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On the roles of cell size and trophic strategy in North Atlantic diatom and dinoflagellate communities

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Abstract

We have examined the inter- and intra-group seasonal succession of 113 diatom and dinoflagellate taxa, as surveyed by the Continuous Plankton Recorder (CPR) in the North Atlantic, by grouping taxa according to two key functional traits: cell size (μg C cell^{-1}) and trophic strategy (photoautotrophy, mixotrophy, or heterotrophy). Mixotrophic dinoflagellates follow photoautotrophic diatoms but precede their obligate heterotrophic counterparts in the succession because of the relative advantages afforded by photosynthesizing when light and nutrients are available in spring. The mean cell size of the sampled diatoms is smallest in the summer, likely because of the higher specific nutrient affinity of smaller relative to larger cells. Contrastingly, we hypothesize that mixotrophy diminishes the size selection based on nutrient limitation and accounts for the lack of a seasonal size shift among surveyed dinoflagellates. Relatively small, heterotrophic dinoflagellates (μg C cell$^{-1} < 10^{-3}$) peak after other, larger dinoflagellates, in part because of the increased abundance of their small prey during nutrient-deplete summer months. The largest surveyed diatoms (μg C cell$^{-1} > 10^{-2}$) bloom later than others, and we hypothesize that this may be because of their relatively slow maximum potential growth rates and high internal nutrient storage, as well as to the slower predation of these larger cells. The new trait database and analysis presented here helps translate the taxonomic information of the CPR survey into metrics that can be directly compared with trait-based models.

We seek to understand how marine phytoplankton communities are regulated by the interplay of constituent species traits, biotic interactions, and the environment (Litchman and Klausmeier 2008). Numerical simulations can quantitatively encapsulate such understanding and may ultimately provide some predictive capability. To date, plankton community models have made considerable progress in resolving key functional groups, and models are increasingly seeking to resolve, and understand the importance of, diversity within those functional groups (Follows et al. 2007; Dutkiewicz et al. 2009). These studies have largely focused on subtropical, prokaryotic populations, where recent advances in molecular methods have revealed intra-group population variations that can be interpreted and simulated in terms of known physiological and biophysical traits of the organisms (Johnson et al. 2006).

We would like to pursue analogous interpretations (and ultimately simulations) of eukaryotic phytoplankton populations in the seasonal, subpolar oceans, but are hindered by limited understanding of how key functional traits structure eukaryotic communities. To address this limitation, we take advantage of a long-term, regional-scale set of observations of more than 100 diatom and dinoflagellate taxa, as captured by the Continuous Plankton Recorder (CPR) survey of the North Atlantic. We seek to characterize the spatial and temporal variations in intra-group community structure from the data, and use knowledge of how cell size and trophic strategy vary among the surveyed taxa to provide a framework for interpreting these population variations.

Diatoms and dinoflagellates in the subpolar North Atlantic—Diatoms and dinoflagellates play instrumental, yet different, roles in marine ecosystems and biogeochemical cycles (Cushing 1989). At the functional group level, a seasonal succession from diatoms to dinoflagellates has been widely observed in mid- to high-latitude surface waters (though perhaps not at depth) and attributed to changes in environmental conditions and predation (Margalef 1978; Leterme et al. 2005; McQuatters-Gollop et al. 2007). Blooms of diatoms are empirically related to turbulent, nutrient-rich conditions and result in a sinking flux of organic matter as well as a transfer of organic carbon and energy to higher trophic levels (Ryther 1969; Smetacek 1985). In contrast, dinoflagellates typically reach their greatest abundance in relatively quiescent and nutrient-deplete periods, common in summer, that are associated with weaker export and surface ocean recycling of organic matter. Transitions between diatom and dinoflagellate populations have also been characterized on interannual to decadal timescales in the North Atlantic (Leterme et al. 2005), potentially affecting the regional balance of surface ocean carbon cycling.

The roles of cell size and trophic strategy—To date, regional analyses have largely focused on intergroup dynamics (Leterme et al. 2005; McQuatters-Gollop et al.

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2007). However, in order to identify and quantify the mechanisms that differentiate taxa within the sampled diatom and dinoflagellate assemblages, we group taxa by key functional traits that are significant for their interactions with their resource environment and predators. An organism's functional traits are characteristics that mediate growth, reproduction, or survival (Violle et al. 2007) and determine its fitness under given environmental and predatory conditions (Litchman and Klausmeier 2008). We focus on two traits that provide intra-group differentiation within the diatoms and dinoflagellates: cell size and trophic strategy.

Cell size is a "master trait" that places important constraints on many key organismal characteristics and biotic interactions, including nutrient affinity (Litchman et al. 2007), light absorption efficiency (Finkel et al. 2010), predation (Hansen et al. 1997), and growth and metabolic rates (Litchman et al. 2007). Cell size is increasingly used to structure trait-based plankton community models, and determines, in part, the roles of the phytoplankton community in biogeochemical cycles and the marine food web (Baird and Suthers 2007; Banas 2011). Thus, the characterization of the CPR survey in terms of cell size will provide a valuable perspective on regional and seasonal variations in sampled populations, as well as a useful benchmark for comparison with trait-based plankton community models.

Trophic strategy is the degree to which phytoplankton acquire nutrients and energy by photoautotrophy, heterotrophy, or some combination (mixotrophy). Here there is a clear intergroup differentiation, as diatoms are exclusively photoautotrophic and dinoflagellates exhibit a range of trophic strategies. Within the dinoflagellates, mixotrophy has been hypothesized to define the ecological niches of many taxa (Smayda 1997; Hansen 2011). Recent evidence suggests that as much as 40–95% of total bacterivory is carried out by small ($\sim$ 5 μm), mixotrophic algae in the temperate North Atlantic Ocean (Zubkov and Tarran 2008), and many harmful algal blooms are also attributed to mixotrophic dinoflagellates (Smayda 1997). However, models of open-ocean plankton communities to date have generally ignored this strategy, perhaps overlooking or misrepresenting the dinoflagellate population entirely. The CPR survey represents a unique opportunity to characterize the seasonal and regional patterns of trophic strategies both between and within diatom and dinoflagellate populations in the subpolar North Atlantic.

Cell size and trophic strategy are not, of course, the only potentially significant traits for diatoms and dinoflagellates: other examples include motility and buoyancy, coloniality, formation of vacuoles, and the production chemicals to mediate resource competition and predation (Litchman and Klausmeier 2008). Though we acknowledge their potential importance, we will not address these further here.

In order to pursue a trait-based analysis of intra-group variations in the CPR diatom and dinoflagellate record, we have compiled a database of published reports on the cell size and trophic strategy for each of the 62 diatom and 51 dinoflagellate taxa considered in the CPR survey. We use this database to differentiate CPR-observed seasonal patterns of abundance for taxa with different size and trophic strategy.

