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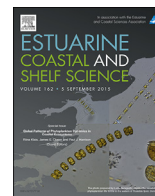
Phytoplankton blooms in estuarine and coastal waters: Seasonal patterns and key species

Jacob Carstensen [a, *], Riina Klais [b], James E. Cloern [c]

[a] Dept. of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde, Denmark
[b] Institute of Ecology and Earth Sciences, Tartu University, Lai 40, 51005 Tartu, Estonia
[c] United States Geological Survey, MS496, 345 Middlefield Road, Menlo Park, CA 94025, USA

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ABSTRACT

Phytoplankton blooms are dynamic phenomena of great importance to the functioning of estuarine and coastal ecosystems. We analysed a unique (large) collection of phytoplankton monitoring data covering 86 coastal sites distributed over eight regions in North America and Europe, with the aim of investigating common patterns in the seasonal timing and species composition of the blooms. The spring bloom was the most common seasonal pattern across all regions, typically occurring early (February–March) at lower latitudes and later (April–May) at higher latitudes. Bloom frequency, defined as the probability of unusually high biomass, ranged from 5 to 35% between sites and followed no consistent patterns across gradients of latitude, temperature, salinity, water depth, stratification, tidal amplitude or nutrient concentrations. Blooms were mostly dominated by a single species, typically diatoms (58% of the blooms) and dinoflagellates (19%). Diatom-dominated spring blooms were a common feature in most systems, although dinoflagellate spring blooms were also observed in the Baltic Sea. Blooms dominated by chlorophytes and cyanobacteria were only common in low salinity waters and occurred mostly at higher temperatures. Key bloom species across the eight regions included the diatoms *Cerataulina pelagica* and *Dactyliosolen fragilissimus* and dinoflagellates *Heterocapsa triquetra* and *Prorocentrum cordatum*. Other frequent bloom-forming taxa were diatom genera *Chaetoceros*, *Coscinodiscus*, *Skeletonema*, and *Thalassiosira*. Our meta-analysis shows that these 86 estuarine-coastal sites function as diatom-producing systems, the timing of that production varies widely, and that bloom frequency is not associated with environmental factors measured in monitoring programs. We end with a perspective on the limitations of conclusions derived from meta-analyses of phytoplankton time series, and the grand challenges remaining to understand the wide range of bloom patterns and processes that select species as bloom dominants in coastal waters.

1. Introduction

Phytoplankton biomass, primary production and community composition are all highly dynamic at the land-sea interface where diverse human actions and climate variability intersect to drive complex patterns of change over time (Cloern and Jassby, 2008). An important pattern is the occurrence of seasonal or episodic bursts of biomass accumulation as blooms, and research in recent decades has identified processes that trigger blooms at the land-sea interface, including: pulsed inputs of nutrients from river inflow (Peierls et al., 2012; Hall et al., 2013), coastal upwelling (Brown and Ozretich, 2009), atmospheric deposition (Paerl, 1997), wind-induced entrainment of bottom water (Iverson et al., 1974; Carstensen et al., 2005), and neap-spring variability of tidal mixing and stratification (Cloern, 1996); seasonal winds that enhance water retention in bays (Yin, 2003); heat waves that set up thermal stratification (Cloern et al., 2005); increasing retention time in flushed systems (Odebrecht et al., 2015); release of benthic grazing pressure (Carstensen et al., 2007; Cloern et al., 2007; Petersen et al., 2008); and seasonal changes in temperature and solar radiation (Shikata et al., 2008). Phytoplankton blooms have ecological and biogeochemical significance because much of the annual primary production in estuarine-coastal ecosystems occurs during these events when photosynthesis exceeds system respiration (Caffrey

et al., 1998). That production is the energy supply that fuels production in food webs supporting fisheries (Houde and Rutherford, 1993), aquaculture harvest (Bacher et al., 1998), system respiration (Hopkinson et al., 2005), and microbial processes that make estuaries biogeochemical hot spots (Cloern et al., 2014). Recent comparisons of chlorophyll *a* time series across a range of estuarine-coastal ecosystem types reveal a surprising diversity of seasonal biomass patterns, that these patterns differ from those in the open ocean (Cloern and Jassby, 2010), and they can change abruptly (Winder and Cloern, 2010).

