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Abstract

Marine net primary production by phytoplankton fuels the marine food web. This chapter summarizes the primary controls on marine net primary production, recent temporal patterns in regional and global net primary production, and projections for net marine primary production over the next century.

Keywords

Net primary production • Primary productivity • Climate change • Carbon cycle • Photosynthesis • Phytoplankton

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Definition

Net Primary Production (NPP)

Net primary production (NPP) is the formation of organic material from inorganic compounds minus the respiratory losses of the photosynthetic organisms. Global marine annual NPP provides an estimate of the organic material available to fuel the ocean's food webs for the year. The majority of NPP in the sea is generated by photosynthesis by phytoplankton: a polyphyletic group of photosynthetic prokaryotic and eukaryotic algal lineages. Satellite ocean color estimates of phytoplankton chlorophyll-*a* (the dominant pigment used to harvest light) are combined with models to estimate global NPP, while ^{14}C incubations have been the most common method for estimating in situ NPP (for a review of these and other methods, see Cullen (2001)). Here we summarize controls on and recent patterns in NPP and model projections for how NPP will change over the next century.

Currently satellite-based ocean color models estimate that annual mean net primary productivity is $407 \text{ mg C m}^{-2} \text{ day}^{-1}$ with a year-to-year standard error of 2.9 over 2003–2010 (data from www.science.oregonstate.edu/ocean.productivity following Behrenfeld and Falkowski (1997)). Integrated over the year marine NPP is ~ 44 to 67 Gt of carbon, approximately half of total global NPP (Field et al. 1998; Westberry et al. 2008). Net primary productivity is spatially and temporally variable. Annual rates of marine net primary productivity are approximately lognormally distributed and range from a minimum value of $7.2 (\pm 0.8)$ to a maximum value of $12500 (\pm 212 \text{ sd}) \text{ mg C m}^{-2} \text{ day}^{-1}$ and are typically lowest in the oceanic gyres and highest in upwelling zones along the coasts (Fig. 15.1). Regionally 21–46 % of NPP occurs in the high latitudes and Southern Ocean, 11–29 % occurs in the gyres, and 40–49 % occurs in the subtropical regions (Westberry et al. 2008). Within local regions NPP varies on daily, monthly, and decadal scales. For example, over 1985–2008 monthly mean daily net primary productivity in the Gullmar Fjord, Sweden, ranges from 50 to over $2000 \text{ mg C m}^{-2} \text{ day}^{-1}$ during the year, and mean annual production varies across years from a low of 182 to a high of $339 \text{ g C m}^{-2} \text{ year}^{-1}$ (Lindahl et al. 2009).

Controls on NPP

Temporal and spatial trends in NPP are regulated by changes in environmental conditions that regulate phytoplankton growth including irradiance; inorganic nutrient concentrations, predominantly nitrogen, phosphorus, and iron; and temperature. For example, over significant areas of the equatorial and subarctic Pacific Ocean and parts of the Southern Ocean, low levels of iron deposition on the sea surface result in chronically low levels of phytoplankton biomass and NPP; ice cover, high winds, and resulting deep surface mixed layers result in low NPP due to chronic light limitation over large areas of the high latitudes for much of the year; nutrient upwelling zones fuel phytoplankton blooms and high NPP in many coastal regions and across the equatorial upwelling (Fig. 15.1). Loss processes such as

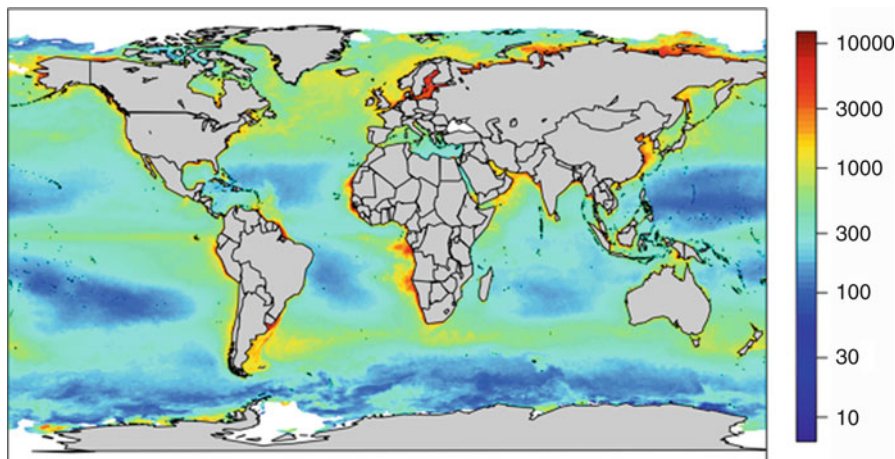


Fig. 15.1 Annual NPP ($\text{mg C m}^{-2} \text{ day}^{-1}$) for 2008 estimated from ocean color and sea surface temperature (MODIS) using the Vertically Generalized Production Model following Behrenfeld and Falkowski (1997). Data courtesy of the Oregon Ocean Productivity Lab: <http://www.science.oregonstate.edu/ocean.productivity/standard.product.php>

