to the coastal ocean via river discharge more than doubled during the 20th century due to increases in fossil-fuel combustion, discharges of human and animal wastes, and the use of industrial fertilizers in coastal watersheds (Peierls et al., 1991; Galloway et al., 2004; Seitzinger et al., 2010). Riverine input of N_r to the coastal ocean is correlated with human population density in and net anthropogenic inputs (NANI)²³ to coastal watersheds (Howarth et al., 2012). NPP in coastal marine and estuarine ecosystems increases with increasing riverine inputs of N_r (Nixon, 1992). Given predicted increases in population density in coastal watersheds and climate-driven changes in the hydrological cycle, global nutrient-export models predict that riverine inputs of N_r to coastal waters will double again by 2050 (Seitzinger et al., 2010). In this context, it is noteworthy that anthropogenic perturbations of the N-cycle caused by NANI already exceed the estimated “planetary boundary” ($35 \times 10^3 \text{ kg yr}^{-1}$) within which sustainable development is possible (Rockstram et al., 2009).

Ocean warming and associated increases in vertical stratification are likely to exacerbate the effects of increases in NANI on phytoplankton NPP in coastal waters (Rabalais et al., 2009). As a consequence, excess NPP and the global extent of coastal eutrophication are likely to continue increasing, especially in coastal waters near large watersheds, population centres and areas of industrial agriculture (Kroeze and Seitzinger, 1998; Dayton et al., 2005; Seitzinger et al., 2005; UNESCO, 2008; Kemp et al., 2009; Rabalais et al., 2009; Sherman and Hempel, 2009).

5.2 *Ocean warming*

5.2.1 *Global impacts on NPP*

Henson et al., (2013) used the results of six global biogeochemical models to project the effects of upper ocean warming on the amplitude and timing of seasonal peaks in

²³ Net anthropogenic nitrogen input (NANI) is the sum of synthetic N fertilizer used, N fixation associated with agricultural crops, atmospheric deposition of oxidized N, and the net movement of N into or out of the region in human food and animal feed.

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 (Malone, 1980; Azam et al., 1983; Cushing, 1990; Kiørboe, 1993; Legendre and Rassoulzadegan, 1996; Shurin et al., 2006; Pomeroy et al., 2007; Marañón, 2009; Barnes et al., 2010; Finkel et al., 2010; Suikkanen et al., 2013; and section 6.3.2).

In today's ocean, the proportion of NPP accounted for by small phytoplankton (cells with an equivalent spherical diameter < 10 μm) generally increases with increasing water temperature in the ocean (Atkinson et al., 2003; Daufresne et al., 2009; Marañón, 2009; Huete-Ortega et al., 2010; Morán et al., 2010; Hilligsøe et al., 2011) and with increasing vertical stratification of the euphotic zone (Margalef, 1978; Malone, 1980; Kiørboe, 1993). Small cells also have a competitive advantage over large cells in nutrient-poor environments (Malone, 1980a; Chisholm, 1992; Kiørboe, 1993; Raven, 1998; Marañón, 2009). Thus, as the upper ocean warms and becomes more stratified, it is likely that the small phytoplankton species will account for an increasingly large fraction of NPP (Morán et al., 2010) resulting in increases in energy flow through microbial food webs and decreases in fish stocks and organic carbon export to the deep sea (see section 6.1.1 and references therein).

This trend may be exacerbated by increases in temperature that are likely to stimulate plankton metabolism, enhancing both NPP and microbial respiration. Recent studies (Montoya and Raffaelli, 2010; Sarmiento et al., 2010; Behrenfeld, 2011; Taucher and Oschlies, 2011; Taucher et al., 2012) suggest that predicted climate-driven increases in the temperature of the upper ocean will stimulate the NPP of smaller picophytoplankton cells (equivalent spherical diameter < 2 μm), despite predicted decreases in nutrient inputs to the euphotic zone from the deep sea in permanently stratified regions of the ocean (e.g., the oligotrophic, subtropical central gyres).

However, if this does occur, it will not result in an increase in fishery production or in the ocean's uptake of atmospheric CO₂, because increases in picophytoplankton NPP will be accompanied by equivalent increases in the respiratory release of CO₂ by bacterioplankton and other heterotrophic microbial consumers in the upper ocean (Sarmiento et al., 2010; Behrenfeld, 2011).

