Why large cells dominate estuarine phytoplankton

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Abstract

Surveys across the world oceans have shown that phytoplankton biomass and production are dominated by small cells (picoplankton) where nutrient concentrations are low, but large cells (microplankton) dominate when nutrient-rich deep water is mixed to the surface. I analyzed phytoplankton size structure in samples collected over 25 yr in San Francisco Bay, a nutrient-rich estuary. Biomass was dominated by large cells because their biomass selectively grew during blooms. Large-cell dominance appears to be a characteristic of ecosystems at the land–sea interface, and these places may therefore function as analogs to oceanic upwelling systems. Simulations with a size-structured NPZ model showed that runs of positive net growth rate persisted long enough for biomass of large, but not small, cells to accumulate. Model experiments showed that small cells would dominate in the absence of grazing, at lower nutrient concentrations, and at elevated (\(+5^\circ C\)) temperatures. Underlying these results are two fundamental scaling laws: (1) large cells are grazed more slowly than small cells, and (2) grazing rate increases with temperature faster than growth rate. The model experiments suggest testable hypotheses about phytoplankton size structure at the land–sea interface: (1) anthropogenic nutrient enrichment increases cell size; (2) this response varies with temperature and only occurs at mid-high latitudes; (3) large-cell blooms can only develop when temperature is below a critical value, around 15°C; (4) cell size diminishes along temperature gradients from high to low latitudes; and (5) large-cell blooms will diminish or disappear where planetary warming increases temperature beyond their critical threshold.

“the biomass spectrum has an important future in marine ecology” (Platt 1985).

A grand challenge of limnology and oceanography is to understand the processes that shape phytoplankton communities. Individual phytoplankton species appear while others disappear, for reasons largely unexplained, to reshape communities over time scales of weeks or even days. The challenge is visualized in Fig. 1, showing images of phytoplankton sampled at nearby locations in San Francisco Bay on different dates. The image conveys information about community variability at two levels: cell morphology that defines communities as assemblages of species, and cell size that ranges over 9 orders of magnitude (Finkel et al. 2010).

The mechanisms of phytoplankton community variability at the species level remain mysterious. Experiments (Benincà et al. 2008) and models (Huisman and Weissing 1999) demonstrate how species interactions, such as resource competition, can generate chaotic fluctuations in plankton food webs, even in the absence of environmental variability. Predictability of chaotic systems decays quickly over time and, as a result, “long-term prediction of species abundances can be fundamentally impossible” (Benincà et al. 2008). Novel modeling approaches show promise in forecasting blooms of individual species (McGowan et al. 2017), and data syntheses (e.g., Boyd et al. 2010) and ecosystem models (e.g., Follows and Dutkiewicz 2011) have greatly advanced our knowledge of the environmental controls on and biogeographical distributions of algal functional groups across the world oceans. However, we still struggle to explain variability of phytoplankton communities at the species level.

On the other hand, notable advances have been made in recent decades to understand and even predict variability at the other level of community structure depicted in Fig. 1—the level of cell size. These advances build from the universal scaling laws of biological processes with organism size, recognized by Elton nearly a century ago who “formulated all of the principles on which the modern theory of the pelagic ecosystem is based” (Platt 1985). These scaling laws prescribe rates of processes regulating phytoplankton population variability—photosynthesis, respiration, sinking, grazing, nutrient uptake, biosynthesis, cell division—as functions of cell size (e.g., Eppley and Sloan 1966; Banse 1976; Irwin et al. 2006; Edwards et al. 2012). Five patterns explained by these
scaling laws have emerged from surveys of size structure across different oceanic domains:

Pattern 1: there is an inverse relationship between phytoplankton abundance and cell size (e.g., Irwin et al. 2006); this is a universal scaling law of biology.

Pattern 2: there is a positive relationship between mean cell size and phytoplankton biomass (e.g., Kiørboe 1993).

Pattern 3: there are size-based limits to the accumulation of biomass; small cells dominate when biomass is low, but larger cells are selectively added as biomass builds (Chisholm 1992).

Pattern 4: as a consequence of Pattern 3, blooms are dominated by large cells (e.g., Bautista and Harris 1992).

Pattern 5: as a consequence of Pattern 4, biomass variability of large cells is much higher than variability of small cells (Malone 1980).

These patterns are common features of phytoplankton community variability with important ecological and biogeochemical implications. They bring some order to the chaotic and unpredictable oscillations of individual species. They have largely emerged from surveys across ocean domains of size-fractionated chlorophyll (Malone 1971) or cell-size distributions measured by microscopy (Irigoin et al. 2004) or flow cytometry (Li 2002). Their broader generality can be tested by comparison with phytoplankton size patterns in other ecosystem types. Here, we ask if these patterns hold in high-nutrient ecosystems at the land–sea interface where phytoplankton biomass is 10–100 times greater than in the open ocean (Cloern and Jassby 2008). First, we explore patterns of cell size from a multidecadal record of phytoplankton sampling in San Francisco Bay as an example of a

Fig. 1. The range of phytoplankton (and ciliate) cell sizes measured with an Imaging FlowCytobot (http://ifcb-data.whoi.edu/about). The images are of samples collected from October 2016 to June 2017 between USGS Sta. 18 and 22 (Fig. 2). Images courtesy of the Raphael Kudela Laboratory, University of California-Santa Cruz.
nutrient enriched temperate estuary. Then we explore processes underlying those patterns using a simple size-based model.

**Methods**

**Site description**

San Francisco Bay is a site of long-term study by the U.S. Geological Survey (USGS) to understand how ecosystems at the land–sea interface respond to human activities and climate variability. The Bay system includes two connected, but different, estuary types. South Bay (Fig. 2) is a marine lagoon situated in an urban landscape. North Bay, including San Pablo and Suisun Bays, is a river-dominated estuary with primary freshwater inflow from the Sacramento and San Joaquin Rivers. The Central Bay bridges these two estuary types and is connected to the NE Pacific Ocean through the Golden Gate. This coastal ecosystem has been used to measure estuarine processes and variability in a setting influenced by urban runoff, wastewater discharge, runoff from California’s agricultural Central Valley, and exchange with shelf waters situated in an eastern boundary current upwelling system. Nutrient inputs from urban and agricultural sources have enriched this estuary with nitrogen and phosphorus, providing an opportunity to explore patterns of phytoplankton cell size where nutrient limitation of growth is rare (Cloern 1999).

