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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 eight 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 reported in the literature 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 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 1 year. The accuracy of these values is unknown but probably low, given the large interannual and spatial variability within ecosystems. Finally, global assessments are confounded by measurements that are not intercomparable because they were made with different 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's surface, their CO_2 emissions are globally significant – estimated at $0.43 \, Pg \, C \, yr^{-1}$ (Borges, 2005). The 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 requires globally distributed measurements of primary production, external supplies of organic carbon, and respiration across the diversity of estuarine ecosystems.

The organic carbon supplied 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 may be old (Raymond and Bauer, 2001), is 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 annual phytoplankton primary production (APPP) 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. Although we do not consider primary production by benthic microalgae, this supply of labile organic matter is comparable to that of phytoplankton in some estuaries (Underwood and Kromkamp, 1999) and it plays a similarly important role in the dynamics of ecosystem metabolism and energetics.

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 systems such as the Baltic Sea (Elmgren, 1984), South San Francisco Bay (Jassby et al., 1993), and Moreton Bay (Eyre and McKee, 2002). Much of the annual production occurs during seasonal or episodic blooms when 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, methyl mercury (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 food. Annual phytoplankton production is highly correlated with fishery landings (Nixon, 1988), biomass of benthic invertebrates (Herman et al., 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-year 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 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 terrestrial and marine biomes. Annual net primary production in the world oceans is on the order of 60 Pg C (Behrenfeld et al., 2005), and areal rates range from about $160\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in oligotrophic regions of the open ocean to about $1300\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ 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-Madriñán and Fischer, 2013). Therefore, our knowledge of phytoplankton 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 APPP from direct measurements reported in the readily accessible scientific literature as an update to the last review published three decades ago by Walter Boynton and colleagues (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 APPP 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 measurements of APPP 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 APPP in estuarine-coastal ecosystems, reliability of APPP estimates at the global scale, and steps required to reduce the large uncertainty of those estimates.

2 An inventory of annual phytoplankton primary production measurements

We compiled measurements of APPP reported in references found through searches in Scopus, Google Scholar, and Web of Science. Our target was reported values of depth-integrated APPP 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 a description of the methods used, sampling frequency and period, or if the sampling locations were not specified. The final compilation (summarized in the Supplement Table S1) includes 1148 values of APPP from 483 sampling sites within 131 ecosystems (places). Primary production 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 APPP. In order to streamline our presentation we define our uses of "primary production" as the phytoplankton contribution to system production; "production" as either the process or the mass of carbon fixed over a period of time; and "productivity" as a rate of production – usually an hourly or daily rate.

The compilation includes 389 measurements of APPP 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 to be strong evidence of a reduced effort at measuring APPP 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 APPP measurements from studies in Asia (31), South/Central America (15), Australia/New Zealand (13), and Africa (1). Phytoplankton 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).
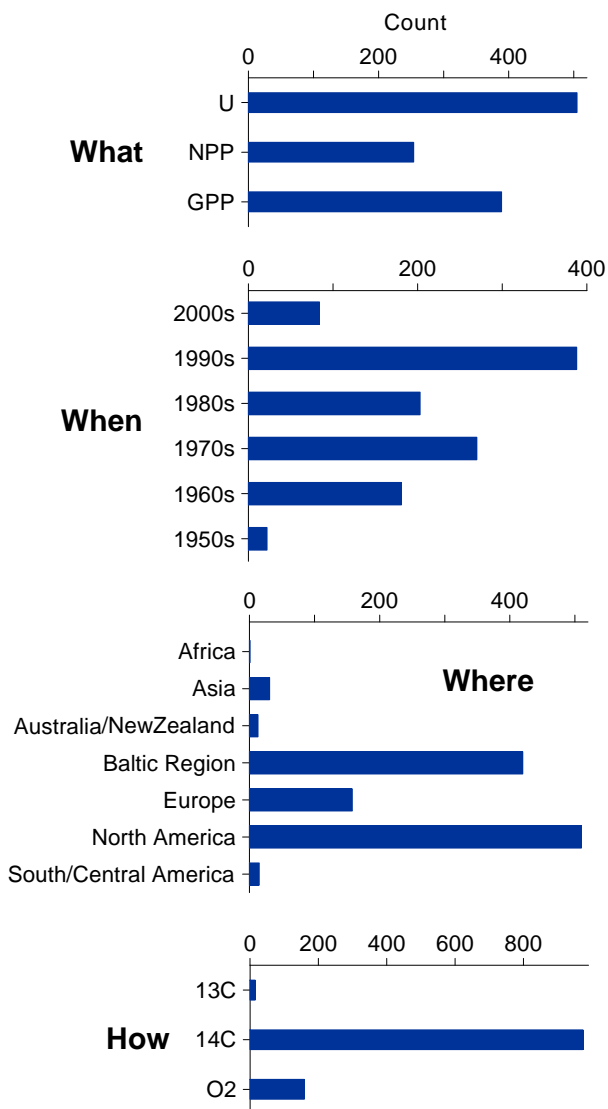
Fig. 1. Summary statistics of 1148 measurements of annual phytoplankton primary production (APPP) in estuarine-coastal ecosystems. Top panel shows what was reported: U = unspecified; NPP = net primary production; GPP = gross primary production. Panels below show the distribution of measurements by decade, region, and method. Median APPP and data sources for each of 131 ecosystems are given in the Supplement Table S1.

3 Patterns of variability

3.1 Latitudinal patterns

APPP at individual sites ranged from $-692 \, \mathrm{g \, C \, m^{-2} \, yr^{-1}}$ (net pelagic production, which includes respiration by heterotrophs) at site 2 in the Scheldt Estuary during 2002 (Gazeau et al., 2005) to $1890 \, \mathrm{g \, C \, m^{-2} \, yr^{-1}}$ (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 measurements at sites binned within 20° latitudinal bands (Fig. 2). Of the 1148 reported values, 958 come from sites between 30 and 60° N. This highly skewed distribution of effort reflects the exceptional number of APPP 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 reported measurements of APPP for sites south of 20° N, none between the equator and 25° S, and only 15 in the Southern Hemisphere. Therefore, our knowledge of annual phytoplankton 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 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), constrains our ability to answer a fundamental question: does APPP vary systematically with latitude?

3.2 Variability between sampling sites

From 1148 individual measurements of APPP we calculated median values at the 483 sites where measurements have been reported. Median APPP ranged across sites from $-278 \, \mathrm{g \, C \, m^{-2} \, yr^{-1}}$ (net pelagic production) at station 2 in the Scheldt Estuary to $1890 \, \mathrm{g \, C \, m^{-2} \, yr^{-1}}$ (net phytoplankton production) at one site in 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 the median APPP measured 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 APPP measured at sites in other regions is skewed by 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 ($174 \, \mathrm{g \, C \, m^{-2} \, yr^{-1}}$). Based on the median APPP 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 APPP 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 1 year, but the others represent
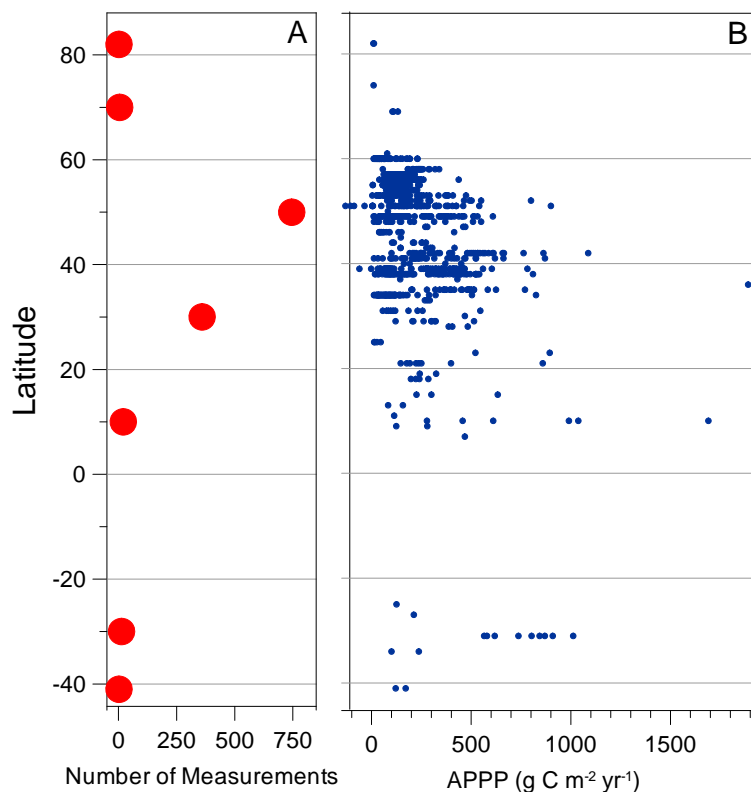
Fig. 2. (A) Distribution of effort, as the number of APPP measurements reported within 20° latitudinal bands, and **(B)** latitudinal distribution of 1148 APPP measurements (one value of $-692\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ from the Scheldt Estuary is not shown).

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 APPP measurements reported for the world's estuarine-coastal ecosystems. The overall median is 185 and mean is $252\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$. 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 APPP between regions of the world oceans (Chavez et al., 2010). As an index of how the empirical record has grown we also show in Fig. 4 the ranked distribution of APPP reported for 45 estuaries by Boynton et al. (1982), which averaged $190\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ and ranged from 19 to $547\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$.

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, these ecosystem types are characterized by large spatial variability of primary production (high-resolution visualizations of spatial patterns are begin-

ning to emerge from remote sensing data and improved bio-optical models for estuaries; Son et al., 2014). We selected 11 examples where APPP was measured at multiple (minimum 9) sites during 1 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 ($=$ Scheldt Estuary) during 1991. Annual phytoplankton production does not follow a normal distribution (e.g., Figs. 3, 4; Shapiro–Wilk test $W = 0.780$, $p < 0.0001$; Shapiro and Wilk, 1965), so we used the ratio of median absolute deviation (MAD) to median APPP as a robust index of dispersion (Ruppert, 2011) that can be compared within and between ecosystems. For a univariate data set, the MAD is defined as the median of the absolute deviations from the series median. The ratio MAD : median of APPP within ecosystems ranged from 0.20 to 0.83 (Fig. 5a) – i.e., the characteristic deviation from the median APPP within an ecosystem ranged from about 20 % to about 80 % of that median. For comparison, the MAD : median of the median APPP between the 11 ecosystems was 0.74. This comparison shows that the spatial variability of APPP within some ecosystems can be comparable to the variability between ecosystems. Therefore, measurements at single sites are unlikely to yield reliable estimates
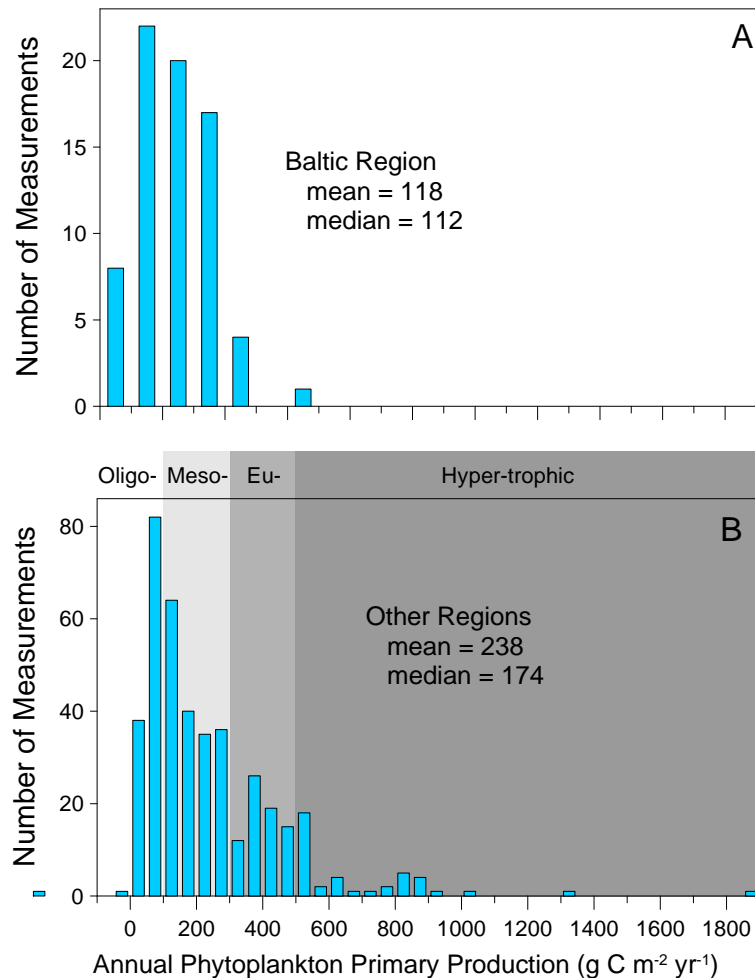
Fig. 3. Frequency distributions of median APPP measured (**A**) at 74 sites in the Baltic region, and (**B**) at 409 sites in other regions. Shaded regions (**B**) partition measurements into Nixon's classification (Nixon, 1995) of 4 trophic states, from oligotrophic ($< 100\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) to hypertrophic ($> 500\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$).