Methods

Cell size database—From published literature we have compiled estimates of cell size (cell volume and cell carbon content) for each of the diatom and dinoflagellate taxa that are identified in the CPR database. This new database is an improvement over similar, existing descriptions of CPR phytoplankton taxa, and allows us to approximate many of the size-linked functional traits of the constituent taxa. Cell size of the individual taxon is expected to vary because of several factors, including changes in cell size over the cell cycle, decreases in average diatom cell size associated with asexual reproduction, and environmental and biological selection for specific cell size. Thus, we have collected as many estimates as possible and produced an estimate of average cell size. We specifically consider the size of individual cells, not their aggregates such as chains or mats.

A limited compilation of cell size estimates for the CPR taxa has been previously published (Matishov et al. 2000). Their cell weight estimates were calculated using tables of average cell volumes (Solovieva 1976) and wet weights (Makarevich et al. 1993) compiled for the Barents Sea. Cell volumes were estimated by application of the most appropriate geometric shape(s). Makarevich et al. (1993) converted cell volumes (μm^3) to wet weight (μg) by dividing cell volumes by 10^{-6} μm^3 μg^{-1}. Here we have converted their wet weights back to cell volumes.

Building upon Matishov et al. (2000), our updated compilation details cell mass (μg C $cell^{-1}$) for 62 diatoms and 51 dinoflagellates (Table 1). Further details, including standard deviation of cell mass, number of samples and source publications, are provided in the Web Appendix (www.aslo.org/lo/toc/vol_58/issue_1/0254a.html). Linear cell dimensions, cell volume, and cell carbon estimates were compiled. If only linear dimensions were provided, volume was estimated using standard formulas for the closest geometric shapes (Hillebrand et al. 1999; Olenina et al. 2006). For any single source, if both cellular carbon and cell volume estimates were provided, cell volume was used and converted to cell carbon using standard allometric conversion factors (Menden-Deuer and Lessard 2000). For a few sources (Wiltshire and Durselen 2004) the carbon data were used directly. When provided, every individual size measurement was used in the calculation of average cell size (Olenina et al. 2006), but most studies only provided estimates of the average size of each taxon. In cases where one of the observations for a taxon differed in excess of an order or magnitude from other observations it was not used. For the aggregated generic categories, each species was treated as a separate individual observation in the computation of the mean to prevent any one species from excessively dominating the estimate of size. For example, to estimate the average size of *Chaetoceros* (*Hyalochaete*) and *Chaetoceros* (*Phaeoceros*), 219 cell volume and cell carbon estimates of 54 identified species (and 2 unidentified *Hyalochaete* sp.) were gathered. The species were identified as *Hyalochaete* or *Phaeoceros*, and then the average size of

Table 1. Log_{10} cell mass (μg C cell^{-1}) and volume (μm^3) for CPR survey diatoms (62) and dinoflagellates (51), and trophic strategy for dinoflagellates (M = mixotroph, H = heterotroph). All diatoms are considered to be photoautotrophic. *See* Web Appendix for detailed cell size and trophic strategy sources.

Taxon	Log_{10} cell mass (μg C cell^{-1})	Log_{10} cell volume (μm^3)	Trophic strategy
Diatoms			
Paralia sulcata	−3.82	3.29	
Skeletonema costatum	−4.39	2.71	
Thalassiosira spp.	−2.96	4.51	
Dactyliosolen antarcticus	−2.23	5.37	
Dactyliosolen mediterraneus	−3.10	4.30	
Rhizosolenia imbricata shrubsolei	−2.81	4.65	
Rhizosolenia styliformis	−1.91	5.70	
Rhizosolenia hebetata semispina	−2.65	4.85	
Rhizosolenia alata indica	−2.32	5.22	
Rhizosolenia alata alata	−2.66	4.87	
Rhizosolenia alata inermis	−2.65	4.81	
Chaetoceros (*Hyalochaete*) spp.	−3.79	3.47	
Chaetoceros (*Phaeoceros*) spp.	−3.50	3.81	
Biddulphia sinensis	−1.69	6.05	
Asterionella glacialis	−4.08	3.05	
Thalassiothrix longissima	−3.51	3.84	
Thalassionema nitzschioides	−4.17	2.95	
Nitzschia seriata	−4.09	3.05	
Nitzschia delicatissima	−4.70	2.31	
Actinoptychus spp.	−2.98	4.41	
Asteromphalus spp.	−3.13	4.24	
Bacillaria paxillifer	−3.68	3.53	
Bacteriastrum spp.	−3.53	3.74	
Bellerochea malleus	−2.48	5.15	
Biddulphia alternans	−2.86	4.75	
Biddulphia aurita	−2.92	4.55	
Biddulphia granulata	−2.32	5.20	
Biddulphia regia	−1.94	5.61	
Biddulphia rhombus	−2.05	5.69	
Cerataulina pelagica	−2.94	4.44	
Climacodium frauenfeldianum	−3.43	3.84	
Corethron criophilum	−2.76	4.71	
Coscinodiscus concinnus	−1.08	6.67	
Coscinodiscus spp.	−0.76	7.09	
Detonula confervacea	−3.99	3.18	
Ditylum brightwellii	−2.60	4.88	
Eucampia zodiacus	−3.27	4.08	
Fragilaria spp.	−4.07	3.97	
Guinardia flaccida	−2.38	5.12	
Gyrosigma spp.	−2.85	4.60	
Hemiaulus spp.	−3.12	4.31	
Lauderia borealis	−3.00	4.40	
Leptocylindrus danicus	−3.90	3.30	
Navicula spp.	−3.57	3.75	
Nitzschia closterium	−4.47	2.62	
Rhaphoneis amphiceros	−3.89		
Planktoniella sol	−3.19	4.85	
Rhizosolenia acuminata	−0.92	6.93	
Rhizosolenia bergonii	−1.96	5.67	
Rhizosolenia calcar avis	−2.07	5.52	
Rhizosolenia delicatula	−3.40	4.00	
Rhizosolenia fragilissima	−3.16	4.23	
Rhizosolenia setigera	−2.27	5.30	
Rhizosolenia stolterfothii	−2.89	4.58	
Schroederella delicatula	−3.10	4.32	
Stephanopyxis spp.	−2.40	5.13	
Streptotheca tamesis	−2.71	4.79	
Surirella spp.	−2.41	5.23	
Nitzschia spp.	−3.57	3.87	

Table 1. Continued.

