REVIEW

# Patterns and ecological implications of historical marine phytoplankton change

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ABSTRACT: There is growing evidence that average global phytoplankton concentrations have been changing over the past century, yet published trajectories of change are highly divergent. Here, we review and analyze 115 published phytoplankton trend estimates originating from a wide variety of sampling instruments to explore the underlying patterns and ecological implications of phytoplankton change over the period of oceanographic measurement (1889 to 2010). We found that published estimates of phytoplankton change were much less variable when estimated over longer time series and consistent spatial scales and from the same sampling instruments. Average phytoplankton concentrations tended to increase over time in near-shore waters and over more recent time periods and declined in the open oceans and over longer time periods. Most published evidence suggests changes in temperature and nutrient supply rates as leading causes of these phytoplankton trends. In near-shore waters, altered coastal runoff and increased nutrient flux from land may primarily explain widespread increases in phytoplankton there. Conversely, in the open oceans, increasing surface temperatures are strengthening water column stratification, reducing nutrient flux from deeper waters and negatively influencing phytoplankton. Phytoplankton change is further affected by biological processes, such as changes in grazing regimes and nutrient cycling, but these effects are less well studied at large scales. The possible ecosystem consequences of observed phytoplankton changes include altered species composition and abundance across multiple trophic levels, effects on fisheries yield, and changing patterns of export production. We conclude that there is evidence for substantial changes in phytoplankton concentration over the past century, but the magnitude of these changes remains uncertain at a global scale; standardized long-term measurements of phytoplankton abundance over time can substantially reduce this uncertainty.

KEY WORDS: Phytoplankton · Marine · Trend · Drivers · Consequences · Global · Change · Ecological

## INTRODUCTION

Marine phytoplankton are a diverse group of pelagic photosynthetic microbes that provide over 90% of marine primary production (Charpy-Roubaud & Sournia 1990). Individual cells range over 4 orders of magnitude in size (~0.2 to 1000 µm; Fig. 1A; Sheldon

et al. 1972, Margalef 1978, Falkowski et al. 2004) and are globally distributed. Although marine phytoplankton account for only 0.2% of global photosynthetic carbon biomass, they generate 46.2% of the primary production (Field et al. 1998). To achieve this, the global standing stock of phytoplankton turns over every 2 to 6 d on average (Behrenfeld & Fal-

kowski 1997). Due to this rapid turnover (Fig. 1A), phytoplankton growth often depletes available nutrient resources.

Over a century of scientific research has shown that marine phytoplankton play an important role in determining the structure and functioning of marine ecosystems (Chavez et al. 2003, Richardson & Schoeman 2004) and can have large effects on fisheries yields (Ryther 1969, Chavez et al. 2003, Ware & Thomson 2005, Chassot et al. 2007, 2010), biogeochemical cycles (Redfield 1958, Falkowski et al. 1998), climate regulation (Charlson et al. 1987, Murtugudde et al. 2002), and weather patterns (Gnanadesikan et al. 2010). Reflecting this scientific interest, the proportion of peer-reviewed scientific studies of marine phytoplankton has increased markedly over time (Fig. 1B).