**Hydrographic and water-quality measurements**

The USGS observational program includes hydrographic and water-quality measurements at sampling stations along a 150-km transect from the lower South Bay to the lower Sacramento River (Fig. 2). Vertical profiles of salinity, temperature, chlorophyll fluorescence, and photosynthetically active radiation (PAR) were made with a Seabird Electronics CTD, submersible fluorometer, and a quantum sensor. Near-surface and near-bottom water samples were collected each cruise at a subset of stations to measure chlorophyll a (Chl a).

**Fig. 2.** Map of the San Francisco Bay system showing locations of USGS sampling stations along a transect from lower South Bay (Sta. 36) to the lower Sacramento river (Sta. 657).
Table 1. Ranges and median values of water-quality measurements where phytoplankton samples were collected in San Francisco Bay from 1992 to 2017.

| Salinity | Temperature (°C) | Extinction coefficient k (m⁻¹) | Chl a (mg m⁻²) | DIN (μM) | DRP (μM) | DSi (μM) |
|----------|-----------------|--------------------------------|----------------|----------|----------|----------|
| Minimum  | 0.05            | 7.9                            | 0.3            | 0.3      | 0.1      | 0.4      | 0        |
| Median   | 24.3            | 15.8                           | 1.5            | 5.6      | 27.6     | 3        | 89.8     |
| Maximum  | 33.3            | 24.8                           | 17.1           | 157      | 197      | 28.8     | 363      |

concentration and calibrate the fluorometer. Dissolved inorganic nutrient (nitrate + nitrite, ammonium, phosphate, and silicate) concentrations were measured in 799 of the water samples where phytoplankton were analyzed. The light attenuation coefficient k (m⁻¹) was calculated as slope of the regression of ln(PAR) vs. depth (m). Daily incident PAR (Einst. m⁻² d⁻¹) was measured near the shoreline of South San Francisco Bay using a LiCor 190S quantum sensor. Detailed descriptions of methods, how they changed over time, and steps of data validation are provided by Schraga and Cloern (2017). All data are available online (Cloern and Schraga 2016).

Phytoplankton taxonomy, enumeration, and cell measurements

Samples for phytoplankton community analysis were collected at a subset of the hydrographic stations. Most-frequently sampled stations were distributed along the salinity gradients of North and South Bay: 657, 6, 13, 18, 27, 32, and 36 (Fig. 2). Near-surface water samples were preserved in acid Lugol’s solution and analyzed by light microscopy. Samples collected from 1992 through 2013 were concentrated by settling and examined with a phase-contrast inverted microscope using the method of Utermöhl (1958). Aliquots of 2–50 mL were settled in chambers for 6–24 h. Entire aliquots were examined at ×1250 magnification and all cells >30 μm diameter were enumerated. Cells smaller than 30 μm were counted at ×1250 magnification; a minimum 100 cells of the most numerous taxon were counted using the strip-count method (APHA 1989). Diatoms and dinoflagellates were identified after clearing with 30% hydrogen peroxide and mounting in Hyrax Mounting Medium. Cell volumes of dominant taxa were estimated by measuring 50–100 cells and applying the geometric formulas of Wetzel and Likens (1991). The biovolume of each taxon was computed as the product of its abundance (cells mL⁻¹) and its cell volume (μm³ cell⁻¹). These data are available online (Nejad et al. 2017).

Samples collected after 2013 were analyzed by a different laboratory using the membrane filtration technique (McNabb 1960). A target tally of minimum 400 natural units (colonies, filaments, unicells) was counted and identified to the lowest possible taxonomic level from each sample using three steps. In step 1, a minimum 100 natural units of organisms smaller than 5 μm (greatest axial linear dimension) were identified and counted from random fields at ×630 using a Leica DMLB compound microscope. In step 2, a minimum 300 natural units larger than 5 μm were identified and counted in random fields at ×630. In step 3, a transect at ×630 and half chamber scan at ×400 were examined for any large taxa missed in the random fields count. Cell biovolumes were estimated from measurements of 10 individuals per taxon in each sample, where possible.

Mean cell volume (μm³ cell⁻¹) was computed for each sample as total cell biovolume (μm³ mL⁻¹) divided by total cell abundance (cells mL⁻¹). Mean cell size (μm) was computed as the equivalent spherical diameter (ESD) of mean cell volume, and analyses that follow used log transformation of ESD because phytoplankton cell size follows a lognormal distribution (Acevedo-Trejos et al. 2015). Although microscopic procedures changed after 2013, the statistical relationships between mean cell size and sample biovolume (see below) did not differ between methods, so the pre- and post-2013 samples were pooled.

Data analyses

All analyses were done in the R environment (R Development Core Team 2012). Generalized additive models (GAMs) were used to explore patterns of cell-size variability, using the R package mgcv (Wood 2006).

Results

San Francisco Bay as a high-nutrient estuary

Phytoplankton samples analyzed here were collected across the salinity gradient of a temperate, turbid, high-nutrient estuary that supports blooms reaching biomass >100 mg Chl a m⁻³ (Table 1). Salinity in waters sampled for phytoplankton ranged from 0.05 to 33.3, but the median salinity (24.3) indicates that the data set is mostly representative of estuarine waters having a larger proportion of seawater than freshwater. The median light extinction coefficient k was 1.5 m⁻¹, corresponding to a photic depth (1% surface irradiance) of 3 m. This turbidity is primarily associated with river-derived fine-grained sediments suspended by wind waves and tidal currents (May et al. 2003). The median concentrations of dissolved inorganic nitrogen (DIN), dissolved reactive phosphorus (DRP), and dissolved silica (DSi) all greatly exceeded the half saturation constants for phytoplankton growth (Table 1). High

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turbidity and nutrient concentrations create an environment where phytoplankton growth and photosynthesis are usually limited by light (Cloern 1999). The largest phytoplankton blooms developed in South Bay during spring, often triggered by salinity stratification following inputs of freshwater during the wet season (Cloern 1996). Concentrations of dissolved inorganic N, P, and Si were depleted by uptake during years of exceptionally large blooms. These wide ranges of factors that regulate phytoplankton growth and community composition provide an opportunity to learn how the growth environment might also regulate cell size along the salinity gradient of estuaries.