Taxon	Log_{10} cell mass (μg C cell^{-1})	Log_{10} cell volume (μm^3)	Trophic strategy
Odontella mobiliensis	−2.19	5.50	
Asterionella kariana	−4.40	2.65	
Stauroneis membranacea	−3.01	4.39	
Dinoflagellates			
Ceratium fusus	−2.27	4.70	M
Ceratium furca	−2.24	4.73	M
Ceratium lineatum	−2.39	4.57	M
Ceratium tripos	−1.94	5.05	M
Ceratium macroceros	−2.28	4.67	M
Ceratium horridum	−1.86	5.16	M
Ceratium longipes	−2.18	4.81	M
Ceratium arcticum	−2.09	4.87	M
Protoceratium reticulatum	−2.65	4.28	M
Ceratium kofoidii	−2.46	4.49	M
Pyrophacus spp.	−2.02	4.96	M
Ceratium falcatum	−1.91	5.07	M
Amphisolenia spp.	−1.39	5.63	H
Ceratium arietinum	−1.94	5.04	M
Ceratium azoricum	−2.16	4.80	M
Ceratium belone	−1.92	5.07	M
Ceratium bucephalum	−1.94	5.04	M
Ceratium buceros	−2.60	4.34	M
Ceratium candelabrum	−2.08	4.89	M
Ceratium carriense	−1.71	5.29	M
Ceratium compressum	−1.61	5.39	M
Ceratium declinatum	−2.31	4.64	M
Ceratium extensum	−1.91	5.40	M
Ceratium gibberum	−1.51	5.50	M
Ceratium hexacanthum	−1.35	5.67	M
Ceratium inflatum	−2.55	4.38	M
Ceratium karstenii	−1.54	5.46	M
Ceratium lamellicorne	−1.61	5.39	M
Ceratium massiliense	−1.81	5.18	M
Ceratium minutum	−2.72	4.21	M
Ceratium pentagonum	−1.92	5.06	M
Ceratium petersii	−1.80	5.18	M
Ceratium platycorne	−1.61	5.39	M
Ceratium praelongum	−2.01	4.95	M
Ceratium pulchellum	−2.02	4.95	M
Ceratium setaceum	−2.21	4.75	M
Ceratium teres	−2.30	4.66	M
Ceratium trichoceros	−2.51	4.43	M
Ceratium vultur	−1.91	5.07	M
Ceratocorys spp.	−2.17	4.79	M
Cladopyxis spp.	−3.41	3.47	H
Dinophysis spp.	−2.26	4.70	H
Exuviaella spp.	−2.51	4.43	M
Gonyaulax spp.	−2.41	4.56	M
Oxytoxum spp.	−3.13	3.77	H
Protoperidinium spp.	−2.06	4.91	H
Podolampas spp.	−2.26	4.69	H
Pronoctiluca pelagica	−3.25	3.64	H
Prorocentrum spp.	−2.90	4.02	M
Ceratium falcatiforme	−2.22	4.73	M
Ceratium longirostrum	−2.46	4.48	M

these groups was calculated using the average carbon and volume estimates of the individual species within these categories.

Additional taxonomic information on synonyms was gathered from the World Register of Marine Species (Appeltans et al. 2011). According to Appeltans et al. (2011), all marine *Ceratium* should be assigned to *Neoceratium*, *Ceratium bucephalum* is a synonym of *Ceratium arietinum*, and *Ceratium lamellicorne* is a synonym of *Ceratium platycorne*. The same size information was applied to all synonyms in the CPR database. No size information was obtained for *Ceratium compressum*, but it can be confused with *C. platycorne*, and therefore it was assigned the size of *C. platycorne*.

Trophic strategy database—Based upon published reports, we categorized each of the CPR taxa simply as a photoautotroph, mixotroph, or heterotroph using the criteria described below (Table 1). Those taxa, notably the diatoms, containing plastids and photosynthetic pigments, but with no evidence for consumption of organic particles or prey, are considered to be photoautotrophic. Because of the ubiquity of mixotrophy among dinoflagellates and the difficulty of ruling out heterotrophic behaviors in dinoflagellates (Stoecker 1999), we assume for this analysis that no dinoflagellates are purely photoautotrophic all of the time. Dinoflagellates in this classification scheme are, therefore, mixotrophs or heterotrophs. Mixotrophic dinoflagellates contain plastids and photosynthetic pigments, and show evidence for the consumption of organic particles or prey, such as the presence of food vacuoles or direct observation of feeding (Hansen and Calado 1999). We have not quantified the relative importance of photoautotrophy or heterotrophy for mixotrophic dinoflagellates, and have not distinguished between native plastids or pigments and kleptochloroplasts or algal symbionts (Hansen 2011). Pure heterotrophic dinoflagellates contain no functioning plastids or photosynthetic pigments, and show evidence for consumption of organic particles or prey. We assume that those *Ceratium* taxa that have no published accounts regarding trophic strategy are mixotrophic. Although this trophic partitioning simplifies a vast array of behaviors (Hansen 2011), it allows us to compare patterns of seasonal succession among broad groups organized by trophic function.

Analysis of CPR data—The CPR survey, with its broad spatial, temporal, and taxonomic coverage and internally consistent methodology, provides a unique observational record of plankton ecological dynamics in the North Atlantic. These data have been used to study plankton seasonal cycles (Leterme et al. 2005) and biogeography (Barnard et al. 2004), as well as long-term changes in total phytoplankton biomass (Hinder et al. 2012). The Sir Alister Hardy Foundation for Ocean Science (SAHFOS) has operated the CPR survey in the North Atlantic with consistent taxon-level phytoplankton measuring techniques since 1958 (Richardson et al. 2006). Ships of opportunity tow the plankton recorder at roughly 7–9 m depth on quasi-regular routes, and plankton caught on the spooling filtering mesh (270 μm on a side) are enumerated microscopically upon return to the laboratory. The microscopic analysis of the filtering meshes is converted empirically to a semiquantitative measure of cell number density (cells volume^{-1}), which we term "abundance" throughout the manuscript. We prefer semiquantitative abundance to the more commonly used metrics of number density or biomass because the exact volume of filtered water is unknown (Jonas et al. 2004).

For each taxon and standard survey area (there are 41 survey areas in the North Atlantic; Fig. 1), SAHFOS provided us with monthly mean abundance and sampling frequency data for 1958–2006. The sampling frequency simply describes the number of distinct observations that were compiled by SAHFOS to calculate the monthly mean abundance for a given year, taxon, and zone. We considered only the 62 diatom and 51 dinoflagellate taxa that were routinely monitored across all zones and years (Table 1); these taxa represent a subset of common, but not all, diatoms and dinoflagellates. Next, we describe the methods by which we averaged the CPR database over multiple years, areas, and taxa.