Despite these increased research efforts, one of the most fundamental questions in phytoplankton research remains poorly resolved: How are average marine phytoplankton biomass concentrations changing over the long term? Answering this seemingly simple question is complicated by the fact that phytoplankton concentrations are highly variable in space and time and are difficult to distinguish from other marine microbes and particles, making it difficult to obtain direct measurements of their carbon biomass. As a consequence, the total concentration of the light-harvesting pigment chlorophyll, which is present in all phytoplankton cells, has been used as a first-order proxy of abundance and biomass. Despite documented variability in the phytoplankton chlorophyll:carbon ratio (Geider 1987), chlorophyll continues to be the most practical and extensively used proxy of phytoplankton carbon biomass over large spatial scales (Huot et al. 2007, Henson et al. 2010). This review deals with changes in phytoplankton concentrations as measured via ocean color and chlorophyll assessed over the era of oceanographic measurement, 1889 to 2010, and at regional to global scales. We did not attempt to include the literature on phytoplankton cell counts or species composition and make only limited inferences on changes in primary production. Following this, we review the physical and biological drivers of long-term marine phytoplankton change. We conclude by summarizing some potential ecosystem consequences of phytoplankton change both across ecosystems and globally.
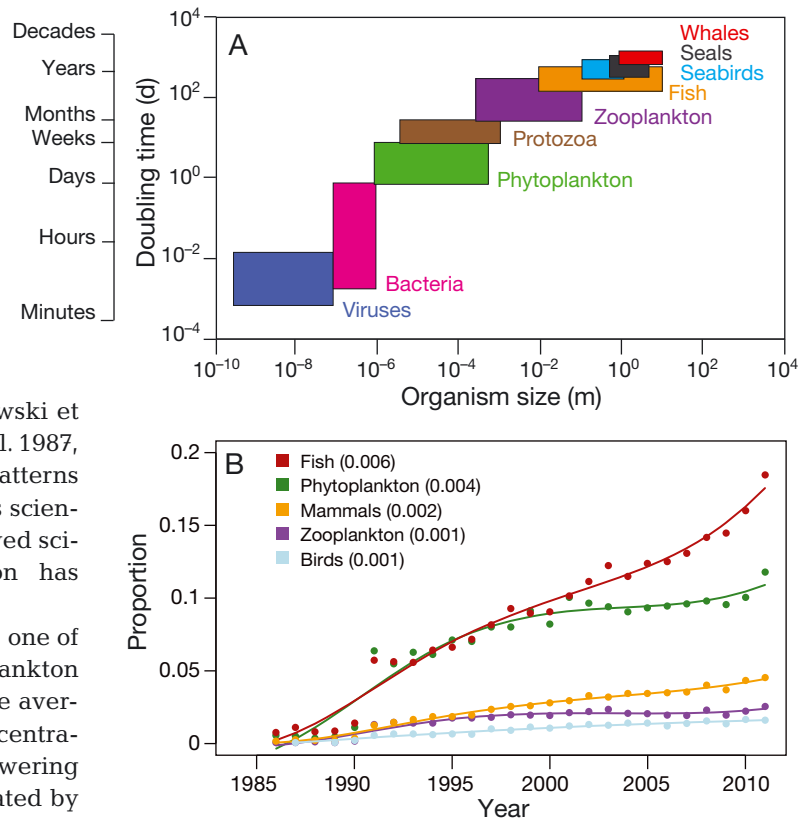


Fig. 1. Phytoplankton in the scientific literature. (A) Dominant space and time scales at which major groups of marine organisms operate. The average size range (*x*-axis) is plotted as a function of the average doubling time (*y*-axis) for various marine groups. Phytoplankton are represented in green. Figure was adapted after Murphy et al. (1988). (B) Time trends in the scaled proportion of peer-reviewed studies reporting on major marine species groups (1985–2010; see Supplement at www.int-res.com/articles/suppl/m534p251_supp.pdf for details). Taxonomic groups are represented as colors, with the linear rates of change over time reported in brackets

## MATERIALS AND METHODS

### Phytoplankton trends

We systematically searched scientific databases to identify peer-reviewed studies of temporal marine phytoplankton change. Our literature search covered a minimum of ~22 million articles from over 16 500 peer-reviewed journals. We limited our search to publications estimating phytoplankton change from chlorophyll concentrations or ocean color collected from the upper ocean at multi-year scales (>5 yr). Studies conducted in fresh or brackish waters were not included. We extracted 115 phytoplankton time series and estimates of temporal phytoplankton change from 25 publications (Table 1).

To standardize measurements that were reported in different units, we extracted the estimated total percentage change in phytoplankton over the available time span as reported by the authors. In some cases, data extraction software was used to extract and calculate these rates (www.getdata-graph-digitizer.com). Where the time series were extracted from the publication, we fitted linear time series models to the observations and calculated the total percentage change as the difference between the average concentration at the start and end of the fitted time series referenced to the initial value. The percent change was then divided by the length of the time series to yield the standardized percent change per year, relative to the initial phytoplankton concentration. To spatially standardize the rates of change, we binned all estimates into 5° × 5° cells. This resolution was selected because the majority of published phytoplankton time series were estimated over spatial domains equal to or greater than 5°. The extracted trends were also referenced according to the sampling instrumentation used to generate the underlying time series: (1) *in situ*, (2) contemporary remote sensing, (3) Secchi disk, (4) continuous plankton recorder (CPR), (5) Forel-Ule, and (6) multi-sensor. Multi-sensor trends are those which were generated by combining measurements from 2 or more of these sampling instruments.