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), so we might expect comparably high inter-annual variability of APPP. We probed the data inventory to explore interannual variability of APPP, using studies at 10 sites where phytoplankton production was measured during at least 7 consecutive years. Annual phytoplankton 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, interannual 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 of APPP) at these 10 sites was 0.23, smaller than the index of vari-

ability between the sites of 0.57. Although the number of records is small, the available data suggest that variability of APPP between ecosystems > spatial variability within ecosystems > variability between years. Therefore, the highly skewed geographic distribution of APPP measurements (Fig. 2) differs markedly from the global distribution of sampling 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 APPP increases with series duration (Jassby et al., 2002). We found only eight APPP series longer than a decade, but these represent notable advances since the 1980s when none were available (Boynton et al., 1982). The longest series were from Tampa Bay (29 years; Johansson, 2010; J. O. R. Johansson, personal communication, August 2013), Gullmar Fjord (23 years; Lindahl et al., 1998; O. Lindahl, personal communication, June 2009), and Rhode River Estuary (20 years;
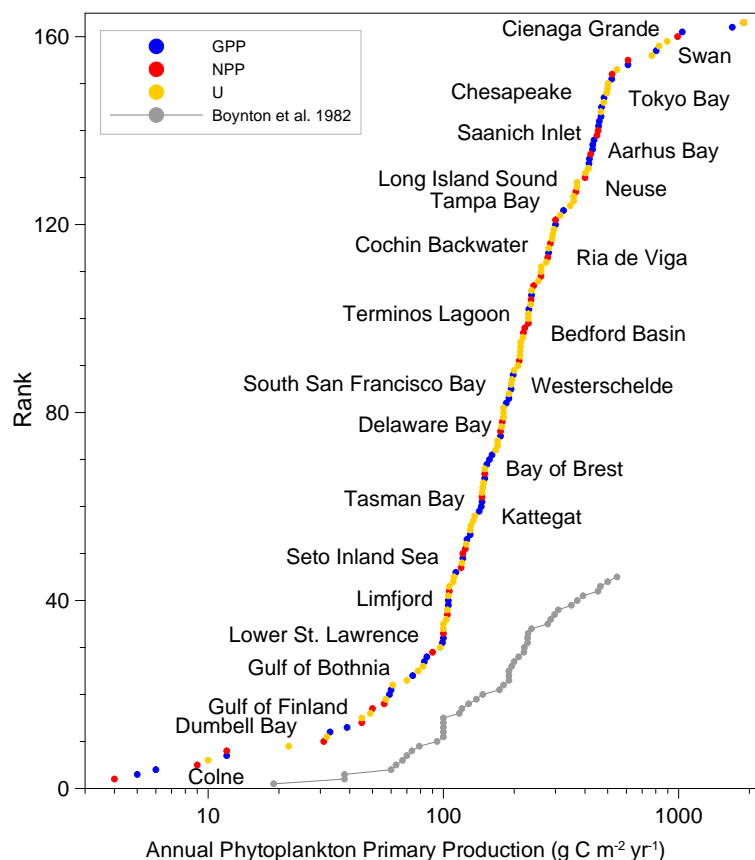
Fig. 4. Ranked distribution of median APPP reported for 131 estuarine-coastal ecosystems. U = unspecified; NPP = net primary production; GPP = gross primary production (values and data sources for each ecosystem are given in the Supplement Table S1). Thirty ecosystems are represented twice because both GPP and NPP were reported. One negative value ($-105\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) from the Scheldt Estuary is not shown. For comparison, the gray line and circles show the ranked distribution of the 45 measurements of APPP available when Boynton et al. (1982) last reviewed phytoplankton production in estuaries.

Gallegos, 2014; C. L. Gallegos, personal communication, May 2013). The scarcity of decadal time series precludes assessments of change over time to complement assessments of climate-driven changes in oceanic primary production (e.g., Behrenfeld et al., 2006).

4 What drives this variability?

4.1 A conceptual model

The values of APPP reported here are the time integral of daily, depth-integrated primary productivity measured in discrete water samples. Primary productivity is the product of plant biomass times its turnover rate, so the variability of APPP described above is ultimately determined by processes that drive temporal and spatial variability of phytoplankton biomass and growth rate within estuaries (Fig. 6). Potential biomass production 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 dynamic processes: (1) transport processes including import of ocean-derived phytoplankton biomass, export by washout during events of high river flow, and sinking; (2) biomass growth; and (3) mortality that includes losses to grazers 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) and Boynton and colleagues (Boynton et al., 1982), links these processes and provides a framework for exploring the drivers of APPP variability over time, within and between estuaries.

The construct of primary productivity as biomass times growth rate is the basis for models of varying complexity used to estimate phytoplankton primary production and to compare the strength of different controls. The simplest model describes primary productivity as a linear function of phytoplankton biomass B (as chlorophyll a concentration,
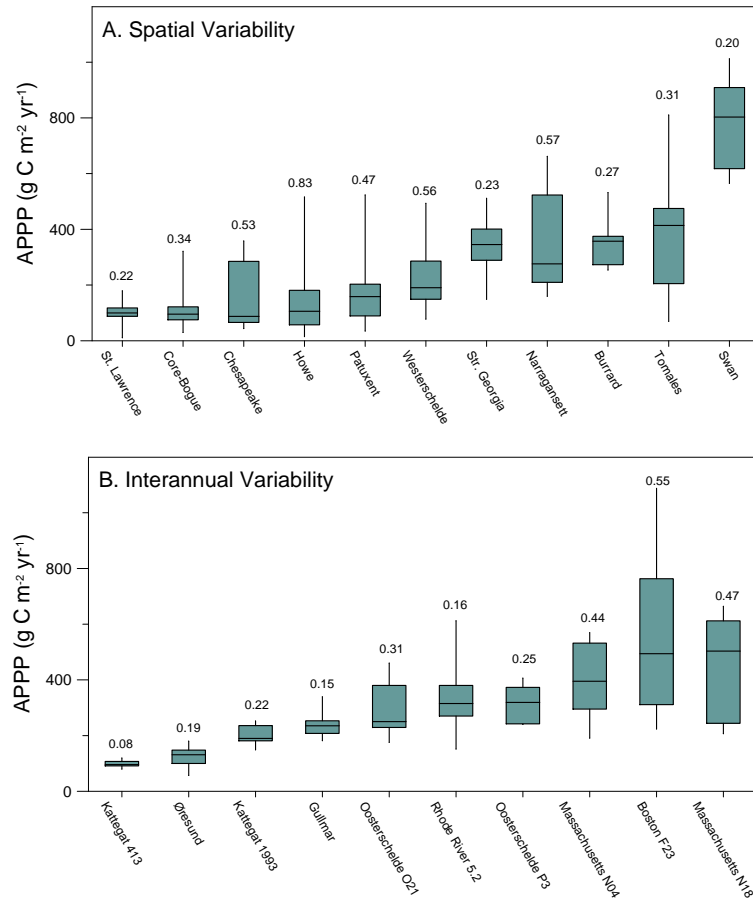
Fig. 5. Examples of (**A**) spatial variability of APPP across multiple sites within estuarine-coastal ecosystems, and (**B**) interannual variability of APPP at individual sites. Boxplots show median, interquartile ranges (boxes), and ranges (vertical lines). Numbers above are median absolute deviation (MAD) divided by median APPP 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 in the 1960s (Flemer, 1970); Howe Sound (Stockner et al., 1977); Patuxent River Estuary (Flemer et al., 1970); Westerschelde (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, 25 June 2009); Oosterschelde sites O21 and P3 (Wetsteyn and Kromkamp, 1994); Rhode River site 5.2 (Gallegos, 2014); Massachusetts Bay sites N04 and N18 and Boston Harbor site F23 (Oviatt et al., 2007).

chl a), which varies 500-fold across estuarine-coastal ecosystems (Cloern and Jassby, 2008). For example, 64 % of the daily variability of phytoplankton productivity in Saanich Inlet is explained by daily fluctuations of chl a (Grundle et al., 2009), and 81 % of the variability of APPP 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 productivity as a linear function of $\Psi \cdot B \cdot I$ (Behrenfeld and Falkowski, 1997), where the coefficient 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 daily primary-productivity 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 primary-productivity variability in other estuaries such as the Chesapeake (Harding et al., 2002), Rhode River Estuary (Gallegos, 2014), 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 Sect. 5.1) fluctuates with seasonal temperature variability or with variability of dissolved inorganic carbon along the estuarine salinity gradient (Gallegos, 2012). Models based on this last approach are the foundation for computing oceanic
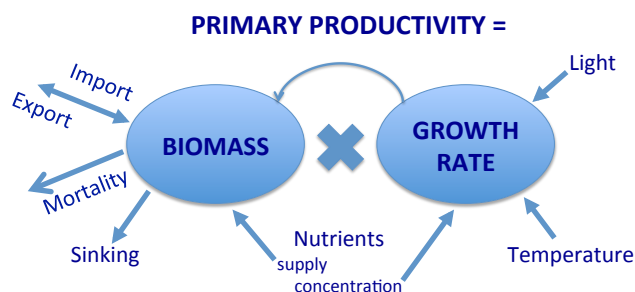
Fig. 6. Primary productivity is the product of phytoplankton biomass (regulated by import, export, sinking, mortality, nutrient supply, and growth rate) times phytoplankton growth rate (regulated by light, temperature, and nutrient concentrations).

primary production from remotely sensed chl a, water temperature, and optical properties of the upper ocean. Accurate estimates of primary production from all these model classes requires calibrations that capture seasonal and regional variations in photosynthetic efficiency expressed as p_{max} (Saux Picart et al., 2014).