We first calculated the mean annual cycle of abundance for each taxon within each area. In doing so, we weighted the monthly mean abundance by sampling frequency such that better sampled periods have more weight in the mean. Second, we evaluated a basin-wide mean annual cycle for each taxon. In this case, each zone was weighed by its geographic area (km^2). Third, we calculated the average over multiple taxa, and have given each taxon equal weight in the mean. We considered only areas, months, and years with greater than two samples and have not attempted to interpolate for missing data. The averaging, as we have done here, is inherently a trade-off between having enough data for robust statistics and retaining taxon- and area-specific patterns. The spatial and temporal averaging also has the effect of smoothing over short-duration or local-scale ecological events.

Next, we describe how we estimate the uncertainty associated with the monthly mean abundance measurements, and outline a method for how this error estimate propagates when we average over years, areas, and taxa. In essence, the goal of this analysis is to place the mean successional patterns in the context of uncertainty associated with natural ecosystem variability and sampling intensity. To this end, we calculated the standard error ($\delta^{est}_{i,j,k}$) for each month (i = 1, …, 12), taxon (j = 1, …, 113), and area (k = 1, …, 41):

$$\delta^{est}_{i,j,k} = \frac{\sigma_{i,j,k}}{\sqrt{l'_{i,j,k} - 1}} \quad (1)$$

where $l'_{i,j,k}$ is the number of years with available data within the temporal range (l = 1958, …, 2006) and $\sigma_{i,j,k}$ is the standard deviation for the available data. This error estimate was then propagated through successive averaging over years, zones, and taxa, which we describe in detail below.

When averaging monthly mean abundances over multiple years to obtain the mean seasonal cycle for each area and taxon, we assume that the errors from year to year are

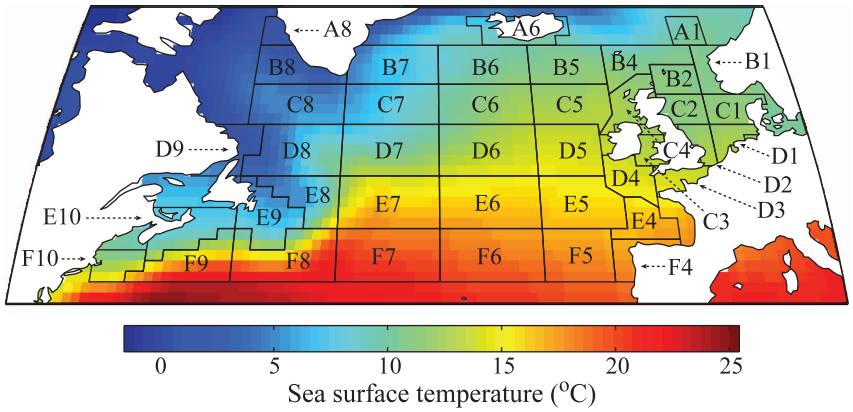

Fig. 1. Map of CPR Standard Survey Areas, superimposed upon the annual mean sea surface temperature climatology for 1971–2000 (Smith and Reynolds 2003).

random and uncorrelated, and that the estimate of uncertainty, $\delta^{est}_{i,j,k}$, is equal over all years. Thus, the estimated error in the mean annual cycle for each taxon and area is (Taylor 1997)

$$\delta_{i,j,k} = \left[\sum_{l} \left(\frac{w_{i,j,k,l}}{\sum_{l} w_{i,j,k,l}} \right)^2 (\delta^{est}_{i,j,k})^2 \right]^{\frac{1}{2}} \quad (2)$$

where the weights, $w_{i,j,k,l}$, are the sampling frequency for each taxon, area, month, and year. When calculating the error associated with averaging over the basin, we also assume that area-to-area errors are uncorrelated and random, such that error propagates as

$$\delta_{i,j} = \left[\sum_{k} \left(\frac{w_{i,j,k}}{\sum_{k} w_{i,j,k}} \right)^2 (\delta_{i,j,k})^2 \right]^{\frac{1}{2}} \quad (3)$$

where the weights, $w_{i,j,k}$, are the geographic area (km^2) of each survey area. Unlike when averaging over multiple years and zones, when averaging over multiple taxa observed at the same place and time, we assume the errors are correlated, such that the error estimate is

$$\delta_i = \frac{\sum_{j} \delta_{i,j}}{j'} \quad (4)$$

where j' is the number of taxa averaged. The assumption of uncorrelated errors on interannual and basin scales, but correlated errors for species measured in the same place and time, is reasonable considering the characteristic time and space scales of coordinated variability in marine ecosystems at this latitude (Doney et al. 2003).

Interpretation of the CPR data—Though the CPR database is a rich and unparalleled record of ecological variability in the North Atlantic, aspects of the CPR sampling methodologies that guide our interpretations of the data warrant additional discussion here.

The CPR sampling mesh (270 μm on a side) does not efficiently sample smaller phytoplankton, such as any of the picoplankton (< 2 μm), and it misses the majority of the nanoplankton (2–20 μm). It does capture a diverse, but perhaps incomplete, set of the microplankton (> 20 μm), including the diatom and dinoflagellate taxa considered in this study. Thus, we stress that our results and discussion refer only to those diatom and dinoflagellate taxa covered by the survey. The size of the filtering mesh also implies that relatively small surveyed diatoms and dinoflagellates may be undersampled relative to larger ones simply because smaller cells pass more readily through the mesh (Richardson et al. 2006). As a consequence, we examine patterns of seasonal change within taxonomic groups or size classes or robust metrics of surveyed community change, but not differences in relative abundance between size classes or taxonomic groupings.

It is also possible that relatively small taxa are preferentially caught when the filtering mesh is clogged by other, larger cells. We expect that this bias would cause a strong, positive correlation between the abundance of small and large cells and that this correlation would increase with total biomass and subsequent clogging. We have correlated the abundance time series for the smallest and largest (by cell mass) quartiles of diatoms and dinoflagellates and plotted the correlation coefficient (r) against the median, summed abundance for each region (Fig. 2). The abundances of smaller and larger diatoms and dinoflagellates are positively correlated, yet the strength of correlation does not scale with total abundance, suggesting that the sampling bias due to mesh clogging is not dominating patterns in the dataset.

There are several reasons why this may be the case. Most of the diatoms, and some of the dinoflagellates, form chains or aggregates that dramatically increase their linear dimension and probability of being caught by the mesh. Similarly, many of the surveyed taxa have a linear dimension that greatly exceeds their equivalent spherical diameter. For example, many *Ceratium* have long horns and diatoms have spines that increase their effective probability of mesh capture.