## Variability of phytoplankton trends

The direction and magnitude of phytoplankton time trends reported in the literature have been widely conflicting (Venrick et al. 1987, Falkowski & Wilson 1992, Antoine et al. 2005, Gregg et al. 2005, Behrenfeld et al. 2006, Boyce et al. 2010, 2014, Wernand et al. 2013). To better understand the factors that may explain this variability, we estimated the standard deviation ($\sigma$) of the standardized phytoplankton trends that were available within each 5° × 5° cell. We then used statistical models to estimate what combination of predictors would best explain the variability in the phytoplankton trend estimates ($\sigma$). To account for the spatial dependence between trend variances ($\sigma$) within each 5° × 5° cell, we estimated the

trend variability as a function of several covariates within a generalized least-squares model as:

$$\log_{10}[\sigma_i] = \beta_0 + \beta_1 Predictor_i + \varepsilon_i \quad (1)$$

where $\sigma_i$ is the standard deviation of the trends in cell$_i$, which was log transformed to ensure normality; $\beta_0$ is the model intercept; $\beta_1$ is the rate of response change as a function of the predictor in question; and $\varepsilon_i$ is the model error, specified as:

$$\varepsilon \sim N(0,\delta) \quad (2)$$

where 0 is the mean, and $\delta$ is the error covariance matrix. To account for spatial autocorrelation, the covariance parameters of $\delta$ were assumed to follow a spatially dependent process, whereby the correlation between them decreases exponentially with increasing spatial separation (Cressie 1993). Using this approach, we quantitatively estimated the influence of several predictors on the variability of phytoplankton time trends. Predictor variables tested include the number and type of sampling instrument, range and variance of the spatial and temporal extent of the trends, average time series length, average baseline year of the trend, distance of the cell from the nearest coast, measurement units of the trend, and ocean basin where the trend was estimated.

Table 1. Published phytoplankton time series reviewed here. CPR: continuous plankton recorder; BU: bottom-up; TD: top-down; B: both; −: not investigated

| Reference | Start-end year | Span (yr) | Instrument | Driver |
|---|---|---|---|---|
| Aebischer et al. 1990 | 1955–1987 | 32 | CPR | BU |
| Aksnes & Ohman 2009 | 1949–2007 | 58 | Secchi | BU |
| Antoine et al. 2005 | 1979–2002 | 23 | Satellite | − |
| Behrenfeld et al. 2006 | 1997–2006 | 9 | Satellite | BU |
| Boyce et al. 2010 | 1899–2008 | 109 | Blended | BU |
| Boyce et al. 2014 | 1890–2010 | 120 | Blended | BU |
| Chavez et al. 2011 | 1989–2009 | 20 | *In situ* | − |
| Falkowski & Wilson 1992 | 1900–1981 | 81 | Secchi | − |
| Frank et al. 2005 | 1962–2002 | 40 | CPR | TD |
| Goes et al. 2005 | 1997–2004 | 7 | Satellite | BU |
| Gregg & Conkright 2002 | 1979–2000 | 21 | Blended | − |
| Gregg et al. 2005 | 1998–2003 | 5 | Satellite | − |
| Head & Pepin 2010 | 1998–2006 | 8 | CPR | − |
| Karl et al. 2001 | 1969–1998 | 29 | *In situ* | BU |
| Saba et al. 2010 | 1990–2007 | 17 | *In situ* | B |
| McQuatters-Gollop et al. 2007 | 1948–2003 | 55 | CPR | − |
| McQuatters-Gollop et al. 2011 | 1948–2008 | 60 | CPR | − |
| Montes-Hugo et al. 2009 | 1978–2006 | 28 | Satellite | BU |
| Motoda et al. 1987 | 1949–1969 | 20 | *In situ* | B |
| Raitsos et al. 2005 | 1948–2002 | 54 | CPR | − |
| Shiomoto et al. 1997 | 1985–1994 | 9 | *In situ* | TD |
| Sugimoto & Tadokoro 1997 | 1972–1973 | 21 | *In situ* | B |
| Suikkanen et al. 2007 | 1979–2003 | 24 | *In situ* | BU |
| Venrick et al. 1987 | 1968–1985 | 17 | *In situ* | BU |
| Wernand et al. 2013 | 1889–1999 | 110 | Forel-Ule | − |