The use of different model classes implies that the physical and biological regulators of primary production shown in Fig. 6 take on varying degrees of 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 phytoplankton biomass. This relationship has been formalized by C. Gallegos (http://www.biogeosciences-discuss.net/10/C7574/2013/bgd-10-C7574-2013-supplement.pdf) as an alternative conceptual model for understanding variability of APPP over time (Fig. 5b), within (Fig. 5a), and between (Fig. 4) estuarine-coastal ecosystems as a process tightly tied to processes of phytoplankton biomass variability. We use case studies to illustrate responses to four of these processes.

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 APPP 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 Ciénaga 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; and 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 phytoplankton 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 phytoplankton growth such as shallow depth (Ciénaga 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 a spatial pattern of decreasing phytoplankton production 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 the lower Chesapeake Bay after the 1950s in response to increased loadings of reactive nitrogen (N) and phosphorus (P) (Harding, 1997); APPP in the western Wadden Sea ranged between 100 and $200\,g\,C\,m^{-2}\,yr^{-1}$ in the 1960s and 1970s, but increased to $300–400\,g\,C\,m^{-2}\,yr^{-1}$ in the 1980s after riverine nutrient inputs to the North Sea increased (Cadée and Hegeman, 1993); APPP 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 APPP in Kaneohe Bay was $894\,g\,C\,m^{-2}\,yr^{-1}$ in 1976 when total N (TN) loading was $25.6\,kmol\,N\,d^{-1}$, but it fell to $294\,g\,C\,m^{-2}\,yr^{-1}$ in 1978 after TN loading was reduced to $6.1\,kmol\,N\,d^{-1}$ by diverting sewage to the ocean (Smith et al., 1981). Similar changes were measured in the upper Tampa Bay where mean annual GPP declined from $750\,g\,C\,m^{-2}\,yr^{-1}$ to $410\,g\,C\,m^{-2}\,yr^{-1}$

after inputs of dissolved inorganic N were reduced from > 3000 to $< 1000 \, kg \, N \, d^{-1}$ (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. Phytoplankton 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 APPP is only $9 \, g \, C \, m^{-2} \, yr^{-1}$ (Apollonio, 1980); APPP is $10 \, g \, C \, m^{-2} \, yr^{-1}$ in Young Sound ($74° \, N$) where the ice-free season is 2 months (Rysgaard et al., 1999). These values of annual phytoplankton production are smaller than the peak daily phytoplankton production ($16 \, g \, C \, m^{-2} \, d^{-1}$) in the tropical Ciénaga 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 pelagic 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). Model simulations 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 $50 \, mg \, L^{-1}$ (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 (m^{-1}) – exceeds 5. The empirical record supports these generalizations. Annual phytoplankton production in the inner Bristol Channel is only $6.8 \, g \, C \, m^{-2} \, yr^{-1}$ 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 estuar-

ies have ultra-low phytoplankton production, such as Roskeeda Bay with NPP of $4 \, g \, C \, m^{-2} \, yr^{-1}$ (Raine and Patching, 1980), Colne Estuary with GPP of $5 \, g \, C \, m^{-2} \, yr^{-1}$ (Kocum et al., 2002), and turbid regions of the Ems-Dollard (Colijn and Ludden, 1983) and Columbia River (Small et al., 1990) estuaries with APPP of 26 and $38 \, g \, C \, m^{-2} \, yr^{-1}$, 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 phytoplankton 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 phytoplankton production in shallow regions where the optical depth 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 to fuel 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 phytoplankton production can be positive, even in deep turbid estuaries, when the water column stratifies to establish a surface layer where the optical depth < 5 and phytoplankton biomass grows rapidly. Much of the annual phytoplankton 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 phytoplankton production dynamics are tied to variability of river discharge. In tidal estuaries both stratification and turbidity oscillate over the fortnightly neap–spring cycle, with the 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 productivity (Cloern, 1996). Variability of primary productivity 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 the 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 phytoplankton production that occurs during seasonal blooms. For example, March–April phytoplankton production in South San Francisco Bay was $67\,g\,C\,m^{-2}$ during a year (1990) of relatively calm spring winds and low turbidity, but only $18\,g\,C\,m^{-2}$ 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 the 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 phytoplankton production (Cloern and Jassby, 2012).

4.4 Top-down regulation

While the growth 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 growth and mortality including consumption by grazers (Fig. 6). Rates of growth 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 APPP in productive estuaries (Calbet, 2001), but year-to-year variability in the seasonal timing of copepod population growth can be an important regulator of APPP. For example, anomalous low APPP 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 APPP (Keller et al., 2001).

Although micro- and meso-zooplankton consume most phytoplankton production in the open ocean (Calbet, 2001; Calbet and Landry, 2004), their role as grazers can be 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 timescales 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). It is also evident from case studies of changing phytoplankton biomass after bivalve populations either abruptly increased or decreased. Phytoplankton primary production in the low-salinity habitats of northern San Francisco Bay decreased from 106 to $39\,g\,C\,m^{-2}\,yr^{-1}$ 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 the South San Francisco Bay after the NE Pacific shifted to its cool phase in 1999 when bivalve biomass declined and APPP increased from $<200\,g\,C\,m^{-2}\,yr^{-1}$ to $>400\,g\,C\,m^{-2}\,yr^{-1}$ (Cloern and Jassby, 2012). 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 timescales 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 phytoplankton 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 phytoplankton production are positively correlated with freshwater inflow to many estuaries including the 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 phytoplankton 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 northern 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 timescale (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 the longest flushing times and retain nutrients and phytoplankton biomass (Gilmartin and Revelante, 1978). For example, the yield of chl *a* per unit nitrogen input is five times higher in Chesapeake Bay than the Hudson River Estuary, in part because gravitational circulation retains nutrients within the Chesapeake Bay, whereas a large fraction of the nutrients delivered to the Hudson River Estuary is exported to the coastal plume (Malone et al., 1988). However, other examples show that long retention does not necessarily promote accumulation of phytoplankton biomass and high primary production. The New and Neuse Estuary examples illustrate a nonmonotonic relationship, with peak phytoplankton 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 losses of phytoplankton biomass to grazing and respiration. The principle of long retention and high production does not hold when these losses exceed GPP. In those circumstances phytoplankton biomass is inversely related to retention time (Lucas et al., 2009). Phytoplankton production is thus governed by the relative timescales 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 phytoplankton production. Whereas freshwater inflow is a source of buoyancy that stratifies estuaries to promote blooms as episodes of fast phytoplankton production, tidal currents are a source of mechanical energy to break down stratification. Variability of phytoplankton production is 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 constrain phytoplankton production. As a result of these processes, low-energy microtidal estuaries (tidal amplitude < 2 m) have a 10-fold 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 phytoplankton productivity 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). Phytoplankton production in Saldhana Bay is similarly supported by nutrients imported from shelf waters during the summer 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 APPP in Tomales Bay (see Fig. 5a) which is highest ($810 \, \text{g C m}^{-2} \, \text{yr}^{-1}$) at the estuary mouth and lowest ($70 \, \text{g C m}^{-2} \, \text{yr}^{-1}$) 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 transported 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 an APPP 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 > 100 and $> 300 \, \mu\text{g L}^{-1}$, 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 oscillations of these large-scale climate patterns 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 APPP 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 primary production during these blooms can be significant components of annual 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, 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 phytoplankton 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 (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 APPP 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 years and its interpretation has been the subject of many studies, uncertainty persists about what ^{14}C assimilation measures because of the confounding effects of light and dark algal respiration, refixation of respired ^{14}C, excretion of radiolabeled carbon, and grazing (Marra, 2002). Further, there is uncertainty about the comparability of ^{14}C-based primary production measurements between studies using different incubation protocols (Harrison et al., 1985).

Standard methods have been developed for using ^{14}C assays to measure phytoplankton 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 phytoplankton 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, 2014) 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 coefficients (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 APPP 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 phytoplankton productivity. Different approaches have been used to estimate NPP 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 (Tillman et al., 2000; Langdon, 1993).

5.1 A model to simulate incubation assays for measuring phytoplankton primary productivity

How much variability can be expected between these methods, and is that variability large enough to confound comparisons of APPP 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 (distinct from models of ^{14}C assimilation and recycling, e.g., Marra, 2002) describes 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:

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

t is time (h); p_b is C-assimilation rate (mg C mg^{-1} chl a h^{-1}); Chl:C is the ratio of phytoplankton chl a to carbon biomass; $p_b \cdot$ Chl:C is growth rate (h^{-1}); and R is phytoplankton respiration rate (h^{-1}). Phytoplankton C-assimilation rate is a function of irradiance (I):

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

p_{max} is maximum C-assimilation rate; $I_{z,t}$ is photosynthetically active radiance PAR (µmol quanta 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): $I_{max} = 1250$ µmol quanta m^{-2} s^{-1}; $D = 14$ h; $k = 0.92$ m^{-1} (i.e., euphotic depth $z_p = 5$ m); $\alpha = 0.02$ [(mg C mg^{-1} chl a h^{-1})/(µmol quanta 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 respiration rate R was fixed at 0.004 h^{-1}, such that respiration loss is 15 % of GPP – within the range measured in 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 $\Delta t = 0.05$ h and initial condition $B = 200$ mg C m^{-3}. Gross production (mg C m^{-3}) was computed at each incubation depth as the cumulative sum of $B(p_b \cdot$ Chl:C$)\Delta t$, 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 primary production was computed with trapezoidal integration of production at each simulated depth from the surface to z_p. This yielded daily, depth-integrated net phytoplankton productivity PN and gross productivity PG ($\mathrm{mg\,C\,m^{-2}\,d^{-1}}$) for 24 h incubations. For shorter incubations we used a variety of approaches reported in the literature to convert production measured over several hours into daily production.

5.2 Comparison of phytoplankton productivity 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 primary productivity over a 24 h period, beginning at sunrise and using parameters listed above. The goal of primary production measurements is an accurate estimation of the time and depth integral of this function. The upper panel of Fig. 7 shows the prescribed diel cycle of incident 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 2 (surface and z_p) to 16 depths. We first used the model to calculate PN for a protocol of incubating samples at 25 depths for 24 h beginning at sunrise, similar to the JGOFS protocol. We use PN from this simulation, $879\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$, as a benchmark for comparing outcomes of other protocols.

We then used the model to simulate 16 other protocols representing a subset of the many different approaches used to measure daily phytoplankton productivity in estuarine-coastal waters. The simulations were organized into three 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 timing of incubations and computations used to convert short-term C-assimilation rates into daily productivity. Computed PN ranged from 527 to $1551\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ among the 17 simulated assays (Table 1), revealing a potential 3-fold range of measured daily productivity by a phytoplankton community having fixed initial biomass and photosynthetic efficiency in a prescribed light field, depending on the method used. Experiment 1 shows that one source of variability is the error from measuring phytoplankton primary productivity at a small number of depths in the exponential light gradient in a water column (Fig. 7). Incubation of samples at only two depths, surface and z_p, yielded PN of $1551\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$, 77 % above the benchmark. Computed PN then decreased continuously as the number of simulated incubation depths was increased (Table 1). This variability

expresses the error from approximating a continuous non-linear function with a small number of straight lines (trapezoidal depth integration). This error is small when the number of sample depths is about eight, but many published values of PN are based on sample incubations at only one to six depths.

