Biogeographic distribution of diversity and size-structure of organic-walled dinoflagellate cysts

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ABSTRACT: Global biogeographic patterns and environmental correlates of diversity and size structure of extant marine organic dinoflagellate cysts were determined. Dinoflagellate cyst diversity, like that of many other terrestrial and marine groups, is lowest at the poles and higher at lower latitudes. Temperature is responsible for much of the positive correlation between dinoflagellate cyst diversity and latitude. In contrast, the most obvious correlate with the median size of dinoflagellate cysts is the depth of the water column, especially in warm-water regions, perhaps due to changes in mixing regime and the advantages associated with the lower sinking rates and lower nutrient requirements of smaller species in offshore waters. The unique biogeographic pattern in dinoflagellate cyst diversity may reflect the unique physiological features of dinoflagellates: preference for warm, stable water columns, slower inherent growth rates, and their ability to act as mixotrophs or heterotrophs. Dinoflagellates tend to be 'gleaners', slow-growers adapted to oligotrophic conditions and less sensitive to inorganic nutrient supply, as compared to inorganic resource 'opportunists' with high growth rates, such as diatoms. These ecophysiological differences between dinoflagellates and other functional groups, such as diatoms and coccolithophores, may account for the major differences in the biogeographic and latitudinal diversity gradients between these groups.

KEY WORDS: Dinoflagellate cysts · Biogeography · Diversity · Size

INTRODUCTION

Diversity and size structure of organisms in communities are influenced by environmental conditions, and have the capacity to alter the structure and function of food webs and the biogeochemical cycling of key elements (Hutchinson 1959, Brown et al. 2004, Finkel et al. 2007, 2010). Large-scale patterns of biodiversity and community size structure can provide insights into the underlying mechanisms that shape ecosystem structure and function (Brown 1995, Rosenzweig 1995, Gaston & Blackburn 2000, Li 2002, Allen & Gillooly 2006). Currently, it is unclear what factors control plankton richness and size structure in the sea, whether there are differences between taxonomic groups, whether environmental selection on species affects biogeographic patterns in species richness and size structure, and, in turn, whether these biogeographic patterns reflect peculiar selective environmental conditions.

Higher species diversity at low latitudes have been predicted for marine phytoplankton (Barton et al. 2010) and have been observed for marine bacterioplankton (Fuhrman et al. 2008), coccolithophorids (Cermeño et al. 2008a), tintinnid ciliates (Dolan et al. 2006), and copepods (Woodd-Walker et al. 2002), but not for diatoms or mixed phytoplankton assemblages (Cermeño et al. 2008a,b). There are some general trends in phytoplankton size structure in response to temperature, light, and nutrient concentration. For example, average phytoplankton cell size within communities tends to increase with nutrient availability and decrease with in-

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creasing temperatures, but exceptions are not uncom-
mon (Li 2002, Finkel et al. 2009, Kostadinov et al. 2009,
Mei et al. 2009, Chen & Liu 2010). Observational data
on the biogeographic distributions of different plankton
functional groups and their environmental correlates
can be used to test hypotheses about the controls on
community diversity and size structure and improve
predictions for how future environmental and climate
change may alter the biogeographic distributions of
these important organisms. In the present paper, we
have quantified the global biogeographic patterns and
environmental correlates of diversity and size structure
of extant marine organic dinoflagellate cyst communi-
ties, for which a large data set of recent dinoflagellate
cyst abundances from core tops has been made publicly
available (Marret & Zonneveld 2003, Radi & de Vernal
2008). As these samples were all collected from surface
sediments, the data set is a compilation of present-day
distributional patterns of marine extant organic dino-
gellate cysts (Marret & Zonneveld 2003). Traditionally,
correlations between modern environmental conditions
and the dinoflagellate cyst community structure from
core tops have been applied to down-core communities
to reconstruct paleoenvironmental conditions; here we
focus on modern environmental correlates related to di-
noflagellate community size structure and diversity.

Dinoflagellates are important primary producers,
and some also play a significant role as herbivores in
the microbial food web (Margalef 1978, Azam et al.
1983, Hansen 1992, Sherr & Sherr 2007). Dinoflagel-
lates are motile and have some unique physiological
features compared to other plankton functional
groups, including a preference for water stability, an
ability to live as mixotrophs or heterotrophs, and the
ability of some species to form cysts (Taylor 1987,
Smayda 1997, Litchman 2007). Approximately 20%
dinoflagellate species can form resting cysts as part of
their life cycle (Taylor 1987), which can act to protect
the species under unfavorable conditions and seed
new dinoflagellate communities under favorable con-
ditions (Anderson & Wall 1978, Lewis et al. 1999). Cyst
formation may be triggered by environmental stress
such as nutrient depletion in laboratory cultures
(Anderson et al. 1985a). In the field, however, induc-
tion of sexuality and encystment of dinoflagellates has
also been associated with optimal temperature, light,
and nutrient conditions, as well as other endogenous
factors (Anderson et al. 1985a, Kremp & Heiskanen
1999). Cyst formation in dinoflagellates may be a
survival strategy to minimize lateral dispersal into
unfavorable regions as opposed to avoidance of envi-
ronmental stress (Smetacek 1985). We hypothesize
that the unique eco-physiological features of the cyst-
forming dinoflagellates may result in distributional
patterns different from those of other functional groups

with distinctly different physiological traits and trade-
offs.