## Average phytoplankton trends

Based on the results of the analysis of trend variance in the previous paragraph (Eqs. 1 & 2), we calculated the mean rate of phytoplankton change from the extracted trend estimates for each individual 5° × 5° cell while minimizing the major factors influencing trend variation (see 'Results' for details). As an additional sensitivity check, we calculated mean rates of phytoplankton change weighted by the length of the time series used to generate the trend (years), but this did not influence the results.

## Patterns of phytoplankton change

To explore patterns of similarity and dissimilarity among the phytoplankton trends, we identified reported trends which were coincident in space and time. Published estimates where the proportion of spatial and temporal overlap of the trends was greater than 50% were identified as coincident. We then looked for patterns within these coincident trends concerning the degree of agreement in the direction and magnitude of the time trends.

## RESULTS AND DISCUSSION

### Summary of phytoplankton trends

The majority of the extracted phytoplankton trends spanned less than 23 yr, were initiated after 1978, and extended over areas less than $73 \times 10^5$ km$^2$ (approximately half the size of the Arctic Ocean; Fig. 2A). The majority of the trends were estimated from time series derived from *in situ* (36%), satellite remote sensing (32%), or multiple (31%; Fig 2A, inset) sampling instruments. The remaining trends were inferred from time series of water column transparency measurements using the standardized Secchi disk (15%; Secchi 1886), CPR (13%), or semi-quantitative assessments of ocean color using the Forel-Ule color scale (3%; Forel 1890). The extracted trend estimates were globally distributed, but their availability was greatest in the Northern Hemisphere and closer to the coasts, and they were sparsely distributed at high latitudes and in the Southern Hemisphere (Fig. 2B). The estimates of phytoplankton change were observed to be larger and more variable over shorter time intervals (Fig. 2C).

## Variability of phytoplankton trends

The variability between estimated phytoplankton time trends within each 5° × 5° cell was found to differ spatially (Fig. 3A) and was well predicted by both intrinsic and extrinsic factors (Table 2). Phytoplankton trend variability was best predicted by the ocean basin where the trend was recorded (r$^2$ = 0.66; p < 0.0001), trend variability being highest in the North Indian and North Atlantic Oceans and lowest in the Arctic and Southern Oceans (Fig. 3B). Phytoplankton trends also become progressively more variable when more sampling instruments were used (r$^2$ = 0.6; p < 0.0001), when estimated over shorter (i.e. less than ~55 yr; r$^2$ = 0.51; p < 0.0001) and more recent (i.e. after ~1975; r$^2$ = 0.48; p < 0.0001) time periods, and when the trends were estimated over different spatial extents (r$^2$ = 0.25; p < 0.0001; Fig. 3C–E). The type of sampling instrument used was also a significant predictor in some cases. Trend variability within a cell (σ) was significantly increased by the addition of trends derived from remote sensing (r$^2$ = 0.62; p < 0.0001) or Forel-Ule (r$^2$ = 0.24; p < 0.0001) observations. Since trends derived from multiple sampling instruments were available in all 5° × 5° cells globally, it was not possible to explore what effect including or removing these trends would have on the trend variance in a given cell. However, separating trends into those which were estimated from single instruments and those which used multiple instruments suggested that trends estimated by combining measurements from multiple instruments were typically less variable than those estimated from single instruments (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m534p251_supp.pdf). This pattern may partly be driven by the generally longer time series length of trends estimated from combined data sources.