Results from experiment 2 illustrate that different protocols include different processes and, therefore, are expected to yield different outcomes. The benchmark PN represents the general approach of computing depth-integrated phytoplankton productivity from C-assimilation measured in samples incubated in situ for 24 h. 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 (gross) productivity from measures of phytoplankton biomass, incident irradiance and the light attenuation coefficient. Platt et al. (1990) derived an accurate series approximation of daily integral productivity based on this approach, which yields a PG of $620\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ – 40 % smaller than the benchmark PG of $1034\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ (Table 1). This deviation arises because the benchmark approach includes the process of phytoplankton biomass change – in this particular case growth and accumulation in bottles during the 24 h incubation. However, the approach of Platt et al. (1990), and others used to estimate oceanic primary productivity from satellite-derived ocean color, assumes that phytoplankton biomass is static. The difference in simulated primary productivity derived from in situ incubation compared to that derived from C-assimilation numbers is determined by the sign and magnitude of phytoplankton biomass change over the incubation period – i.e., the balance between biomass production and loss (e.g., grazing). If losses exceed production then the productivity derived from time- and depth-integration of the $p_b - I$ function will be larger than productivity measured in situ. If losses equal production the two methods will yield similar outcomes, so there is no general scaling of productivity values derived from these two common approaches. This is confirmed with experimental comparisons of the two approaches that have yielded varying results (e.g., Harrison et al., 1985; Lohrenz et al., 1992). We considered another process – production and excretion of dissolved organic carbon during an incubation period. Simulated PN was $1072\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ when we accounted for excreted production by assuming it is 22 % of particulate C-assimilation (Tillman et al., 2000).

In Experiment 3 we explored variability arising from differences in incubation duration and timing, and procedures for computing daily productivity. We simulated incubations at 25 depths over 2, 4, 6 and 12 h periods centered around solar noon, and used a common approach of time integration as the product of hourly-mean production during the incubation (PN_{inc}) times the ratio of daily incident irradiance (E) to incident irradiance during the incubation period (E_{inc}). Results showed a progressive increase in computed PN from $527\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ (2 h incubation) to
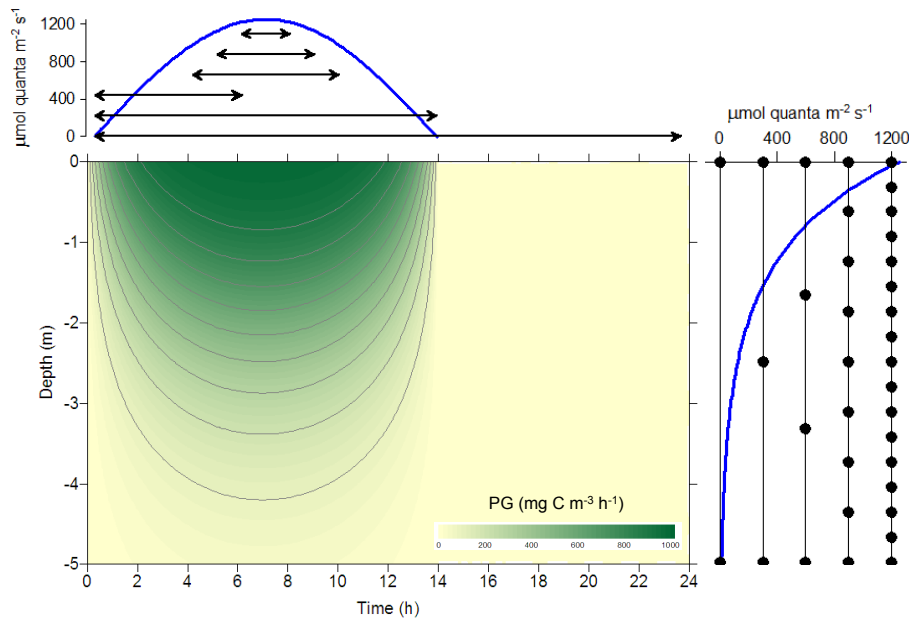
Fig. 7. Schematic showing the 24 h diel cycle of incident photosynthetically active radiance (blue line, upper panel) beginning at sunrise ($t = 0$), and depth distribution of PAR at solar noon (blue line, right panel) representative of summer conditions at a temperate latitude. The contour plot, lower left, shows the diel and vertical variability of hourly gross phytoplankton primary productivity (PG) 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 protocols compared in Table 1.

Table 1. Computed depth-integrated daily primary productivity ($mg\,C\,m^{-2}\,d^{-1}$) of a common phytoplankton sample across a range of protocols. D is photoperiod and D_{inc} is incubation duration (h); t_i is start time of an incubation (t_0 is sunrise); t_f is end time; E is daily PAR and E_{inc} is PAR during the incubation period ($mol\,quanta\,m^{-2}\,d^{-1}$); PN_{inc} is net production and PG_{inc} is gross production during the incubation period ($mg\,C\,m^{-2}$).

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
879	25	24	0	24	40.2	879	1034	benchmark method		trapezoidal depth integration	Harding et al. (2002)
1551	2	24	0	24	40.2	1551	1747	benchmark method, 2 incubation depths	1	trapezoidal depth integration	
997	3	24	0	24	40.2	997	1160	benchmark method, 3 incubation depths	1	trapezoidal depth integration	Grøntved and Steemann Nielsen (1957)
921	4	24	0	24	40.2	921	1079	benchmark method, 4 incubation depths	1	trapezoidal depth integration	
886	8	24	0	24	40.2	886	1042	benchmark method, 8 incubation depths	1	trapezoidal depth integration	Cole (1989)
880	16	24	0	24	40.2	880	1035	benchmark method, 16 incubation depths	1	trapezoidal depth integration	
620					40.2		620	assumes static biomass	2	series solution to the time and depth integration	Platt et al. (1990)
1072	25	24	0	24	40.2	1072	1261	include excreted production	2	$1.22 \cdot$ benchmark	Tillman et al. (2000)
527	25	2	6	8	9.0	118	126	2 h incubation around noon	3	$(E/E_{inc}) \cdot PN_{inc}$	Oviatt (2002)
586	25	4	5	9	17.5	255	273	4 h incubation around noon	3	$(E/E_{inc}) \cdot PN_{inc}$	Mallin et al. (1991)
657	25	6	4	10	25.1	410	439	6 h incubation around noon	3	$(E/E_{inc}) \cdot PN_{inc}$	
919	25	12	1	13	39.2	896	962	12 h incubation	3	$(E/E_{inc}) \cdot PN_{inc}$	Kuenzler et al. (1979)
697	25	6	7	13	19.6	340	369	6 h incubation PM	3	$(E/E_{inc}) \cdot PN_{inc}$	Anderson (1964)
623	25	6	7	13	19.6	340	369	6 h incubation PM	3	$(D-3) \cdot$ hourly mean PN_{inc}	Parker et al. (2012)
714	25	7	7	14	20.1	357	390	7 h incubation PM	3	$2 \cdot PN_{inc}$	Taguchi et al. (1977)
826	25	2	6	8	9.0	118	126	2 h incubation noon	3	$D \cdot$ hourly mean PN_{inc}	Rysgaard et al. (1999)
893	25	4	5	9	17.5	255	273	4 h incubation around noon	3	$D \cdot$ hourly mean PN_{inc}	Grundle et al. (2009)

$919\,mg\,C\,m^{-2}\,d^{-1}$ (12 h incubation). This variability again reflects the accumulation of phytoplankton biomass as incubations proceed in nutrient-rich estuarine waters (measured, e.g., by Alpine and Cloern, 1988). As incubation dura-

tion lengthens, phytoplankton biomass accumulates (or it decreases if losses exceed production) continuously in bottles, so measured daily PN yields 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 657 and 697 mg C m^{-2} d^{-1}, respectively (Table 1). The underestimation of PN from short-term incubations relative to the benchmark also reflects errors from the computation of daily productivity (the time integral of nonlinear functions of p_b vs. I and I vs. time, Fig. 7) as a linear function of PN$_{inc}$. A further source of variability is the variety of linear multipliers used across studies, such as E/E_{inc}, D, D-3, and 2 (Table 1). This source of error is avoided with numerical integrations of short-term C-assimilation rates over time (e.g., Fee, 1973; Platt and Sathyendranath, 1995). Lastly, we remind readers of processes not included in our model – respiration and subsequent refixation of assimilated ^{14}C – that further confound interpretation of ^{14}C assays for measuring primary productivity (Marra, 2002).

The central points of this analysis are (1) many different approaches have been used to measure APPP in estuarine-coastal waters – there is nothing approaching a standard method; (2) method matters because simulations show that the measurement of depth-integrated daily productivity of a defined sample in a common light environment can vary by (at least) a factor of two (Table 1) depending on processes included or excluded, incubation duration and timing, and computational procedures. This variability between methods is small relative to the wide span of APPP between ecosystems (Fig. 4), consistent with the principle that phytoplankton biomass and light attenuation are the key components of primary production variability. However, differences between methods can be large enough to confound comparisons across studies. For example, the simulations presented here suggest that 2-fold differences of APPP between sites or over time (e.g., Parker et al., 2012) cannot be judged significant unless they are derived from common methods.

5.3 Recommendations

On the basis of these simulations we endorse two practices that have been recommended by others in the past. First, protocols for measuring phytoplankton primary productivity should be tailored to study objectives, and those objectives should be explicitly stated. If the objective is gross productivity analogous to satellite-derived rates in the ocean then an appropriate method is short-term measurements of C-assimilation rates across a light gradient and then integration of those rates over time and depth with the series approximation of Platt et al. (1990). In our standard case this yielded a rate of 620 g C m^{-2} d^{-1} (Table 1). If the objective is net productivity of particulate organic carbon that includes biomass change during incubations then an appropriate method is 24 h in situ (or simulated in situ) incubations distributed over the euphotic zone, measurement of assimilated ^{14}C collected on filters, and numerical depth-integration of C-assimilation rates. In our standard case this yielded a rate of 879 g C m^{-2} d^{-1}. If the objective is total net

productivity then this protocol can be modified to measure production of both dissolved and particulate organic carbon. In our standard case this yielded a rate of 1072 g C m^{-2} d^{-1}.

Our second recommendation is to minimize errors in the time and depth integration of measured C-assimilation rates. Our simulated incubations at a small number of depths resulted in large overestimates of productivity relative to the benchmark. Accurate depth integration requires incubations at a minimum of 8 depths, which yielded a 1 % error (relative to the benchmark) in our standard case. Time-integration is inherent in 24 h incubations and this is a compelling reason for the use of dawn–dawn incubations. If shorter incubations are used then the nonlinear variability of productivity over the diel light cycle should be integrated numerically, and the implications of phytoplankton biomass change during the incubation period should be considered when interpreting results and comparing them against values derived from other methods.

6 Advances since 1982 and two grand challenges for the future

Our goal was to compile and synthesize measurements of annual phytoplankton primary production in estuarine-coastal waters as a fundamental process that drives variability of water quality, biogeochemical processes, and production at higher trophic levels. Most primary production measurements in estuaries have been made since the 1982 review of Boynton et al. (1982) when APPP was available for 45 estuaries – most (32) from North America. The record now includes APPP measurements from 131 estuaries and its geographic coverage has expanded, particularly in Europe. Increased sampling has captured a larger range of variability: mean APPP across 45 estuaries ranged between 19 and 547 g C m^{-2} yr^{-1} (Boynton et al., 1982) compared to -105 and 1890 g C m^{-2} yr^{-1} in the latest compilation (Fig. 4). Enhanced sampling has led to discoveries that APPP can vary up to 10-fold within estuaries and 5-fold from year to year (this is probably an underestimate); some tropical-subtropical estuaries sustain very high rates of primary production, so global upscaling of APPP from measurements in temperate estuaries might have substantial errors; synthesis of estuarine APPP is confounded by the use of many methods; and daily depth-integrated primary productivity can be modeled as a function of phytoplankton biomass, light availability and photosynthetic efficiency that varies seasonally and regionally (Son et al., 2014). In the past three decades we have also developed a deeper understanding that variability of phytoplankton production at the land–sea interface cannot be explained by a single factor, such as nutrient loading rate (Cloern, 2001). Contemporary conceptual models now recognize that nutrient loading sets the potential for biomass production in estuaries, but the realization of that potential changes over time (Duarte et al., 2008) and is

shaped by variability of hydrology, optical properties, transport processes, inputs of heat, light and mixing energy, and top-down control of phytoplankton biomass growth (Fig. 6).

