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Review: phytoplankton primary production in the world's estuarine-coastal ecosystems

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Abstract

Estuaries are biogeochemical hot spots because they receive large inputs of nutrients and organic carbon from land and oceans to support high rates of metabolism and primary production. We synthesize published rates of annual phytoplankton primary production (APPP) in marine ecosystems influenced by connectivity to land – estuaries, bays, lagoons, fjords and inland seas. Review of the scientific literature produced a compilation of 1148 values of APPP derived from monthly incubation assays to measure carbon assimilation or oxygen production. The median value of median APPP measurements in 131 ecosystems is 185 and the mean is 252 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, but the range is large: from −105 (net pelagic production in the Scheldt Estuary) to 1890 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (net phytoplankton production in Tamagawa Estuary). APPP varies up to 10-fold within ecosystems and 5-fold from year-to-year (but we only found 8 APPP series longer than a decade so our knowledge of decadal-scale variability is limited). We use studies of individual places to build a conceptual model that integrates the mechanisms generating this large variability: nutrient supply, light limitation by turbidity, grazing by consumers, and physical processes (river inflow, ocean exchange, and inputs of heat, light and wind energy). We consider method as another source of variability because the compilation includes values derived from widely differing protocols. A simulation model shows that different methods can yield up to 3-fold variability depending on incubation protocols and methods for integrating measured rates over time and depth.

Although attempts have been made to upscale measures of estuarine-coastal APPP, the empirical record is inadequate for yielding reliable global estimates. The record is deficient in three ways. First, it is highly biased by the large number of measurements made in northern Europe (particularly the Baltic region) and North America. Of the 1148 reported values of APPP, 958 come from sites between 30° N and 60° N; we found only 36 for sites south of 20° N. Second, of the 131 ecosystems where APPP has been reported, 37 % are based on measurements at only one location during one year. The accuracy of these values is unknown but probably low, given the large inter-annual and spatial variability within ecosystems. Finally, global assessments are confounded by measurements that are not intercomparable because they were made with a broad range of methods.

Phytoplankton primary production along the continental margins is tightly linked to variability of water quality, biogeochemical processes including ocean-atmosphere CO_2 exchange, and production at higher trophic levels including species we harvest as food. The empirical record has deficiencies that preclude reliable global assessment of this key Earth-system process. We face two grand challenges to resolve these deficiencies: (1) organize and fund an international effort to use a common method and measure APPP regularly across a network of coastal sites that are globally representative and sustained over time, and (2) integrate data into a unifying model to explain the wide range of variability across ecosystems and to project responses of APPP to regional manifestations of global change as it continues to unfold.

1 Introduction

Estuaries have large supplies of organic carbon because of their connection to land that delivers organic matter from runoff and nutrients that support high rates of primary production (Hopkinson et al., 2005). As a result, estuaries function as fast biogeochemical reactors that operate on the energy derived from respiration of their external and internal supplies of fixed carbon. Total annual ecosystem respiration generally exceeds gross primary production (Caffrey, 2004; Gattuso et al., 1998), so most estuaries are heterotrophic ecosystems that transform organic matter into inorganic nutrients and CO_2, are oversaturated in CO_2 with respect to the atmosphere and, unlike the open ocean, are sources of CO_2 to the atmosphere. Although estuaries occupy a small fraction of the Earth surface their CO_2 emissions are globally significant – estimated at $0.43\,\mathrm{Pg\,C\,yr^{-1}}$ (Borges, 2005). Addition of this term to CO_2 budgets reverses the function of the coastal ocean from being a net sink to a net source of CO_2, and this term reduces the calculated global ocean CO_2 uptake by 12 %. Therefore, sound understanding of ocean-atmosphere CO_2 exchange as a climate regulator requires globally distributed measurements of primary production, external supplies of organic carbon, and respiration across the diversity of estuarine ecosystems.

The supply of organic carbon to estuaries is packaged in different forms. Detritus delivered by land runoff is derived primarily from terrestrial vegetation and is an important energy supply that fuels estuarine metabolism. This pool of organic matter is old (Raymond and Bauer, 2001), refractory, has low nitrogen content, is metabolized primarily by microbial decomposers and has little direct food value for herbivores (Sobczak et al., 2005). Much of the organic matter produced by vascular plants and macroalgae is also routed through decomposers or exported; only about 20 % of seagrass, marsh and macroalgal primary production is consumed by herbivores (Cebrian, 1999). A third supply is primary production by microalgae, including phytoplankton and benthic forms. The biogeochemical and ecological significance of microalgal production differs from the other forms because it is enriched in nitrogen and lipids including essential fatty acids, packaged in a form easily accessible to consumer organisms, and because this pool turns over rapidly – on the order of days (Furnas, 1990). Most (∼ 90 %) phytoplankton production is consumed or decomposed to support local heterotrophic metabolism, whereas a substantial fraction of macrophyte production (24–44 %) is exported or buried and does not contribute to local metabolism (Duarte and Cebrian, 1996). Therefore, the different forms of organic matter are metabolized through different routes and have different ecological and biogeochemical ramifications. We focus on phytoplankton primary production as a supply of labile organic carbon that plays a central role in the ecological and biogeochemical dynamics of estuaries and other marine ecosystems influenced by connectivity to land.

With the exception of very turbid estuaries such as the Scheldt (Gazeau et al., 2005), net planktonic production is positive in estuaries so it is an autotrophic component operating within heterotrophic ecosystems. Phytoplankton production is the primary source of organic carbon to some estuarine-coastal system such as the Baltic Sea (Elmgren, 1984), South San Francisco Bay (Jassby et al., 1993), and Moreton Bay (Eyre and McKee, 2002). The rate of phytoplankton production is highly variable in space and time because algal cells divide daily (or faster) under optimal growth conditions. Dynamics of phytoplankton production are characterized by seasonal periods or episodic bursts of rapid photosynthesis as blooms develop. These events are transformative as phytoplankton photosynthesis exceeds total system respiration and estuaries shift temporarily to a state of autotrophy (Caffrey et al., 1998), leading to: depletion of inorganic nutrients as they are converted into organic forms incorporated into algal biomass (Kemp et al., 1997); drawdown of CO_2 (Cloern, 1996) and shifts in pH; oversaturation of dissolved oxygen (Herfort et al., 2012); rapid phytoplankton uptake of contaminants such as PCBs, methylmercury (Luengen and Flegal, 2009), and dissolved trace metals such as cadmium, nickel and zinc (Luoma et al., 1998); increased growth and production of copepods (Kiørboe and Nielsen, 1994) and bivalve mollusks (Beukema and Cadée, 1991) as the algal food supply increases; and sedimentation of phytoplankton-derived organic carbon that accelerates benthic respiration and nutrient regeneration rates (Grenz et al., 2000).

Trophic transfer of the energy and essential biochemicals contained in phytoplankton biomass is the resource base supporting production at higher trophic levels including those we harvest for protein. Annual phytoplankton production is highly correlated with fishery landings (Nixon, 1988), biomass of benthic invertebrates (Herman, 1999), and sustainable yield of cultured shellfish (Bacher et al., 1998). Increasing nutrient runoff during the past century has provoked increases of phytoplankton production supporting 3–8 fold increases of fish biomass in the Baltic Sea, Japan's Seto Inland Sea, northern Adriatic Sea, shelf waters of the Black Sea, and the Nile Delta (Nixon and Buckley, 2002; Caddy, 2000). However, the increased phytoplankton production of organic carbon has exceeded the assimilative capacity of these and other ecosystems, leading to the global expansion of marine dead zones (Diaz and Rosenberg, 2008), loss of habitat for seagrasses, demersal fish and shellfish (Carstensen et al., 2003), and shifts in fish communities (Kemp et al., 2005; Caddy, 2000). The link between phytoplankton production and estuarine biogeochemistry is illustrated in a compelling way by the systemic changes that occurred in Narragansett Bay during a 25 yr warming period when the winter-spring phytoplankton bloom disappeared, primary production declined 40–50 %, benthic metabolism slowed, and the bay switched from being a net consumer to a net producer of fixed nitrogen (Nixon et al., 2009). Therefore, understanding variability of phytoplankton primary production is a key to understanding variability of ecosystem respiration and metabolism; cycling of nutrients, carbon, and trace metals; water and habitat quality; secondary production by herbivores; fish catch; production of cultured shellfish; and the cumulative value of all these ecosystem services, judged to be highest in estuaries among all biomes (Costanza et al., 1997).

Frequent and globally-distributed satellite observations of ocean color have provided a robust understanding of the rates and patterns of primary production across the terrestrial and marine biomes. Total annual primary production in the world oceans is on the order of 60 Pg C (Behrenfeld et al., 2005), and areal rates range from about 160 $\mathrm{g\,C\,m^{-2}}$ in oligotrophic regions of the open ocean to about 1300 $\mathrm{g\,C\,m^{-2}}$ in the most productive (Peruvian) upwelling system (Chavez et al., 2010). However, satellite-based methods have not yet been developed for routinely measuring phytoplankton production in shallow coastal waters where suspended sediments, dissolved organic matter, and interference from land confound interpretation of ocean color (Moreno-Madrinan and Fischer, 2013). Therefore, our knowledge of primary production in estuaries and other shallow coastal domains is based almost entirely on direct measurements, which are labor-intensive and therefore distributed much more sparsely in time and space than can be accomplished through remote sensing.

Here we present an inventory of annual phytoplankton primary production from direct measurements reported in the readily-accessible scientific literature as an update to the last review published three decades ago (Boynton et al., 1982). This work follows recent syntheses of the seasonal patterns (Cloern and Jassby, 2008), scales of variability (Cloern and Jassby, 2010), and phenology of phytoplankton biomass (Winder and Cloern, 2010) in estuarine-coastal ecosystems. Our objectives are to summarize the patterns and rates of phytoplankton production contained in the available data records, and to determine if they contain sufficient spatial and temporal coverage to establish reliable global assessments of this important Earth system process. We first summarize the data compilation to show where, how and when primary production measurements have been made, and then explore the data to illustrate patterns of variability over time, between and within ecosystems. We then provide a synthesis of the literature to summarize what is known about the underlying causes of this variability. We use a simulation model to estimate how much of the between-ecosystem variability could result from the substantial differences in methods used across studies. We end with perspectives on the contemporary state of knowledge of phytoplankton production in estuarine-coastal ecosystems, reliability of production estimates at the global scale, and steps required to reduce the large uncertainty of those estimates.