## Average phytoplankton trends

We calculated average rates of phytoplankton change within each 5° × 5° cell using extracted trend estimates which were approximately coincident in time and estimated with the same sampling instruments. Following these guidelines, we calculated average time trends in phytoplankton over 4 intervals:

(1) Oceanographic era: 1890–1920 to 1980–2010, derived from direct measurements of ocean color, Secchi depth, and *in situ* chlorophyll concentrations (4 studies; 3 instruments).
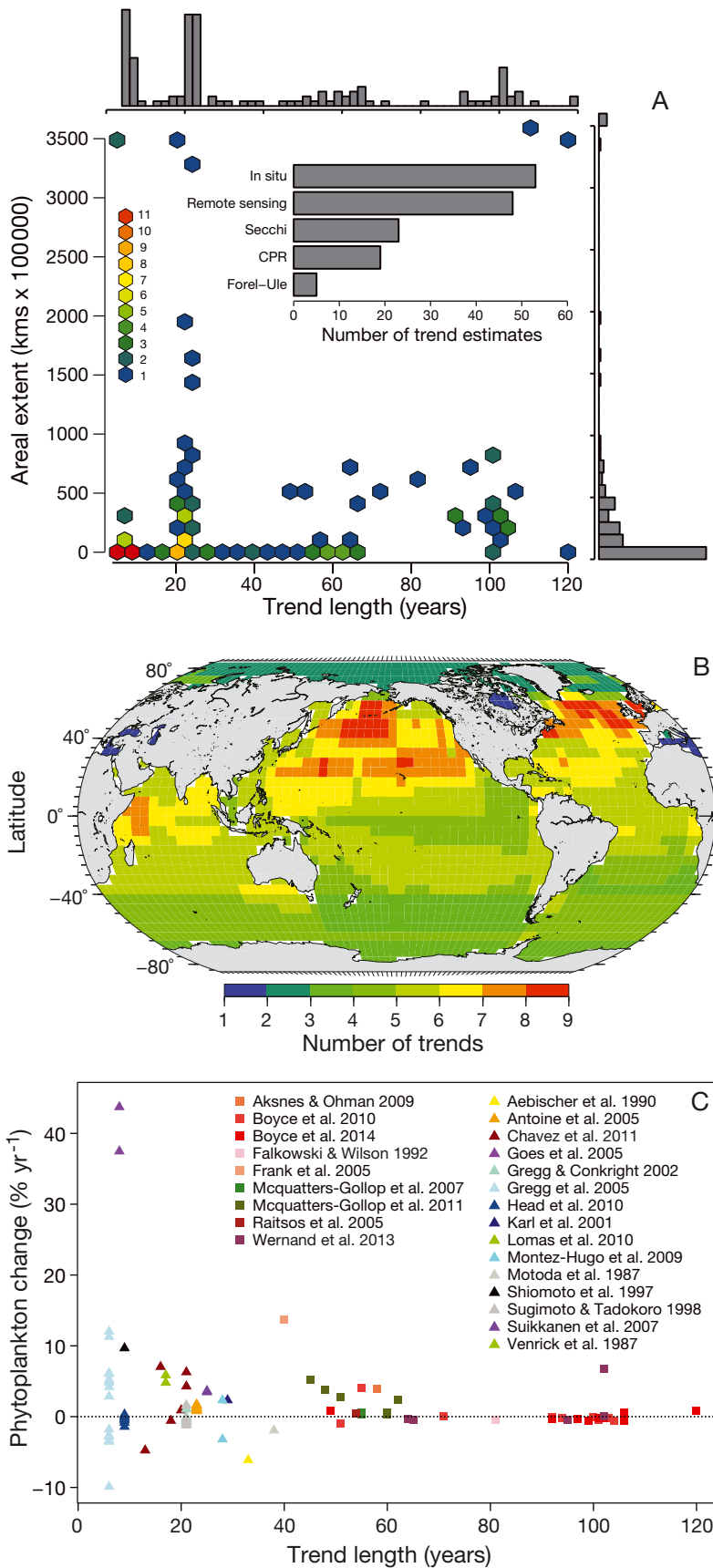
(2) Early satellite era: 1975 to 2000–2010, derived using remote sensing measurements (3 studies; 2 instruments);

(3) Contemporary satellite era: 1995–2005 to 2005–2010, derived using remote sensing measurements (3 studies; 1 instrument);

(4) CPR era: 1945–1955 to 1990–2010, derived using CPR measurements (4 studies; 1 instrument).