As coastal science moves forward in the 21st century, a grand challenge is to discover how these multiple drivers interact to generate the large spatial and temporal variability of APPP inherent to estuaries and other shallow marine ecosystems. This challenge is important because we have also discovered over the past three decades 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 rates of coastal production as global change proceeds.

A second grand challenge is to design and implement a program to measure estuarine-coastal phytoplankton 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). However, potentially larger sources of uncertainty must arise from the uneven spatial distribution of APPP 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 phytoplankton production in the world oceans is driven by variability in the transport of deep, nutrient-rich water to the surface (Behrenfeld et al., 2006). However, the much wider span of APPP 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 in-

fluenced 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 phytoplankton 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. 4) 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 are 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 phytoplankton 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 remain limited.

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 Ciénaga 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 undersampled tropical and subtropical sites. To put the undersampling problem into a 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 1 year. Yet we know from a few well-sampled places that production varies up to 10-fold within estuaries (Fig. 5a) and up to 5-fold 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 direct measurements of phytoplankton production in estuarine-coastal ecosystems include nonstandard 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 adopt a common method and measure primary productivity 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. Recent advances in development of bio-optical algorithms for turbid coastal waters (e.g., Son et al., 2014) indicate that remote sensing will play an increasingly important role in meeting this grand challenge.

Supplementary material related to this article is available online at http://www.biogeosciences.net/11/ 2477/2014/bg-11-2477-2014-supplement.pdf.

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References

Abreu, P. C., Bergesch, M., Proença, L. A., Garcia, C. A. E., and Odebrecht, C.: Short- and Long-Term Chlorophyll a Variability in the Shallow Microtidal Patos Lagoon Estuary, Southern Brazil, Estuar. Coast., 33, 554–569, doi:10.1007/s12237-009-9181-9, 2009.

Adolf, J. E., Yeager, C. L., Miller, W. D., Mallonee, M. E., and Harding Jr., L. W.: Environmental forcing of phytoplankton floral composition, biomass, and primary productivity in Chesapeake Bay, USA, Estuar. Coast. Shelf S., 67, 108–122, doi:10.1016/j.ecss.2005.11.030, 2006.

Alpine, A. E. and Cloern, J. E.: Phytoplankton Growth-Rates in a Light-Limited Environment, San-Francisco Bay, Mar. Ecol.-Prog. Ser., 44, 167–173, 1988.

Alpine, A. E. and Cloern, J. E.: Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary, Limnol. Oceanogr., 37, 946–955, 1992.

Anderson, G. C.: The Seasonal and Geographic Distribution of Primary Productivity Off the Washington and Oregon Coasts, Limnol. Oceanogr., 9, 284–302, 1964.

Apollonio, S.: Primary production in Dumbell Bay in the Arctic Ocean, Mar. Biol., 61, 41–51, 1980.

Ara, K., Yamaki, K., Wada, K., Fukuyama, S., Okutsu, T., Nagasaka, S., Shiomoto, A., and Hiromi, J.: Temporal variability in physicochemical properties, phytoplankton standing crop and primary production for 7 years (2002–2008) in the neritic area of Sagami Bay, Japan, J. Oceanogr., 67, 87–111, doi:10.1007/s10872-011-0010-y, 2011.

Ærtebjerg, G., Jacobsen, T. S., Gargas, E., and Buch, E.: The Belt Project. Evaluation of the physical, chemical and biological measurements, Denmark, 122 pages, ISBN 8750335324 9788750335320, 1981.

Azevedo, I., Duarte, P., and Bordalo, A.: Pelagic metabolism of the Douro estuary (Portugal) – Factors controlling primary production, Estuar. Coast. Shelf S., 69, 133–146, doi:10.1016/j.ecss.2006.04.002, 2006.

Bacher, C., Duarte, P., Ferreira, J. G., Heral, M., and Raillard, O.: Assessment and comparison of the Marennes-Oléron Bay (France) and Carlingford Lough (Ireland) carrying capacity with ecosystem models, Aquat. Ecol., 31, 379–394, 1998.

Banas, N. S., Hickey, B. M., Newton, J. A., and Ruesink, J. L.: Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA, Mar. Ecol.-Prog. Ser., 341, 123–139, doi:10.3354/meps341123, 2007.

Becacos-Kontos, T.: Primary production and environmental factors in an oligotrophic biome in the Aegean Sea., Mar. Biol., 42, 93–98, 1977.

Behrenfeld, M. J. and Falkowski, P. G.: A consumer's guide to phytoplankton primary productivity models, Limnol. Oceanogr., 42, 1479–1491, 1997.

Behrenfeld, M. J., Randerson, J. T., McClain, C. R., Feldman, G. C., Los, S. O., Tucker, C. J., Falkowski, P. G., Field, C. B., Frouin, R., Esaias, W. E., Kolber, D. D., and Pollack, N. H.: Biospheric primary production during an ENSO transition, Science, 291, 2594–2597, doi:10.1126/science.1055071, 2001.

Behrenfeld, M. J., Boss, E., Siegel, D. A., and Shea, D. M.: Carbon-based ocean productivity and phytoplankton physiology from space, Global Biogeochem. Cy., 19, GB1006, doi:10.1029/2004gb002299, 2005.

Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., Milligan, A. J., Falkowski, P. G., Letelier, R. M., and Boss, E. S.: Climate-driven trends in contemporary ocean productivity, Nature, 444, 752–755, doi:10.1038/nature05317, 2006.

Beukema, J. J., and Cadée, G. C.: Growth-rates of the bivalve *Macoma balthica* in the Wadden Sea during a period of eutrophication – relationships with concentrations of pelagic diatoms and flagellates, Mar. Ecol.-Prog. Ser., 68, 249–256, 1991.

Borges, A. V.: Do We Have Enough Pieces of the Jigsaw to Integrate CO_2 Fluxes in the Coastal Ocean?, Estuaries, 28, 3–27, 2005.

Bouman, H. A., Nakane, T., Oka, K., Nakata, K., Kurita, K., Sathyendranath, S., and Platt, T.: Environmental controls on phytoplankton production in coastal ecosystems: A case study from Tokyo Bay, Estuar. Coast. Shelf S., 87, 63–72, doi:10.1016/j.ecss.2009.12.014, 2010.

Boynton, W. R., Kemp, W. M., and Keefe, C. W.: A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production, in: Estuarine Comparisons, edited by: Kennedy, V. S., Academic Press, New York, 1982.

Brussaard, C. P. D.: Viral control of phytoplankton populations – A review, J. Eukaryot. Microbiol., 51, 125–138, 2004.

Bukaveckas, P. A., Barry, L. E., Beckwith, M. J., David, V., and Lederer, B.: Factors Determining the Location of the Chlorophyll Maximum and the Fate of Algal Production within the Tidal Freshwater James River, Estuar. Coast., 34, 569–582, doi:10.1007/s12237-010-9372-4, 2011.

Burford, M. A., Webster, I. T., Revill, A. T., Kenyon, R. A., Whittle, M., and Curwen, G.: Controls on phytoplankton productivity in a wet-dry tropical estuary, Estuar. Coast. Shelf S., 113, 141–151, doi:10.1016/j.ecss.2012.07.017, 2012.

Caddy, J. F.: Marine catchment basin effects versus impacts of fisheries on semi-enclosed seas, ICES J. Mar. Sci., 57, 628–640, 2000.

Cadée, G. C. and Hegeman, J.: Persisting High Levels of Primary Production at Declining Phosphate Concentrations in the Dutch Coastal Area (Marsdiep), Neth. J. Sea Res., 31, 147–152, 1993.

Caffrey, J. M.: Factors controlling net ecosystem metabolism in US estuaries, Estuaries, 27, 90–101, 2004.

Caffrey, J. M., Cloern, J. E., and Grenz, C.: Changes in production and respiration during a spring phytoplankton bloom in San Francisco Bay, California, USA: implications for net ecosystem metabolism, Mar. Ecol.-Prog. Ser., 172, 1—12, 1998.

Calbet, A.: Mesozooplankton grazing effect on primary production: A global comparative analysis in marine ecosystems, Limnol. Oceanogr., 46, 1824–1830, 2001.

Calbet, A. and Landry, M. R.: Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems, Limnol. Oceanogr., 49, 51–57, 2004.

Carstensen, J., Conley, D., and Muller-Karulis, B.: Spatial and temporal resolution of carbon fluxes in a shallow coastal ecosystem, the Kattegat, Mar. Ecol.-Prog. Ser., 252, 35–50, 2003.

Cebrian, J.: Patterns in the fate of production in plant communities, Am. Nat., 154, 449–468, doi:10.1086/303244, 1999.

Cermeño, P., Maranon, E., Perez, V., Serret, P., Fernandez, E., and Castro, C.: Phytoplankton size structure and primary production in a highly dynamic coastal ecosystem (Ría de Vigo, NW-Spain): Seasonal and short-time scale variability, Estuar. Coast. Shelf S., 67, 251–266, doi:10.1016/j.ecss.2005.11.027, 2006.

Chavez, F. P., Messié, M., and Pennington, J. T.: Marine primary production in relation to climate variability and change, Annu. Rev. Mar. Sci., 3, 227–260, doi:10.1146/annurev.marine.010908.163917, 2010.

Cloern, J. E.: Does the benthos control phytoplankton biomass in South San Francisco Bay?, Mar. Ecol.-Prog. Ser., 9, 191–202, 1982.

Cloern, J. E.: Temporal dynamics and ecological significance of salinity stratification in an estuary (South San Francisco Bay, USA), Oceanol. Acta, 7, 137–141, 1984.

Cloern, J. E.: Turbidity as a control on phytoplankton biomass and productivity in estuaries, Cont. Shelf Res., 7, 1367–1381, 1987.

Cloern, J. E.: Annual variations in river flow and primary production in the South San Francisco Bay Estuary (USA), in: Estuaries and Coasts: Spatial and Temporal Intercomparisons, edited by: Elliott, M. and Ducrotoy, D., Olsen and Olsen, Fredensborg, 91–96, 1991.

Cloern, J. E.: Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California, Rev. Geophys., 34, 127–168, 1996.

Cloern, J. E.: The relative importance of light and nutrient limitation of phytoplankton growth: a simple index of coastal ecosystem sensitivity to nutrient enrichment, Aquat. Ecol., 33, 3–16, 1999.

Cloern, J. E.: Our evolving conceptual model of the coastal eutrophication problem, Mar. Ecol.-Prog. Ser., 210, 223–253, 2001.

Cloern, J. E. and Jassby, A. D.: Complex seasonal patterns of primary producers at the land-sea interface, Ecol. Lett., 11, 1294–1303, doi:10.1111/J.1461-0248.2008.01244.X, 2008.

Cloern, J. E. and Jassby, A. D.: Patterns and Scales of Phytoplankton Variability in Estuarine-Coastal Ecosystems, Estuar. Coast., 33, 230–241, doi:10.1007/S12237-009-9195-3, 2010.