We also note that the three smallest surveyed dinoflagellates, *Cladopyxis* spp., *Oxytoxum* spp., and *Pronoctiluca pelagica*, do not tend to form chains and have linear dimensions far below the 270 μm mesh size, suggesting that

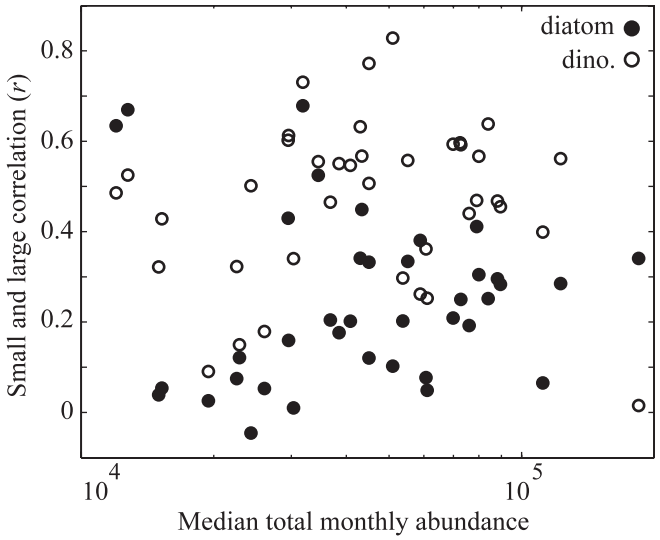

Fig. 2. Correlation (r) between monthly mean time series for the smallest and largest size quartiles of diatoms (filled circle) and dinoflagellates (dino., open circle) for each area as a function of the median summed abundance over all species in that area. There is no significant increase in correlation with total abundance for either diatoms or dinoflagellates.

they would be taxa whose sampling would be likely to be biased by clogging of the mesh. However, the smallest dinoflagellates are most abundant in summer (*see* Results), during a period with low total abundance and, presumably, relatively minor mesh clogging. This suggests that clogging is not dramatically biasing the observation of these smaller cells. Therefore, we conclude that temporal changes in abundance of the different size fractions of diatoms and dinoflagellates captured by the CPR can provide insight into the selection for traits under different abiotic and biotic conditions.

Results

In addition to reporting the basin-wide, seasonal patterns of abundance for surveyed diatoms and dinoflagellates (Figs. 3–5), we examine the successional patterns for the six nearly zonal bands of CPR survey areas, from A (farthest north) to F (farthest south; *see* map Fig. 1), spanning from subpolar to near-subtropical waters. Each band includes both coastal (far eastern and western zones) and pelagic habitats.

Diatoms sampled by the CPR survey reach a maximum abundance in spring (February–May) and decline through the summer (June–August; Fig. 3, top panel). The diatom spring maximum is followed by a peak in CPR dinoflagellate abundance in summer (defined here as the sum of abundance for heterotrophic and mixotrophic dinoflagellates), which is in turn followed by a fall diatom bloom. Though we show the summed dinoflagellate abundance only for the basin mean, the successional pattern is broadly consistent across latitudes (Areas A–F) and in coastal vs. open ocean locations within the CPR survey area. This succession has been observed widely enough to become a paradigm of surface waters in temperate seas (Margalef 1978), and it has also been observed previously in CPR data (Leterme et al. 2005; McQuatters-Gollop et al. 2007). The annual peaks of both the spring diatom bloom and summer dinoflagellate abundance are later and stronger in more northerly zones, driven by latitudinal variations in light, temperature, restratification, and predation (Taylor et al. 1993).

In addition to these successional patterns among the aggregated diatom and dinoflagellate groups, we find evidence for novel intra-group patterns related to variations in cell size and trophic strategy. When differentiating CPR dinoflagellates according to trophic strategy, we find that an early bloom in photoautotrophic diatoms is followed, in sequence, by mixotrophic and heterotrophic dinoflagellates (Fig. 3). The peak in heterotrophic abundance coincides with the summer diatom minimum. In terms of timing of the seasonal cycles, photoautotrophs and heterotrophs are nearly out of phase. Contrasting the signals by latitude band (Areas A–F) reveals that mixotrophic and heterotrophic dinoflagellates tend to peak at roughly the same time in northern latitudes, whereas the mixotrophic peak precedes that of heterotrophs by up to 2 months in the south. Throughout, the abundance of heterotrophic dinoflagellates exhibits a stronger seasonal cycle than the mixotrophs, with a noticeably stronger winter decline.

We also differentiate the seasonal cycles of abundance between equal, logarithmically spaced size classes of diatoms and dinoflagellates sampled by the CPR survey, averaged across all areas and years (Fig. 4). The size classes are as follows (m=cell mass; units are μg C cell^{-1}): (1) $m > 10^{-2}$ (7 diatoms, 19 dinoflagellates), (2) $10^{-2} > m > 10^{-3}$ (26 diatoms, 29 dinoflagellates), (3) $10^{-3} > m > 10^{-4}$ (21 diatoms, 3 dinoflagellates), and (4) $m < 10^{-4}$ (8 diatoms, 0 dinoflagellates). We illustrate only the basin-average results, but the seasonal trends are qualitatively similar on a regional basis. In the basin average, the spring blooms of the three smallest diatom size classes increase and peak in the same month. The abundance of the largest diatoms exhibits a slower increase and peak abundance a month or two later than the smaller size classes (Fig. 4B). Among the dinoflagellates, the abundance of the two larger groups peaks earlier than the smallest group by approximately 1 month. The peak of the smallest group coincides with the summer minimum in diatoms (Fig. 4B). It is notable that the smallest size class of dinoflagellates exhibits the strongest seasonality, with very low winter abundances, of any of the groupings in this analysis (Fig. 4A,C). This is consistent with the strong winter decline of heterotrophic dinoflagellates (Fig. 3), as three of the seven dinoflagellates identified as purely heterotrophic are the three smallest dinoflagellate cell sizes (Table 1; *Cladopyxis* spp., *Oxytoxum* spp., and *P. pelagica*).