5.2.2 Regional impacts on NPP

Regional trends in phytoplankton NPP are less controversial. The area of low NPP in the subtropical central gyres increased by 1-4 per cent yr⁻¹ from 1998 through 2006 (Polovina et al., 2008; Vantrepotte and Mélin, 2009), a trend that is likely to continue through this century (Polovina et al., 2011). Decreasing NPP has been attributed to climate-driven (ocean warming) increases in vertical stratification and associated decreases in nutrient fluxes from deep water to the euphotic zone in the permanently stratified subtropical gyres (Rost et al., 2008; Jang et al., 2011; Polovina et al., 2011; Capotondi et al., 2012; Moore et al., 2013). In the North Atlantic, upper ocean warming and increases in stratification have been accompanied by decreasing NPP in waters south of ~50°N, whereas warming and increases in stratification to the north have been accompanied by increasing NPP (Richardson and Shoeman, 2004; Bode et al., 2011). These divergent responses to stratification reflect increases in the availability of sunlight in nutrient-rich, well-mixed subpolar waters and increases in nutrient limitation in nutrient-poor, permanently stratified²⁴ subtropical waters (Richardson and Shoeman, 2004; Steinacher et al., 2010; Bode et al., 2011; Capotondi et al., 2012).

Polar ecosystems are particularly sensitive to climate change (Smith et al., 2001; Anisimov et al., 2007; Bode et al., 2011; Doney et al., 2012; Engel et al., 2013), and the impacts of shrinking ice cover on NPP are expected to be especially significant in the Arctic Ocean (Wang and Overland, 2009). Loss of Arctic sea ice has accelerated in recent years (with a record low in 2012),²⁵ a trend that is correlated with an increase in annual NPP by an average of 27.5 Tg C yr⁻¹ since 2003, with an overall increase of 20 per cent from 1998 to 2010 (Arrigo et al., 2008; Arrigo and van Dijken, 2011; Brown and Arrigo, 2012). Of this increase, 30 per cent has been attributed to a decrease in the spatial extent of summer ice and 70 per cent to a longer growing season (the spring bloom is occurring earlier). The change in NPP is not spatially homogeneous. Positive trends are most pronounced in seasonally ice-free regions, including the eastern Barents shelf, Siberian shelves (Kara and east Siberian seas), western Mackenzie shelf, and the Bering Strait. NPP is expected to continue increasing during this century due to continued sea-ice retreat and the associated increase in available sunlight. However, this trend may be short-lived if nitrate supplies from deep water are insufficient (Tremblay and Gagnon, 2009). Neglecting the latter, Arrigo and van Dijken (2011) project a > 60 per cent increase in NPP for a summer ice-free Arctic using a linear extrapolation of the historical

²⁴ The permanent or main thermocline extends from ~50° N to ~50° S. North Atlantic Deep Water and Antarctic Bottom Water formation take place at higher latitudes.

²⁵ <http://nsidc.org/arcticseaicenews//>.

trend. Should these trends continue, additional loss of ice during Arctic spring could boost NPP more than three-fold above 1998-2002 levels and alter marine ecosystem structure and the degree of pelagic-benthic coupling. However, predictions of future trends in Arctic NPP are uncertain, given the possibility of nitrate limitation (Vancoppenolle et al., 2013). Reducing uncertainty for both nitrate fields and rates of biogeochemical processes in the sea-ice zone should improve the skill of projected changes in NPP needed to anticipate the impact of climate change on Arctic food webs and the carbon cycle.

The coastal marine ecosystem of the West Antarctic Peninsula supports massive spring-summer phytoplankton blooms upon which the production of Antarctic krill depends. NPP associated with these blooms is correlated with the spatial and temporal extent of ice cover during the previous winter. Air temperatures over the West Antarctic Peninsula have warmed by 7°C since the 1970s, resulting in a 40 per cent decline in winter sea-ice cover and a decrease in phytoplankton NPP (Flores et al., 2012; Ducklow et al., 2013; Henley, 2013). Continued declines in the extent of winter sea-ice cover is likely to drive decadal-scale reductions in NPP and the production of krill, reducing the food supply for their predators (marine mammals, seabirds and people).