Cloern, J. E. and Jassby, A. D.: Drivers of change in estuarine-coastal ecosystems: discoveries from four decades of study in San Francisco Bay, Rev. Geophys., 50, RG4001, doi:10.1029/2012RG000397, 2012.

Cloern, J. E., Alpine, A. E., Cole, B. E., Wong, R. L. J., Arthur, J. F., and Ball, M. D.: River discharge controls phytoplankton dynamics in the northern San Francisco Bay estuary, Esuar. Coast. Shelf S., 16, 415–429, 1983.

Cloern, J. E., Cole, B. E., Wong, R. L. J., and Alpine, A. E.: Temporal dynamics of estuarine phytoplankton – a case study of San Francisco Bay, Hydrobiologia, 129, 153–176, 1985.

Cloern, J. E., Cole, B. E., and Hager, S. W.: Notes on a *Mesodinium rubrum* red tide in San Francisco Bay (California, USA), J. Plankton Res., 16, 1269–1276, 1994.

Cloern, J. E., Grenz, C., and Vidergar Lucas, L.: An empirical model of the phytoplankton chlorophyll:carbon ratio – The conversion factor between productivity and growth rate, Limnol. Oceanogr., 40, 1313–1321, 1995.

Cloern, J. E., Schraga, T. S., Lopez, C. B., Knowles, N., Labiosa, R. G., and Dugdale, R.: Climate anomalies generate an exceptional dinoflagellate bloom in San Francisco Bay, Geophys. Res. Lett., 32, L14608, doi:10.1029/2005gl023321, 2005.

Cole, B. E.: Temporal and Spatial Patterns of Phytoplankton Production in Tomales Bay, California, U.S.A., Estuar. Coast. Shelf S., 28, 103–115, 1989.

Cole, B. E. and Cloern, J. E.: An Empirical Model for Estimating Phytoplankton Productivity in Estuaries, Mar. Ecol.-Prog. Ser., 36, 299–305, 1987.

Cole, J. J., Caraco, N. F., and Peierls, B. L.: Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary?, Limnol. Oceanogr., 37, 1608–1617, 1992.

Colijn, F. and Ludden, E.: Primary production of phytoplankton in the Ems-Dollard estuary, in: Primary Production in the Ems-Dollard estuary, edited by: Colijn, F., Rijksuniversiteit Groningen, 38–99, 1983.

Costanza, R., d'Arge, R., deGroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., Oneill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., and vandenBelt, M.: The value of the world's ecosystem services and natural capital, Nature, 387, 253–260, 1997.

Diaz, R. J. and Rosenberg, R.: Spreading dead zones and consequences for marine ecosystems, Science, 321, 926–929, 2008.

Duarte, C. M. and Cebrian, J.: The fate of marine autotrophic production, Limnol. Oceanogr., 41, 1758–1766, 1996.

Duarte, C. M., Conley, D. J., Carstensen, J., and Sánchez-Camacho, M.: Return to Neverland: Shifting Baselines Affect Eutrophication Restoration Targets, Estuar. Coast., 32, 29–36, doi:10.1007/s12237-008-9111-2, 2008.

Durbin, E. G., Krawiec, R. W., and Smayda, T. J.: Seasonal studies on the relative importance of different size fractions of phytoplankton in Narragansett Bay (USA), Mar. Biol., 32, 271–287, 1975.

Edwards, R. R. C.: Ecology of a coastal lagoon complex in Mexico, Estuar. Coast. Mar. Sci, 6, 75–92, 1978.

Elmgren, R.: Trophic dynamics in the enclosed, brackish Baltic Sea, Rapp. P. -v. Reun. Cons. Int. Explor. Mer, 183, 152–169, 1984.

Eppley, R. W.: Temperature and phytoplankton growth in the sea, Fish. B.-NOAA, 70, 1063–1085, 1972.

Eyre, B. D. and McKee, L. J.: Carbon, nitrogen, and phosphorus budgets for a shallow subtropical coastal embayment (Moreton Bay, Australia), Limnol. Oceanogr., 47, 1043–1055, 2002.

Fee, E. J.: A numerical model for determining integral primary production and its application to Lake Michigan, J. Fish. Res. Board Can., 30, 1447–1468, 1973.

Figueiras, F. G., Labarta, U., and Reiriz, M. J. F.: Coastal upwelling, primary production and mussel growth in the Rías Baixas of Galicia, Hydrobiologia, 484, 121–131, doi:10.1023/a:1021309222459, 2002.

Flemer, D. A.: Primary Production in the Chesapeake Bay, Chesapeake Science, 11, 117–129, 1970.

Flemer, D. A., Hamilton, D. H., Keefe, C. W., and Mihursky, J. A.: Final technical report to Office of Water Resources Research on the effects of thermal loading and water quality on estuarine primary production. Office of Water Resources Research, U.S. Department of Interior, Washington, D.C. NRI Ref. No. 71-6, Chesapeake Biological Laboratory, 210, 1970.

Flint, R. W.: Phytoplankton production in the Corpus Christi Bay Estuary, Contrib. Mar. Sci., 27, 65–83, 1970.

Flores-Verdugo, F. J., Day, J. W., Mee, L., and Briseño-Dueñas, R.: Phytoplankton production and seasonal biomass variation of seagrass, *Ruppia maritima* L., in a tropical Mexican lagoon with an ephemeral inlet, Estuaries, 11, 51–56, 1988.

Furnas, M. J.: Insitu growth rates of marine phytoplankton – approaches to measurement, community and species growth rates, J. Plankton Res., 12, 1117–1151, doi:10.1093/plankt/12.6.1117, 1990.

Gallegos, C. L.: Phytoplankton photosynthetic capacity in a shallow estuary: environmental correlates and interannual variation, Mar. Ecol.-Prog. Ser., 463, 23–37, 2012.

Gallegos, C. L.: Long-term variations in primary production in a eutrophic sub-estuary: 1. Seasonal and spatial variability, Mar. Ecol.-Prog. Ser., 502, 53–67, doi:10.3354/meps10712, 2014.

Gameiro, C., Zwolinski, J., and Brotas, V.: Light control on phytoplankton production in a shallow and turbid estuarine system, Hydrobiologia, 669, 249–263, doi:10.1007/s10750-011-0695-3, 2011.

Garnier, J., Servais, P., Billen, G., Akopian, M., and Brion, N.: Lower Seine river and estuary (France) carbon and oxygen budgets during low flow, Estuaries, 24, 964–976, doi:10.2307/1353010, 2001.

Gattuso, J.-P., Frankignoulle, M., and Wollast, R.: Carbon and carbonate metabolism in coastal aquatic ecosystems., Annu. Rev. Ecol. Syst., 29, 405–433, 1998.

Gazeau, F., Gattuso, J.-P., Middelburg, J., Brion, N., Schiettecatte, L.-S., Frankignoulle, M., and Borges, A.: Planktonic and whole system metabolism in a nutrient-rich estuary (the Scheldt estuary), Estuar. Coast., 28, 868–883, doi:10.1007/bf02696016, 2005.

Gilmartin, M.: The primary production of a British Columbia fjord, J. Fish. Res. Board Can., 21, 505–538., 1964.

Gilmartin, M. and Revelante, N.: The phytoplankton characteristics of the barrier island lagoons of the Gulf of California, Estuar. Coast Mar. Sci., 7, 29–47, 1978.

Glé, C., Del Amo, Y., Sautour, B., Laborde, P., and Chardy, P.: Variability of nutrients and phytoplankton primary production in a shallow macrotidal coastal ecosystem (Arcachon Bay, France), Estuar. Coast. Shelf S., 76, 642–656, doi:10.1016/j.ecss.2007.07.043, 2008.

Gocke, K., Cortés, J., and Murillo, M. M.: The annual cycle of primary productivity in a tropical estuary: The inner regions of the Golfo de Nicoya, Costa Rica, Rev. Biol. Trop., 49, 289–306, 2001.

Goebel, N. L., Kremer, J. N., and Edwards, C. A.: Primary production in Long Island Sound, Estuar. Coast., 29, 232–245, 2006.

Greene, V. E., Sullivan, L. J., Thompson, J. K., and Kimmerer, W. J.: Grazing impact of the invasive clam *Corbula amurensis* on the microplankton assemblage of the northern San Francisco Estuary, Mar. Ecol.-Prog. Ser., 431, 183–193, doi:10.3354/meps09099, 2011.

Grenz, C., Cloern, J. E., Hager, S. W., and Cole, B. E.: Dynamics of nutrient cycling and related benthic nutrient and oxygen fluxes during a spring phytoplankton bloom in South San Francisco Bay (USA), Mar. Ecol.-Prog. Ser., 197, 67–80, 2000.

Grøntved, J. and Steemann Nielsen, E.: Investigations on the Phytoplankton in Sheltered Danish Marine Localities. Meddelser fra Kommissionen for Danmarks Fiskeri- og Havundersøgelser, Serie Plankton, bd. 5, no. 6, 1957.

Grundle, D. S., Timothy, D. A., and Varela, D. E.: Variations of phytoplankton productivity and biomass over an annual cycle in Saanich Inlet, a British Columbia fjord, Cont. Shelf Res., 29, 2257–2269, doi:10.1016/j.csr.2009.08.013, 2009.

Haas, L. W.: The effect of the spring-neap tidal cycle on the vertical salinity structure of the James, York and Rappahannock Rivers, Virginia, USA, Estuar. Coast. Mar. Sci., 5, 485–496, 1977.

Harding Jr., L. W.: Long-term increase of phytoplankton biomass in Chesapeake Bay, 1950–1994, Mar. Ecol.-Prog. Ser., 157, 39–52, 1997.

Harding Jr., L. W., Mallonee, M. E., and Perry, E. S.: Toward a Predictive Understanding of Primary Productivity in a Temperate, Partially Stratified Estuary, Estuar. Coast. Shelf S., 55, 437–463, doi:10.1006/ecss.2001.0917, 2002.

Harrison, W. G., Platt, T., and Lewis, M. R.: The utility of light-saturation models for estimating marine primary productivity in the field – a comparsion with convential simulated insitu methods, Can. J. Fish. Aquat. Sci., 42, 864–872, doi:10.1139/f85-110, 1985.

Herman, P. M. J., Middelburg, J. J., Van de Koppel, J., Heip, C. H. R.: Ecology of estuarine macrobenthos, in: Advances in Ecological Research, vol. 29: Estuaries, edited by: Nedwell, D. B and Raffaelli, D. G., Elsevier Academic Press Inc., San Diego, 195–240, 1999.

Henry, J. L., Mostert, S. A., and Christie, N. D.: Phytoplankton production in Langebaan Lagoon and Saldanha Bay, T. Roy. Soc. S. Afr., 42, 383–398, 1977.

Herfort, L., Peterson, T. D., Prahl, F. G., McCue, L. A., Needoba, J. A., Crump, B. C., Roegner, G. C., Campbell, V., and Zuber, P.: Red Waters of *Myrionecta rubra* are Biogeochemical Hotspots for the Columbia River Estuary with Impacts on Primary/Secondary Productions and Nutrient Cycles, Estuar. Coast., 35, 878–891, doi:10.1007/s12237-012-9485-z, 2012.

Hernandez, C. A. and Gocke, K.: Productividad primaria en la Ciénaga Grande de Santa Marta, Colombia., Anales del Instituto de Investigaciones Marinas de Punta de Betin, 19–20, 101–119, 1990.

Hickey, B. M. and Banas, N. S.: Oceanography of the U.S. Pacific Northwest coastal ocean and estuaries with application to coastal ecology, Estuaries, 26, 1010–1031, 2003.