With the goal of identifying the primary environmen-
tal controls of diversity and size structure of plankton
communities, we address the following specific ques-
tions: (1) What are the primary environmental corre-
lates of dinoflagellate cyst diversity and size structure?
(2) Do the large-scale distributional patterns in richness
and community size structure of organic cyst-forming
dinoflagellates differ from those of other phytoplankton
groups with different ecophysiological traits? (3) If
there are differences, what are the likely mechanisms
generating such differences? Our approach was to map
the community diversity and size structure of dinofla-
gellate cysts and determine their statistical relation-
ships to the environmental variables latitude, tempera-
ture, nutrient concentrations, and water depth. These
results should provide insight into the environmental
conditions that support dinoflagellate diversity in the
water column and cause encystment.

MATERIALS AND METHODS

We analyzed a global database of extant organic
dinoflagellate cysts from a number of literature sources
covering the Arctic Ocean, sub-Arctic, North Atlantic
and adjacent areas, and eastern North Pacific (Radi &
de Vernal 2008 [1171 samples]), Benguela upwelling
system (Zonneveld et al. 2001 [41 samples], Holzwarth
et al. 2007 [54 samples]), tropical African margin in the
eastern Atlantic (Marret 1994 [46 samples], Marret &
Zonneveld 2003 [39 samples]), western equatorial At-
lantic (Vink et al. 2000 [34 samples]), Atlantic sector of
the Southern Ocean (Esper & Zonneveld 2002 [32 sam-
ples]), Antarctic waters near the Falkland Islands (Har-
land et al. 1998 [14 samples]), southern Indian and
Pacific (Marret & de Vernal 1997 [67 samples]), and
mid-African area in the eastern Atlantic influenced by
the Congo River plume (Dale et al. 2002 [34 samples]).
Calcareous or siliceous cysts were excluded because
they may reflect separate functional groups respond-
ing differently to environmental conditions, including
different nutrient requirements (e.g. only the siliceous
forms need silicate) and resistance to decay. The final
data set consisted of 1532 samples of organic-walled
dinoflagellate cysts collected from surface sediments
(upper centimeter), representing 10 to 1000 yr, depen-
ding on sedimentation rates and bioturbation (Fig. 1;
Marret & Zonneveld 2003, Radi & de Vernal 2008). All
species in the study are extant. The samples were
treated and examined using comparable up-to-date
methodology to assure consistency (Marret & Zonn-
eveld 2003, Radi & de Vernal 2008). An excellent sum-
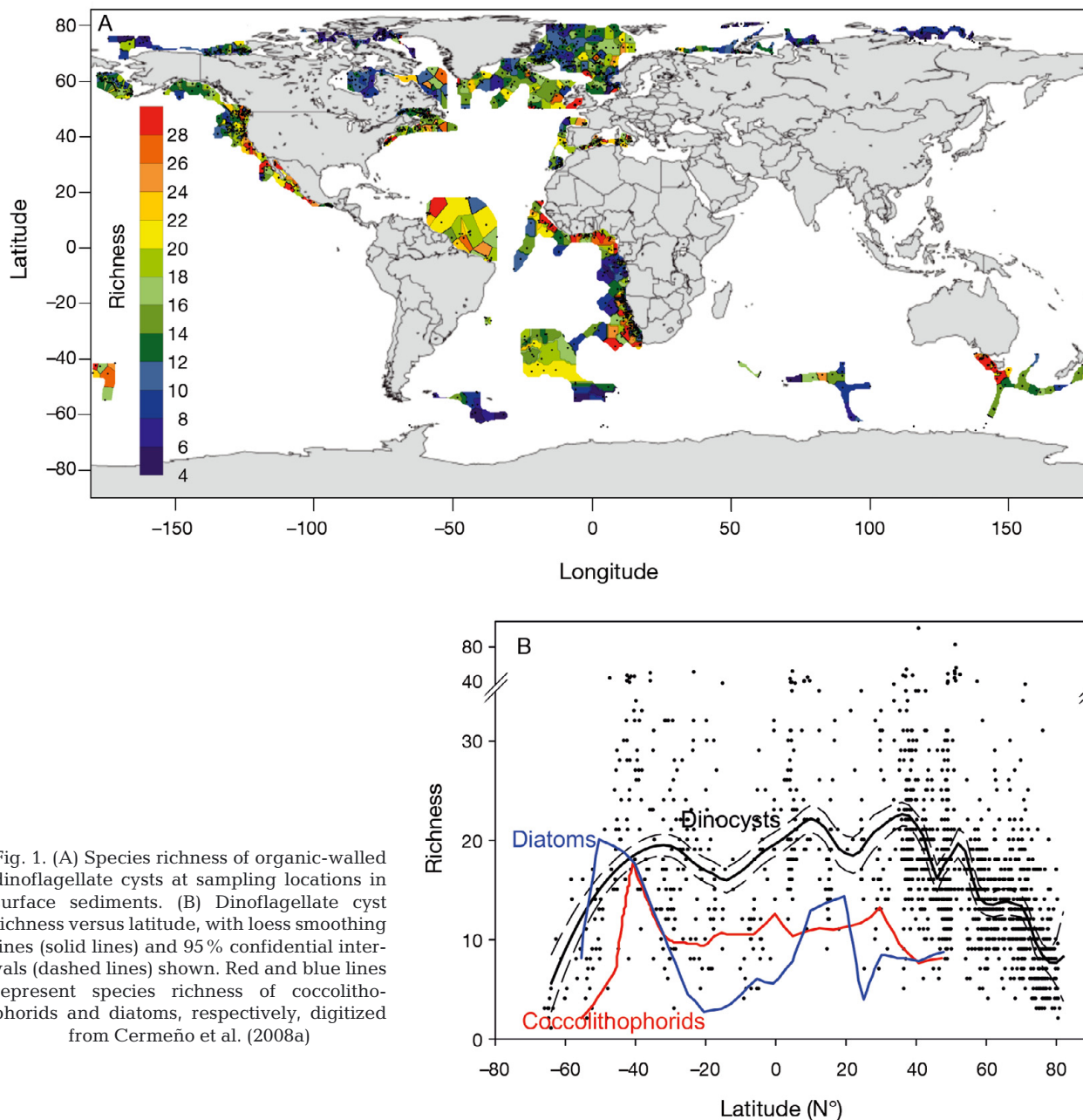mary of much of this data set, including background