The phytoplankton community

A total of 1214 phytoplankton samples were collected from 01 April 1992 to 18 April 2017 and analyzed by light microscopy. The data record includes 24,850 measurements of abundance and cell size of 986 taxa, including heterotrophic dinoflagellates. Most taxa occurred rarely—the median number of occurrences was only 4, and 248 taxa were observed only once. The community was composed primarily of a small number of frequently-occurring taxa, mostly diatoms, dinoflagellates, and cryptophytes (Table 2). Heterotrophic dinoflagellates were an important component of the community, contributing a mean 9% of cell biovolume. The most-frequently occurring heterotrophic taxa included Phalacroma oxytoxoides, Miniscula bipes, Gyrodinium spirale, Noctiluca scintillans, Protoperidinium spp., and Polykrikos schwartzii. These forms are large, with mean ESD of 33.5 μm. They were removed from the data record to assess cell-size attributes of the pigmented, auto- and mixo-trophic phytoplankton.

Patterns of phytoplankton cell size in San Francisco Bay

**Pattern 1: Cell size and abundance**

Measured volumes of 23,862 phototrophic phytoplankton cells ranged from 1 μm³ to 5.9 × 10⁶ μm³ (Fig. 3A), and they followed the universal pattern of decreasing cell density as cell size increases. Wide variability around this pattern reflects, in part, the large errors inherent in measuring cell abundances and estimating their biovolume by microscopy.

**Pattern 2: Mean cell size and biomass**

The total cell biovolume in individual samples ranged from 660 μm³ mL⁻¹ to 3.1 × 10⁶ μm³ mL⁻¹, and cell densities ranged from 3 cells mL⁻¹ to 1.1 × 10⁶ cells mL⁻¹. This translates into ranges of sample-mean cell volumes between 1.5 μm³ and 9.7 × 10⁴ μm³, and sample-mean ESD between 1.4 μm and 57.0 μm. A GAM of log-transformed ESD against log-transformed sample biovolume was highly significant (p < 2 × 10⁻¹⁶), and it explained 39% of the deviance in sample-mean cell size (Fig. 3B). Similar GAM’s showed that environmental factors summarized in Table 1 explained less than 10% of cell-size deviance: salinity, temperature, light extinction coefficient, DIN, and DRP concentrations. Therefore, variability of sample-mean cell size in this estuary

| Taxonomic identification | Number of occurrences |
|--------------------------|-----------------------|
| Teleaulax amphioxeia     | 626                   |
| Thalassiosira spp.       | 620                   |
|Skeletonema costatum     | 589                   |
| Paralia sulcata         | 524                   |
| Thalassiosira eccentrica| 503                   |
| Plagioselmis prolunga var. nordica | 466 |
| Cyclotella atomus        | 457                   |
| Actinoptychus senarius  | 441                   |
| Plagioselmis prolunga   | 392                   |
| Ceratonemis closterium  | 381                   |
| Nitzschia spp.          | 359                   |
| Nannochloropsis spp.    | 349                   |
| Hemiselmis sp.          | 327                   |
| Heterocapsa triquetra   | 318                   |
| Thalassiosira hendeyi   | 317                   |
| Cyclotella striata      | 304                   |
| Heterocapsa rotundata   | 298                   |
| Thalassiosira angulata  | 269                   |
| Nannochloris spp.       | 253                   |
| Cyclotella choctawhatcheana | 251 |
| Cyclotella sp.          | 243                   |
| Pyramimonas spp.        | 237                   |
| M. rubrum               | 233                   |
| Thalassionema nitzschioides | 225 |
| Thalassiosira visurgis  | 221                   |
| Ditylum brightwellii    | 213                   |
| Rhodomonas salina       | 205                   |
| Thalassiosira punctigera| 200                   |
| Prorocentrum cordatum   | 189                   |
| Pleurosigma strigosa    | 188                   |
| Eutrepia lanwii         | 180                   |
| Pseudocurculfieldia marina | 173          |
| Komma caudata           | 172                   |
| Rhizosolenia setigera   | 170                   |
| Plagioselmis nanoplanctica | 167               |
| Navicula spp.           | 165                   |
| P. oxytoxoides          | 164                   |
| Chaetoceros subtilis    | 152                   |
| Cyclotella meneghiniana | 148                   |
| Teleaulax sp.           | 148                   |
| Gyrosigma fasciola      | 139                   |
| Pyramimonas plurioculata| 138                   |
| Teleaulax acuta         | 138                   |
| Thalassiosira rotula    | 135                   |
| Gymnodinium sp.         | 134                   |
| Nitzschia longissima    | 129                   |
| Thalassionema sp.       | 126                   |
| Cryptomonas sp.         | 122                   |
| M. bipes               | 122                   |

**Table 2.** The 50 most frequently occurring phytoplankton taxa in 1214 samples collected in San Francisco Bay from 1992 to 2017.
appears to be more strongly tied to variability of phytoplankton biovolume than it is to variability of factors that regulate growth and community composition.

Diatoms were the dominant component of phytoplankton in San Francisco Bay, as they are in other nutrient-rich estuaries (Carstensen et al. 2015). They contributed 80% of the summed biovolume in all samples (Fig. 3C). Cryptophytes contributed 6.1%, phototrophic dinoflagellates 5.2%, the phototrophic ciliate *Myrionecta rubrum* 3.8%, and chlorophytes 3.6%.

**Pattern 3: Limits on biomass accumulation of small cells**

To explore this pattern, I binned the phytoplankton into five size classes based on the distribution of all cell-size measurements (Fig. 4). Quintiles of the distribution identified size-class breaks at ESD of 5.26 μm (20th percentile), 7.90 μm, 11.71 μm, and 20.97 μm (80th percentile). Table 3 lists mean cell size of the 10 most important taxa in each size class. Cells in the largest size class contributed 67% of the summed biovolume in all samples; cells in the three intermediate sizes each contributed about 10%; and cells in the smallest size class contributed only 2.4% (Fig. 3D). Therefore, small cells (ESD < 5.26 μm) are a minor phytoplankton component in San Francisco Bay. This conclusion could result from bias inherent to light microscopy, an inappropriate method for counting micron-size cells. However, in an earlier study, we used an epifluorescent microscope to analyze formaldehyde-preserved samples collected onto 0.2-μm polycarbonate filters. Results showed that picocyanobacteria (*Synechococcus* sp.) were widespread, reached maximum densities of $5 \times 10^5$ cells mL$^{-1}$, contributed up to 15% of Chl $a$ during non-bloom conditions, but only 2% during the spring bloom (Ning et al. 2000). A recent 4-yr study of algal pigments in San Francisco Bay showed that cyanobacteria contributed, on average, 4% of Chl $a$ (Peacock et al. unpubl.). Finally, Chisholm (1992) noted that the maximum potential biomass of pico-plankton is about 0.5 mg Chl $a$ m$^{-3}$, less than 10% of the median Chl $a$ in samples analyzed here (Table 1). Therefore, although methods used here underestimate the contribution of picoplankton, independent analyses show that the error is