Hopkinson, C. J., Smith, E. M., del Giorgio, P. A., and Williams, P. J. le B.: Estuarine respiration: an overview of benthic, pelagic and whole system respiration, in: Respiration in Aquatic Ecosystems, edited by: del Giorgio, P. A. and Williams, P. J. le B., Oxford University Press, New York, 2005.

Houde, E. D. and Rutherford, E. S.: Recent trends in estuarine fisheries – predictions of fish production and yield, Estuaries, 16, 161–176, 1993.

Howarth, R. W.: Nutrient limitation of net primary production in marine ecosystems, Annu. Rev. Ecol. Syst., 19, 89–110, 1988.

Jassby, A. D., Cloern, J. E., and Powell, T. M.: Organic-carbon sources and sinks in San-Francisco Bay – variability induced by river flow, Mar. Ecol.-Prog. Ser., 95, 39–54, 1993.

Jassby, A. D., Cloern, J. E., and Cole, B. E.: Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal ecosystem, Limnol. Oceanogr., 47, 698–712, 2002.

Johansson, J. O. R.: Long-term and seasonal trends in phytoplankton production and biomass in Tampa Bay, Florida, in: Proceedings, Tampa Bay Area Scientific Information Symposium, BASIS 5: 20–23 October 2009, edited by: Cooper, S. T., available at: http://www.tbeptech.org/BASIS/BASIS5/BASIS5.pdf (last access: 2 November 2013), 73–94, 2010.

Joint, I. R. and Pomroy, A. J.: Primary production in a turbid estuary, Estuar. Coast. Shelf S., 13, 303–316, 1981.

Kaas, H., Møhlenberg, F., Josefson, A., Rasmussen, B., Krause-Jensen, D., Jensen, H. S., Svendsen, L. M., Windolf, J., Middelboe, A. L., Sand-Jensen, K., and Pedersen, M. F.: Danske fjorde – status over miljøtilstand, årsagssammenhoenge og udvikling. Faglig rapport fra DMU, nr. 179, Miljø- og Energiministereriet, Danmarks Miljøundersøgelser, Roskilde., available at: http://www2.dmu.dk/1_viden/2_Publikationer/3_fagrapporter/rapporter/fr179.pdf (last access: 2 May 2014), 1996.

Keller, A. A., Taylor, C., Oviatt, C., Dorrington, T., Holcombe, G., and Reed, L.: Phytoplankton production patterns in Massachusetts Bay and the absence of the 1998 winter-spring bloom, Mar. Biol., 138, 1051–1062, 2001.

Kemp, W. M., Smith, E. M., Marvin-DiPasquale, M., and Boynton, W. R.: Organic carbon balance and net ecosystem metabolism in Chesapeake Bay, Mar. Ecol.-Prog. Ser., 150, 229–248, doi:10.3354/meps150229, 1997.

Kemp, W. M., Boynton, W. R., Adolf, J. E., Boesch, D. F., Boicourt, W. C., Brush, G., Cornwell, J. C., Fisher, T. R., Glibert, P. M., Hagy, J. D., Harding Jr., L. W., Houde, E. D., Kimmel, D. G., Miller, W. D., Newell, R. I. E., Roman, M. R., Smith, E. M., and Stevenson, J. C.: Eutrophication of Chesapeake Bay: historical trends and ecological interactions, Mar. Ecol.-Prog. Ser., 303, 1–29, doi:10.3354/meps303001, 2005.

Ketchum, B. H.: Relation between circulation and planktonic populations in estuaries, Ecology, 35, 191–200, 1954.

Kimmerer, W., Gartside, E., and Orsi, J. J.: Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay, Mar. Ecol.-Prog. Ser., 113, 81–94, 1994.

Kiørboe, T. and Nielsen, T. G.: Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 1. Copepods, Limnol. Oceanogr., 39, 493–507, 1994.

Knap, A.: JGOFS Protocols – June 1994, Chapter 2. Shipboard Sampling Procedures, section 4.0 Primary Production, available at: http://usjgofs.whoi.edu/JGOFS_19.pdf (last access: 11 January 2014), 1994.

Kocum, E., Underwood, G. J. C., and Nedwell, D. B.: Simultaneous measurement of phytoplanktonic primary production, nutrient and light availability along a turbid, eutrophic UK east coast estuary (the Colne Estuary), Mar. Ecol.-Prog. Ser., 231, 1–12, 2002.

Koseff, J. R., Holen, J. K., Monismith, S. G., and Cloern, J. E.: Coupled Effects of Vertical Mixing and Benthic Grazing on Phytoplankton Populations in Shallow, Turbid Estuaries, J. Mar. Res., 51, 843–868, 1993.

Kromkamp, J. and Peene, J.: Possibility of net phytoplankton primary production in the turbid Schelde Estuary (SW Netherlands), Mar. Ecol.-Prog. Ser., 121, 249–259, 1995.

Kromkamp, J., Peene, J., Rijswijk, P., Sandee, A., and Goosen, N.: Nutrients, light and primary production by phytoplankton and microphytobenthos in the eutrophic, turbid Westerschelde estuary (The Netherlands), Hydrobiologia, 311, 9–19, doi:10.1007/bf00008567, 1995.

Kuenzler, E. J., Stanley, D. W., and Koenings, J. P.: Nutrient kinetics of phytoplankton in the Pamlico River, North Carolina, Report –

Water Resources Research Institute of The University of North Carolina, 1979.

Langdon, C.: The significance of respiration in production measurements based on oxygen, ICES Mar. Sc., 197, 69–78, 1993.

Lawrenz, E., Smith, E. M., and Richardson, T. L.: Spectral Irradiance, Phytoplankton Community Composition and Primary Productivity in a Salt Marsh Estuary, North Inlet, South Carolina, USA, Estuar. Coast., 36, 347–364, doi:10.1007/s12237-012-9567-y, 2013.

Laws, E. A. and Bannister, T. T.: Nutrient- and light-limited growth of *Thalassiosira fluviatilis* in continuous culture, with implications for phytoplankton growth in the oecan, Limnol. Oceanogr., 25, 457–473, 1980.

Laws, E. A., Landry, M. R., Barber, R. T., Campbell, L., Dickson, M.-L., and Marra, J.: Carbon cycling in primary production bottle incubations: inferences from grazing experiments and photosynthetic studies using ^{14}C and ^{18}O in the Arabian Sea, Deep-Sea Res. Pt. II, 47, 1339–1352, 2000.

Lindahl, O., Belgrano, A., Davidsson, L., and Hernroth, B.: Primary production, climatic oscillations, and physico-chemical processes: The Gullmar Fjord time-series data set (1985–1996), ICES J. Mar. Sci., 55, 723–729, 1998.

Lohrenz, S. E., Wiesenburg, D. A., Rein, C. R., Arnone, R. A., and Taylor, C. D.: A comparison of *in situ* and simulated *in situ* methods for estimating oceanic primary production, J. Plankton Res., 14, 201–221, 10.1093/plankt/14.2.201, 1992.

Lucas, L. V., Koseff, J. R., Cloern, J. E., Monismith, S. G., and Thompson, J. K.: Processes governing phytoplankton blooms in estuaries. I: The local production-loss balance, Mar. Ecol.-Prog. Ser., 187, 1–15, 1999.

Lucas, L. V., Thompson, J. K., and Brown, L. R.: Why are diverse relationships observed between phytoplankton biomass and transport time?, Limnol. Oceanogr., 54, 381–390, 2009.

Luengen, A. C. and Flegal, A. R.: Role of phytoplankton in mercury cycling in the San Francisco Bay estuary, Limnol. Oceanogr., 54, 23–40, doi:10.4319/lo.2009.54.1.0023, 2009.

Luoma, S. N., van Geen, A., Lee, B. G., and Cloern, J. E.: Metal uptake by phytoplankton during a bloom in South San Francisco Bay: Implications for metal cycling in estuaries, Limnol. Oceanogr., 43, 1007–1016, 1998.

Mallin, M. A., Paerl, H. W., and Rudek, J.: Seasonal phytoplankton composition, productivity and biomass in the Neuse River estuary, North Carolina, Estuar. Coast. Shelf S., 32, 609–623, 1991.

Mallin, M. A., Paerl, H. W., Rudek, J., and Bates, P. W.: Regulation of estuarine primary production by watershed rainfall and river flow, Mar. Ecol.-Prog. Ser., 93, 199–203, 1993.

Malone, T. C., Kemp, W. M., Ducklow, H. W., Boynton, W. R., Tuttle, J. H., and Jonas, R. B.: Lateral variation in the production and fate of phytoplankton in a partially stratified estuary, Mar. Ecol.-Prog. Ser., 32, 149–160, 1986.

Malone, T. C., Crocker, L. H., Pike, S. E., and Wendler, B. W.: Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary, Mar. Ecol.-Prog. Ser., 48, 235–249, 1988.

Marra, J.: Approaches to the measurement of plankton production, in: Phytoplankton Productivity: Carbon Assimilation in Marine and Freshwater, edited by: Williams, P. J. le B., Thomas, D. N., and Reynolds, C. S., Blackwell Science Ltd., Oxford, 78–108, 2002.

Martin, M. A., Fram, J. P., and Stacey, M. T.: Seasonal chlorophyll a fluxes between the coastal Pacific Ocean and San Francisco Bay, Mar. Ecol.-Prog. Ser., 357, 51–61, 2007.

May, C. L., Koseff, J. R., Lucas, L. V., Cloern, J. E., and Schoellhamer, D. H.: Effects of spatial and temporal variability of turbidity on phytoplankton blooms, Mar. Ecol.-Prog. Ser., 254, 111–128, 2003.

Medina-Gómez, I. and Herrera-Silveira, J. A.: Primary production dynamics in a pristine groundwater influenced coastal lagoon of the Yucatan Peninsula, Cont. Shelf Res., 26, 971–986, doi:10.1016/j.csr.2006.03.003, 2006.

Meeuwig, J. J.: Predicting coastal eutrophication from land-use: an empirical approach to small non-stratifed estuaries, Mar. Ecol.-Prog. Ser., 176, 231–241, 1999.

Moll, R. A.: Phytoplankton in a temperate-zone salt marsh: net production and exchanges with coastal waters., Mar. Biol., 42, 109–118, 1977.

Monbet, Y.: Control of phytoplankton biomass in estuaries: A comparative analysis of microtidal and macrotidal estuaries, Estuaries, 15, 563–571, 1992.

Montes-Hugo, M. A., Alvarez-Borrego, S., and Gaxiola-Castro, G.: Annual phytoplankton production in a coastal lagoon of the southern California Current System, Mar. Ecol.-Prog. Ser., 277, 51–60, 2004.

Morán, X. A. G.: Annual cycle of picophytoplankton photosynthesis and growth rates in a temperate coastal ecosystem: a major contribution to carbon fluxes, Aquat. Microb. Ecol., 49, 267–279, doi:10.3354/ame01151, 2007.

Moreno-Madriñán, M. J. and Fischer, A. M.: Performance of the MODIS FLH algorithm in estuarine waters: a multi-year (2003–2010) analysis from Tampa Bay, Florida (USA), Int. J. Remote Sens., 34, 6467–6483, doi:10.1080/01431161.2013.804227, 2013.

Murrell, M. C. and Hollibaugh, J. T.: Microzooplankton grazing in northern San Francisco Bay measured by the dilution method, Mar Ecol.-Prog. Ser., 15, 53–63, 1998.