5.2.3 *Distribution and abundance of toxic phytoplankton species*

The socioeconomic impacts of toxic dinoflagellate species are increasing globally (Van Dolah, 2000; Glibert et al., 2005; Hoagland and Scatista, 2006; Babin et al., 2008; UNESCO, 2012), and their distribution and abundance are sensitive indicators of the impacts of anthropogenic nutrient inputs and climate-driven increases in water temperature and vertical stratification on ecosystem services (see section 6.3.2).

Alexandrium tamarense represents a group of species that cause paralytic shellfish poisoning (PSP) (*Alexandrium catenella*, *A. fundyense*, *Pyrodinium bahamense* and *Gymnodinium catenatum*) globally (Boesch et al., 1997). Since the 1970s, PSP episodes have spread from coastal waters of Europe, North America and Japan to coastal waters of South America, South Africa, Australia, the Pacific Islands, India, all of Asia and the Mediterranean (Lilly et al., 2007). Climate-driven shifts in the geographic ranges of *Ceratium furca* and *Dinophysis spp.* in the NE Atlantic have also occurred (Edwards et al., 2006), and the abundance of dinoflagellates in the North Sea have been positively correlated with the North Atlantic Oscillation (NAO) and sea surface temperature (Edwards et al., 2001).

5.2.4 *Distribution and abundance of indicator zooplankton species*

The distribution and abundance of calanoid copepods are also sensitive indicators of climate-driven increases in upper ocean temperature and basin-scale oscillations (Hays et al., 2005; Burkill and Reid, 2010; Edwards et al., 2010) including poleward shifts in species distributions (Beaugrand et al., 2002; Beaugrand et al., 2003; Cheung et al., 2010; Chust et al., 2014), decreases in size, and higher growth rates (e.g., Beaugrand et al., 2002; Richardson, 2008; Mackas and Beaugrand, 2010). There have also been phenological changes, with the seasonal peak in abundance advancing to earlier in the

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 their seasonal peak in abundance.²⁶ Water temperature also influences the annual cycle of *Neocalanus plumchrus* biomass in the Northeast Pacific, where decadal-scale variations include a shift to an earlier occurrence of the seasonal biomass peak, as well as a decrease in the duration of the bloom under warm ocean conditions (Mackas et al., 2007; Batten and Mackas, 2009).

The frequency and magnitude of gelatinous zooplankton blooms may be important indicators of the status and performance of marine ecosystems (Hay, 2006; Graham et al., 2014). Both predators (medusa and ctenophores) and herbivores (tunicates) can affect the fate of NPP (Pitt et al., 2009; Lebrato and Jones, 2011). Predators disrupt metazoan food webs by consuming copepods and small fish (Richardson et al., 2009). Tunicates reduce the transfer of NPP to upper trophic levels and to the deep sea as their gelatinous remains are degraded via microbial food webs (Lebrato and Jones, 2011).

Although, there is no evidence for an increase in the frequency and magnitude of gelatinous zooplankton on a global scale (Condon et al., 2012), decadal scale increases have been reported in several coastal marine ecosystems (Brodeur et al., 2002; Kideys, 2002; Lynam et al., 2006; Uye, 2008; Licandro et al., 2010). A rigorous analysis of multi-decadal (using a 1950 baseline) abundance data for 45 Large Marine Ecosystems, Brotz et al., 2012 found that 28 (62 per cent) exhibited increasing trends while 3 (7 per cent) exhibited decreasing trends. Thus, while increases of jellyfish populations may not be globally universal, they are both numerous and widespread. The most likely causes of these trends include ocean warming, overfishing, coastal eutrophication, habitat modification, aquaculture, and introductions of non-indigenous gelatinous species (Brotz et al., 2012; Purcell, 2012). While direct evidence is lacking for most of these pressures, jellyfish tend to be most abundant in warm waters with low forage fish populations, and it is likely that ocean warming will provide a rising baseline of abundance leading to increases in the magnitude of jellyfish blooms and associated impacts on ecosystem services (Graham et al., 2014).