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**Fig. 3.** Five patterns of phytoplankton cell size in San Francisco Bay: (A) decreasing cell size with increasing cell density in 23,862 microscopic measurements; (B) increasing mean cell size (ESD) with increasing biovolume in 1214 samples; and comparisons across five phytoplankton size classes of their (D) mean biovolume, (E) ratio of median biovolume in bloom samples to median biovolume in non-bloom samples, and (F) standard deviation of biovolume in 1214 samples. Panel (C) shows the relative contributions of the five most important phytoplankton groups to summed biovolume in all 1214 samples.
small relative to the 28-fold ratio of biovolume in the largest to smallest size class in this estuary (Fig. 3D).

**Pattern 4: Blooms dominated by large cells**

The overall biomass dominance of large cells (Fig. 3D), their high variability (Fig. 3F), and the positive relationship between mean cell size and sample biovolume (Fig. 3B), suggest that large cells play important roles in bloom dynamics. To test this hypothesis, I defined bloom samples as those having total biovolume above the 90th percentile, and then compared the median biovolumes in bloom and non-bloom samples for each size class. Median biovolume of each size class was higher during blooms than non-blooms. However, the magnitude of biovolume amplification during blooms differed among the size classes, ranging from 1.6 for the smallest size class to 59 for the largest size class (Fig. 3E). Therefore, blooms are events of highly elevated biovolume of large cells, but not the smaller cells.

**Pattern 5: Biomass variance highest in the large-cell component**

The standard deviation of biovolume also increased with cell size (Fig. 3F), and it was nearly 60-fold higher in the largest size class ($1.1 \times 10^5$) than in the smallest size class ($2.0 \times 10^3$). Therefore, based on the metric of biovolume, the San Francisco Bay phytoplankton community is dominated by large cells—those traditionally labeled “microplankton.” The large-cell component was highly variable, while the smaller-cell components were comparatively stable over time.

The pattern of large cells becoming increasingly dominant as biomass builds has been observed elsewhere in other ways, such as measures of size-fractionated Chl a along biomass gradients (Raimbault et al. 1988). This pattern reveals limits on the biomass accumulation of phytoplankton that are based on cell size. As blooms develop: population growth of the smallest cells (picoplankton) reaches a plateau at low biomass; growth of intermediate size cells (nanoplankton) continues and reaches a higher plateau; biomass of the largest cells (microplankton) continues to build toward a higher peak that is ultimately set by the nutrient supply (Chisholm 1992). This pattern of nutrient- and size-based limits on biomass accumulation is a fundamental feature of phytoplankton ecology. It is central to our understanding of why picoplankton dominate in subtropical ocean gyres (Ward et al. 2012), while microplankton (diatoms in particular) dominate in nutrient-rich coastal waters (Moisan et al. 2017), upwelling systems (Dugdale and Wilkerson 1998), and estuaries (Carstensen et al. 2015). It also underlies three patterns of phytoplankton cell size in San Francisco Bay: (1) mean size increases as biovolume increases (Fig. 3B); (2) mean cell size is large because biovolume is composed mostly of large cells (Fig. 3D); (3) variability of biovolume is mostly attributed to variability of the largest cells (Fig. 3F). These patterns all arise from the selective accumulation of large cells during blooms (Fig. 3E).

How, then, is the biomass growth of phytoplankton limited by cell size? A rich literature addresses this question, and the answers are often tied to: nutrient supply; size-based traits that determine the balance between phytoplankton population growth and mortality, grazing in particular; and temperature regulation of those traits. Next, I describe a simple model that integrates these regulating factors and

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**Fig. 4.** Frequency distribution of 23,862 cell-size measurements as ln(ESD). Vertical lines break the distribution into quintiles used to partition the phytoplankton into five size classes, from smallest (ESD < 5.26 μm) to largest (ESD > 20.97 μm).
reproduces the patterns of cell size observed in San Francisco Bay. Model results provide insights about the selective accumulation of large cells during blooms in this, and other high-nutrient estuaries. While oceanographers have asked “why are the oligotrophic oceans dominated by picoplankton?” (Chisholm 1992), here we ask the complementary question of why estuaries are dominated by large cells.

An explanatory model

Model description

I used a size-structured NPZ (nutrient, phytoplankton, zooplankton) model to search for processes underlying the patterns of phytoplankton size distribution described above (Fig. 3). The model is a variation of that developed by Poulin and Franks (2010) and Taniguchi et al. (2014), tailored to the phytoplankton community and environmental conditions of San Francisco Bay. Its key features are simple representation of a pelagic food web, and rates of phytoplankton growth and grazing that follow empirically-derived functions of producer and consumer size. The phytoplankton component included five size classes, P₁–P₅, based on size distributions in San Francisco Bay (Fig. 4). The zooplankton component included five size classes Z₁–Z₅, where size of consumers was defined as the largest cell size in the corresponding phytoplankton class (Table 4). Zooplankton were treated as herbivores, and their consumption was restricted to feeding only from their corresponding phytoplankton size class—i.e., model version 1 of Taniguchi et al. (2014).