2 An inventory of phytoplankton primary production measurements

We compiled measurements of phytoplankton primary production reported in references found through searches in SCOPUS, Google Scholar, and Web of Science. Our target was reported values of depth-integrated annual primary production across the world's estuaries, bays, lagoons, tidal rivers, inland seas, and nearshore coastal marine waters influenced by connectivity to land. We only included values derived from direct measurements of oxygen evolution or carbon assimilation that were made at least once each month, except at high latitudes where winter measurements are not made under ice. Reports were excluded if they did not include description of the methods used, sampling frequency and period, or if the sampling locations were not specified. The final compilation (summarized in Supplement Table A1) includes 1148 values of annual phytoplankton production from 483 sampling sites within 131 ecosystems (places). Primary productivity has been measured in many other studies (e.g. Gilmartin, 1964; Henry et al., 1977), but the results were not reported with the information required to calculate depth-integrated annual production.

The compilation includes 389 measurements reported as gross primary production (GPP), 254 measurements reported as net primary production (NPP) that include measures of either net phytoplankton production in the euphotic zone (e.g. Moll, 1977; Rivera-Monroy et al., 1998) or net pelagic production (e.g. Gazeau et al., 2005), and 505 measurements reported only as "primary production" (Fig. 1). Phytoplankton production measurements became routine components of some research and monitoring programs after the 1950s and we found around 200 annual measurements each decade from the 1960s to 1980s. Reported measurements peaked at 388 in the 1990s, but we found only 84 from the first decade of the 21st century (Fig. 1). This seems strong evidence of reduced effort at measuring phytoplankton production in estuarine-coastal ecosystems. The overwhelming majority of measurements were reported from European (more than half from the Baltic region) and North American estuarine-coastal waters. We found a total of only 58 annual production measurements from studies in Asia (31), South–Central America (15), Australia–New Zealand (13), and Africa (1). Primary production was most commonly (974 of 1148) made as measures of ^{14}C assimilation; 159 were made from rates of oxygen production; and 15 from ^{13}C assimilation (Fig. 1).

3 Patterns of variability

3.1 Latitudinal patterns

Annual production at individual sites ranged from $-692\,\mathrm{g\,C\,m^{-2}}$ (net pelagic production, which includes respiration by heterotrophs) at site 2 in the turbid Scheldt Estuary during 2002 (Gazeau et al., 2005) to $1890\,\mathrm{g\,C\,m^{-2}}$ (net phytoplankton production) in the Tamagawa Estuary during 1988 (Yamaguchi et al., 1991). We show the distribution of individual measurements by latitude, and the geographic distribution of effort as the number of reported production measurements at sites binned within 20° latitudinal bands (Fig. 2). Of the 1148 reported values, 958 come from sites between

30° N and 60° N. This highly skewed distribution of effort reflects the exceptional number of production measurements made in the Baltic Sea and nearby coastal waters (420), mostly in Danish or Swedish coastal waters (368), and notably in the Kattegat where 249 measurements have been reported – 23 % of the global total. We found only 36 measurements of annual production reported for sites south of 20° N, none between the equator and 25° S, and only 15 in the Southern Hemisphere. Therefore, our knowledge of phytoplankton primary production in the world's estuarine-coastal ecosystems is strongly biased by the high concentration of sampling effort at northern latitudes and particularly in the Baltic region. In contrast, we found remarkably little published information about the annual production of estuarine-coastal phytoplankton in tropical-subtropical ecosystems and in the Southern Hemisphere. The highly skewed geographic distribution of sampling, coupled with the large variability within latitudinal bands (Fig. 2), severely constrains our ability to answer a fundamental question: does phytoplankton production vary systematically with latitude?

3.2 Variability between sampling sites

From 1148 individual annual primary production measurements we calculated median values at the 483 sites where measurements have been reported. Median production ranged across sites from net pelagic production of $-278\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ at station 2 in the Scheldt Estuary to $1890\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in the Tamagawa Estuary. Given the large weight of measurements from the Baltic region we separated these from sites in other world regions. The mean and median of median annual primary production at sites in the Baltic region are similar, 118 and $112\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, respectively (Fig. 3a). However, the distribution of median annual production at sites in other regions is skewed toward a small number of high values (Fig. 3b), so the overall mean ($238\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) is larger than the median ($174\,\mathrm{C\,m^{-2}\,yr^{-1}}$). Based on the median primary production values reported at these 409 non-Baltic sites, 121 are classified as oligotrophic ($< 100\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), 178 as mesotrophic ($100–300\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), 69 as eutrophic ($300–500\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), and

41 as hypertrophic ($> 500\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), following Scott Nixon's classification (Nixon, 1995).

3.3 Variability between ecosystems

We used the 1148 individual measurements to calculate median annual primary production for the 131 ecosystems where measurements have been reported. We use the word "ecosystem" in the sense of a place, either an individual bay or estuary or a subregion of the Baltic Sea or connected coastal waters (e.g., Gulf of Finland, Kattegat). Forty-seven of these values are single measurements made at one site during one year, but the others represent the medians of measurements made at multiple sites and/or during multiple years (see Fig. 5). The ranked distribution of median values is shown in Fig. 4, which provides a summary of annual phytoplankton primary production measurements reported for the world's estuarine-coastal ecosystems. The overall median is 183 and mean is $254\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$. However, the spread around these measures of central tendency is from -105 to $1890\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, considerably larger than variability of primary production between regions of the world oceans (Chavez et al., 2010).

3.4 Variability within ecosystems

Many of the 131 ecosystems represented in the data compilation are estuaries, fjords, bays or lagoons – aquatic habitats situated within the land-ocean continuum that have large spatial gradients of phytoplankton biomass and environmental factors that regulate phytoplankton growth rate, such as nutrient concentrations, bathymetry, mixing, turbidity, and grazing losses. As a result, high spatial variability of primary production is a characteristic of these ecosystem types. We selected 11 examples where annual phytoplankton production was measured at multiple (minimum 9) sites during one year (Fig. 5a). Spatial variability is large within some of these ecosystems, e.g. ranging from 70 to $810\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in Tomales Bay during 1985, from 15 to $516\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in Howe

Sound during 1974, and from 78 to 493 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in the Westerschelde during 1991. Primary production measurements do not follow a normal distribution (e.g. Figs. 3 and 4; Shapiro–Wilk test $W = 0.780$, $p < 0.0001$; Shapiro and Wilk, 1965), so we used the ratio median absolute deviation (mad) to median production as a robust index of dispersion (Ruppert, 2011) that can be compared within and between ecosystems. This ratio ranged from 0.20 to 0.83 (Fig. 5a) – i.e., the characteristic deviation from the median production within an ecosystem ranged from about 20 % to about 80 % of that median. For comparison, the mad : median of the median annual production between the 11 ecosystems was 0.74. This comparison shows that the spatial variability of primary production across sites within some ecosystems can be comparable to the variability of median production between ecosystems. Therefore, measurements at single sites are unlikely to yield reliable estimates of ecosystem-scale phytoplankton production (Jassby et al., 2002).

Phytoplankton biomass in estuarine-coastal ecosystems can fluctuate substantially from year-to-year (Cloern and Jassby, 2010). We probed the data inventory to explore inter-annual variability of phytoplankton production, using studies at 10 sites where primary production was measured during at least 7 consecutive years. Annual production at some sites, such as Kattegat station 413 (measured from 1989 to 1997) and Gullmar Fjord (from 1985 to 2008) was stable over time (Fig. 5b). However at other sites, such as Massachusetts Bay station N18 and Boston Harbor station F23, inter-annual variability was large, ranging from 207 to 664 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ and 224 to 1087 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$, respectively, during the 1995–2005 study period. The median index of interannual variability (mad:median production) at these 10 sites was 0.23, smaller than the index of variability between the sites of 0.57. Although the number of records is small, the available data suggest that variability of annual phytoplankton primary production between ecosystems > spatial variability within ecosystems > variability between years. Therefore, the highly skewed geographic distribution of phytoplankton production measurements (Fig. 2) differs markedly from the global distribution of sampling that would be required to adequately capture the largest component of variability – between ecosystems. The available data probably underestimate interannual variability because most records are short and variance of primary production increases with series duration (Jassby et al., 2002). We found only 8 series of annual primary production longer than a decade; the longest were from Tampa Bay (29 yr; Johansson, 2010; J. O. R. Johansson, personal communication, August 2013), Gullmar Fjord (23 yr; Lindahl et al., 1998; O. Lindahl, personal communication, June 2009), and Rhode River Estuary (20 yr; Gallegos, 2013; C. L. Gallegos, personal communication, May 2013). The rarity of decadal time series precludes assessments of change over time to complement assessments of climate-driven changes in oceanic primary production (Behrenfeld et al., 2006).

4 What drives this variability?

4.1 A conceptual model

Primary productivity is the product of plant biomass times its turnover rate, so its variability can be understood by exploring processes that drive variability of biomass and growth rate (Fig. 6). Potential biomass is set by the nutrient supply rate (Howarth, 1988), but the realization of that potential varies greatly across estuaries (Cloern, 2001) and is determined by the balance between three sets of processes: (1) transport processes including import of ocean-derived phytoplankton, export by washout during events of high river flow, and sinking; (2) biomass growth through cell division; and (3) mortality that includes grazing losses to consumers and cell lysis induced by viral infection (Brussaard, 2004). Phytoplankton growth rate is regulated by water temperature, nutrient concentrations and forms, and the amount and quality of photosynthetically available radiation (PAR). The conceptual model depicted in Fig. 6, grounded in the foundational work of coastal scientists such as Bostwick Ketchum (Ketchum, 1954), links these processes and provides a framework for exploring underlying causes of the large variability of primary production over time, within and between estuaries.

The construct of primary production as the product of biomass and growth rate is the basis for models of varying complexity used to estimate primary production and to compare the strength of different controls. The simplest model describes primary production as a linear function of biomass B (chl a concentration), which varies 500-fold across estuarine-coastal ecosystems (Cloern and Jassby, 2008). For example, 64 % of the daily variability of phytoplankton production in Saanich Inlet is explained by daily fluctuations of chl a (Grundle et al., 2009), and 81 % of the variability of annual production in Boston Harbor–Massachusetts Bay is explained by variability of annual mean chl a (Keller et al., 2001). A second class of models describes primary production as a linear function of $\Psi \cdot B \cdot I$ (Behrenfeld and Falkowski, 1997), where the constant Ψ is an index of light-utilization efficiency (a physiological component) and I is a proxy for light availability such as depth-averaged PAR. Models of this form explain 60–95 % of the primary production variability in estuarine-coastal ecosystems such as San Francisco Bay, Puget Sound, Neuse River Estuary, Delaware Bay, Hudson River Estuary plume (Cole and Cloern, 1987), Tomales Bay (Cole, 1989), the Sacramento–San Joaquin Delta (Jassby et al., 2002), and Escambia Bay (Murrell et al., 2007). A further level of complexity is required to explain the full range of production variability in other estuaries such as Chesapeake Bay (Harding et al., 2002), Rhode River Estuary (Gallegos, 2013), and Tokyo Bay (Bouman et al., 2010). In these places the photosynthetic efficiency Ψ varies significantly because the maximum carbon-assimilation rate $p_{\max}$ (see below) fluctuates with seasonal temperature variability or variability of dissolved inorganic carbon along the estuarine salinity gradient (Gallegos, 2012). Models based on this last approach are the foundation for deriving oceanic primary production from remotely sensed chl a, water temperature, and optical properties of the upper ocean (Behrenfeld et al., 2006).