grazing, viral and parasitoid attack, cell death, remineralization by bacteria and fungi, and sinking further regulate total net primary production through changes in the total standing stock of phytoplankton and the supply of nutrient.

Recent Trends in NPP: Global Analyses

Year-over-year trends in NPP can be driven by natural physical forcing (patterns in atmospheric and ocean circulation, mixed layer dynamics) overlaid by anthropogenic perturbations including eutrophication of coastal regions and changes in CO_2 and ocean pH and reduction of ozone over the poles. Climate change is expected to cause changes in the magnitude and temporal and spatial patterns in NPP, but over the short term may be difficult to detect over natural variability. Statistical analyses indicate an NPP time series of ~ 40 years duration is required to unambiguously detect an anthropogenic climate change signal (Henson et al. 2010).

Global analysis of ocean color indicates NPP has decreased between 1979–2002 and 1997–2006 (Gregg et al. 2003; Behrenfeld et al. 2006). Typical monthly changes in the NPP anomaly over the period of 1997–2007 are $1 \text{ mg C m}^{-2} \text{ day}^{-1}$ per year, with maximal changes on the order of $30\text{--}40 \text{ mg C m}^{-2} \text{ day}^{-1}$ per year (Henson et al. 2010). Gregg et al. (2003) found that much of the decrease in NPP over 1979–2002 ($\sim 70\%$) occurred in the high latitudes. In contrast NPP increased between 7% and 14% in 3 of the 4 low-latitude basins analyzed. Gregg et al. (2003) hypothesize the $>10\%$ decline in NPP in the Antarctic is due to a combination of a decrease in iron deposition and increase in wind stress. Behrenfeld et al. (2006), using an ocean color model from 1997 to 2006, find a global decline in

NPP starting in 1999 that is highly correlated with a multivariate El Niño-Southern Oscillation index and hypothesize that this decline in global NPP (from 1999 to 2006) may be due to climate warming and increased stratification. Changes in NPP due to climate change is expected to be difficult to detect over natural interannual, decadal, and multi-decadal variability inherent in the NPP signal on the decade scale (Henson et al. 2010). Differences in the individual satellite data sets, calibrations used, and the temporal range of observations are likely responsible for some of the differences in results and conclusions between studies.

Recent Trends in NPP: Regional Analyses

Low Latitudes

Long-term measurements of NPP across the globe indicate changes in NPP over the last decades are complex and diverse. Increases in sea surface temperature in the subtropics are expected to increase surface water stratification, decrease nutrient supply to the surface, resulting in a decrease in NPP (Behrenfeld et al. 2006). In situ and ocean color-based model evidence for recent low-latitude decreases in NPP is equivocal (Gregg et al. 2003; Behrenfeld et al. 2006; Saba et al. 2010). A large decrease in primary productivity has been documented in the Cariaco Basin over the last 15 years as part of the Carbon Retention In A Colored Ocean (CARIACO) time series project (Müller-Karger et al. 2000). In contrast, NPP from in situ ^{14}C tracer measurements at the Bermuda Atlantic Time-series Study site (BATS: 31° N , 64° W) and Hawaii Ocean Time-series site (HOT: 22° N , 158° W), both in subtropical gyres, has been increasing by $\sim 10\text{ mg C m}^{-2}\text{ day}^{-1}\text{ year}^{-1}$ from 1988 to 2006 (Saba et al. 2010). The decadal increases in NPP at these sites have been attributed to changes in subsurface water mass dynamics, changes in community composition, and increases in nitrite+nitrate availability in the surface (Saba et al. 2010).