Fig. 1. (A) Species richness of organic-walled dinoflagellate cysts at sampling locations in surface sediments. (B) Dinoflagellate cyst richness versus latitude, with loess smoothing lines (solid lines) and 95 % confidential intervals (dashed lines) shown. Red and blue lines represent species richness of coccolithophorids and diatoms, respectively, digitized from Cermeño et al. (2008a)

oceanographic information and descriptions of the species, is provided by Marret & Zonneveld (2003).

Species diversity of the cyst assemblages is calculated as species richness

$$S = S_{obs} + \frac{a(a-1)}{2(b+1)}$$

(Colwell 2005), in which S_{obs} is the total number of observed species, a is the number of species counted once, and b is the number of species counted twice. Other diversity estimates, such as the Shannon index, give similar patterns as species richness (data not shown).

The length and width (µm) of each cyst in the database, not including processes, was extracted from literature sources, and the largest cross-sectional area (µm^2) of each cyst species was calculated based on appropriate geometric shapes (the detailed size data of each individual species and a list of references are provided in Table S1 in the supplement at www.int-res.com/articles/suppl/m425p035_supp.pdf). The area of each cyst species was log$_{10}$-transformed to achieve variance homogeneity. Median log area of the community in each sediment sample was calculated as the median size of the species present, not weighted

by abundance to focus on the size changes of the cyst community caused by species turnover and how many species can be sustained within a particular environment (i.e. to avoid interference by changes in relative abundances of individual species). The 25th and 75th percentiles of the log area of each sample were also calculated. Twenty-four species for which we could not find size information were excluded from the analysis. These are generally rare species. In analyzing the relationships between cyst size structure and environmental factors, we discarded the samples in which the numerical abundances of the species without size information exceeded 25% of the total abundances (29 samples) and with species richness values <3 (6 samples). This resulted in a data set containing 1495 samples, comprising 78 species with size information, covering latitudes from 81°N to 66°S.

Annual mean sea-surface (0 m) temperature (°C) and nitrate and phosphate (μmol l^{-1}) data for each sampling location were interpolated from the monthly climatology data downloaded from the World Ocean Atlas 2005 using the *k*-nearest-neighbor classification method in the R package class (Ripley 1996). We assumed that the cysts had not been horizontally transported far from where they grew originally as vegetative cells (see discussion in Marret & Zonneveld 2003). Field evidence suggests that secondary transport generally has a minor, predominately local influence on cyst distribution, perhaps due to high sinking rates (Marret & Zonneveld 2003). The spatial resolution of the temperature, nitrate, and phosphate climatology data is 1° in latitude and longitude. Bathymetry data were obtained directly from the original data sources whenever possible. For samples without bathymetry (mostly in northern Atlantic and Arctic regions), the data were downloaded from the United States Naval Oceanographic Office. Spearman rank correlation was used throughout to restrict violation of normal distribution. The maps were drawn using Surfer 7.03 (Golden Software), with the global map (downloaded from www. aquarius.geomar.de) using Lambert azimuthal projection. The interpolations were conducted with the kriging or nearest-neighbor method in Surfer. Local polynomial regression fitting (loess) and the 95% confidential intervals were calculated using R (R Development Core Team 2009). As many variables are correlated with each other, partial correlations (Sokal & Rohlf 1994) were used to investigate the relationships between one environmental variable and diversity/size with a third controlled variable (i.e. to examine the correlations between residuals resulting from linear regressions of diversity/size with the third variable and of the target variable with the third variable, respectively).

RESULTS

Latitudinal patterns in dinoflagellate cyst species richness and size structure

There is a geographic structure in the species richness of dinoflagellate cysts, which varies from a minimum of 1 to a maximum of 101 (Fig. 1A). Average species richness increases from low values (mean ± SE: 5.6 ± 1.5) in polar regions to higher values (22.1 ± 0.6) at ~40° and varies between 16.9 ± 0.8 and 21.8 ± 0.7 from 40°S to 40°N (Fig. 1B). Species richness is significantly negatively rank correlated with absolute latitude (Table 1). Richness is usually low throughout Arctic regions, while hotspots occur in the Celtic Sea, the Californian upwelling region, the Gulf of Guinea, and the sector of the Southern Ocean south of Australia (Fig. 1A). To compare with the diversity patterns of diatoms and coccolithophorids, we digitized the diversity data of diatoms and coccolithophorids from data reported by Cermeño et al. (2008a). While species richness of diatoms, coccolithophorids, and dinoflagellate cysts tends to be low in the Southern Ocean, there are significant differences in the latitudinal pattern in richness between the 3 groups (Fig. 1B). The latitudinal diversity pattern of diatoms largely follows nutrient availability (Cermeño et al. 2008a), but dinoflagellate cyst richness does not decrease with decreasing nutrient concentration in the tropics/subtropics (Fig. 1B).