The use of different model classes implies that the physical and biological regulators of primary production shown in Fig. 6 take on varying importance across the diversity of ecosystem types at the land–sea interface. However, underlying all models is a strong empirical relationship between primary production and biomass. The mechanisms of annual phytoplankton production variability over time (Fig. 5b), within (Fig. 5a), and between (Fig. 4) estuarine-coastal ecosystems are thus tightly tied to the mechanisms of biomass variability. We use case studies to illustrate responses to four fundamental mechanisms of biomass variability.

4.2 Nutrient supply

Estuaries receive larger nutrient inputs than any other ecosystem type (Howarth, 1988), and the importance of nutrient supply is reflected in the wide distribution of annual production measurements shown in Fig. 4. The hypertrophic systems at the upper end of this distribution sustain exceptionally high phytoplankton biomass, with peak chl *a* concentrations of 98 $\mu g L^{-1}$ in Tamagawa Estuary (Yamaguchi et al., 1991), $> 100\,\mu g L^{-1}$ in Swan River Estuary (Thompson, 1998), and 181 $\mu g L^{-1}$ in Cienaga Grande de Santa Marta (Hernandez and Gocke, 1990). These compare with chl *a* concentrations $\sim 0.1\,\mu g L^{-1}$ in oligotrophic ocean domains. All hypertrophic ecosystems have large nutrient supplies, either from urban sources including sewage (e.g. Tamagawa Estuary, Yamaguchi et al., 1991; Boston Harbor, Oviatt et al., 2007; Kaneohe Bay before sewage diversion, Smith et al., 1981; Swan River Estuary, Thompson, 1998; western Long Island Sound, Goebel et al., 2006), or runoff from agricultural watersheds (e.g. Golfo de Nicoya, Gocke et al., 2001; Huizache–Caimanero Lagoon, Edwards, 1978; Ciénaga Grande de Santa Marta, Hernandez and Gocke, 1990). By contrast, the low-production ecosystems at the other end of the distribution include those with small nutrient inputs such as Biscayne Bay (Roman et al., 1983) and Petalion Gulf in the oligotrophic Aegean Sea where nitrate concentrations are typically $< 0.1\,\mu M$ (Becacos-Kontos, 1977). Therefore, nutrient supply is a key mechanism of variability across ecosystems.

However, nutrient loading alone is not a good predictor of primary production because individual estuaries have attributes that regulate their efficiency at converting exogenous nutrients into phytoplankton biomass (Cloern, 2001). The hypertrophic estuaries, bays and lagoons have high production efficiency because they have features that either promote fast growth such as shallow depth (Cienaga Grande de Santa Marta, Hernandez and Gocke, 1990) or a long growing season in the tropics (Golfo de Nicoya; Gocke et al., 2001), or slow transport processes that retain nutrients and phytoplankton biomass (Chesapeake Bay, Harding et al., 2002; Swan River Estuary, Thompson, 1998). Other nutrient-rich estuaries, such as northern San Francisco Bay and the Scheldt estuary, are inefficient at converting exogenous nutrients into phytoplankton biomass because of fast grazing or strong light limitation (see below). The distribution of nutrients along the land-ocean transition can generate spatial variability of primary production such that it decreases with distance away from the nutrient source – e.g., river inflow to the Douro Estuary (Azevedo et al., 2006) or sewage discharges to Long Island Sound (Goebel et al., 2006).

Nutrient supply to estuaries is strongly influenced by human activities, and changes in nutrient supply over time have caused significant changes in phytoplankton biomass and production, especially since the mid 20th century. Chlorophyll *a* concentrations increased 5- to 10-fold in lower Chesapeake Bay after the 1950s in response to increased loadings of reactive nitrogen (N) and phosphorus (P) (Harding, 1997); annual phytoplankton production in the western Wadden Sea ranged between 100–200 $\mathrm{g\,C\,m^{-2}}$ in the 1960s and 1970s, but increased to 300–400 $\mathrm{g\,C\,m^{-2}}$ in the 1980s after riverine nutrient inputs to the North Sea increased (Cadée and Hegeman, 1993); annual phytoplankton production in the Kattegat more than doubled after the 1950s and is significantly correlated with annual N loading (Carstensen et al., 2003). Equally compelling case studies show significant reductions of phytoplankton biomass and production following steps to reduce anthropogenic nutrient input. Net annual phytoplankton production in Kaneohe Bay was 894 $\mathrm{g\,C\,m^{-2}}$ in 1976 when total N (TN) loading was 25.6 $\mathrm{kmol\,N\,d^{-1}}$, but it fell to 294 $\mathrm{g\,C\,m^{-2}}$ in 1978 after TN loading was reduced to 6.1 $\mathrm{kmol\,N\,d^{-1}}$ by diverting sewage to the ocean (Smith et al., 1981). Similar changes were measured in upper Tampa Bay where mean annual GPP declined from 750 $\mathrm{g\,C\,m^{-2}}$ during 1980–85 to 410 $\mathrm{g\,C\,m^{-2}}$ during 1999–2008 after inputs of dissolved inorganic N were reduced from >3000 to <1000 $\mathrm{kg\,N\,d^{-1}}$ (Johansson, 2010). Therefore, long-term observations confirm linkages between nutrient supply and phytoplankton biomass and primary production. However, steps to reduce nutrient inputs have not always led to expected declines of phytoplankton biomass or production (Duarte et al., 2008), and this experience confirms also that the efficiency of incorporating nutrients into biomass is regulated by processes that vary across ecosystems and change over time. We highlight three of these processes.

4.3 Light limitation

Phytoplankton growth rate in nutrient-rich estuaries is determined in large part by light availability measured as mean PAR (Alpine and Cloern, 1988), which varies with incident solar irradiance, turbidity, and depth of the mixed layer (Wofsy, 1983). All three components play major roles in regulating phytoplankton production. Primary production at high latitudes is constrained by a short growth season because solar irradiance does not reach the water surface when it is covered by ice and snow. The open-water season in Dumbell Bay (80°30′ N) lasts about a month, so annual net production is only $9\,\mathrm{g\,C\,m^{-2}}$ (Apollonio, 1980); annual production is $10\,\mathrm{g\,C\,m^{-2}}$ in Young Sound (74° N) where the ice-free season is two months (Rysgaard et al., 1999). These values of annual production are smaller than the peak daily production ($16\,\mathrm{g\,C\,m^{-2}}$) in the tropical Cienaga Grande de Santa Marta (Hernandez and Gocke, 1990).

Many estuaries have high concentrations of mineral sediments delivered by land runoff and kept in suspension by wind waves and tidal currents (May et al., 2003). Sediment-associated turbidity constricts the photic zone to a thin layer, leading to light limitation of photosynthesis over the water column and slow incorporation of nutrients into phytoplankton biomass. The Scheldt Estuary is an iconic example of a high-nutrient estuary where mean PAR in the water column is insufficient to support positive net production (Gazeau et al., 2005). Wofsy (1983) developed a steady-state model to explore relationships between phytoplankton growth and turbidity from suspended particulate matter (SPM). Simulations with the model are consistent with observations that: phytoplankton biomass in nutrient-rich estuaries is inversely related to SPM concentration;

blooms cannot develop when SPM concentration exceeds about 50 $\mathrm{mg\,L^{-1}}$ (except in shallow waters); and phytoplankton respiration exceeds photosynthesis when the optical depth – the product of mixed depth H (m) times the light attenuation coefficient k ($\mathrm{m^{-1}}$) – exceeds 5. The empirical record supports these generalizations. Annual phytoplankton production in the inner Bristol Channel is only 6.8 $\mathrm{g\,C\,m^{-2}}$ because of "severe light limitation" of photosynthesis by suspended sediments where the euphotic zone is less than 50 cm deep (Joint and Pomroy, 1981). Other nutrient-rich high-SPM estuaries have ultra-low primary production, such as Roskeeda Bay with NPP of 4 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Raine and Patching, 1980), Colne Estuary with GPP of 5 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Kocum et al., 2002), and turbid regions of the Ems–Dollard (Colijn and Ludden, 1983) and Columbia River (Small et al., 1990) estuaries with annual production of 26 and 38 $\mathrm{g\,C\,m^{-2}}$, respectively. These examples are important reminders that phytoplankton require both light energy and nutrients as essential resources. Simple models (e.g. Cloern, 1999) provide tools for assessing the relative importance of light and nutrient limitation of phytoplankton growth and making comparisons of resource limitation across estuaries and over time.

Much of the spatial variability (Fig. 5a) of primary production within some estuaries is a consequence of SPM gradients that generally decrease along the river-ocean continuum as sediments sink and their concentrations are diluted by clear ocean water. A characteristic pattern of high production near the estuary mouth and low production near the river source of SPM or in the estuarine turbidity maximum, is seen in many estuaries including Corpus Christi Bay (Flint, 1970), Howe Sound (Stockner et al., 1977), Bristol Channel (Joint and Pomroy, 1981), Ems Dollard Estuary (Colijn and Ludden, 1983), Delaware Bay (Pennock and Sharp, 1986), San Francisco Bay (Cloern, 1987), and the Seine Estuary (Garnier 2001). The water column of turbid estuaries can support positive net production in shallow regions where the optical depth $H \cdot k$ is less than 5. Thus, lateral shallows of coastal plain estuaries such as South San Francisco Bay (Cloern et al., 1985), Chesapeake Bay (Malone et al., 1986), and James River Estuary (Bukaveckas et al., 2011) are zones of high phytoplankton biomass and they function as autotrophic domains that export phytoplankton biomass that fuels metabolism in deeper heterotrophic domains (Caffrey et al., 1998). Thus, complex spatial patterns of phytoplankton production and net ecosystem metabolism are established across estuarine gradients of bathymetry and SPM concentration (Lucas et al., 1999).