Although 36% of all extracted trends were derived from *in situ* sampling instruments, most of these could not be incorporated into our analysis, as they tended to be available over time periods which did not coincide with any other studies. Further, the average rates of change over the oceanographic era were derived from 4 studies which were similar in the spatio-temporal extent but estimated time trends using 3 different sampling instruments.

Long-term rates of change suggested declining trends over much of the ocean, except for the North Atlantic, where large increases were driven by possibly unrealistic estimates (6.7% yr$^{-1}$) derived from semi-quantitative Forel-Ule ocean color measurements (Wernand et al. 2013; Fig. 4A). Most estimates over this period suggested declining trends across the North and equatorial Pacific oceans. This contrasts greatly with satellite-derived

Fig. 2. Phytoplankton time series data. (A) Standardized number of phytoplankton trend estimates as a function of trend length and areal extent. Colours denote the number of phytoplankton trend estimates. Histograms in the outer margins depict the frequency distribution of the trends as a function of trend length and areal extent. Inset depicts the number of phytoplankton time trends estimated using measurements collected from different sampling instruments. (B) Spatial distribution of all phytoplankton trend estimates. Colors depict the number of trends per 5° × 5° cell. (C) Standardized rate of phytoplankton change over time as a function of trend length. Long-term trends that transcend scales of natural variability (35 yr; Henson et al. 2010, Beaulieu et al. 2013) are shown as squares; all others are shown as triangles. Colors identify the source publication. The horizontal dashed line denotes no change. CPR: continuous plankton recorder
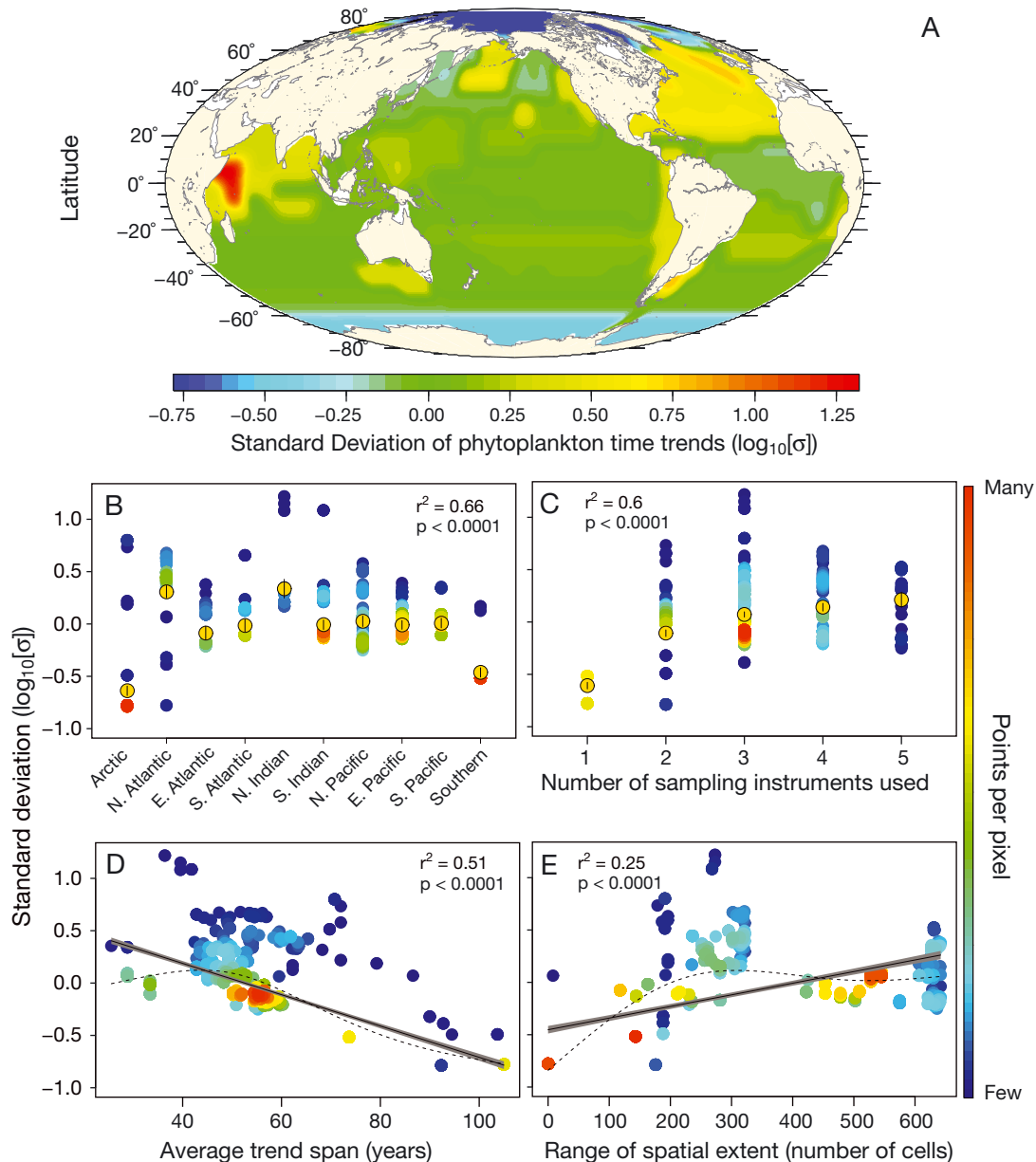
Fig. 3. Phytoplankton trend variability. (A) Standard deviation between extracted trends within each 5° × 5° cell. Colors depict the $\log_{10}$-transformed standard deviation calculated within each cell using all available phytoplankton trend estimates and spatial interpolation. (B–E) Strong univariate predictors of phytoplankton trend variability across all 5° × 5° cells. (B) Ocean basin where the trend was reported, (C) number of sampling instruments present in the cell, (D) average length of time spanned by all trends in a cell, and (E) differences (range) between the spatial extent of trends in a cell. For (B–E), colours depict the density of the points, where blue represents few and red represents many points per pixel. Yellow points (B,C) and trend lines (D,E) are generalized least squares model-predicted phytoplankton trend variability values (standard deviation). Vertical lines (B,C) or shaded regions (D,E) are the 95% confidence limits about the model estimates. Broken lines in (D) and (E) are estimates from generalized additive models (GAMs). All relationships are statistically significant (p < 0.0001)