The sizes of individual dinoflagellate cyst species range from 314.2 to 3959.2 μm^2 in area and exhibit a skewed log-normal frequency distribution (Fig. 2A). The median size of the dinoflagellate cyst community varies with latitude, but not in the same fashion as species richness. Median cell size of the dinoflagellate cyst communities is largest (log area mean ± SE: 3.28 ± 0.01 log μm^2) in the highest southern latitudes (66°S), decreases to 3.14 log μm^2 from 66 to 36°S, then increases from 36°S to 20°N (3.19 ± 0.01 log μm^2), decreases to 3.12 log μm^2 at 44°N, and is relatively invariant to 80°N (Fig. 2C). The dramatic increase of median size in the Southern Ocean (south of 40°S) is a combined result of the presence of a large endemic species, *Selenopemphix antarctica*, and the loss of small species (Table 1; 25th and 75th percentiles). The peak in median size at 20°N is a function of the specific ranges of the cosmopolitan species, such as *Selenopemphix quanta*, and endemic species, such as *Bitectatodinium spongium*, restricted to warm temperate and tropical waters. The most prominent geographic pattern in median size is an onshore–offshore gradient in the Californian upwelling, equatorial and southern Atlantic regions (Fig. 2B).

Table 1. Spearman rank correlation and partial correlation coefficients among cyst richness, size, and environmental factors (For total data set, n = 1532 for richness and n = 1495 for size. For ≤13°C, n = 975 for richness and 965 for size; for >13°C, n = 557 for richness and 530 for size). |Lat|: absolute latitude; Temp.: annual mean temperature (°C); log [NO_3]: $\log_{10}$ transformed nitrate concentration at 0 m (µmol l^{-1}); log [PO_4]: $\log_{10}$ transformed phosphate concentration at 0 m (µmol l^{-1}); Depth: water depth (m); Median: median size (log µm^2); 25%Q: 25th percentile size (log µm^2); 75%Q: 75th percentile size (log µm^2); **: p < 0.01, *: p < 0.05