5.3 *Ocean acidification*

The oceans are becoming more acidic due to increases in uptake of atmospheric CO₂ (Calderia and Wickett, 2003; Calderia and Wickett, 2005; Doney et al., 2009; Beardall et al., 2009), and most of the upper ocean is projected to be undersaturated with respect to aragonite within 4-7 decades (Orr et al., 2005) with undersaturation expected to occur earliest at high latitudes (> 40°) and in upwelling systems where the aragonite saturation horizon is expected to shoal most rapidly (Feely et al., 2009, Gruber et al., 2009). These chemical changes in turn affect marine plankton via several mechanisms

²⁶ http://www.pices.int/publications/pices_press/volume16/v16_n2/pp_19-21_CPR_f.pdf.

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 CO₂ decrease the energy requirements for photosynthetic organisms to synthesize biomass. Such biological effects are likely to perturb marine biogeochemical cycles including carbon export to the deep sea via the biological pump which may have a positive feedback on the buildup of CO₂ in the upper ocean and atmosphere. However, assessments of the impacts of ocean acidification on NPP and nutrient cycling remain controversial and are a subject of much research (cf., Delille et al., 2005; Doney et al., 2009; Shi et al., 2009; Shi et al., 2010; Shi et al., 2012; Moy et al., 2009; Kristy et al., 2010). For example, increases in CO₂ may stimulate N₂ and carbon fixation by colonial cyanobacterial diazotrophs (Barcelos e Ramos et al., 2007). In addition, as the upper ocean warms, the geographic range of diazotrophs will expand. These effects may combine to enhance N₂ fixation by as much as 35-65 per cent by the end of this century (Hutchins et al., 2009). It is noteworthy interesting that projected increases in N₂ fixation are about the same magnitude as increases in denitrification projected by Oschlies et al., (2008). Although both of these estimates have large uncertainties, if input and output fluxes accelerate at about the same rate, the ocean's global inventory of N_r would not change, whereas NPP could increase (Sarmiento et al., 2010; Behrenfeld, 2011).

In regard to macrophytes, photosynthetic rates of calcifying macroalgae do not appear to be stimulated by elevated CO₂ conditions, i.e., the majority of studies to date have shown a decrease or no change in photosynthetic rates under elevated CO₂ conditions (Hofmann and Bischof, 2014). On the other hand, there is clear evidence that ocean acidification (higher pCO₂) stimulates seagrass NPP resulting in increases in above- and below-ground biomass suggesting that the capacity of seagrasses to sequester carbon may be significantly increased (Garrard and Beaumont, 2014).

5.4 *Sea-level rise, coastal development and macrophyte NPP*

Sea levels have increased globally since the 1970s, mainly as a result of global mean sea-level rise due in part to anthropogenic warming causing ocean thermal expansion and glacier melting (Chapter 4 of this Assessment). Sea-level rise will not be uniform globally. Regional differences in sea-level trends will be related to changes in prevailing winds, ocean circulation, gravitational pull of polar ice sheets, and subsidence, so that sea-level rise will exceed the global mean in some regions and will actually fall in others.²⁷

To date, the global decline in macrophyte habitats has been primarily due to coastal development, artificially hardened shorelines, aquaculture operations, dredging and eutrophication. This will change with sea-level rise (Short and Neckles, 1999; Nicholls

²⁷ <http://tidesandcurrents.noaa.gov/sltrends/>.

and Cazenave, 2010). Macrophyte habitats are projected to be negatively affected by sea-level rise and subsidence, especially where distributions are constrained on their landward side by geomorphology and human activities along the shoreline (Pernetta, 1993; Short and Neckles, 1999; Orth et al., 2006; Alongi, 2008; Gilman et al., 2008; Silliman et al., 2009; Waycott et al., 2009; Donato et al., 2011). Together, sea-level rise, subsidence, coastal development and aquaculture operations are destroying mangrove forests, tidal marshes and seagrass beds at an alarming rate. The combination of sea-level rise and the loss of these coastal habitats will decrease the capacity of coastal ecosystems to provide services, including climate regulation (carbon sequestration), protection against coastal flooding and erosion, and the capacity to support biodiversity and living marine resources.