Net production can be positive, even in deep turbid estuaries, when the water column stratifies to establish a surface layer where $H \cdot k < 5$ and phytoplankton biomass grows rapidly. Much of the annual production in estuaries occurs during blooms, and surface blooms develop under conditions of salinity stratification in many estuaries such as Chesapeake Bay (Malone et al., 1986), South San Francisco Bay (Cloern, 1996), and Tokyo Bay (Bouman et al., 2010). The primary source of buoyancy to stratify estuaries is freshwater inflow, so stratification and production dynamics are tied to variability of river discharge as a source of low-density fresh water. In tidal estuaries both stratification and turbidity oscillate over the fortnightly neap-spring cycle, with lowest SPM concentrations, strongest stratification and highest phytoplankton biomass during the low-energy neap tides followed during spring tides by the breakdown of stratification, increases of SPM by suspension of bottom sediments, and rapid declines of phytoplankton biomass and primary production (Cloern, 1996). Variability of primary production over the neap-spring tidal cycle is a prominent feature of phytoplankton dynamics in Puget Sound, Saanich Inlet, Lower Saint-Lawrence Estuary (Sinclair et al., 1981), subestuaries of Chesapeake Bay (Haas, 1977), and South San Francisco Bay (Cloern, 1984). Light availability to phytoplankton also fluctuates with wind stress that breaks down stratification and generates waves that penetrate to suspend bottom sediments in shallow estuaries. Wind mixing can be a mechanism of annual variability of the primary production that occurs during seasonal blooms. For example, March–April primary production in South San Francisco Bay was 67 $\mathrm{g\,C\,m^{-2}}$ during a year (1990) of relatively calm spring winds and low turbidity, but only 18 $\mathrm{g\,C\,m^{-2}}$ the following year when winds were stronger, SPM concentrations higher, and the spring bloom was suppressed by high turbidity (May et al., 2003). Human modifications of hydrologic systems have altered sediment discharge in many of the world's rivers, with downstream effects on estuarine primary producers. SPM concentrations and turbidity of northern San Francisco Bay have decreased 50 % since 1975 following decades of channelizing and damming its tributary rivers. This implies a doubling of the euphotic-zone depth, illustrating that changes in sediment supply can be a process of long-term change in estuarine primary production (Cloern and Jassby, 2012).

4.4 Top-down regulation

While the division rate of phytoplankton cells is determined by temperature, nutrient concentrations and light availability, the rate of biomass change is determined by the balance between rates of cell division and mortality including consumption by grazers (Fig. 6). Rates of cell division and consumption are often in balance, except following events such as lengthening of the photoperiod in spring (Riley, 1967), pulsed inputs of nutrients (Ara et al., 2011), germination of phytoplankton resting stages (Shikata et al., 2008), or setup of stratification (Pennock, 1985) when phytoplankton growth rate temporarily exceeds grazing rate and biomass builds. The most probable fate of phytoplankton cells is to be consumed by grazers that include fast-growing microzooplankton (flagellates, ciliates, mixotrophic phytoplankton) and mesozooplankton such as copepods. On an annual basis the grazing loss to mesozooplankton is a small fraction ($\sim$ 10 %) of primary production in productive estuaries (Calbet, 2001), but year-to-year variability in the seasonal timing of copepod population growth can be an important regulator of annual primary production. For example, anomalous low primary production occurred across all sampling sites in Massachusetts Bay in 1998, a year with an unusually warm winter and early growth of copepods whose grazing suppressed the winter-spring bloom that normally contributes over 40 % of annual primary production (Keller et al., 2001).

Although micro- and meso-zooplankton consume most primary production in the open ocean (Calbet, 2001; Calbet and Landry, 2004), their role as grazers is less important in shallow estuaries and bays where benthic suspension feeders, especially bivalve molluscs, are the dominant grazers (Murrell and Hollibaugh, 1998). Bivalves are the important grazers in shallow waters because they can filter the overlying water column on time scales of days (Cloern, 1982) and because they both compete with zooplankton for the phytoplankton food resource and prey upon microzooplankton (Greene et al., 2011) and copepod nauplii (Kimmerer et al., 1994). Grazing by bivalves can be a strong regulator of phytoplankton biomass and production. This regulation is evident from phytoplankton biomass budgets that compare seasonal rates of growth with grazing by zooplankton and bivalves (Cloern, 1982). It is evident from comparative analyses showing that mean annual phytoplankton biomass (chl *a*) is inversely correlated with mussel biomass in 59 Danish estuaries ($r = -0.71$; Kaas et al., 1996) and 15 estuaries of Prince Edward Island ($r = -0.92$; Meeuwig, 1999). And it is evident from case studies of changing phytoplankton biomass after bivalve populations either abruptly increased or decreased. Annual phytoplankton production in the low-salinity habitats of northern San Francisco Bay decreased from 106 to 39 $\mathrm{g\,C\,m^{-2}}$ after the nonnative clam *Potamocorbula amurensis* was introduced and rapidly colonized bottom sediments in 1987 (Alpine and Cloern, 1992). An equally large and abrupt decline of phytoplankton biomass followed colonization of the Ringkøbing Fjord by the clam *Mya arenaria* after water exchange with the North Sea was modified (Petersen et al., 2008). The inverse pattern developed in South San Francisco Bay (Cloern and Jassby, 2012) after the NE Pacific shifted to its cool phase in 1999 when bivalve biomass declined and annual phytoplankton production increased from $< 200\,\mathrm{g\,C\,m^{-2}}$ to $> 400\,\mathrm{g\,C\,m^{-2}}$. Similarly, the loss of oysters from Chesapeake Bay is a contributing factor to the increased phytoplankton biomass and production in this high-nutrient estuary (Kemp et al., 2005). Therefore, grazing by pelagic and especially benthic suspension feeders is a key process of phytoplankton production variability over time and between estuarine-coastal ecosystems.

4.5 Physical processes

Phytoplankton production is tightly regulated by physical processes that deliver nutrients, control the efficiency with which nutrients are converted into biomass, and transport nutrients and biomass away from and into estuaries and bays. The key physical forcings operate across the interfaces between estuaries and their tributary rivers, the coastal ocean, and atmosphere (Cloern, 1996).

4.5.1 River flow

Empirical observations over decades have established a strong association between river discharge and phytoplankton primary production in estuaries. However, the relationship between the two is complex, system specific, multidimensional, and is best understood through comparisons of the time scales of biomass production, loss, and transport (Lucas et al., 1999). Complexity arises because variability of river inflow drives variability of some processes that promote and other processes that suppress biomass accumulation and production. Positive associations derive from rivers as a source of both nutrients and low-density fresh water that stratifies estuaries and creates a horizontal density gradient that drives gravitational circulation and retains phytoplankton biomass within estuaries. As a result, seasonal and annual variability of primary production are positively correlated with freshwater inflow to many estuaries including South San Francisco Bay (Cloern, 1991), Neuse Estuary (Mallin et al., 1993), Chesapeake Bay (Adolf et al., 2006), Escambia Bay (Murrell et al., 2007), Patos Lagoon (Abreu et al., 2009), and Sagami Bay (Ara et al., 2011).

However, river inflow is also a source of sediments (Wetsteyn and Kromkamp, 1994) and colored dissolved organic matter (Lawrenz et al., 2013) that constrain primary production by attenuating light and altering its spectral quality. Freshwater inflow also drives seaward advective transport that can be faster than phytoplankton growth rate and prevent biomass accumulation during periods of high discharge. Thus, seasonal phytoplankton biomass and production are inversely related to river inflow to other estuaries such as North San Francisco Bay (Cloern et al., 1983), and Norman River Estuary (Burford et al., 2012). These contrasting examples illustrate the dual functions of river inflow as both a nutrient source that promotes biomass growth and a transport process that can prevent its accumulation within estuaries. The balance between these functions varies with river flow so the functional relationships are complex, as observed in the New and Neuse River estuaries where the transport time scale (freshwater flushing time) ranges from < 2 h to > 7 months. Phytoplankton biomass in these estuaries is maximal when flushing time is about 10 days. At longer flushing times (low flow) biomass growth rate is limited by nutrient exhaustion; at shorter flushing times (high flow) biomass accumulation is limited by washout (Peierls et al., 2012).

A generally-accepted principle of estuarine ecology is that phytoplankton production is highest in coastal systems that have longest flushing times and retain nutrients and biomass (Gilmartin and Revelante, 1978). For example, the chlorophyll yield per unit nitrogen input is five times higher in Chesapeake Bay than the Hudson River Estuary, in part because gravitational circulation retains nutrients within Chesapeake Bay whereas a large fraction of the nutrients delivered to Hudson River Estuary are exported to the coastal plume (Malone et al., 1988). However, other examples show that long retention does not necessarily promote high biomass accumulation and primary production. The New and Neuse Estuary examples illustrate a nonmonotonic relationship, with peak biomass at the inflow that optimizes the balance between riverine nutrient supply and downstream transport loss (Peierls et al., 2012). A further level of complexity emerges when we consider phytoplankton losses to grazing and respiration. The principle of long-retention and high-production does not apply when these losses exceed gross primary production. In those circumstances phytoplankton biomass is inversely related to retention time (Lucas et al., 2009). Phytoplankton primary production is thus governed by the relative time scales of net growth and transport (Fig. 6), both of which are directly related to river inflow.

4.5.2 Ocean exchange

Physical processes that propagate into estuaries from the coastal ocean play an equally important role in regulating primary production. Whereas freshwater inflow is a source of buoyancy that stratifies estuaries to promote blooms as episodes of high primary production, tidal currents are a source of mechanical energy to break down stratification. Production dynamics are therefore tied to seasonal inputs of freshwater but also to inputs of tidal energy that vary over hourly, semidiurnal and neap-spring periods (Koseff et al., 1993). Tidal stresses on the bottom also maintain sediments in suspension that attenuate light and limit primary production. As a result of these processes, low-energy microtidal estuaries (tidal amplitude $< 2\,\mathrm{m}$) have a tenfold higher yield of chl *a* per unit nitrogen than energetic macrotidal estuaries (Monbet, 1992), and many of the eutrophic and hypertrophic systems shown in Fig. 4 have no or weak tides.