|	Total data set				≤13°C				>13°C			
	Richness	Median	25%Q	75%Q	Richness	Median	25%Q	75%Q	Richness	Median	25%Q	75%Q
Spearman rank correlation												
|Lat|	−0.52**	−0.11**	0.29**	−0.29**	−0.54**	0.01	0.25**	−0.29**	0.14**	−0.25**	−0.15**	0.01
Temp.	0.57**	0.14**	−0.26**	0.35**	0.63**	0.11**	−0.19**	0.43**	−0.08	0.22**	0.23**	−0.06
Log [NO_3]	−0.13**	0.03	0.09**	0.16**	0.15**	0.16**	−0.02	0.39**	0	−0.03	−0.07	0.10*
Log [PO_4]	−0.17**	0.01	0.09**	0.06**	0.12**	0.07*	−0.05	0.18**	−0.09*	0.06	−0.02	0.20**
Depth	0.23**	−0.15**	−0.34**	0.15**	0.16**	−0.06	−0.21**	0.24**	0.01	−0.47**	−0.40**	−0.35**
Partial correlation (holding Temp. constant)												
|Lat|	0.06*	−0.01	0.09**	0.06*	−0.02	0.06	0.16**	0.09*	0.10*	−0.04	0.06	−0.03
Log [NO_3]	0.11**	0.16**	0.03	0.36**	0	0.17**	0.06	0.35**	−0.05	0.24**	0.14**	0.16**
Log [PO_4]	0.04	0.15**	0.02	0.26**	−0.05	0.15**	0	0.19**	−0.11*	0.21**	0.15**	0.19**
Depth	−0.03	−0.25**	−0.28**	0.01	−0.06	0.01	−0.17**	0.20**	−0.06	−0.51**	−0.39**	−0.36**
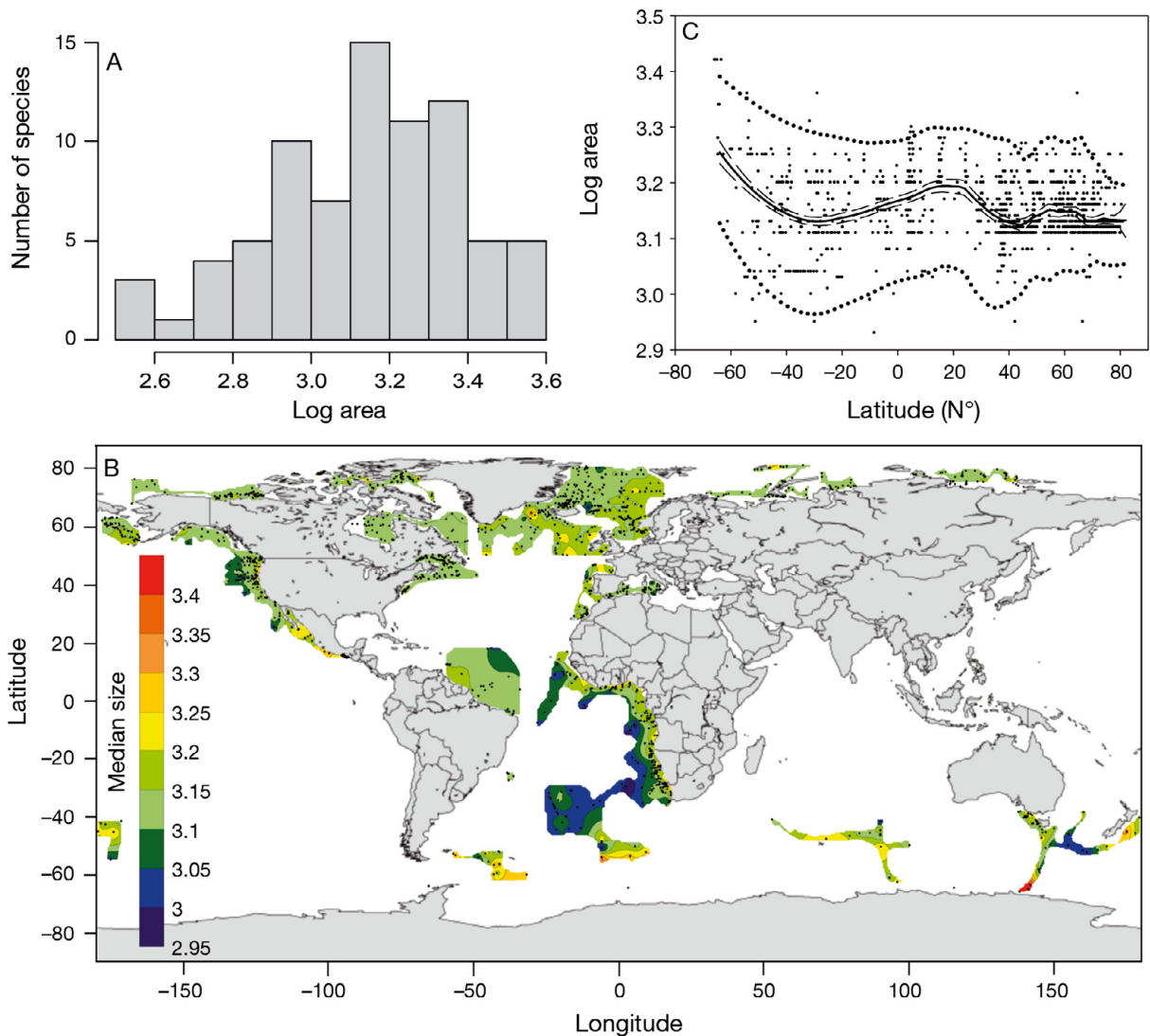
Fig. 2. (A) Frequency distribution histogram of dinoflagellate cyst size (log area, µm^2). (B) Contour maps of the median size (log µm^2) of dinoflagellate cyst communities. (C) Median cyst size (log µm^2) versus latitude, with loess smoothing line (solid line) and 95% confidence intervals (dashed lines) shown. Dotted lines: 25th and 75th percentile sizes

Environmental controls on dinoflagellate cyst species richness and size

Temperature and latitude appear to be the most important environmental factors affecting richness. Dinoflagellate cyst species richness is positively rank correlated with annual mean temperature (Table 1, Fig. 3A), negatively rank correlated with nitrate (log [NO_3]) and phosphate (log [PO_4]), and positively correlated with water depth (Table 1, Fig. 3B, C). Temperature accounts for most of the correlation between richness and latitude. The effect of temperature on cyst richness is most pronounced in cold waters <13°C (Table 1, Fig. 3A). In contrast, macronutrient concentration and depth are only marginally correlated with richness. If temperature is held constant, richness is weakly positively correlated with log [NO_3] and log [PO_4], but not correlated with depth (Table 1).

Environmental correlates for size structure differ from species richness. Increasing temperature tends to relate to an increase in the size range (maximum to minimum size) of the dinoflagellate cysts within samples, increasing 2.5-fold from −1.4 to 28.5°C. The 75th percentile is positively rank correlated with temperature, while the 25th percentile is negatively correlated with temperature (Table 1). At higher temperatures, the higher species richness allows for a higher variability in size (increase in size range) among species. In contrast, the median size of the dinoflagellate cyst assemblages is not highly correlated with temperature when temperature is <20°C, but does increase with temperature >20°C (Fig. 3D).

Instead of temperature, water depth appears to be the strongest correlate for median cyst size in warm regions, particularly in the southern Atlantic and off western California (Table 1, Fig. 2B). Loess average median size generally decreases with water depth, and increasing depth is always associated with a decrease in the size of the 25th percentile (Table 1, Fig. 3F). Although macronutrient concentrations in the euphotic zone often tend to be lower in deeper waters, the correlation between depth and cyst size is much stronger than that between nutrient concentration and cyst size (Table 1). The effect of macronutrient concentrations on median size is most pronounced in the Southern Ocean, where larger median size coincides with higher nitrate concentrations (Fig. 3E). Overall, the effect of macronutrient concentrations on size is weakly positive and most evident for the 75th percentile (Table 1, Fig. 3E).

Relationship between cyst species richness and size

At low richness, the median size can range from small to large, while, at high richness, the median size converges to a medium value (Fig. 4). Overall, richness is only weakly correlated with median size (Spearman r = 0.10, p < 0.001, n = 1495). Temperature appears to be the major factor causing the weak correlation. When factoring in temperature using partial correlation, the relationship between richness and median size disappears (Table 1).