5.5 *Regions of special interest*

5.5.1 *Coastal river plumes*

Increases in land-based anthropogenic inputs of N and P to coastal waters is driving increases in annual phytoplankton NPP in estuaries and coastal marine ecosystems near population centres and areas of industrial agriculture in large river basins (sections 6.2.1 and 6.2.2). This may lead to further increases in the spatial extent and/or number of coastal ecosystems experiencing eutrophication and oxygen-depleted dead zones associated with the coastal plumes of major river-coastal systems, including the Yangtze (E. China Sea), Mekong (S. China Sea), Niger (Gulf of Guinea), Nile (Mediterranean Sea), Parana (Atlantic Ocean), Mississippi (Gulf of Mexico), and Rhine (North Sea) (UNESCO, 2012).

5.5.2 *Polar waters and subtropical gyres*

Ocean warming appears to be driving opposing trends in phytoplankton NPP in polar waters (interannual increases in NPP) and subtropical gyres (interannual decreases in NPP) and a global expansion of oxygen minimum zones associated with upwelling systems. Regions of special interest include the Arctic Ocean, coastal waters of the western Antarctic Peninsula, permanently stratified subtropical gyres of the North Pacific and North Atlantic, and major coastal upwelling centers (Cariaco Basin and California, Humboldt, Canary, Benguela and Somali Currents).

5.5.3 *Subpolar waters*

Early expressions of the impacts of ocean acidification on upper ocean plankton are most likely to occur at high latitudes. Pteropods and foraminifera (dominated by *Globigerina bulloides*) are most abundant at high latitudes (> 40°N) in surface waters of the North Atlantic (Barnard et al., 2004; Fraile et al., 2008; Bednaršek et al., 2012), whereas the coccolithophore *E. huxleyi* is most abundant in the

“Great Southern Coccolithophore Belt” of the Southern Ocean²⁸ 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 declines in these regions, likely impacts will be to reduce the capacity of the oceans to take up CO₂, 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 affecting 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 Feeley, 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 Process²⁹ 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 its coastal module (UNESCO, 2012; Malone et al., 2014a; Malone et al., 2014b). The essential variables required to compute key indicators of ecosystem health include species richness, chlorophyll-*a*, dissolved N_r, and dissolved BAP (UNESCO, 2012). Routine and sustained measurements of these variables over a range of temporal and spatial scales are required for rapid and timely detection of changes in NPP and nutrient cycles and the impacts of these changes on ecosystem services on regional (e.g., Large Marine Ecosystems) to global scales. Although satellite imagery, limited *in situ* measurements and numerical models are making it possible to detect interannual and decadal changes in NPP on these scales, the same cannot be said for observations of species richness and nutrient distributions (UNESCO, 2012).

²⁸ The belt is centered around the sub-Antarctic front and has a spatial extent of 88 x 106 km² (~25 per cent of the global ocean).

²⁹ http://www.un.org/Depts/los/global_reporting/global_reporting.htm.

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., 2009). For details on requirements, advantages and limitations of satellite-based remote sensing of ocean colour, see IOCCG (1998), Sathyendranath (2000), and UNESCO (2006, 2012).

Two related activities, both contributions to the Global Ocean Observing System, provide the core of an integrated observing system needed to provide data required to assess the state of the marine environment in terms of both time-space variations in phytoplankton NPP and the impacts of these variations on ecosystem services: the Chlorophyll Global Integrated Network (ChloroGIN)³⁰ (Sathyendranath et al., 2010) and Societal Applications in Fisheries and Aquaculture using Remotely-Sensed Imagery (SAFARI) (Forget et al., 2010). FARO (Fisheries Applications of Remotely Sensed Ocean Colour) has recently been initiated to coordinate the development of ChloroGIN and SAFARI for the provision of ocean-colour data and data products for use in fisheries research and ecosystem-based management of living marine resources.³¹ Likewise, the GEO Biodiversity Observation Network, the Global Biodiversity Information Facility (GBIF), and the Ocean Biogeographical Information System (UNESCO, 2012) provide data and information on the species richness of marine primary producers.