The coastal ocean can be an important source of nutrients to estuaries, and phytoplankton responses are most clearly observed in estuaries and bays connected to eastern boundary current systems dominated by wind-driven coastal upwelling (Hickey and Banas, 2003). Mean primary production in Spain's Rías Baixas is $2.4\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$ (with peaks up $4\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$) during the summer upwelling season, but only $1\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$ during the spring and autumn when upwelling is weaker (Figueiras et al., 2002). Short-term variability around these seasonal means is large because upwelling events bring cold, salty, nutrient-rich shelf water to the surface that is advected into the Rías by density-driven circulation and promotes phytoplankton biomass growth; downwelling events reverse the circulation pattern and retain that biomass within the Rías (Figueiras et al., 2002). Summer production in Saldhana Bay is similarly supported by nutrients imported from shelf waters during the upwelling season (Pitcher and Calder, 1998). Upwelling systems can also be a source of phytoplankton biomass that is produced in shelf waters and transported into estuaries and bays, such as those connected to the California Current system: Tomales Bay (Smith and Hollibaugh, 1997), San Francisco Bay (Martin et al., 2007), and Willapa Bay (Banas et al., 2007). The import of ocean-derived phytoplankton is an important exogenous source of organic carbon to fuel estuarine metabolism (Smith and Hollibaugh, 1997) and supply food to herbivores including commercially harvested oysters (Banas et al., 2007) and mussels (Figueiras et al., 2002). The ocean supply of both nutrients and phytoplankton biomass sets up the spatial variability of primary production in Tomales Bay (see Fig. 5a) which is highest ($810\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) at the estuary mouth and lowest ($70\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) at the estuary head

(Cole, 1989). A similar spatial pattern develops in Willapa Bay where chl *a* decreases within the estuary because ocean-derived phytoplankton biomass is consumed rapidly as it is advected by tidal currents over dense oyster beds (Banas et al., 2007).

The rate and direction of ocean exchange vary with oceanographic conditions, basin topography of estuaries, and hydrology. For example, the net flux of phytoplankton biomass (chl *a*) is into San Francisco Bay during the summer upwelling season, but out of the bay during other seasons (Martin et al., 2007). Coastal lagoons in Mexico with restricted openings to the sea and long water retention have primary production 6 times larger than lagoons with direct and continuously open connections and faster water exchange with the ocean (Flores-Verdugo et al., 1988). Many estuaries in arid climates are closed to ocean exchange after blockage by sand bars during the dry season, and phytoplankton biomass can accumulate when they are closed. South Africa's Mdloti and Mhlanga estuaries receive large nutrient supplies from treated sewage. When they are closed, phytoplankton biomass accumulates to extremely high levels (chl *a* concentrations above 100 and 300 $\mu g\,L^{-1}$, respectively) and these estuaries must enter a hypertrophic state when closed (Thomas et al., 2005).

Shelf waters connected to estuaries and bays are strongly influenced by regional climate trends and basin-scale climate oscillations captured in indices such as the North Atlantic Oscillation and Pacific Decadal Oscillation. Observational records are now becoming long enough to reveal that these large-scale climate processes induce variability of phytoplankton primary production within estuaries. Mean winter temperature of coastal waters off the northeastern US have warmed 1.7 °C since 1970, and this regional warming trend is synchronous with a trend of increasing winter cloudiness and a 40–50 % decline of primary production in Narragansett Bay (Nixon et al., 2009). South San Francisco Bay was transformed from an oligotrophic-mesotrophic estuary to a mesotrophic-eutrophic estuary after the Pacific Decadal Oscillation and North Pacific Gyre Oscillation reversed signs in 1999, signaling a shift of the NE Pacific to its cool phase (Cloern and Jassby, 2012). The mechanism of this regime shift was a climate-induced trophic cascade that began with increased production of marine predators (flatfish, crabs, shrimp) that migrated into the bay, preyed on bivalve molluscs, and released their grazing pressure on phytoplankton.

4.5.3 Heat, light and wind energy

Physical processes impinging on the water surface of estuaries and bays also regulate the production and accumulation of phytoplankton biomass. Gordon Riley and his contemporaries understood that spring blooms in North Atlantic estuaries are triggered by seasonal increases in photoperiod and daily solar radiation (Riley, 1967). Variable heat input has two effects. First, water temperature sets an upper limit to phytoplankton growth rate (Eppley, 1972) and photosynthetic efficiency (p_{max}) fluctuates significantly with seasonal variability of water temperature in Narragansett Bay (Durbin et al., 1975), Bristol Channel (Joint and Pomroy, 1981), Chesapeake Bay (Harding et al., 2002), Tokyo Bay (Bouman et al., 2010), Tagus Estuary (Gameiro et al., 2011), Rhode River Estuary (Gallegos, 2012), and Neuse Estuary (Peierls et al., 2012). Second, warming during heat waves can thermally stratify estuaries and trigger intense blooms of motile phytoplankton such as the dinoflagellate *Akashiwo sanguinuea* (Cloern et al., 2005) and the phototrophic ciliate *Mesodinium (Myrionecta) rubrum* (Cloern et al., 1994). Bursts of production during these blooms can be significant components of ecosystem-scale primary production (Herfort et al., 2012). Wind stress on the water surface mixes estuaries, sets up waves that suspend bottom sediments, and drives coastal currents that can influence residence time of phytoplankton in coastal bays. For example, high-productivity red tide blooms develop in Mirs Bay and Tolo Harbor during the winter monsoon when NE winds drive landward surface currents that retain phytoplankton biomass by slowing exchange with coastal waters of the South China Sea (Yin, 2003).

Therefore, physical processes operating within estuaries (horizontal and vertical mixing, advection, sediment suspension, light absorption) and across their interfaces with watersheds (freshwater, nutrient, sediment input), the coastal ocean (tidal oscillations, exchanges of salt, heat, nutrients, plankton and predators), and atmosphere (heat exchange, wind stress, photon flux to the water surface) all play essential roles in driving the variability of phytoplankton production in ecosystems at the land–sea interface (Cloern, 1996).

5 Methods as a source of variability

"*No currently used method gives an unambiguous measure of photosynthesis.*" (Laws et al., 2000)

We next consider another source of primary-production variability – that associated with methods. All measurements reported here are based on rates of oxygen production or CO_2 assimilation in water samples contained in bottles incubated at different depths or irradiance. It is well established that the two approaches measure different quantities (e.g. Laws et al., 2000), and the ratio of oxygen produced to carbon fixed (photosynthetic quotient PQ) is not constant. Among the studies included here the reported PQ ranged from 1 (Flores-Verdugo et al., 1988) to 1.4 (Cermeño et al., 2006). However, 85 % of the annual production values in our compilation were derived from measurements of ^{14}C assimilation rates and we might be tempted to assume these values are intercomparable. Although the ^{14}C method has been used for 60 yr and its interpretation has been the subject of many studies, uncertainty persists about what ^{14}C-assimilation measures (Marra, 2002) because of the confounding effects of light and dark algal respiration, refixation of respired ^{14}C, excretion of radiolabeled carbon, and grazing. Further, there is uncertainty about the comparability of ^{14}C-based primary production measurements between studies using different incubation protocols.

Standard methods have been developed for using ^{14}C assays to measure primary production in the ocean, such as the US Joint Global Ocean Flux Study (JGOFS) protocol that prescribes dawn-dusk in situ incubations at 8 depths (Knap, 1994). However, a surprisingly varied suite of protocols for handling and incubating water samples and integrating rates over depth and time have been used to measure primary production in estuaries. Some protocols included screening of water samples to remove mesozooplankton grazers (Thayer, 1971) while others did not; some included measures of ^{14}C in dissolved organic carbon fixed by phytoplankton and excreted during the incubation period (Sellner, 1976) but most did not; some included correction for isotopic discrimination of the heavy isotope ^{14}C (Becacos-Kontos, 1977); some (Gallegos, 2013) included corrections to account for changing spectral quality of light with depth; the euphotic depth was assumed to be either 0.1 % (Kromkamp and Peene, 1995) or 1 % (Gazeau et al., 2005) of surface irradiance, and it was determined from measured light attenuation coefficient (e.g. Morán, 2007), or a transformation of Secchi depth (e.g., Medina-Gómez and Herrera-Silveira, 2006), or estimated from other quantities such as wind and tidal currents (e.g. Montes-Hugo et al., 2004). The frequencies of measurements yielding annual production ranged from twice weekly (Glé et al., 2008) to monthly (most studies), the number of incubation depths or irradiance exposures ranged from 1 (Flores-Verdugo et al., 1988) to 20 (Bouman et al., 2010), and incubation durations ranged from 20 min (Thompson, 1998) to 72 h (Apollonio, 1980). Incubations were done in-situ (e.g. Steemann Nielsen, 1952), in outdoor incubators exposed to natural sunlight (e.g. Umani et al., 2007), or in laboratory incubators exposed to artificial light (Azevedo et al., 2006). In addition, a wide variety of approaches have been used to integrate results of bottle incubations over the euphotic (or water) depth and over time to compute daily, depth integrated primary production. Different approaches have been used to estimate net phytoplankton production from ^{14}C assays, such as assuming that phytoplankton respiration is a fixed proportion of p_{max} (e.g. Cole et al., 1992) or a dynamic quantity modeled to include components of light and dark respiration (Langdon, 1993; Tillman et al., 2000).

5.1 A model to simulate incubation assays for measuring primary productivity

How much variability can be expected between these methods, and is that variability large enough to confound comparisons of primary production between studies? We constructed a model to simulate incubation assays of carbon fixation, and used the model to measure this variability across a range of incubation protocols and computational procedures reported in the literature. The model is a mass-balance equation to describe the time evolution of phytoplankton biomass B (mg C m^{-3}) in a bottle during an incubation period, and it applies the equation set developed by Platt et al. (1990) to compute daily integral photosynthesis:

$$dB/dt = B(p_b \cdot \mathrm{Chl:C} - G - R) \tag{1}$$

t is time (h); p_b is assimilation rate (mg C mg^{-1} chl a h^{-1}); Chl : C is the ratio of phytoplankton chl a to carbon biomass, and $p_b \cdot \mathrm{Chl:C}$ is growth rate (h^{-1}); G is mesozooplankton grazing rate (h^{-1}); and R is phytoplankton respiration rate (h^{-1}). Assimilation rate is computed as a function of irradiance:

$$p_b = p_{\max}[1 - \exp(-I_{z,t} \cdot \alpha / p_{\max})] \tag{2}$$

$p_{\max}$ is maximum assimilation rate; $I_{z,t}$ is photosynthetically active radiance PAR (µEinst m^{-2} s^{-1}) at time t and depth z (m); α is photosynthetic efficiency as initial slope of the $p_b - I$ curve. Instantaneous irradiance is given by:

$$I_{0,t} = I_{\max}[\sin(\pi t / D)] \tag{3}$$

$$I_{z,t} = I_{0,t}[1 - \exp(-k \cdot z)] \tag{4}$$

$I_{0,t}$ is incident PAR at time t; $I_{\max}$ is incident PAR at solar noon; D is photoperiod; and k is the vertical light attenuation coefficient.