The model includes a set of 11 ordinary differential equations describing rates of phytoplankton (P) and zooplankton (Z) population growth, and uptake and regeneration of

Table 3. The 10 most important phytoplankton species in San Francisco Bay within each of five size classes. Species within each class are ordered by their cumulative biovolume in all samples, beginning with the highest. Mean cell size (ESD) is the average cell size for each species across all samples where it occurred. Some species were grouped into two size classes, reflecting variability of size within species.

| Size class 1 | ESD (µm) | Size class 2 | ESD (µm) | Size class 3 | ESD (µm) |
|--------------|----------|--------------|----------|--------------|----------|
| Thalassiosira spp. | 4.0 | S. costatum | 6.7 | P. sulcata | 10.1 |
| Nannochloropsis spp. | 1.6 | C. subtilis | 6.7 | T. amphioxeia | 9.1 |
| Hemiselmis sp. | 3.4 | C. chloactawhatcheena | 7.0 | Myrionecta rubrum | 10.0 |
| Nannochloris spp. | 2.0 | Plagioselmis prolunga var. nordica | 6.5 | Chaetoceros gracilis | 9.9 |
| P. marina | 3.6 | R. salina | 5.8 | Alexandrium tamarense | 10.7 |
| S. costatum | 4.2 | Nitzschia supralitorea | 7.3 | Melosira nummuloides | 10.2 |
| P. prolunga | 4.2 | P. prolunga | 6.1 | S. costatum | 9.4 |
| P. plurioculata | 3.9 | T. amphioxeia | 7.2 | N. longissima | 9.4 |
| Nitzschia spp. | 4.5 | C. closterium | 6.7 | C. atomus | 9.3 |
| C. atomus | 4.6 | K. caudata | 6.1 | T. nitzschioides | 9.9 |

| Size class 4 | ESD (µm) | Size class 5 | ESD (µm) |
|--------------|----------|--------------|----------|
| Aulacoseira granulata | 14.9 | D. brightwellii | 68.2 |
| Cyclotella sp. | 14.3 | T. eccentrica | 37.0 |
| H. triquetra | 15.9 | T. punctigera | 62.6 |
| Closteriopsis sp. | 15.8 | T. rotula | 31.3 |
| Thalassiosira spp. | 15.5 | P. strigosum | 27.2 |
| P. sulcata | 13.8 | T. hendeyi | 50.5 |
| A. senarius | 16.6 | M. rubrum | 29.4 |
| T. angulata | 15.5 | R. setigera | 30.0 |
| P. cordatum | 15.7 | T. visurgis | 26.1 |
| C. striata | 15.3 | A. tamarense | 25.9 |

Table 4. Sizes of five phytoplankton and zooplankton size classes, and parameter values for each used in the NPZ model.

| Phytoplankton | P₁ | P₂ | P₃ | P₄ | P₅ |
|---------------|----|----|----|----|----|
| Mean ESD (µm) | 3.48 | 6.52 | 9.64 | 15.54 | 39.41 |
| Q₁₀ | 1.62 | 1.62 | 1.62 | 1.62 | 1.62 |
| µmax at 20°C (d⁻¹) | 1.11 | 1.01 | 0.95 | 0.88 | 0.76 |
| ks (µM N) | 0.60 | 0.81 | 1.09 | 1.23 | 1.92 |

| Zooplankton | Z₁ | Z₂ | Z₃ | Z₄ | Z₅ |
|-------------|----|----|----|----|----|
| Size (µm) | 5.26 | 7.90 | 11.71 | 20.97 | 224 |
| Q₁₀ | 2.48 | 2.48 | 2.48 | 2.48 | 2.48 |
| gmax at 20°C (d⁻¹) | 11.37 | 8.68 | 6.69 | 4.56 | 0.95 |
| kz (µM N) | 6.20 | 4.77 | 3.71 | 2.56 | 0.56 |
nitrates measured in San Francisco Bay of about 0.5 mg m$^{-2}$.

Equation 1 defines the rate of phytoplankton population change as the balance between rates of growth and grazing. Growth rate is determined by temperature-regulated maximum growth rate $\mu_0$, light availability $I$, and nutrient limitation described as a Michaelis-Menten function with size-dependent half saturation constant $k_s$ (Table 4). Maximum growth rate was computed as a function of the size-dependent maximum growth rate $\mu_{\text{max}}$ at 20°C (Table 4) and temperature $T$ (°C), using a $Q_{10}$ of 1.62 (Taniguchi et al. 2014):

$$\mu_i = \mu_{\text{max}} \cdot 1.62^{(T-20)/10}$$  \hspace{1cm} (4)

Light limitation $I$ was computed as a linear function of $E$, the depth-averaged photosynthetically available radiation, using a scaling factor $le$ of 0.128. This approach was based on the linear relationship between photosynthetic efficiency (daily carbon fixed per unit Chl a) and water-column mean irradiance determined from 14C assays in San Francisco Bay (Supporting Information Fig. 5, Cloern et al. 2007). $E$ was computed from incident PAR (Einst. m$^{-2}$ d$^{-1}$), the light attenuation coefficient $k$ (m$^{-1}$), and water depth $H$, fixed at 10 m:

$$I = leE = le \text{PAR}/(KH)$$  \hspace{1cm} (5)

Grazing rate was computed as a Michaelis-Menten formulation of phytoplankton biomass, with size-dependent half saturation constant $k_z$ (Table 4). The biomass-specific zooplankton grazing rate $g_i$ (d$^{-1}$) was computed as a function of size- and temperature-dependent maximum grazing rate $g_{\text{max}}$ at 20°C (Table 4), using a $Q_{10}$ of 2.48 (Taniguchi et al. 2014):

$$g_i = g_{\text{max}} \cdot 2.48^{(T-20)/10}$$  \hspace{1cm} (6)

I modified the grazing equation from the original approach of Taniguchi et al. (2014) by prescribing a low phytoplankton biomass $pm$ (= 0.1 μM N) at which grazing was set to zero. This allowed a minimum phytoplankton biomass in the simulations comparable to the minimum Chl a concentrations measured in San Francisco Bay of about 0.5 mg m$^{-3}$.

Equation 2 defines the rate of zooplankton change as the balance between rates of production (food assimilation) and mortality $m_z$. Food assimilation was computed as grazing rate multiplied by growth efficiency $ge$, set at 0.32 (Taniguchi et al. 2014). NPFZ models, including this one, are sensitive to specifications of zooplankton mortality that constrain the rate of biomass growth at the upper trophic level. I selected a value $m_z = 0.06$ d$^{-1}$ because this yielded simulations where the mean biomass fraction of the largest phytoplankton size class (0.69) matched that in the observational data (0.67).

Equation 3 defines the rate of change of DIN concentration (N) as the balance between rates of phytoplankton assimilation (production) and recycling by zooplankton metabolism [(1 - $ge$) × consumption] and mortality. These equations describe a vertically mixed and closed system where total nitrogen $N_T$ is constant.