Comparison of chlorophyll *a* time series across sites has been useful for discovering how the patterns of phytoplankton biomass variability are shaped by features that distinguish estuarine-coastal ecosystems from the open ocean − nutrient enrichment, tidal mixing, freshwater inflow, shallow depth and tight benthic-pelagic coupling, sharp vertical and horizontal gradients (Cloern, 1996). Progress has been slower in solving the much more challenging problem of understanding how these and other processes select those phytoplankton species that grow fast enough to develop blooms. Our general conceptual understanding recognizes one seasonal pattern that starts with a spring bloom dominated by large, fast-growing diatoms, followed by a number of summer blooms comprised of diatoms, flagellates, and dinoflagellates, and autumn blooms dominated by diatoms and dinoflagellates (Tett et al., 1986; Mallin et al., 1991). However, there are many deviations from this classical pattern. Blooms in San Francisco Bay are dominated by diatoms throughout the year (Cloern and Dufford, 2005), and blooms of nitrogen-fixing cyanobacteria typically develop in low salinity waters during summer (Jurgensone et al., 2011) when dissolved inorganic nitrogen is depleted from the surface layer and temperatures are high (Paerl and Huisman, 2009). Dinoflagellates dominate spring blooms in parts of the Baltic Sea (Klais et al., 2011). The highly variable physical environment and nutrient regime in estuaries and coastal waters promote different strategies at different times (Margalef, 1978), and bloom species are often selected among those present at suitable inoculum levels prior to the bloom (Smayda and Reynolds, 2001). Given the complexity of the problem, we have not yet identified consistent seasonal patterns of bloom occurrence by individual species or species groups in coastal waters.

Understanding bloom dynamics at the species level has been elusive partly because we are not making sufficient effort to study life-cycle processes such as sexual reproduction (Sarno et al., 2010), germination of resting stages (Shikata et al., 2008), allelopathy and mutualism between species (Smayda, 1997; Smayda and Reynolds, 2001). Second, the information contained in the many empirical records of phytoplankton community variability has not been synthesized to search for common patterns of bloom occurrence and composition. We extend the approach of comparing time series across sites to explore patterns of variability in phytoplankton communities and, particularly, species that develop blooms in estuaries, bays, and shallow coastal waters. To do this we assembled phytoplankton time series from 86 estuarine and coastal sites, and then probed this compilation to explore four basic ecological questions:

Q1. Which species and higher taxa dominate phytoplankton blooms in shallow, nutrient-enriched coastal waters?
Q2. Are there characteristic seasonal patterns of bloom occurrence?
Q3. Are blooms dominated by a common set of phytoplankton groups or species?
Q4: Does bloom frequency vary consistently along gradients of habitat attributes such as salinity, temperature, light availability, nutrients, or mixing?

Answers to these fundamental questions are essential for expanding our still-limited knowledge of the natural history of phytoplankton species succession and blooms.

2. Methods

We used long-term monitoring data from a diverse set of marine ecosystems in North America and Northwestern Europe to identify blooms as observations of unusually high phytoplankton biomass. Differences in the frequencies and phytoplankton taxonomic composition of these blooms were examined across 86 coastal sites ranging from estuaries and lagoons typically affected by land runoff to embayments and nearshore coastal systems (Fig. 1). For simplicity we refer to these as estuarine-coastal sites, recognising their differences in landscape and hydroclimatic settings. These sites encompass a broad range of salinity, temperature, nutrient concentrations, tidal mixing, stratification patterns, water depth and transparency, providing a unique opportunity to explore phytoplankton bloom patterns across habitat gradients characteristic of the land-sea continuum. For some analyses we grouped phytoplankton data from the 86 sites into 8 geographic regions (Fig. 1), largely based on latitude, salinity, tidal amplitude and stratification patterns.

2.1. Data sources

Time series (minimum 5 years) of phytoplankton species counts and water quality data (all surface data) were collected from different national and regional monitoring programs (Table 1). In addition to salinity, temperature and Secchi depth, water samples were analysed for nutrient and chlorophyll *a* concentrations using standard measurements within the different monitoring programs. The taxonomical composition and biomass of the phytoplankton community was assumed to be analysed by standard techniques (inverted microscope; Utermöhl, 1958) in Lugol's-fixed samples. The taxonomic resolution varied among and even within monitoring programs due to differences in identification expertise of the microscopist and the level of taxonomic aggregation (e.g. specimens identified to genus level only). We assume that the most common bloom-forming species are well recognised throughout the diverse data sets and that differences in taxonomic resolution are most problematic for the less common species that are not addressed in this study. The taxonomy used in all data sets was standardized according to the World Register of Marine Species (http://www.marinespecies.org/) to enable comparison of bloom species across sites (Olli et al., 2015). We recognise limitations to the taxonomy obtained by microscopy (Jakobsen et al., 2015) and that the taxonomical identification in some cases includes cryptic species that include multiple species, which we address below.

In all monitoring programs phytoplankton specimens were identified to a standard taxonomical level (mostly at the species or genus level) and size class. Results of microscopic analyses were reported as either biovolume (NRE and SFB; Table 1) or carbon biomass (all other data sets) of each species using different compendia for translating counts (details were not provided with the data). If carbon biomass was not reported we estimated it for each species using measured biovolumes and conversion factors for diatoms (0.11 pg C μm^{-3}; Strathmann, 1967) and non-diatoms (0.13 pg C μm^{-3}; Edler, 1979). More accurate scaling equations could not be employed because cell volumes were not reported. For each sample, we calculated the total phytoplankton carbon biomass by aggregating biomass of all autotrophic and mixotrophic species. We excluded the mixotrophic ciliate *Mesodinium rubrum* because it was not consistently identified in all monitoring programs, and we