Lastly, we illustrate the seasonal variations in the mean cell mass of the most abundant diatom and dinoflagellate taxa (defined as those taxa comprising greater than 95% of the cumulative abundance within each group in each month; Fig. 5). Though smaller cells are generally more abundant than larger cells, and the most abundant pico-

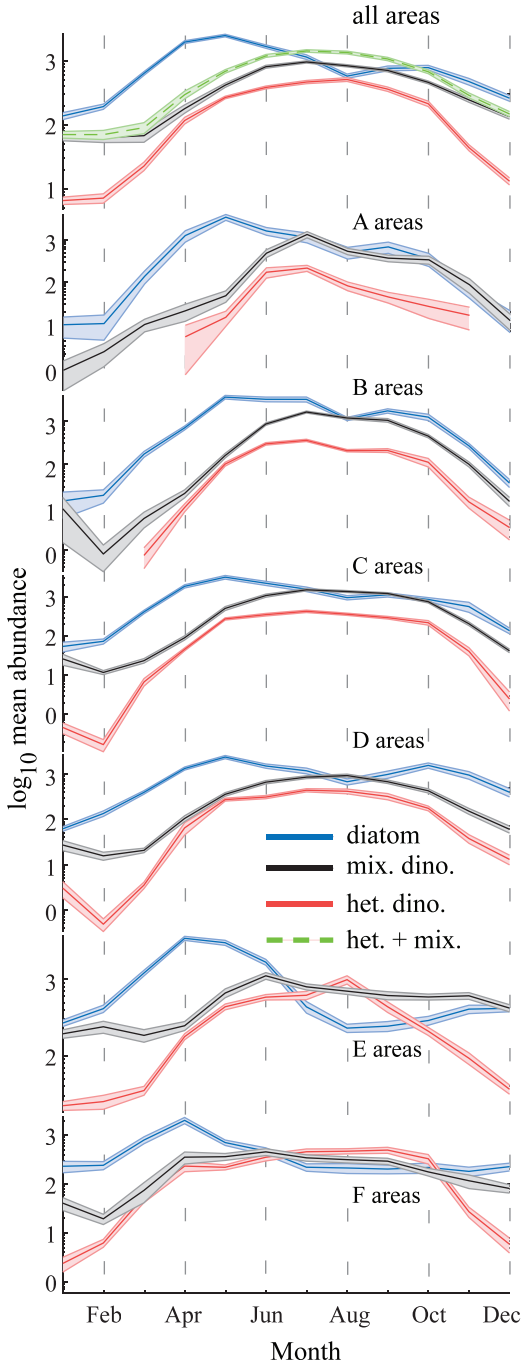

Fig. 3. Log_{10} monthly mean abundance for photoautotrophic diatoms (blue) and mixtotrophic (mix. dino., black), heterotrophic (het. dino., red), and total dinoflagellates (het. + mix.; dashed green), averaged over all CPR survey areas (top panel, All areas) and within each latitude band, from A (farthest north) to F (farthest south). For a map showing locations of CPR survey areas, *see* Fig. 1. Shaded error bars indicate two standard errors ($\pm$ 2σ).

phytoplankton are not recorded in the CPR survey, this simple metric indicates shifts in the relative contributions of the sampled cell types. There is a decline in the mean cell size of diatoms during the summer, but little seasonal change in the dinoflagellates (Fig. 5). A similar seasonal size shift has been observed in temperate coastal waters and is consistent with theoretical predictions about how maximum cell size should decrease with declining nutrient concentration (Kiørboe 2008).

Discussion

Here we interpret these results by addressing the following questions, framed in terms of the two key traits: What role does trophic strategy play in organizing the seasonal succession, in particular the placement of mixotrophic dinoflagellates? Why does the mean cell size of the diatom population decline in the summer, and the abundance of the largest diatoms peak after the bloom of smaller cells? Why do the dinoflagellates exhibit a much smaller range in mean cell size over the course of the year, with the smallest taxa being most abundant in summer and showing the strongest seasonality?

Trophic strategies—Analysis of the CPR data indicates a succession of trophic strategies, from a strong spring increase and subsequent decline in photoautotrophic diatoms to mixotrophic and heterotrophic dinoflagellates, with the latter peaking in summer months. What underpins this succession?

The spring peak of photoautotrophy and subsequent growth of the heterotroph (grazer) population follows a classical view of bloom dynamics. Following wintertime convection, nutrients are plentiful and predators are still relatively scarce. During the spring, increasing insolation and restratification (or a decline in the input of turbulent kinetic energy) promote photoautotrophic growth, and diatoms rapidly bloom (Behrenfeld et al. 2006; Taylor and Ferrari 2011). The termination of the diatom bloom likely reflects the depletion of nutrients (Dale et al. 1999), but the subsequent decline in population is due to losses such as sedimentation and predation.

The abundance of heterotrophic dinoflagellates begins to increase at approximately the same time as the photoautotrophic diatoms, and their population growth slows as the diatom abundance diminishes in summer. Although the diatoms certainly have other predators, such as copepods, and the heterotrophic dinoflagellates other prey, it is known that the dinoflagellates consume diatoms of similar and smaller size (Hansen et al. 1994). Thus, the successional patterns of diatoms and heterotrophic dinoflagellates (Fig. 3) appear consistent with a predator–prey relationship, where the diatoms are a controlling resource for the heterotrophic dinoflagellates during the spring and summer and the dinoflagellates contribute to the cropping of the diatom population in summer. However, additional data or experiments quantifying the ingestion of diatoms by heterotrophic dinoflagellates would be needed to evaluate this hypothesis.

Among the dinoflagellates (Fig. 3), mixotrophs and heterotrophs have similar seasonal cycles of abundance, though the mixotrophs do not decline as significantly in winter and, in southerly latitudes, they reach their maximum abundance slightly earlier than heterotrophs (Fig. 3). Why do the mixotrophs follow photoautotrophic