Coastal Middle Latitudes

Increases in the heat gradient between land and sea associated with climate warming are hypothesized to intensify wind-driven upwelling along areas of the coast and therefore stimulate increases in NPP. Significant increases in NPP have been detected along the California Current from 1997 to 2007, but are not positively correlated with wind stress (Kahru et al. 2009). Changes in nutrient inputs from the continents have had significant impacts on NPP in many coastal systems. For example, primary production in the northern Gulf of Mexico continental shelf has been linked to nutrient inputs from the Mississippi River over the 1980s and 1990s (Lohrenz et al. 1997). In the Baltic entrance region (the Kattegat and Belt Sea), annual NPP has increased from the 1950s to the 1980s and then decreased in the 1990s, attributed in part to changes in nutrient input from land, while higher rates since 1997 are attributed to changes in the methods used to

measure carbon fixation (Rydberg et al. 2006). In the Wadden Sea at Marsdiep, annual NPP has increased since the 1960s, reaching a maximum in the 1990s, and decreasing from the 1990s to 2000 (Cadee and Hegeman 2002). In the Gullmar Fjord off the Swedish Skagerrak coast there is a $\sim 20\%$ increase in NPP from 1985 to a peak in 1992 through 1996 followed by a $\sim 25\%$ decrease to 2008 (Lindahl et al. 2009). The decadal patterns in NPP in the Gullmar Fjord have been attributed to decadal patterns in the North Atlantic Oscillation in conjunction with nutrient inputs and dynamics in the region (Belgrano et al. 1999; Lindahl et al. 2009).

High Latitudes

Regional analyses of Arctic and Southern Ocean NPP indicate recent and projected increases in NPP with ice retreat and associated increases in the area of open water and the length of the phytoplankton growing season (Arrigo et al. 2008; Arrigo and Van Dijken 2011). In the Arctic, net primary production estimated from a satellite-based ocean color model has increased 20 % (441–585 Tg C per year) from 1998 to 2009 following increases in the duration of the open water season (Arrigo and Van Dijken 2011). As ice continues to retreat over the next decades, NPP in the Arctic could increase to ~ 730 Tg C per year, depending on the availability of nutrients (Arrigo and Van Dijken 2011). In the Southern Ocean, NPP estimated from a satellite-based ocean color model from 1978 to 1986 averages 4,414 Tg C per year, with the highest values found in December in the Ross Sea (Arrigo et al. 2008). As ice melt continues in the Southern Ocean, NPP is expected to increase with increasing open water area, meltwater-induced stratification of surface waters near retreating sea ice edges, and input of micronutrients such as iron from the melt of ice (Smith et al. 2007). In situ measurements of primary production in these polar regions, especially the Southern Ocean, are sparse.

Model Projections: NPP Over the Next Century

There is a lack of consensus of how NPP will change over the next century. Projections of NPP from ecosystem-biogeochemical models embedded into three-dimensional ocean–atmosphere general circulation models range from global increases of $>30\%$ to decreases of $>10\%$ by 2100, depending on the model formulation (Bopp et al. 2005; Schmittner et al. 2008; Tagliabue et al. 2011). Models use a variety of different phytoplankton functional types and differ widely in the parameterization of their physiological response to environmental conditions and in some cases the environmental variables that influence growth rate. Only recently have general circulation models with biogeochemistry incorporated flexible elemental stoichiometry and the physiological response to changing $p\text{CO}_2$ (Tagliabue et al. 2011). Most of the models agree that increases in air and sea surface temperature and resultant decreases in surface mixed layer depths and ice retreat are expected to

cause increases in NPP in polar regions, while increased stratification in the subtropics is expected to decrease NPP due to a reduction in surface nutrient availability. Changes in mixed layer depth change irradiance as well as nutrient concentrations. While present models may include the observed increase and eventual saturation of photosynthetic rate with irradiance, the damaging effects of excess irradiance are often neglected. Although the costs associated with avoiding and mitigating photoinhibition are currently poorly quantified, they will impact growth rate and differ across species (Raven 2011) and therefore may contribute to biogeographic patterns in phytoplankton community composition.

Conclusions

NPP is the food that fuels the ocean food web. Currently annual marine NPP is ~44 to 67 Gt of carbon, similar to NPP on land. The impact of future climate change on NPP is unclear. Current expectation is that warming will result in an increase in NPP in polar latitudes due to a decrease in ice cover and increase in surface stratification and the availability of light. In the low-nutrient subtropical oceanic gyres, increased stratification is expected to lead to decreases in nutrient availability and decrease in NPP. Despite these generalities, there is a lack of consensus in model projections of NPP over the next century reflecting significant uncertainties in our understanding of how phytoplankton and NPP will respond to changing climate and other anthropogenic perturbations.

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Cross-References

- ▶ [Ecological Carbon Sequestration in the Oceans and Climate Change](#)
- ▶ [Ocean Acidification and Oceanic Carbon Cycling](#)
- ▶ [Pelagic Ecosystems and Climate Change](#)

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