Central to this model are four allometric equations that prescribe growth and grazing parameters as power functions of cell size $S$ (ESD, μm). These are built from a comprehensive compilation of published experimental measurements (Taniguchi et al. 2014):

$$\mu_{\text{max}} \text{ at } 20^\circC (\text{d}^{-1}) = 1.36 \cdot S^{-0.16} \hspace{1cm} (7)$$

$$k_s (\mu M \text{ N}) = 0.33 \cdot S^{0.48} \hspace{1cm} (8)$$

$$g_{\text{max}} \text{ at } 20^\circC (\text{d}^{-1}) = 33.96 \cdot S^{-0.66} \hspace{1cm} (9)$$

$$k_z (\mu M \text{ N}) = 17.92 \cdot S^{-0.64} \hspace{1cm} (10)$$

The model does not include explicit treatment of N recycling, phytoplankton mortality other than grazing, zooplankton omnivory, or other processes included in more comprehensive and realistic models of pelagic ecosystems (e.g., Ward et al. 2012). The goal here was simple representation of size- and temperature-dependent growth and grazing to search for mechanisms underlying the cell-size patterns observed in San Francisco Bay and other estuaries.

Model implementation

The model equations were solved as an initial value problem using the R package deSolve (Soetaert et al. 2010). Initial values were: $N = 48$ μM (the 1992–2015 January mean DIN concentration in San Francisco Bay); $P_i (= 0.1 \mu M \text{ N})$ and $Z_i (= 0.01 \mu M \text{ N})$ for all size classes $i$. The model was run for the period 1998–2001, using as forcings daily estimates of water temperature and light attenuation coefficient $k$ interpolated from monthly or semimonthly measurements across the USGS sampling network in San Francisco Bay, and daily incident PAR measured in South Bay. Year 1 was used to spin up the model; its ending values were used as initial values for the following 3 yr that were used to extract patterns of cell-size variability. This particular set of differential equations, parameters and forcings appears to be a stiff numerical problem because most of the solvers in the deSolve package did not complete the integrations. I used solver rk45dp6 from the Runge-Kutta family because it integrated the equations to completion and did not yield negative biomass values.
Model results

Results of the 3-yr simulation are shown in Fig. 5, including daily forcings of water temperature and mean irradiance in the water column $E$, computed N concentrations, and biomass of three phytoplankton and zooplankton size classes. Variability of the smaller size classes was characterized by low-amplitude oscillations around small (< 1 $\mu$m N) mean biomass. Biomass of the largest phytoplankton size class $P_5$ peaked during blooms in spring that varied in magnitude across years, depleted the N pool, and were followed by peaks in large zooplankton biomass $Z_5$. These model results are generally representative of seasonal patterns in the saline regions of San Francisco Bay that have spring blooms of large cells and N depletion as the pool of DIN is assimilated into phytoplankton biomass (Cloern 1996). The simulation of daily biomass contained four general patterns of cell size seen in the observational record.

First, mean cell size increased with biomass (Fig. 6A). Here, mean size was computed as the biomass-weighted mean of the five cell sizes $P_1$–$P_5$. Hence, mean size, unlike that in the data (Fig. 3B), is constrained to a maximum of 39.4 $\mu$m—the size of the largest class $P_5$. Most (69%) of the biomass was in the largest size class $P_5$, and the four smaller size classes each contributed about 8% of biomass (Fig. 6B). Biomass of the largest size class was highly variable, but biomass of the smaller size classes was stable (Fig. 6C). Finally, large cells dominated biomass of modeled blooms (Fig. 6D). I defined blooms as events where total phytoplankton biomass exceeded the 90th percentile, and then compared the median biomass in bloom and non-bloom periods for each size class. Median biomass of size classes $P_1$–$P_4$ was not significantly elevated during blooms. However, median biomass in the $P_5$ size class was 70 times higher during blooms compared to non-bloom periods (Fig. 6D). Thus, in the model results, as in the observational data, blooms were events of selective growth and highly amplified biomass of large cells.
The model outputs provide an explanation of why small-cell biomass was stable and low, while large-cell biomass was variable and dominated blooms and overall biomass. Phytoplankton growth rates, computed from cell size and daily temperature, irradiance and N concentration (Eq. 1), ranged from $0.002 \text{ d}^{-1}$ to $0.22 \text{ d}^{-1}$ (Fig. 7A). The mean and range of growth rates decreased monotonically with increasing cell size, following the allometric laws incorporated into the model (Eq. 4). However, grazing rates also decreased monotonically with increasing size (Eq. 6) and, as a result, there was no difference in mean net growth (growth–grazing) rates across size classes (Fig. 7B). Populations grow at the net growth rate, so it’s not obvious why large, but not small, cells developed blooms if they had no difference in mean net growth rate. Large cells had boom-bust cycles between periods of high positive and negative production (Fig. 7C). Smaller cells did not have these boom-bust cycles, and their daily production was always low. The key to this paradox appears to be not in the mean of the net growth rate, but in its pattern of variability over time (Fig. 5, bottom). The largest cells had continuous runs of positive net growth rate sustained long enough each spring for their biomass to reach bloom levels (Fig. 5). Net growth rates of the smaller phytoplankton had high-frequency oscillations between net positive and negative growth rate, so uninterrupted exponential growth was not sustained long enough for biomass to build (Fig. 5, bottom).

These results suggest that the essential difference between large and small cells is the duration of periods when their net growth rate is positive—short for small cells, and long for large cells. This difference reflects size effects on the strength of coupling between producers and their consumers. Small consumers grow fast, so their populations track phytoplankton variability closely. This tight coupling between small producers and consumers has been described as a process that “kills the winner” (Thingstad 1998). Large zooplankton grow more slowly, so their populations have lagged responses to phytoplankton variability (Fig. 5). These lags create opportunities for large cells to “escape predation” (Kiørboe 1993) and sustain biomass growth long enough for blooms to develop. These blooms continue until either the DIN pool is depleted, or the large grazers catch up (Fig. 5).
**Broader implications and future directions**

Although the model used here is a highly simplified representation of diverse and complex communities and trophic linkages (e.g., D’Alelio et al. 2014), it apparently captures key processes through which temperature, nutrients, and plankton size shape these communities. This might reflect two things. First, organisms “must obey basic thermodynamic laws” (Platt 1985). As a result, phytoplankton growth and zooplankton grazing rates follow power functions of size (Eqs. 4, 6) and exponential functions of temperature (Eqs. 7, 9). Second, these functions are grounded in a rich history of experimental measurements that have recently been compiled and synthesized by Taniguchi et al. (2014), building from earlier compilations (e.g., Edwards et al. 2012; Hansen et al. 1997). These scaling laws of size and temperature effects provide a framework for understanding how phytoplankton communities can be shaped by grazing, nutrient supply, and temperature. I used three simple model experiments to illustrate.