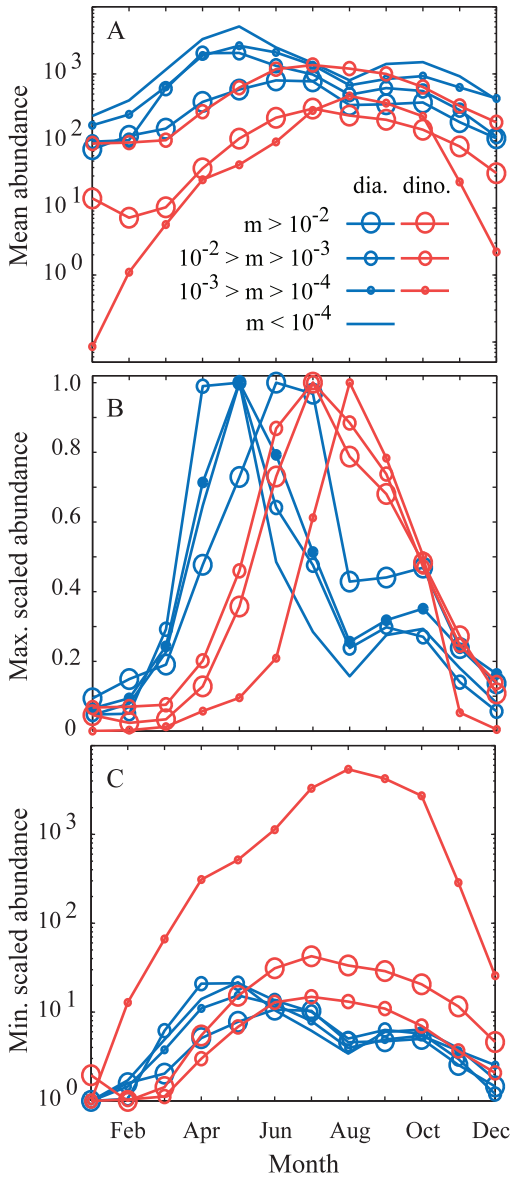

Fig. 4. (A) Monthly mean abundance for equal, logarithmically spaced size classes of diatoms (dia., blue) and dinoflagellates (dino., red), averaged across all areas and years. (B, C) Data are scaled, or normalized, by the maximum (max.) and minimum (min.) of each curve, respectively. The size classes (m=cell mass; units are μg C cell^{-1}) are as follows: (1) m $>$ 10^{-2} (7 diatoms, 19 dinoflagellates), (2) 10^{-2} $>$ m $>$ 10^{-3} (26 diatoms, 29 dinoflagellates), (3) 10^{-3} $>$ m $>$ 10^{-4} (21 diatoms, 3 dinoflagellates), and (4) m $<$ 10^{-4} (8 diatoms, 0 dinoflagellates). Error bars are omitted for clarity.

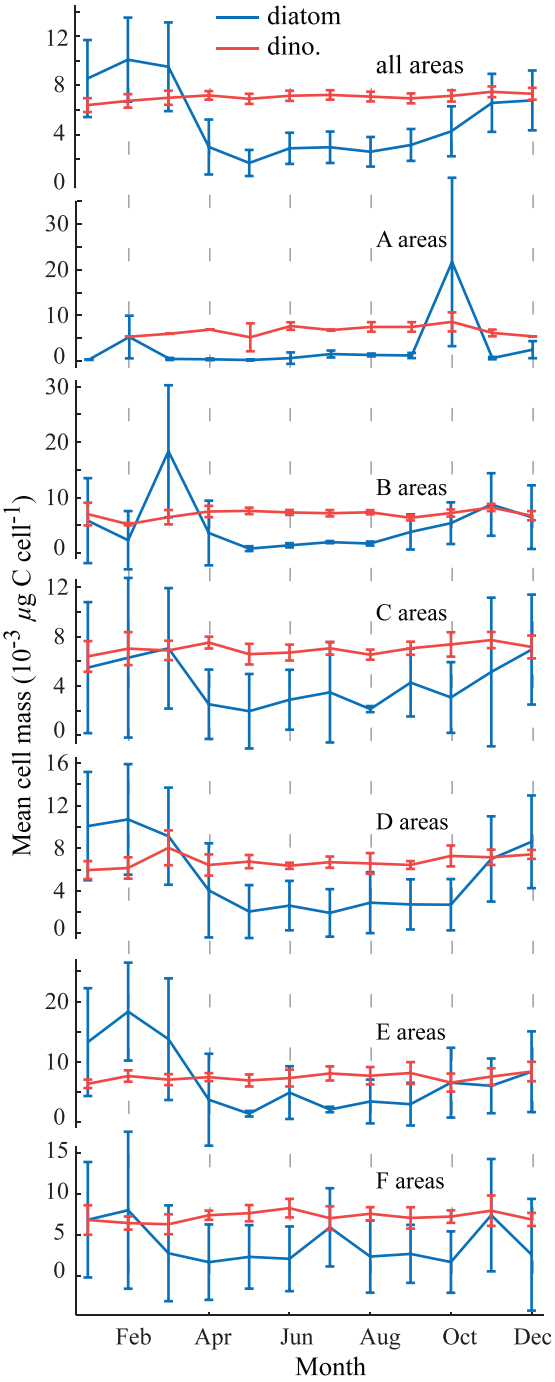

Fig. 5. Mean cell mass (10^{-3} μg C cell^{-1}) of diatom (blue) and dinoflagellate (dino., red) taxa accounting for 95% of the cumulative abundance within each group and month, averaged over all CPR survey areas (top panel, all areas) and within each latitude band, from A (farthest north) to F (farthest south). For a map showing locations of CPR survey areas, *see* Fig. 1. Error bars indicate two standard errors ($\pm$ 2σ).

diatoms but precede heterotrophs in the seasonal succession? During the spring bloom, both obligate photoautotrophic diatoms and mixotrophic dinoflagellates begin to bloom, though the former typically have faster maximum growth rates (for a given cell size; Litchman et al. 2007) and respond more quickly to newly favorable conditions. As inorganic resources are depleted, both mixotrophic and heterotrophic dinoflagellate populations may continue to grow, fueled by the autotrophic prey population. With abundant prey, however, the additional metabolic costs of generalism work against mixotrophs, and the pure heterotrophs tend to have higher potential growth and grazing rates (for ciliates and dinoflagellates; Pérez et al. 1997; Jeong et al. 2010), allowing them to outcompete the

mixotrophs. Yet initially, the mixotrophs have a temporary advantage over the obligate heterotrophs because of their autotrophic ''kick start.'' This is consistent with the interpretation of trophic strategies in a study of phytoplankton assemblages in the New Zealand shelf seas (Chang et al. 2003) and a numerical model of Bruggeman (2009).

It is interesting to speculate whether this ''bet-hedging'' strategy may explain the more significant winter decline of the heterotrophic dinoflagellates relative to the mixotrophic dinoflagellates and photoautotrophic diatoms (Fig. 3). Perhaps, at these northerly CPR latitudes, insolation is sufficient to maintain some photoautotrophic growth throughout the winter, albeit strongly tempered by deep mixing (Dale et al. 1999). Both diatoms and mixotrophic dinoflagellates might maintain a low-density population in this way, especially in the presence of low predator densities. In contrast, the small, heterotrophic dinoflagellates cannot photosynthesize and require relatively small prey that are typical of summer ''microbial loop'' plankton assemblages. Thus, their population declines dramatically in winter.

Though we have argued that resource availability underpins the seasonal succession of trophic strategies, there is limited evidence that temperature could also play a direct role by affecting protistan growth rates. Rose and Caron (2007) found that photoautotrophs grow faster than their protistan predators at lower temperatures typical of spring, whereas the reverse is true at higher, summer temperatures.

Cell size—The analysis indicates that the population of smaller diatoms peaks before their larger counterparts (Fig. 4). At the same time, the mean diatom cell size is a minimum in the summer. In contrast, the mean cell size of dinoflagellates remains fairly constant throughout the year, though the smallest dinoflagellates exhibit a strong seasonal cycle and are most abundant in summer.

Diatoms—Why might larger diatoms peak later than smaller diatoms? One hypothesis is that, within functional groups, larger cells tend to have lower maximum specific growth rates than smaller cells in resource-replete conditions (Irwin et al. 2006). Thus, we would expect the population of smaller cell types to bloom more rapidly, and field studies have shown that smaller cells precede larger cells in phytoplankton succession in temperate seas (Cushing 1989; Taylor et al. 1993) and some lakes (Sommer 1985). Alternatively, the ability of large diatoms to store nutrients to a greater degree than smaller diatoms may allow them to continue growing and dividing after nutrients become limiting (Raven 1987). A third possibility is that a slower response of larger predators (Hansen et al. 1997) allows a later bloom of larger diatoms by opening a grazing ''loophole'' (Irigoien et al. 2005).