DISCUSSION

Large-scale patterns of biodiversity and size on the community level are, in part, an emergent pattern caused by the collective behaviors of each individual species responding to external physical, chemical, and biological conditions. Increased knowledge of the biogeographic patterns of different plankton groups will clarify the contribution of specific physiological and other mechanisms that control community structure. Bridging the gap between our knowledge on organismal physiology and macroscopic distributional patterns is essential to improve our ability to understand and predict the community structure under changing environmental and climatic conditions (Brown 1995, Irwin et al. 2006, Finkel et al. 2010). The correlates between species diversity and average size of dinoflagellate cysts and environmental variables are not necessarily direct indications of cause–effect relationships, but should reveal potential deterministic factors that control plankton community structure or co-vary with key drivers.

Phytoplankton functional groups — biogeography and environmental co-variables

The latitudinal diversity patterns of the phytoplankton groups are consistent with the recent model predictions in which phytoplankton diversity is predominantly regulated by environmental and eco-physiological processes, such as competition and lateral dispersal (Barton et al. 2010). In sub-polar regions with highly variable nutrient supplies, opportunistic species with higher growth rates are favored, resulting in lower species richness, while in stable subtropical and tropical regions, more species are able to coexist (Barton et al. 2010). These predictions and model assumptions can be further tested by analyzing the biogeographic distributions of plankton functional groups and quantifying the photosynthetic and growth responses of typical plankton species from tropical and polar sites.

Fundamental eco-physiological differences between different plankton groups may explain the differences in their biogeographic distribution and, in particular,
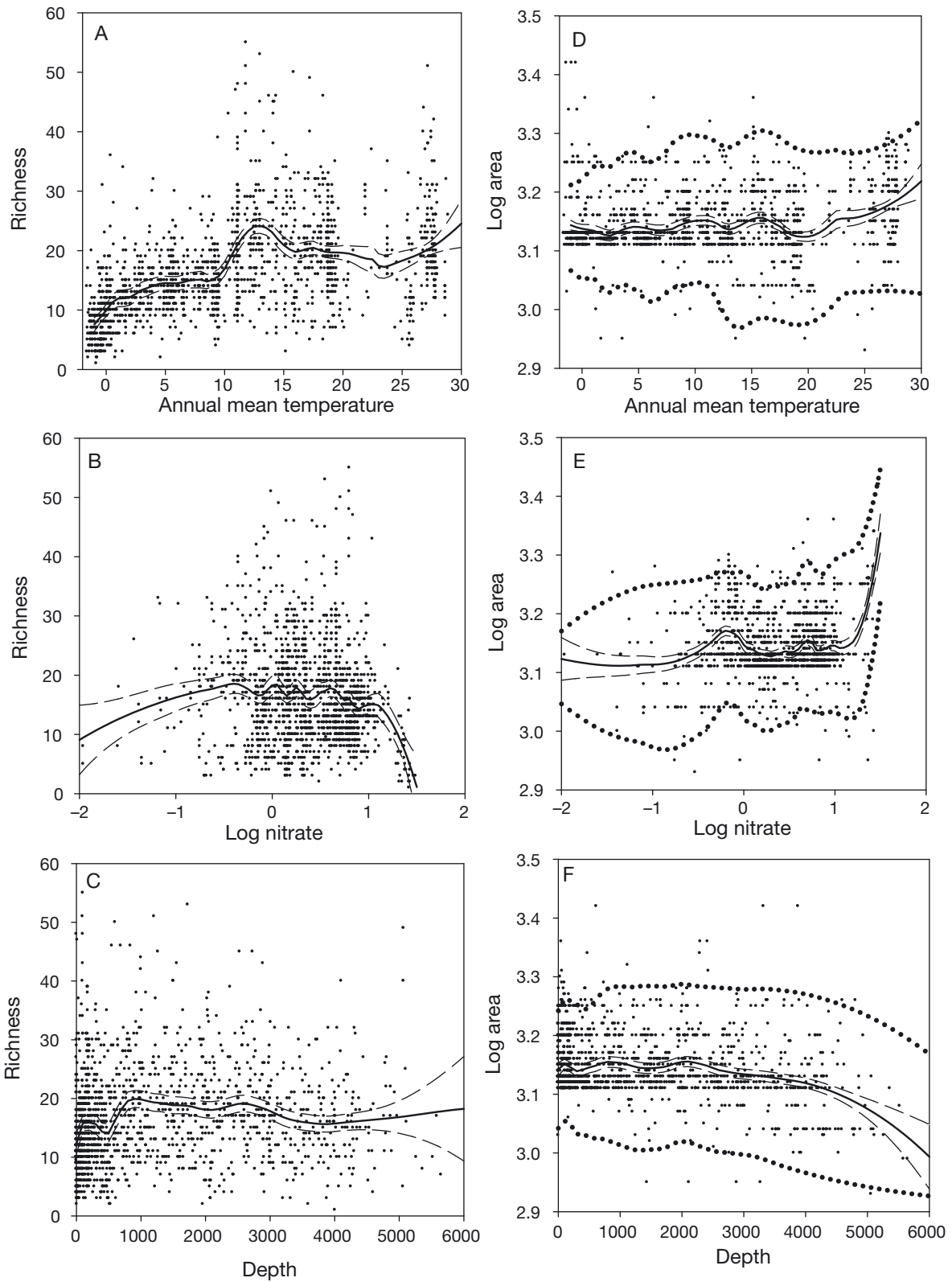
Fig. 3. Richness versus (A) temperature (°C), (B) log nitrate (µmol l^{-1}), and (C) depth (m). Median cyst size (log µm^2) versus (D) temperature (°C), (E) log nitrate (µmol l^{-1}), and (F) depth (m). Loess smoothing lines (solid lines) and 95% confidence intervals (dashed lines) are also shown. Dotted lines: loess smoothing lines of 25th and 75th percentiles. In Panels A to C, 2 data points with richness >60 are not shown, but were included in the calculation
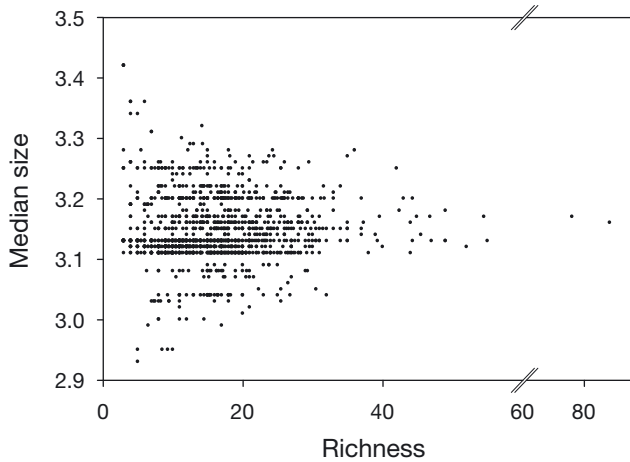
Fig. 4. Median size of dinoflagellate cyst communities (log μm^2) versus richness