**Grazing**

To illustrate the role of size-based grazing, I set grazing rates to zero in the model and compared results against the original base simulation described above. In the zero-grazing case, the N pool was completely assimilated into phytoplankton biomass that reached steady state. The biomass in each size class decreased with increasing cell size—i.e., the inverse pattern of the base simulation when grazing was included (Fig. 8A,B). Mean phytoplankton biomass in the zero-grazing case was 48.5 \( \mu \text{M N} \) compared to 3.7 \( \mu \text{M N} \) in the base case. This example shows that, in the absence of grazing, small cells would rule everywhere, including high-nutrient ecosystems, simply because small cells divide faster than large cells (Eq. 7). In the presence of grazers, large cells gain an advantage through the lagged growth and grazing of their large consumers. This example also is a reminder of the importance of top-down processes on both phytoplankton biomass and size distribution. Even perfect understanding of factors that regulate phytoplankton cell-division rate will not explain community dynamics that are driven by the balance between growth and consumption. Both rates are of equal importance, and both vary systematically with size (e.g., Ward et al. 2012).

**Nutrients**

The ecological and biogeochemical implications of nutrient supply are well established in the ocean, where oligotrophic domains are small-cell recycling systems dominated by the microbial loop, and high-nutrient domains support new production of large cells (e.g., Finkel et al. 2010; Ward et al. 2012). The oceanic patterns suggest that large cells should dominate in coastal ecosystems receiving anthropogenic nutrient inputs, such as estuaries. I used the model to simulate phytoplankton biomass and size structure in San Francisco Bay in an oligotrophic state by reducing the initial N stock from 48 \( \mu \text{M} \) to 1 \( \mu \text{M} \). In this case, mean phytoplankton biomass was only 1 \( \mu \text{M N} \), the largest cells contributed only 7% of biomass, while the four smaller size classes each contributed 21–28% of biomass (Fig. 8C). Nutrient stocks, then,
set the upper limit to which large-cell biomass can build. That limit is high enough in nutrient-rich estuaries like San Francisco Bay to support high-biomass blooms of large cells. Therefore, a consequence of anthropogenic nutrient enrichment, in addition to biomass increase, could be increased phytoplankton cell size. A recent meta-analysis showed that blooms in marine ecosystems receiving nutrient inputs from land are now dominated by large cells and, in particular, diatoms (Carstensen et al. 2015). This may not have always been the case. Spring blooms in today’s Chesapeake Bay are dominated by large cells including diatoms *Cerataulina pelagica* and *Rhizosolenia* spp. (Harding et al. 2016). However, the sediment record does not indicate these large forms were prevalent before the era of nutrient enrichment (Cooper and Brush 1991).

Reconstruction of diatom shifts in sediment records from other estuaries could be a powerful approach for testing the hypothesis that humans have altered phytoplankton size structure through nutrient enrichment. If this hypothesis is true, it has broad ramifications for estuarine-coastal ecosystems and their biological communities. The increase of both diatom production and cell size would increase sedimentation of organic matter and benthic metabolism that drives summer anoxia in Chesapeake Bay (Harding et al. 2016) and other estuaries. Diatoms and dinoflagellates are highly nutritious food resources because they are enriched in essential fatty acids, so another ecological outcome of increased large-cell production could be increased food quality for consumers such as copepods, bivalves, and fish (Winder et al. 2017). Some large forms produce toxins, and those of concern in San Francisco Bay include *Alexandrium* spp., *Karenia mikimotoi*, *Dinophysis* spp., and *Pseudo-nitzschia* spp. If nutrient enrichment selectively increases large-cell production, then reductions of nutrient loading might be a strategy for decreasing the probability of toxin-producing diatom and dinoflagellate blooms (Sutula et al. 2017).

**Temperature**

Observed and modeled blooms of large cells developed in San Francisco Bay during spring, when water temperature was around 15°C (Fig. 9A). The $Q_{10}$ of zooplankton grazing (2.48) is larger than the $Q_{10}$ of phytoplankton growth (1.62), so as seasonal warming progresses grazing rate accelerates faster than growth rate of large cells. For the largest size class $P_5$, the difference between maximum growth rate and maximum grazing rate shifts from positive to negative at 15°C (Fig. 9B), and the runs of positive net growth required for blooms (Fig. 5) shorten. Therefore, temperature above 15°C might be a general threshold beyond which large-cell blooms become less probable because of the differential

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**Fig. 8.** Comparison of three model experiments against (A) the base simulation for San Francisco Bay shown in Fig. 6. Results of each experiment are shown as percent of biomass produced in each phytoplankton size class when: (B) grazing was set to zero; (C) initial N concentration was reduced from 48 μM to 1 μM; (D) temperature was increased by 5°C.
responses of growth and grazing to temperature. To explore this hypothesis, I ran the model as before, but with temperature elevated by 5°C. In this warmer case, maximum grazing rate of the large zooplankton was almost always higher than maximum growth rate of the large phytoplankton (see Fig. 8B). In this warmer case, maximum growth rate of the large phytoplankton was almost always higher than maximum growth rate of the large phytoplankton (see Fig. 8B). Therefore, the hypothesized eutrophication response of increased cell size might be confined to mid and high-latitudes where temperature falls below 15°C.

The decrease of net growth rate with temperature (Fig. 9B) is a scaling law that has not received much attention (but see Chen et al. 2012). It implies that large cells lose their advantage of escaping predation as temperature increases, either seasonally (Fig. 9A), through climate warming, or along latitudinal gradients. An iconic example of change over time was loss of the winter-spring diatom bloom in Narragansett Bay during a warming era. This led to decreased primary production, decreased sedimentation of organic matter, slower benthic metabolism, and a shift in the bay sediments from being a net sink to a net source of nitrogen (Nixon et al. 2009). This scaling law also implies that small cells should rule at lower latitudes, even where nutrient concentrations are high (Fig. 8B). This expectation has not been rigorously tested, but small-cell blooms have been observed in nutrient-rich tropical or subtropical ecosystems such as the Ciénaga Grande de Santa Marta, Colombia (Gocke et al. 2003) and lagoons along Florida’s Atlantic coast (Phlips et al. 2015). Comparative analyses of phytoplankton cell size and grazing rates along latitudinal gradients would be one approach for testing the hypotheses that 15°C is a critical temperature for development of large-cell blooms, and that nutrient enrichment increases cell size only in climates where temperature falls below that threshold.