Murrell, M. C., Hagy III, J. D., Lores, E. M., and Greene, R. M.: Phytoplankton production and nutrient distributions in a subtropical estuary: Importance of freshwater flow, Estuar. Coast., 30, 390–402, 2007.

Nixon, S. W.: Physical energy inputs and the comparative ecology of lake and marine ecosystems, Limnol. Oceanogr., 33, 1005–1025, 1988.

Nixon, S. W.: Coastal marine eutrophication – a definition, social causes, and future concerns, Ophelia, 41, 199–219, 1995.

Nixon, S. W. and Buckley, B. A.: "A strikingly rich zone" – Nutrient enrichment and secondary production in coastal marine ecosystems, Estuaries, 25, 782–796, 2002.

Nixon, S. W., Fulweiler, R. W., Buckley, B. A., Granger, S. L., Nowicki, B. L., and Henry, K. M.: The impact of changing climate on phenology, productivity, and benthic-pelagic coupling in Narragansett Bay, Estuar. Coast. Shelf S., 82, 1–18, 2009.

Oviatt, C.: Annual Primary Production in Narragansett Bay with no Bay-Wide Winter-Spring Phytoplankton Bloom, Estuar. Coast. Shelf S., 54, 1013–1026, doi:10.1006/ecss.2001.0872, 2002.

Oviatt, C. A., Hyde, K. J. W., Keller, A. A., and Turner, J. T.: Production patterns in Massachusetts Bay with outfall relocation, Estuar. Coast., 30, 35–46, 2007.

Parker, A. E., Kimmerer, W. J., and Lidström, U. U.: Reevaluating the generality of an empirical model for light-limited primary production in the San Francisco Estuary, Estuar. Coast., 35, 930–942, doi:10.1007/s12237-012-9507-x, 2012.

Peierls, B. L., Hall, N. S., and Paerl, H. W.: Non-monotonic Responses of Phytoplankton Biomass Accumulation to Hydrologic Variability: A Comparison of Two Coastal Plain North Carolina Estuaries, Estuar. Coast., 35, 1–17, 2012.

Pennock, J. R.: Chlorophyll distributions in the Delaware estuary: Regulation by light-limitation, Estuar. Coast. Shelf S., 21, 711–725, 1985.

Pennock, J. R. and Sharp, J. H.: Phytoplankton production in the Delaware Estuary: temporal and spatial variability, Mar Ecol.-Prog. Ser., 34, 143–155, 1986.

Petersen, J. K., Hansen, J. W., Laursen, M. B., Clausen, P., Carstensen, J., and Conley, D. J.: Regime shift in a coastal marine ecosystem, Ecol. Appl., 18, 497–510, 2008.

Pitcher, G. C. and Calder, D.: Shellfish culture in the Benguela system: phytoplankton and the availability of food for commercial mussel farms in Saldhana Bay, South Africa., J. Shellfish Res., 17, 15–24, 1998.

Platt, T. and Sathyendranath, S.: Software for Use in Calculation of Primary Production in the Oceanic Water Column, available at: http://www.ioccg.org/software/Ocean_Production/rpt.pdf (last access: 26 February 2014), Bedford Institute of Oceanography, Dartmouth NS, 1995.

Platt, T., Sathyendranath, S., and Ravindran, P.: Primary production by phytoplankton: Analytic solutions for daily rates per unit area of water surface, P. Roy. Soc. B, 241, 101–111, 1990.

Raine, R. C. T. and Patching, J. W.: Aspects of carbon and nitrogen cycling in a shallow marine environment, J. Exp. Mar. Biol. Ecol., 47, 127–139, doi:10.1016/0022-0981(80)90107-0, 1980.

Raymond, P. A. and Bauer, J. E.: Riverine export of aged terrestrial organic matter to the North Atlantic Ocean, Nature, 409, 497–500, 2001.

Riley, G.: The plankton of estuaries, in: Estuaries, edited by: Lauff, G., American Association for the Advancement of Science, Publication, No. 83, Washington, DC, 316–328, 1967.

Rivera-Monroy, V., Madden, C., Day, J., Twilley, R., Vera-Herrera, F., and Alvarez-Guillén, H.: Seasonal coupling of a tropical mangrove forest and an estuarine water column: enhancement of aquatic primary productivity, Hydrobiologia, 379, 41–53, doi:10.1023/a:1003281311134, 1998.

Roman, M. R., Reeve, M. R., and Froggatt, J. L.: Carbon production and export from Biscayne Bay, Florida. I. Temporal patterns in primary production, seston and zooplankton, Estuar. Coast. Shelf S., 17, 45–59, doi:10.1016/0272-7714(83)90044-6, 1983.

Ruppert, D.: Modeling Univariate Distributions, in: Statistics and Data Analysis for Financial Engineering, edited by: Casella, G., Fienberg, S., and Olkin, I., Springer Science and Business Media, New York, 118, 2011.

Rysgaard, S., Nielsen, T. G., and Hansen, B. W.: Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland, Mar Ecol.-Prog. Ser., 179, 13–25, 1999.

Saux Picart, S., Sathyendranath, S., Dowell, M., Moore, T., and Platt, T.: Remote sensing of assimilation number for marine phytoplankton, Remote Sens. Environ., 146, 87–96, doi:10.1016/j.rse.2013.10.032, 2014.

Sellner, K. G.: Interpretation of the ^{14}C method of measuring the total annual production of phytoplankton in a South Carolina estuary, Bot. Mar., 19, 119–125, 1976.

Shapiro, S. S. and Wilk, M. B.: An Analysis of Variance test for normality (complete samples), Biometrika, 52, 591–611, 1965.

Shikata, T., Nagasoe, S., Matsubara, T., Yoshikawa, S., Yamasaki, Y., Shimasaki, Y., Oshima, Y., Jenkinson, I. R., and Honjo, T.: Factors influencing the initiation of blooms of the raphidophyte *Heterosigma akashiwo* and the diatom *Skeletonema costatum* in a port in Japan, Limnol. Oceanogr., 53, 2503–2518, doi:10.4319/lo.2008.53.6.2503, 2008.

Sinclair, M., Suba Rao, D. V., and Couture, R.: Phytoplankton temporal distributions in estuaries, Oceanol. Acta, 4, 239–246, 1981.

Small, L. F., McIntire, C. D., MacDonald, K. B., Lara-Lara, J. R., Frey, B. E., Amspoker, M. C., and Winfield, T.: Primary production, plant and detrital biomass, and particle transport in the Columbia River Estuary, Prog. Oceanogr., 25, 175–210, doi:10.1016/0079-6611(90)90007-o, 1990.

Smith, S. V. and Hollibaugh, J. T.: Annual cycle and interannual variability of ecosystem metabolism in a temperate climate embayment, Ecol. Monogr., 67, 509–533, doi:10.1890/0012-9615(1997)067[0509:acaivo]2.0.co;2, 1997.

Smith, S. V., Kimmerer, W. J., Laws, E. A., Brock, R. E., and Walsh, T. W.: Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation, Pac. Sci., 35, 279–395, 1981.

Sobczak, W. V., Cloern, J. E., Jassby, A. D., Cole, B. E., Schraga, T. S., and Arnsberg, A.: Detritus fuels ecosystem metabolism but not metazoan food webs in San Francisco estuary's freshwater Delta, Estuaries, 28, 124–137, 2005.

Soetaert, K., Petzoldt, T., and Setzer, R. W.: Solving differential equations in R: Package deSolve, J. Stat. Softw., 33, 1–25, 2010.

Son, S., Wang, M., and Harding Jr., L. W.: Satellite-measured net primary production in the Chesapeake Bay, Remote Sens. Environ., 144, 109–119, doi:10.1016/j.rse.2014.01.018, 2014.

Steemann Nielsen, E.: The use of radioactive carbon (C^{14}) for measuring organic production in the sea., J. Cons. Int. Explor. Mer., 18, 117–140, 1952.

Stockner, J. G. and Cliff, D. D.: Phytoplankton Ecology of Vancouver Harbor, J. Fish. Res. Board Can., 36, 1–10, 1979.

Stockner, J. G., Cliff, D. D., and Shortreed, K. R. S.: Phytoplankton of the Strait of Georgia, British Columbia, J. Fish. Res. Board Can., 36, 657–666, 1979.

Stockner, J. G., Cliff, D. D., and Buchanan, D. B.: Phytoplankton production and distribution in Howe Sound, British Colombia: a coastal marine embayment-fjord under stress, J. Fish. Res. Board Can., 34, 907–917, 1977.

Taguchi, S., Iseki, K., and Kawamura, T.: The estimate of annual production by phytoplankton in Akkeshi Bay, Japan, J. Oceanogr. Soc. Japan, 33, 97–102, 1977.

Thayer, G. W.: Phytoplankton production and the distribution of nutrients in a shallow unstratified estuarine system near Beaufort, N.C, Chesapeake Science, 12, 240–253, 1971.

Therriault, J.-C. and Levasseur, M.: Control of phytoplankton production in the Lower St. Lawrence Estuary: light and freshwater runoff, Nat. Can., 112, 77–96, 1985.

Thomas, C. M., Perissinotto, R., and Kibirige, I.: Phytoplankton biomass and size structure in two South African eutrophic, tem-

porarily open/closed estuaries, Estuar. Coast. Shelf S., 65, 223–238, 2005.

Thompson, P. A.: Spatial and Temporal Patterns of Factors Influencing Phytoplankton in a Salt Wedge Estuary, the Swan River, Western Australia, Estuaries, 21, 801–817, 1998.

Tillman, U., Hesse, K.-J., and Colijn, F.: Planktonic primary production in the German Wadden Sea, J. Plankton Res., 22, 1253–1276, 2000.

Umani, S. F., Del Negro, P., Larato, C., De Vittor, C., Cabrini, M., Celio, M., Falconi, C., Tamberlich, F., and Azam, F.: Major interannual variations in microbial dynamics in the Gulf of Trieste (northern Adriatic Sea) and their ecosystem implications, Aquat. Microb. Ecol., 46, 163–175, 2007.

Underwood, G. J. C. and Kromkamp, J., Primary production by phytoplankton and microphytobenthos in estuaries, in: Advances in Ecological Research, vol. 29: Estuaries, edited by: Nedwell, D. B and Raffaelli, D. G., Elsevier Academic Press Inc., San Diego, 93–153, 1999.

Wetsteyn, L. P. M. J. and Kromkamp, J. C.: Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (The Netherlands) before, during and after a large-scale coastal engineering project (1980–1990), Hydrobiologia, 282–283, 61–78, doi:10.1007/bf00024622, 1994.

Williams, R. B. and Murdoch, M. B.: Phytoplankton Production and Chlorophyll Concentration in the Beaufort Channel, North Carolina, Limnol. Oceanogr., 11, 73–82, 1966.

Winder, M. and Cloern, J. E.: The annual cycles of phytoplankton biomass, Philos. T. Roy. Soc. B, 365, 3215–3226, doi:10.1098/Rstb.2010.0125, 2010.

Wofsy, S. C.: A simple model to predict extinction coefficients and phytoplankton biomass in eutrophic waters, Limnol. Oceanogr., 28, 1144–1155, 1983.

Yamaguchi, Y., Satoh, H., and Aruga, Y.: Seasonal Changes of Organic Carbon and Nitrogen Production by Phytoplankton in the Estuary of River Tamagawa, Mar. Pollut. Bull., 23, 723–725, 1991.

Yin, K.: Influence of monsoons and oceanographic processes on red tides in Hong Kong waters, Mar Ecol.-Prog. Ser., 262, 27–41, 2003.