We used these equations to simulate outcomes of different experimental protocols using a fixed set of parameters representative of summer conditions at a temperate latitude (e.g., Cloern et al., 1995): $I_{\max} = 1250$ µEinst m^{-2} s^{-1}; $D = 14$ h; $k = 0.92$ m^{-1} (i.e., euphotic depth zp = 5 m); $\alpha = 0.02$ [(mg C mg^{-1} chl a h^{-1})]/[(µEinst m^{-2} s^{-1})]; $p_{\max} = 5$ (mg C mg^{-1} chl a h^{-1}); Chl : C = 0.025 mg chl a mg^{-1} C. The grazing rate G was fixed at 0.0014 h^{-1}, such that mesozooplankton consumption is 6 % of net production (e.g., Lara-Lara et al., 1990). The respiration rate R was fixed at 0.004 h^{-1}, such that respiration loss is 15 % of gross production – consistent with the range measured in chemostat cultures of a marine diatom (Laws and Bannister, 1980).

Equation (1) was solved using the differential equation solver ode in R package deSolve version 1.10–3 (Soetaert et al., 2010), using a time step of 0.05 h and initial condition $B = 200\,\mathrm{mg\,C\,m^{-3}}$. Gross production ($\mathrm{mg\,C\,m^{-3}}$) was computed at each incubation depth as the cumulative sum of $B(p_b \cdot \mathrm{Chl:C} - G)\Delta t$ where Δt is time step, and net production was computed as the cumulative sum of (gross production – $R \cdot B$), from the start (t_i) to ending time (t_f) of a simulated incubation. Depth-integrated production was computed with trapezoidal integration of production at each simulated depth from the surface to zp. This yielded daily, depth-integrated phytoplankton net productivity PN and gross productivity PG ($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) for 24 h incubations. For incubations of shorter duration we used a variety of approaches reported in the literature to convert production over shorter periods into daily production.

5.2 Comparison of production rates derived from different incubation protocols

Our design of simulation experiments is illustrated in Fig. 7. The color contours show the time and depth distribution of hourly productivity over a 24 h period, beginning at sunrise and using parameters listed above. The upper panel shows the prescribed diel cycle of surface irradiance $I_{0,t}$ (blue line) and a set of incubation durations (black horizontal lines) for which simulated PN was computed; these ranged from 2 h incubations centered around noon to 24 h incubations beginning at sunrise ($t_i = 0$). The right panel shows the vertical profile of irradiance at solar noon (blue line) and the depths at which incubations were simulated, shown here ranging from two (surface and zp) to 16 depths. We first used the model to calculate PN for a protocol of incubating samples at 25 depths for a 24 h period beginning at sunrise, similar to the JGOFS protocol. We use PN from this simulation, 812 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$, as a benchmark for comparing outcomes of other protocols.

We then used the model to simulate 19 other protocols representing a subset of the many different approaches used to measure phytoplankton productivity in estuarine-coastal waters. The simulations were organized into four experiments designed to measure sensitivity to: (1) number of depths (irradiances) at which samples are incubated; (2) processes included in the incubation protocols; (3) duration and period of incubations; and (4) computations used to convert short-term C assimilation rates into daily integral production. Daily net primary production ranged from 515 to 1446 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ among the 20 simulated assays (Table 1), revealing a potential 3-fold range of measured production of a phytoplankton community having fixed initial biomass and photosynthetic efficiency in a prescribed light field, depending on method used. Experiment 1 shows that one source of variability is the error from measuring productivity at a small number of depths in the exponential gradient of light attenuation in a water column. Incubation of samples at only two depths, surface and zp, yielded PN of 1466 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$, 81 % above the benchmark. Computed PN then decreased continuously as number of simulated incubation depths was increased (Table 1). This variability expresses the error from approximating a continuous nonlinear function with a series of straight lines (trapezoidal depth integration). This error is small when number of sample depths is about ten, but many published values of PN are based on sample incubations at only 1–6 depths and the simulations explain why these are biased high relative to the benchmark.

The benchmark PN represents the general approach of measuring productivity from C-assimilation measured in samples incubated in-situ or in a light gradient. A second general approach is to: incubate samples in a light gradient over a short period; derive $p_{\max}$ and α from these assays; then, from the resulting $p_b - I$ function, compute daily depth-integrated productivity from measures of phytoplankton biomass, surface irradiance and vertical light attenuation. Platt et al. (1990) derived a series approximation of daily integral production based on this approach, which yields primary productivity of 606 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ – 25 % smaller than the benchmark. This deviation arises because the benchmark approach includes the process of biomass growth and accumulation in bottles during the 24 h incubation period. However, the approach of Platt et al. (1990) and many others used to estimate oceanic primary production from satellite-derived biomass, assumes that phytoplankton biomass is static. This contrast illustrates that different protocols include different processes and, therefore, yield different outcomes. We considered two other processes: mesozooplankton grazing, which is (at least partly) eliminated by pre-screening water samples with a coarse mesh, and inclusion of the dissolved forms of carbon assimilated and excreted during an incubation period. Simulations of pre-screening to remove mesozooplankton (setting $G = 0$) yielded PN of 874 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$. Simulated PN was 991 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ when we accounted for excreted production by assuming it is 22 % of particulate C assimilation (Tillman et al., 2000).

In Experiment 3 we simulated incubations at 25 sample depths over 2 h, 4 h, 6 h and 12 h periods centered around solar noon. Results showed progressive increase in computed daily PN from 515 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ (2 h incubation) to 905 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ (12 h incubation). This variability again reflects the accumulation of phytoplankton biomass in bottles as incubations proceed (e.g. Alpine and Cloern, 1988). Productivity is the product of biomass times growth rate, so as incubation duration lengthens biomass accumulates continuously in bottles exposed to high irradiance (representing the upper region of the euphotic zone where production is concentrated). As a result of this process, estimates of daily integral production from incubation assays will yield different results depending upon incubation duration. The period of incubation also matters, but to a smaller degree: simulated 6 h incubations centered around solar noon and beginning at solar noon yielded PN of 639 and 675 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$, respectively (Table 1).

In Experiment 4 we explored variability arising from differences in computational procedures to: (1) convert C-assimilation rates in short-term assays into daily productivity, and (2) convert a series of C-assimilation rates measured at different light exposures into depth-integrated productivity. The most common approach of time integration (used in Experiments 2 and 3) is to scale hourly-mean productivity during the incubation by the ratio (E/E_{inc}), where E is daily incident irradiance (in our experiments, 40.2 Einst m^{-2} d^{-1}) and E_{inc} is incident irradiance during the incubation period. We compared outcomes from four different approaches of time integration reported in the literature, and these yielded PN ranging from 604 to 868 mg C m^{-2} d^{-1}. Estimates of PN from C-assimilation at a single depth, either the surface or zp, were 1003 and 1219 mg C m^{-2} d^{-1}, respectively (Table 1). Many approaches have been used to calculate daily integral production from short-term productivity rates measured at a few depths. Most are ad-hoc and few are justified, yet the computational approach has a large effect on the value of PN reported, in this case potentially ranging from 604 to 1219 mg C m^{-2} d^{-1}.

The central points of this analysis are that: (1) many different approaches have been used to measure phytoplankton primary production in estuarine-coastal waters – there is nothing approaching a standard method; (2) method matters because integral production derived from simulated incubations of a defined sample and light environment can vary by (at least) a factor of three (Table 1) depending on incubation duration, number of samples incubated, processes included or excluded, and computational procedures. The different protocols reported in the literature measure different quantities and are not intercomparable. Therefore, two- or three-fold differences of phytoplankton primary production across sites or over time (e.g. Parker et al., 2012) cannot be judged significant unless they are derived from common methods.

6 Two grand challenges

Our goal was to summarize measurements of phytoplankton primary production in estuarine-coastal waters as a key Earth-system process that drives variability of water quality, biogeochemical processes, and production at higher trophic levels including species we harvest as food. Place-based studies of annual phytoplankton production have revealed 10-fold variability within some estuarine-coastal ecosystems, nearly 1000-fold variability between ecosystems, and 5-fold variability from year to year at some sites. Therefore, as coastal science advances in the 21st century a grand challenge is to discover how multiple drivers interact to generate this variability. This challenge is important because place-based studies have also demonstrated that phytoplankton production is highly responsive to climate shifts and cycles and human disturbances such as nutrient enrichment, introductions of nonnative species, and water diversions. Mechanistic models will be required to explain the variability of estuarine-coastal primary production summarized here, and to project and plan for changes in coastal production as global change proceeds.

A second grand challenge is to design and implement a program to measure estuarine-coastal primary production and its variability at the global scale. This challenge is important because characteristic values based on sparse data have been upscaled to calculate sustainable yield of estuarine fishery resources (Houde and Rutherford, 1993) and to valuate services provided by estuaries such as food production (Costanza et al., 1997), just as measures of ecosystem metabolism have been upscaled to assess the role of estuaries in the global carbon budget (Borges, 2005). These assessments have inherent errors because of uncertainty in the area of the world's estuaries (Borges, 2005). But potentially larger sources of uncertainty must arise from the uneven spatial distribution of primary production measurements that leave vast knowledge gaps along much of the world's coastline, and an empirical record built from a suite of nonstandard methods that measure different quantities.

6.1 Toward an integrative explanatory model

"The complex structure of estuaries makes them interesting study sites, but frustrating ones from the standpoint of making generalizations, and this observation certainly pertains to developing a predictive understanding of PP [primary production]." (Harding et al., 2002)

Much of the regional, seasonal and interannual variability of primary production in the world oceans can be explained by variability in the transport of deep, nutrient-rich water to the surface (Behrenfeld et al., 2006). However, the wide span of primary production measurements in estuarine-coastal waters (Fig. 2) reflects the many additional processes that operate in shallow systems where land and sea meet: inputs of fresh water, sediments, and nutrients from land runoff; benthic grazing and nutrient regeneration; the balance between the stabilizing effects of heat and freshwater input with mixing by wind and tides; ocean exchange as a source or sink of nutrients and phytoplankton biomass; and retention as influenced by tidal dispersion, gravitational circulation, wind- and river-driven transport.