the differences in their diversity gradients with latitude. Post-depositional lateral transport of cysts from these studies is generally on local scales (Marret & Zonneveld 2003), and there is no evidence that they played a dominant role in determining the large-scale biogeographic patterns in the dinoflagellate cyst diversity observed. The relative abundance and diversity of a taxonomic group is expected to be regulated by environmental conditions that influence growth and survival. Dinoflagellate cyst species richness, which we assume reflects a subset of the diversity of living dinoflagellates, is more highly correlated with sea-surface temperature than latitude, and, when temperature is held constant, latitude is a minor correlate of community richness (Table 1). One interpretation of the data is that warm, stratified, low-latitude regions stimulate more dinoflagellate species to produce cysts, leading to higher cyst species richness. Favorable temperature, light, and nutrient conditions may trigger sexuality and encystment in dinoflagellates *in situ* (Anderson et al. 1985a, Kremp & Heiskanen 1999). We propose that temperature is such a good correlate of dinoflagellate richness because it is an excellent correlate of water-column stability. Dinoflagellates are well known for their inferior ability to compete in turbulent waters (Thomas & Gibson 1990, Peters & Marrasé 2000). Beyond a critical threshold of turbulence, dinoflagellates may stop dividing or lose their flagella, and, as a result, their growth rates can be severely inhibited by small-scale turbulence even for short periods of time (Gibson & Thomas 1995). The inability of most cyst-forming dinoflagellates to thrive in turbulent environments is consistent with decreasing levels of species richness in assemblages poleward of both 40° N and 40° S (Fig. 1) and the high positive correlation between dinoflagellate cyst richness and sea-surface temperature, especially at <13°C (Table 1). Decreases

in sea-surface temperatures <13°C are likely associated with increasing levels of surface mixing and turbulence. The lower correlation between richness and sea-surface temperatures >13°C is likely due to an uncoupling between water-column stability and increasing sea-surface temperatures above this threshold temperature.

The weak correlations between surface macronutrient concentrations and dinoflagellate cyst species richness are consistent with the observation that many dinoflagellates are poor competitors for inorganic nutrients (Litchman 2007). Many dinoflagellate species are mixotrophs or heterotrophs, which may reduce their inorganic nutrient requirements and therefore their need for competitive inorganic nutrient uptake rates (Margalef 1978, Smayda 1997, Litchman 2007). As a result of these collective features, dinoflagellates are expected to attain greater biomass and highest diversities in warm, stratified, oligotrophic regions (Margalef 1978), as confirmed in the present study (Fig. 1) and observed in the fossil record (Fensome et al. 1996, Finkel et al. 2007).

In contrast, diatoms thrive in well-mixed water columns, have high maximal uptake rates for inorganic nutrients and high growth rates relative to other taxonomic groups (Irwin et al. 2006), and often attain great biomass and high diversity in well-mixed, unstable waters (Li 2002, Cermeño et al. 2008a). Turbulence may help replenish the nutrient-depleted diffusive layer around immotile diatom cells, improving growth rates (Thomas & Gibson 1990, Kiørboe 1993, Peters & Marrasé 2000), and mixing minimizes sinking loss of the dense siliceous diatoms out of the euphotic zone. As a group, diatoms can be viewed as opportunist, higher nutrient 'r-strategy' organisms, and dinoflagellates can be viewed as gleaner, lower nutrient, 'K-strategy' organisms (Margalef 1978, Litchman 2007). Other functional groups have different ecophysiological trade-offs that place them intermediately along the r- to K-strategy continuum. Coccolithophorid genera, such as *Emiliania* and *Gephyrocapsa*, have maximum growth rates (for a given size) intermediate between diatoms and dinoflagellates (Irwin et al. 2006), and often bloom under high-light and low-nutrient conditions, as the upper water column stratifies and diatom blooms are in decline (Iglesias-Rodríguez et al. 2002), consistent with the correspondence of their peak diversity with the diatoms between 35 and 55° S (Fig. 1B). Physiological work indicates that some species are well adapted to high light, even under nitrate starvation (Nanninga & Tyrrell 1996, Litchman 2007, Loebl et al. 2010). Their eco-physiological adaptations to a stratifying water column may account for some of the similarities in their biogeographic pattern in species diversity with the organic dinoflagellates cysts (Fig. 1B; Cermeño et al. 2008a).