Why does the mean diatom cell size decline in the summer and increase in periods with more nutrients? If we consider that over the course of the summer, the oligotrophic, stratified waters approach an equilibrium, resource competition perspectives tell us that the smallest cells with the highest specific nutrient affinities and lowest R* (or the minimum steady state subsistence nutrient concentration; Dutkiewicz et al. 2009) should be fittest and dominate the community. Because of the limitation of the CPR sampling, we do not have data on the smallest cell sizes (i.e., the picoplankton), but it is clear that they have not completely excluded all other cell sizes. The diatom population is, however, weighted towards smaller cells in summer. Equilibrium resource competition theory tells us that the biomass of these smaller phytoplankton will be tightly cropped by their quickly growing, small predators (Hansen et al. 1994, 1997), allowing for the accumulation of excess inorganic resource. The extra nutrient allows successively larger size classes of phytoplankton and their predators to persist (Armstrong 1994; Irwin et al. 2006), and this process is thought to explain the positive correlation between inorganic nutrients and cell size (Schartau et al. 2010). Thus, the CPR diatom data are consistent with a persistent population of diatoms enabled by top-down control of the picoplankton, but a greater relative contribution from smaller diatoms in the more oligotrophic summer quasi-equilibrium.

Factors other than resource availability may also be important in driving similar shifts in cell size. Notably, studies have suggested that warmer temperature may favor smaller phytoplankton, independent of nutrient concentrations (Hilligsøe et al. 2011). However, Atkinson et al. (2003) found that for each 1°C decrease in temperature, intraspecific body volume decreases by 2.5%, suggesting that the direct, mechanistic effect of temperature on phytoplankton body volume may be small in comparison with the effect of availability of nutrients. Seasonal variability of turbulence or vertical motion in the surface mixed layer could favor smaller cells in summer and larger cells in winter by affecting sinking and swimming velocities (Kiørboe 1993). We also note that many of the diatoms considered by the CPR survey form chains or aggregates, though we have considered the size of solitary cells in our analysis. Based upon the CPR data, the extent of diatom chain formation or chain size is unknown, and it is, as yet, unclear how chain formation may alter our interpretations.

Dinoflagellates—Why is the seasonal size shift among dinoflagellates much less pronounced than for diatoms? The different trophic strategy of the dinoflagellates leads to a different set of controlling processes. In particular, mixotrophy can alleviate nutrient limitation when inorganic nutrients are scarce (Ward et al. 2011), and weakens the size selection based on the availability of inorganic resources and the size dependence of affinity.

Why do the smallest dinoflagellates have such a pronounced seasonal cycle with very low winter abundances? Interestingly, the three smallest dinoflagellates (μg C cell^{-1} $< 10^{-3}$) that are most abundant in summer, *Cladopyxis* spp., *Oxytoxum* spp., and *P. pelagica*, are all pure heterotrophs. Their prey could include, for example, small diatoms, small dinoflagellates, or other relatively small plankton such as picoplankton (though these are not sampled by the survey) that are relatively abundant in nutrient-deplete, summer conditions. Thus, the summer peak of small, heterotrophic dinoflagellates may be driven by the increased availability of small prey. There is some evidence also that temperature may play a direct role by

increasing heterotrophic growth rates in warm conditions preferentially relative to photoautotrophs (Rose and Caron 2007), though it is unclear the extent to which this mechanism could account for the difference between the smaller and larger dinoflagellate groups, which are predominantly mixotrophic in character.

Wider implications—We have interpreted the intra-group ecological dynamics of diatom and dinoflagellate taxa in the CPR survey by considering the roles of two, key functional traits: trophic strategy and cell size. As well as the expected succession from autotrophs to heterotrophs, the data reveal that mixotrophic dinoflagellates peak earlier than surveyed heterotrophs. This can be understood in terms of a transient, temporal niche where the advantage of a generalist nutritional strategy temporarily outweighs the cost of maintaining both autotrophic and heterotrophic capabilities. During the spring and summer bloom, relatively large diatoms peak later than their smaller relatives, consistent with lower maximum specific growth rates and higher storage capacity for larger cells, as well as a more slowly responding predator population for the larger cells. The mean cell size of the diatom population declines in the summer, consistent with an equilibrium perspective where larger cells persist when total resource loads are larger, and efficient predation limits the growth of the population of smaller cells. In contrast, the mean cell size of dinoflagellates was found to vary little over the annual cycle because, we speculate, mixotrophy frees them from the size selection imposed by nutrient limitation. Notably, the smallest dinoflagellates (μg C cell^{-1} $< 10^{-3}$) peak in summer, consistent with the increased availability of their likely prey.

In order to pursue this trait-based analysis of the CPR survey of phytoplankton, we have developed a new database of cell size and trophic strategy for the recorded taxa. The database represents a substantial improvement on similar, existing resources and provides a valuable reference for this, and future, trait-based analyses. It also provides a link between the taxonomic information of the survey and functional traits that may form the basis of model parameterizations (Baird and Suthers 2007; Banas 2011; Ward et al. 2011). Thus it provides a point of connection between the wealth of observed data and model simulations that might be used to further interpret the regional and seasonal patterns, or form the basis of future climate modeling studies. The trophic strategy database could be improved upon in future studies by attempting to consider more quantitatively the degree of heterotrophy or photoautotrophy among dinoflagellates under different biotic and environmental conditions.

Though we have focused on cell size and trophic strategy, there are other traits that may also be significant and might be treated in a similar fashion (Litchman and Klausmeier 2008). For example, dinoflagellate flagella provide motility in weakly turbulent conditions, allowing them to take advantage of light, access nutrients, and avoid predation (Klausmeier and Litchman 2001). Some dinoflagellates produce and externally release chemicals to mediate resource competition and predation in their favor (Smayda 1997). Mixotrophic dinoflagellates may also eat their nutrient competitors (diatoms, other dinoflagellates) or their predators (other dinoflagellates), liberating resources for their own use (Thingstad et al. 1996). In a similar vein, diatoms have the ability to develop large vacuoles for storage and improving their surface area : volume ratio (Raven 1987), regulate buoyancy (Villareal et al. 1993), or escape predation. Lastly, future studies should consider how the formation of chains and aggregates affects diatom and dinoflagellate fitness by affecting predator–prey interactions, nutrient uptake, sinking, motility, and buoyancy.

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