6.2 *Nitrogen and phosphorus cycles*

The N cycle is more dynamic³² and less well understood than previously thought (Codispoti et al., 2001; Capone and Knapp, 2007; Zehr and Kudela, 2011; Landolfi et al., 2013; Voss et al., 2013). Major impediments to detecting and understanding decadal changes in the marine N cycle are: current uncertainties about the rates (undersampling); distribution and coupling of sources and sinks; sensitivity of N₂ fixation, denitrification, and anammox to anthropogenic inputs of N_r; and changes in the marine environment associated with climate change (warming and increases in stratification of the upper ocean, ocean acidification, oxygen depletion, and sea-level rise).

³⁰ <http://www.chlorogin.org/>.

³¹ <http://www.faro-project.org/index.html>.

³² Estimates of turnover times of N_r have decreased from 10,000 years to 1,500 years (Codispoti et al., 2001).

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 programme³³. Shipboard time-series observations of biogeochemical variables that are being established globally³⁴ should provide deposition data for these plumes. For riverine inputs, rivers that are part of the Global Terrestrial Network for River Discharge (GTN-R)³⁵ and that represent a broad range of volume discharges and catchment-basin population densities are high priorities for monitoring land-based inputs and associated land-cover/land-use practices in their watersheds (UNESCO, 2012).

All global ocean biogeochemistry models require oceanographic data on physical and chemical variables, including temperature, salinity, mixed-layer depth, and the concentration of macro-nutrients (N, P, Si) (Le Quéré et al., 2010). Over the last decade, autonomous technologies for measuring essential physical variables (including temperature, salinity and mixed-layer depth) have revolutionized our ability to observe the sea surface and the ocean's interior. By integrating data from both remote sensing (satellite-based sensors and land-based HF radar) and *in situ* measurements (from ships of opportunity, research vessels and automated moorings, profiling floats, gliders, surface drifters and large pelagic predators), observations of atmospheric and upper ocean geophysics are now made continuously in four dimensions; data are transmitted to data assembly centers in near-real time via satellites, fiber-optic cables, and the internet; and predictions (nowcasts and forecasts) of atmospheric and upper ocean "weather" are made routinely using data assimilation techniques and coupled atmospheric-hydrodynamic models (Hall et al., 2010).

Over the last decade, autonomous technologies have revolutionized our ability to measure nitrate, nitrite, ammonium and reactive phosphate *in situ* (Johnson and Coletti, 2002; ACT, 2003; Sakamoto et al., 2004; Adornato et al., 2010). Efforts are also underway to expand sampling programmes such Repeat Hydrography (Hood 2009), Argo (Rudnick et al., 2004; Testor et al., 2010), and OceanSites³⁶ to incorporate *in situ* nutrient sensors.

³³ <http://www.solas-int.org/>.

³⁴ e.g., For example, <http://www.unesco.org/new/en/natural-sciences/ioc-oceans/sections-and-programmes/ocean-sciences/biogeochemical-time-series/>.

³⁵ <http://www.fao.org/gtos/gt-netRIV.html>; <http://gtn-r.bafg.de>,

http://www.bafg.de/GRDC/EN/Home/homepage_node.html.

³⁶ <http://www.whoi.edu/virtual/oceansites/>

6.3 Plankton species diversity

Sustaining marine species richness³⁷ is the single most important indicator of the capacity of ecosystems to support services valued by society (Worm et al., 2006). A biodiversity observation network (GEO BON)³⁸ has been established to document changes in species biodiversity, and the Ocean Biogeographic Information System (OBIS)³⁹ documents the species diversity, distribution and abundance of life in the oceans. Both are contributions to GEOSS.⁴⁰ A set of sentinel sites should be targeted for sustained observations of species richness including Large Marine Ecosystems and the emerging network of marine protected areas that is nested within them (Malone et al., 2014a). As a group, these sites represent a broad range of species diversity, climate-related changes in the marine environment, and anthropogenic nutrient inputs. Here we underscore the importance of rapid detection of changes in plankton diversity and early warnings of impacts on marine ecosystem services.

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³⁷ Species richness is an unweighted list of species present in an ecosystem that is especially important to monitor because it is the simplest indicator of species diversity and it does not discount rare species that are often the primary concern.

³⁸ <https://www.earthobservations.org/geobon.shtml>

³⁹ <http://www.iobis.org/>

⁴⁰ www.earthobservations.org/geobon.shtml

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