Biogeography of community size-structure and environmental co-variables

Size is an important attribute of all living organisms, affecting resource and habitat requirements, metabolic rate, generation time, and predation risk (Brown et al. 2004). In phytoplankton, cell size influences, and, therefore, community size structure is influenced by, light acquisition, nutrient requirements, nutrient diffusion and active uptake parameters, metabolic rate, sinking rates, and grazing susceptibility (Mei et al. 2009, Finkel et al. 2010). Organism size may also be an important factor determining the strength of the latitudinal richness gradient (Hillebrand & Azovsky 2001, Finlay 2002, Hillebrand 2004). In the case of the dinoflagellate cyst assemblages, the maximum potential size range of the assemblage is positively correlated with the richness of the assemblage, but the median size is independent of species richness (Fig. 4).

In marine systems, the proportion of large phytoplankton in an assemblage tends to increase as standing stock chlorophyll concentration, primary productivity, or nutrient availability increases (Chisholm 1992, Li 2002, Chen & Liu 2010). This suggests that richness and average size and the higher size quartiles should increase with nutrient concentration as nutrient supply relieves larger cells from nutrient limitation (Irwin et al. 2006), if grazing pressure does not bias the size distribution (Kiørboe 1993, Thingstad et al. 2005) and light does not become limiting (Finkel et al. 2009). As temperature and nutrient levels are usually negatively correlated (Kamykowski 1987, Steinhoff et al. 2010), small phytoplankton tend to dominate communities in warm, oligotrophic waters, while large cells become increasingly dominant in cold, nutrient-rich waters (Irwin et al. 2006, Daufresne et al. 2009, Kostadinov et al. 2009, Chen & Liu 2010).

In contrast, median dinoflagellate cyst size is negatively correlated with nutrient concentration. It is not that larger dinoflagellates cannot thrive under higher nutrient conditions, but that their growth and survival is inhibited under well-mixed, colder, turbulent waters that are often characterized by higher nutrient concentrations. At any given sea-surface temperature, there is a significant positive correlation between nitrate and phosphate concentrations in surface waters and the median size of the dinoflagellate cyst community, especially the larger cells (75th percentile) (Table 1). While phytoplankton communities, including diatoms, often exhibit an increase in average size and diversity in well-mixed, high-nutrient, high-chlorophyll waters, dinoflagellate assemblages are more likely to exhibit larger sizes in stable water columns with warmer sea surface temperatures and with intermediate to lower nutrient concentrations (Table 1, Fig. 2). In the Southern Hemisphere the increase in cyst size towards higher latitudes is predominantly due to an increase in the dominance of the large endemic species *Selenopemphix antarctica* in the assemblages. The unique physiological adaptations of this species to the cold and turbulent Southern Ocean and its motile affinity are largely unknown (Marret & Zonneveld 2003).

There is a significant decrease in the size of dinoflagellate cysts moving from onshore to offshore waters in the eastern Pacific and equatorial and southern Atlantic (Table 1, Figs. 2B & 3F), which may be related to the high sinking rates of the larger dinoflagellate cysts (Anderson et al. 1985b), secondary transport by offshore currents, or patterns in grazing and microbial degradation. Sinking velocity estimates for dinoflagellate cysts are limited, but the data available indicate that dinoflagellate cysts may sink much faster than vegetative dinoflagellate cells owing to higher cellular densities (Anderson et al. 1985b). As a result, it may be relatively challenging for large cysts to maintain sizable upper mixed-layer populations in deep offshore waters (Table 1, Fig. 3F). As well as slower sinking velocities, smaller dinoflagellate cyst species may have a growth advantage over larger species in offshore, lower nutrient environments. In addition, higher grazing mortality or selective microbial degradation of smaller cysts in onshore regions might contribute to a reduction in the diversity of smaller species (Persson 2000), perhaps contributing to the strong increase in the 25th percentile of cyst size with decreasing water depth (Table 1, Fig. 3F).

SUMMARY

Species richness of organic dinoflagellate cyst communities is positively correlated with sea-surface temperature, especially in cooler waters, likely due to a suite of physiological adaptations to stable water columns. Macronutrient concentration is a positive correlate for species richness, but is secondary to water-column stability. Water-column depth and nutrient concentration are more important correlates than temperature for the size structure of dinoflagellate cyst assemblages. Smaller cells become an increasingly large component of dinoflagellate cyst communities away from the coast. Significant correlations between environmental conditions, temperature, nutrient concentrations, water depth, and the richness and size structure of the dinoflagellate cyst communities differ from other phytoplankton groups. These differences indicate that the unique physiological features of dinoflagellate cyst communities play an important role in determining the biogeographic patterns in species richness and size structure.

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