We have therefore identified the components of the machine that generates high variability of phytoplankton production in estuarine-coastal ecosystems (Fig. 6). Models have been developed to describe the isolated responses of primary production to variability of some components: temperature (Durbin et al., 1975), light attenuation by sediments (Wofsy, 1983), phytoplankton biomass and irradiance (Cole and Cloern, 1987), tidal energy (Monbet, 1992), light and nutrient limitation of phytoplankton growth rate (Cloern, 1999), nutrient inputs (Carstensen et al., 2003), and hydraulic residence time (Peierls et al., 2012). However, these components have not been integrated into a unifying statistical or mechanistic model to explain the wide range of variability across estuaries (Fig. 5) or to project responses of phytoplankton production to regional manifestations of global change. The biggest challenge for building and testing a unifying model might be the breadth of the data requirement; we're not aware of a single ecosystem where all (or even most) of the controlling processes are measured. Meeting this grand challenge will require new studies across a range of ecosystem types to measure primary production as a component of ecosystem-scale studies that include measurements of process that generate its variability. Until this large hole in the empirical record is filled our capacity for explaining the span of measurements shown in Figs. 2–5, and for developing scenarios of future production in shallow coastal ecosystems, will be constrained.

6.2 Toward a globally representative, consistent set of primary production measurements

"*Single or even a few estimates of annual primary production from estuaries may not be very characteristic of the long-term average. One should therefore question attempts to draw generalizations from multiple estuarine data sets when many of the examples represent single annual estimates, perhaps not even based on comprehensive spatial and seasonal coverage.*" (Jassby et al., 2002)

Estuaries are considered to be among the most productive ecosystems (e.g. Kocum et al., 2002), but this generalization does not apply to phytoplankton production which ranges from trivial to rates as high as primary production of mangroves, tropical forests and salt marshes. Therefore there are bounds on, but no characteristic value of phytoplankton production for estuarine-coastal ecosystems. Most reported values fall in the ranges classified as either mesotrophic or oligotrophic ($< 300\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), but these are heavily weighted to measurements from northern Europe and North America. Much higher phytoplankton production has been measured in some tropical-subtropical systems, such as Cienaga Grande de Santa Marta, Golfo de Nicoya and Huizache–Caimanero Lagoon, suggesting that our current assessments might substantially underestimate primary production in the world's estuarine-coastal ecosystems because we have greatly under-sampled tropical and subtropical sites. To put the under-sampling problem in broader perspective, annual phytoplankton production has been reported for only 131 places along the world's 356 000 km coastline.

Of the 131 places where annual phytoplankton production has been reported, 37 % are based on measurements at only one location during one year. Yet we know from a few well-sampled places that production varies up to tenfold within estuaries (Fig. 5a) and up to fivefold from year to year (Fig. 5b), so there is large uncertainty about how well the single measurements represent ecosystem-scale primary production. Although the models used to derive oceanic primary production from ocean color have uncertainties, the uncertainties are quantified and computations of production across the world oceans are grounded in a robust empirical record with global maps of monthly chl *a* at 4 km spatial resolution (Behrenfeld et al., 2001). In contrast, the empirical measurements of phytoplankton production in estuarine-coastal ecosystems include non-standard methods, are sparsely and unevenly distributed in space and time, most have not been sustained over multiple years, and therefore the empirical record provides an inadequate basis for global upscaling. Thus, a second grand challenge is to organize and fund an international effort to use a common method and measure primary production regularly across a network of coastal sites that are representative of the world's coastline to yield reliable estimates of global primary production, its influence on biogeochemical processes and food production, and its response to global change as it unfolds in the 21st century.

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Table 1. Computed depth-integrated daily primary productivity (mg C m^{-2} d^{-1}) of a common sample across a range of protocols. D_{inc} is incubation duration (h); t_i is start time of an incubation (t_0 is sunrise); t_f is end time; E_{inc} is PAR during the incubation period (Einst m^{-2} d^{-1}); PN_{inc} is net production during the incubation period (mg C m^{-2}); PG_{inc} is gross production during the incubation period (mg C m^{-2}); zp is euphotic depth (m); k is light attenuation coefficient (m^{-1}).

Primary productivity	Number of depths	D_{inc}	t_i	t_f	E_{inc}	PN_{inc}	PG_{inc}	Method variation	Experiment number	Calculation of productivity	Reference for the method
812	25	24	0	24	40.2	812	964	benchmark method		numerical time and depth integration	Harding et al. (2002)
1466	2	24	0	24	40.2	293	330	benchmark method, 2 incubation depths	1	$zp \cdot PN_{inc}$	Mortazavi et al. (2000)
931	3	24	0	24	40.2	931	1085	benchmark method, 3 incubation depths	1	numerical time and depth integration	Grøntved and Steemann Nielsen (1957)
853	4	24	0	24	40.2	853	1008	benchmark method, 4 incubation depths	1	numerical time and depth integration	
819	8	24	0	24	40.2	819	972	benchmark method, 8 incubation depths	1	numerical time and depth integration	Cole (1989)
813	16	24	0	24	40.2	813	965	benchmark method, 16 incubation depths	1	numerical time and depth integration	
606	25	24	0	24	40.2	606	606	assumes static biomass	2	series solution to the time and depth integration	Platt et al. (1990)
874	25	24	0	24	40.2	874	1029	sample screened to remove mesozooplankton	2	benchmark, with $G = 0$	Cole and Cloern (1984)
991	25	24	0	24	40.2	812	964	include excreted production	2	1.22 · benchmark	Tillman et al. (2000)
515	25	2	6	8	9.0	115	123	2 h incubation around noon	3	$(E/E_{inc}) \cdot PN_{inc}$	Oviatt (2002)
571	25	4	5	9	17.5	248	266	4 h incubation around noon	3	$(E/E_{inc}) \cdot PN_{inc}$	Mallin et al. (1991)
639	25	6	4	10	25.1	398	427	6 h incubation around noon	3	$(E/E_{inc}) \cdot PN_{inc}$	
675	25	6	7	13	19.6	329	357	6 h incubation PM	3	$(E/E_{inc}) \cdot PN_{inc}$	Anderson (1964)
905	25	12	1	13	39.2	882	949	12 h incubation	3	$(E/E_{inc}) \cdot PN_{inc}$	Kuenzler et al. (1979)
604	25	6	7	13	19.6	329	357	6 h incubation PM	4	(D-3) · hourly mean PN_{inc}	Parker et al. (2012)
687	25	7	7	14	20.1	343	377	7 h incubation PM	4	$2 \cdot PN_{inc}$	Taguchi et al. (1977)
804	25	2	6	8	9.0	115	123	2 h incubation around noon	4	D · hourly mean PN_{inc}	Rysgaard et al. (1999)
868	25	4	5	9	17.5	248	266	4 h incubation around noon	4	D · hourly mean PN_{inc}	Grundle et al. (2009)
1003	1	3	5.5	8.5	13.3	86[*]	89[*]	3 h incubation around noon	4	(zp · D/2) · hourly mean surface PN_{inc}	Cadée and Hegeman (1979)
1219	1	4	5	9	8.8	109[*]	113[*]	4 h incubation around noon	4	$(D/D_{inc}) \cdot (2.94/k) \cdot PN_{inc}$ at depth of 50 % E	Thayer (1969)

[*] mg C m^{-3} h^{-1}

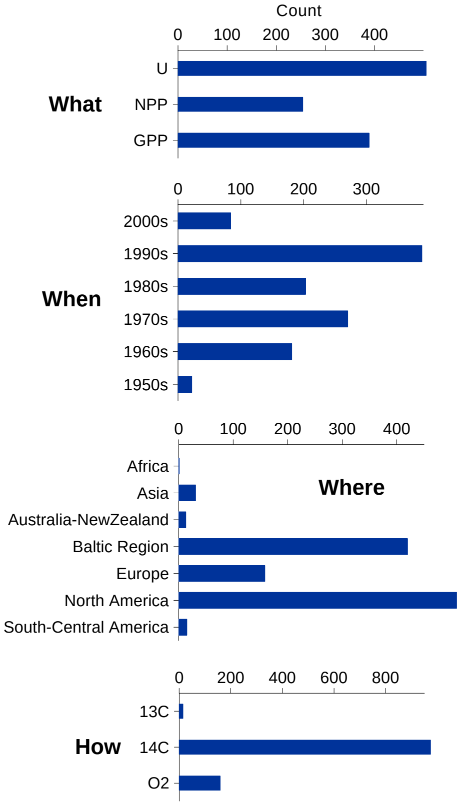

Fig. 1. Summary statistics of 1148 measurements of annual phytoplankton primary production in estuarine-coastal ecosystems. Top panel shows what was reported (U = unspecified; NPP = net primary production; GPP = gross primary production). Panels below show the distribution of measurements by decade, region, and method. Median primary production and data sources for each of 131 ecosystems are given in Supplement Table A1.

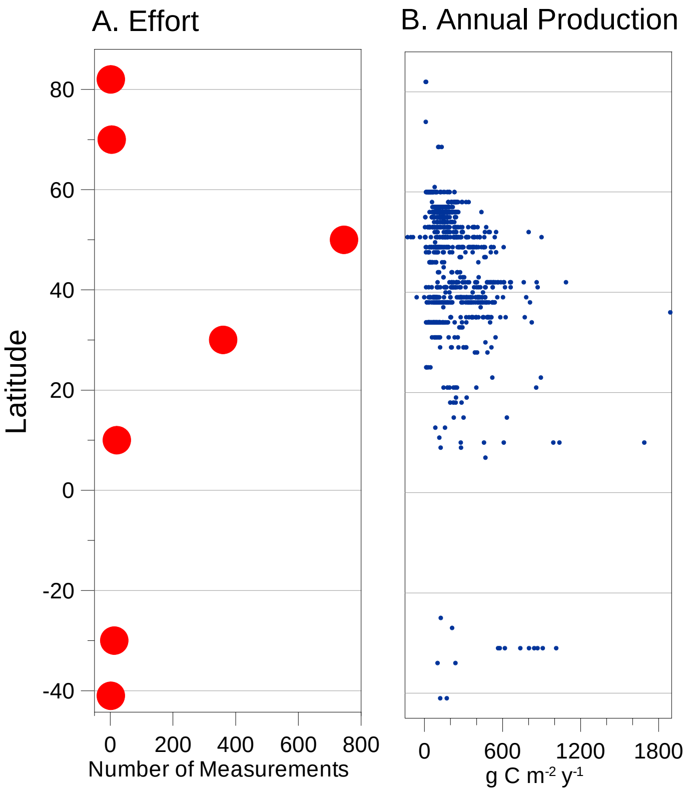

Fig. 2. (A) Distribution of effort, as the number of annual phytoplankton production measurements reported within 20° latitudinal bands, and **(B)** latitudinal distribution of 1148 annual production measurements (one value of $-692\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ from the Scheldt Estuary is not shown).