Rules and rule breakers

The patterns described here are those we would expect if phytoplankton communities were shaped only by the scaling laws of size- and temperature-dependent growth and grazing. However, there is substantial variability around the general patterns that represent exceptions to the rules. Twenty-five years ago, Sallie Chisholm explained: “The simplicity of the general relationships serves as a stable backdrop against which the exceptions can shine. By understanding the forces that have driven the design of these exceptions, we can begin to understand the ecology that has shaped past and present planktonic ecosystems” (Chisholm 1992). In the intervening years, we have accumulated, and learned from, many examples of exceptions to the rules.

The model used here was designed specifically to explore effects of size-based relationships. There are no realistic conditions under which this model can simulate high-biomass blooms of small cells. However, there are many well-documented cases of, sometimes spectacular, small-cell blooms. Examples include the regular surface accumulations of *Nodularia spumigena* across the Baltic Sea during summer (Kahru and Elmgren 2014), an 8-yr bloom of *Aureoumbra lagunensis* in Laguna Madre U.S. (Buskey et al. 2001), green tides of picocyanobacteria and small chlorophytes in Florida lagoons (Phlips et al. 2015), and an expansive bloom of *Chrysochromulina polylepis* that caused fish kills in Scandinavian coastal waters (Maestrini and Graneli 1991). Each of these events was facilitated by traits unrelated to cell size that allowed these species to break the size-based rules. *N. spumigena* fixes nitrogen and escapes predation through its buoyancy and chain formation. The spectacular bloom of *A. lagunensis* in Laguna Madre was facilitated by this species’ tolerance of hypersalinity and its production of extracellular polymeric substances that inhibit growth and grazing of protozoans (Buskey et al. 2001). Blooms of picocyanobacteria and small eukaryotes in Banana River Lagoon were

![Fig. 9.](image-url)
facilitated by the capability of these taxa to utilize dissolved organic N and P (Philips et al. 2015). *C. polylepis* can reach bloom densities because it produces toxins that inhibit growth of competitors and repel grazers. These traits are examples of what Thingstad (1998) described as strategies “to escape from the limitations imposed by the mechanisms of the size-structured model.”

**Large cells in the Anthropocene**

We now have a solid theoretical and empirical foundation for understanding how phytoplankton communities can be structured by size- and temperature-dependent rates of growth, nutrient uptake, and grazing. That foundation includes many experiments and observations showing that small cells dominate in low-nutrient environments (Fig. 10) because of their high uptake efficiency. Large cells can only dominate in the quadrant of low temperature and high nutrient concentrations (Fig. 10), and the model used here suggests that “low” means temperature less than about 15°C (Fig. 8). Small cells dominate at high temperatures (Fig. 10), partly because large cells lose their advantage of predation escape when temperature exceeds about 15°C.

We have also accumulated enough evidence to know that phytoplankton production in estuarine-coastal ecosystems at mid-high latitudes is dominated by large cells, primarily diatoms, and secondarily dinoflagellates (Carstensen et al. 2015). These ecosystems function as analogs to coastal upwelling systems that receive inputs of “new” nutrients, either from the deep ocean or from land. Those nutrients are transformed into large-cell biomass that sustains high rates of primary production, and is routed efficiently to higher-level consumers through short food chains. Large-cell biomass includes biochemicals essential to animals, so is of high nutritional quality. As a result, the efficiency of fish production is higher in estuaries and upwelling systems than in other aquatic ecosystems (Nixon 1988; Brett and Müller-Navarra 1997). A framework developed from basic scaling laws (Fig. 10) identifies conditions shared by upwelling systems and estuaries that select for large-cell production: high nutrients that raise the limit to which biomass can accumulate, and seasonal temperatures cool enough to slow grazing by large-cell consumers.

The contemporary state of diatom dominance may, or may not, be a characteristic feature of estuaries, but the requirement for high nutrients (Fig. 10) suggests that anthropogenic nutrient enrichment is one factor that has contributed to this state. Riverine inputs of reactive nitrogen to coastal areas increased globally from 27 Tg to 47.8 Tg between 1860 and the mid-1990s (Galloway et al. 2004), but there are no observational baselines of phytoplankton communities for detecting changes in large-cell biomass during this enrichment era. Perhaps the only approach for testing this hypothesis is by measuring changes in diatom size recorded in sediment cores, following Cooper and Brush (1991). The world population is growing, N loading to rivers is projected to reach 63 Tg by 2050 (Galloway et al. 2004), and we might anticipate growing dominance of large cells where N loadings are increasing most rapidly. Testing this hypothesis will require repeated observations of phytoplankton communities and nutrient concentrations sustained over the upcoming decades across a range of ecosystem types at the land–sea interface.

Although there is compelling evidence that estuarine-coastal phytoplankton communities respond to climate variability, including multi-decadal temperature trends (e.g., Kahru and Elmgren 2014), we cannot say with certainty that global warming of recent decades has led to the decreased importance of large cells expected from the patterns in Fig. 10. However, projected increases of global temperature are large enough—up to +3°C by 2050 (Swain and Hayhoe 2015)—that we can hypothesize a constriction of the latitudes where large-cells dominate in estuaries. Testing this hypothesis will require repeated observations at a network of coastal sites spaced between tropical and polar latitudes. The simulation result of a temperature threshold for large-cell blooms (Fig. 10) is intriguing, but untested. This hypothesis has implications important enough for testing through a range of approaches, including mesocosm experiments to follow evolution of plankton size structure across temperature treatments spanning 15°C.

Regardless of how future research agendas unfold, there are sound reasons for us to expect that estuarine-coastal phytoplankton communities have been changed by humans and will continue to change in the future. Surveillance is
essential, as is expanded research to understand how and why individual species deviate from the size-based general patterns considered here—the “stable backdrop” of Chisholm (1992).

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Acknowledgments
I thank my colleagues Lisa Lucas and Alan Jassby for their thoughtful comments that greatly strengthened this paper, and appreciate the positive evaluations of two reviewers. This research was supported by the USGS National Research Program (Water Mission Area), USGS Priority Ecosystem Science, the Regional Monitoring Program for San Francisco Bay Water Quality, and the San Francisco Bay Nutrient Management Strategy.

Conflict of Interest
None declared.

Submitted 01 September 2017
Revised 24 October 2017
Accepted 05 October 2017

Associate editor: Susanne Menden-Deuer