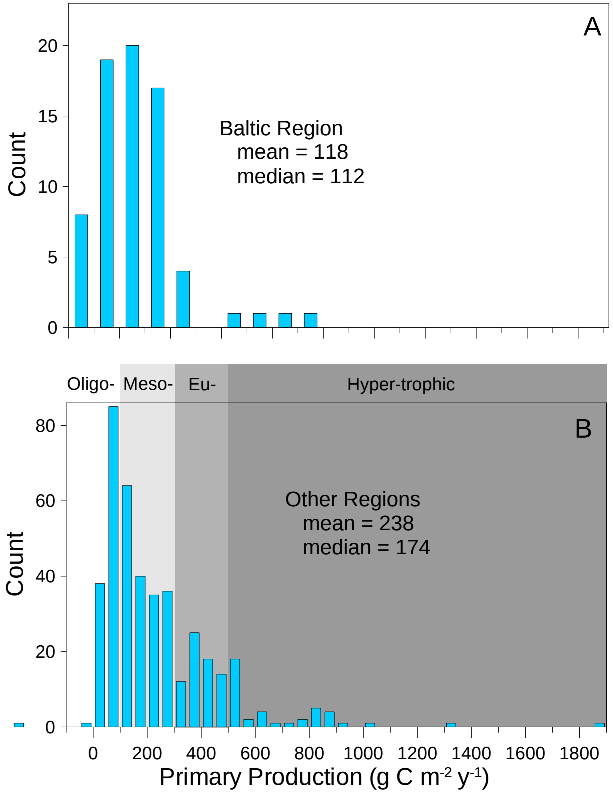

Fig. 3. Frequency distributions of median annual phytoplankton primary production measured **(A)** at 74 sites in the Baltic region, and **(B)** at 409 sites in other geographic regions. Shaded regions **(B)** partition measurements into Nixon's classification (Nixon, 1995) of 4 trophic states, from oligotrophic (< 100 g C m^{-2} yr^{-1}) to hypertrophic (> 500 g C m^{-2} yr^{-1}).

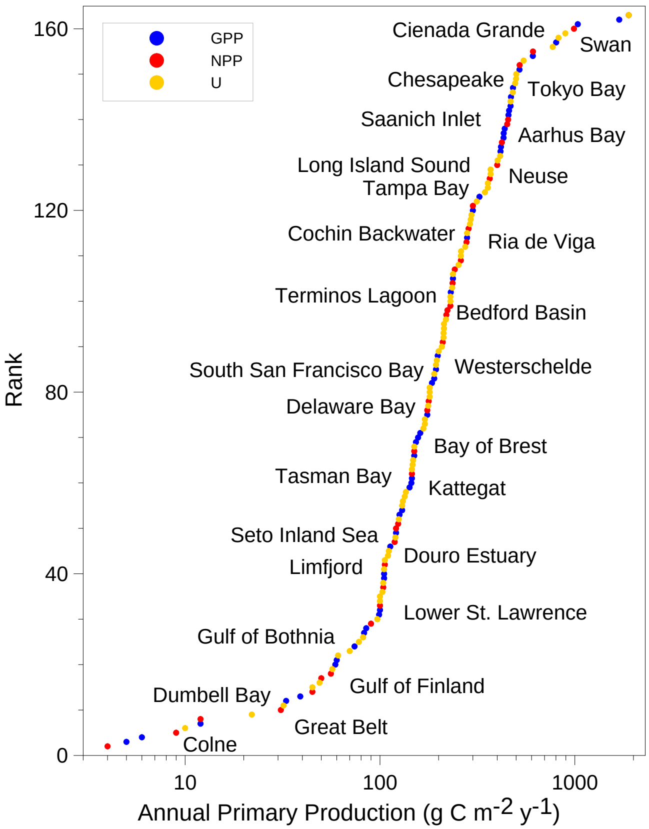

Fig. 4. Ranked distribution of median annual primary production reported for 131 estuarine coastal ecosystems. U = unspecified; NPP = net primary production; GPP = gross primary production (values and data sources for each ecosystem are given in Supplement Table A1). Thirty ecosystems are represented twice because both GPP and NPP were reported. One negative value ($-105\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) from the Scheldt Estuary is not shown.

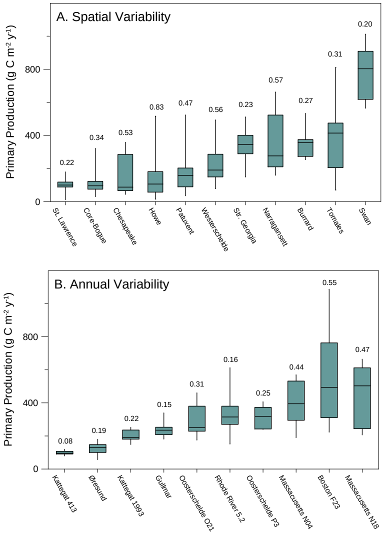

Fig. 5. Examples of **(A)** spatial variability of annual phytoplankton primary production across multiple sites within estuarine-coastal ecosystems, and **(B)** inter-annual variability of primary production at individual sites. Boxplots show median, interquartile ranges (boxes), and ranges (vertical lines). Numbers above are median absolute deviation divided by median production for individual ecosystems or sites. These compare to mad:median of 0.74 between ecosystems in **(A)** and 0.34 between sites in **(B)**. **(A)** Lower St. Lawrence River Estuary (Therriault and Levasseur, 1985); Core-Bogue Estuarine system (Williams and Murdoch, 1966); Chesapeake Bay (Flemer, 1970); Howe Sound (Stockner et al., 1977); Patuxent River Estuary (Flemer et al., 1970); Westershelde (Kromkamp et al., 1995); Strait of Georgia (Stockner et al., 1979); Narragansett Bay (Oviatt, 2002); Burrard Inlet (Stockner and Cliff, 1979); Tomales Bay (Cole, 1989); and Swan River Estuary (Thompson, 1998). **(B)** Kattegat sites 413 and 1993 (Carstensen et al., 2003); Øresund (Ærtebjerg, 1981); Gullmar Fjord (O. Lindahl, personal communication, 2009); Oosterschelde sites O21 and P3 (Wetsteyn and Kromkamp, 1994); Rhode River site 5.2 (Gallegos, 2013); Massachusetts Bay sites N04 and N18 and Boston Harbor site F23 (Oviatt et al., 2007).

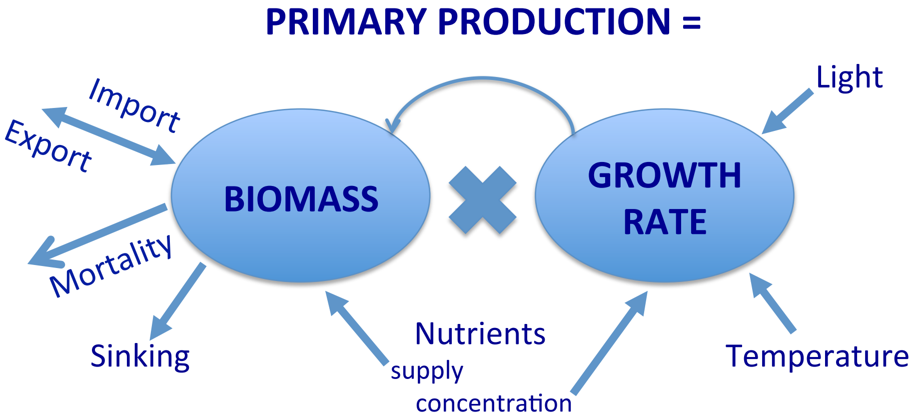

Fig. 6. Phytoplankton primary production is the product of biomass (regulated by import, export, sinking, mortality, nutrient supply, and growth rate) and growth rate (regulated by light, temperature, and nutrient concentrations).

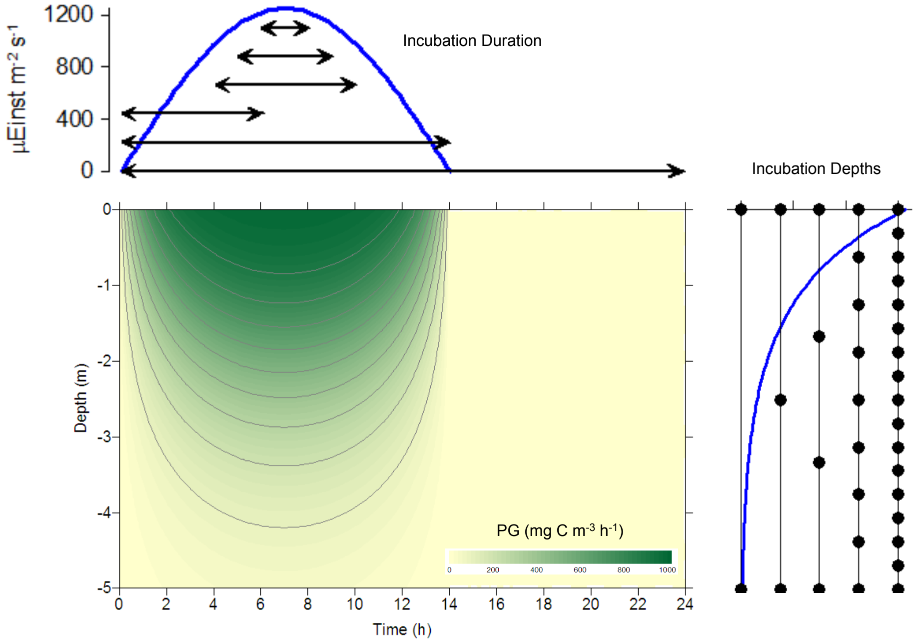

Fig. 7. Schematic showing the 24 h diel cycle of incident photosynthetically active radiance (blue line, upper panel) beginning at sunrise ($t = 0$), and depth distribution of PAR at solar noon (blue line, right panel) representative of summer conditions at a temperate latitude. Contour plot, lower left, shows the diel and vertical variability of gross primary productivity based on equations, initial phytoplankton biomass and photosynthetic parameters described in the text. Horizontal arrows (upper panel) and filled circles (right panel) show incubation periods and depths prescribed to simulate outcomes of different measurement protocols compared in Table 1.