estimates since the late 1970s, suggestive of large-scale phytoplankton increases, except in the Southern Ocean (Fig. 4B). Again, these trends were largely driven by one study, which reported coherent increases in phytoplankton biomass since 1979 (Antoine et al. 2005). Satellite estimates since 1997

suggest spatially variable rates of change, with declines in open ocean regions and increases in nearshore areas (Fig. 4C). Estimates derived from CPR measurements indicate large increases across the temperate North Atlantic Ocean (35 to 65°N) since ~1955 (Fig. 4D).

Table 2. Summary of univariate generalized least-squares model estimation of the factors influencing phytoplankton time trend variability. Akaike's information criterion (AIC) indicated the information-theoretic quality of the selected model; lower values denote higher quality. CPR: continuous plankton recorder

| Predictor | Effect | $r^2$ | AIC |
|---|---|---|---|
| Ocean basin | Ocean basin where trend was estimated | 0.66 | −1231 |
| Data: remote sensing | Inclusion of remote sensing-derived trends | 0.62 | −1645 |
| Sampling instrument | Number of sampling instruments used to derive estimates in the cell | 0.60 | −1314 |
| Time series span | Average trend length within cell | 0.51 | −1431 |
| Trend start year | Minimum baseline year of all trends | 0.48 | −1389 |
| Spatial range | Difference between spatial coverage of trends in cell | 0.25 | −750 |
| Data: Forel-Ule | Inclusion of CPR-derived trends | 0.24 | −588 |
| Spatial variability | Variability between spatial coverage of trends in cell | 0.22 | −677 |
| Data: CPR | Inclusion of CPR-derived trends | 0.08 | −369 |
| Units | Number of trend response units in cell | 0.05 | −353 |
| Data: *in situ* | Inclusion of *in situ*-derived trends | 0.02 | −342 |
| Data: Secchi | Inclusion of Secchi-derived trends | 0.02 | −322 |
| Distance | Distance of cell from the coastline | 0.01 | −321 |
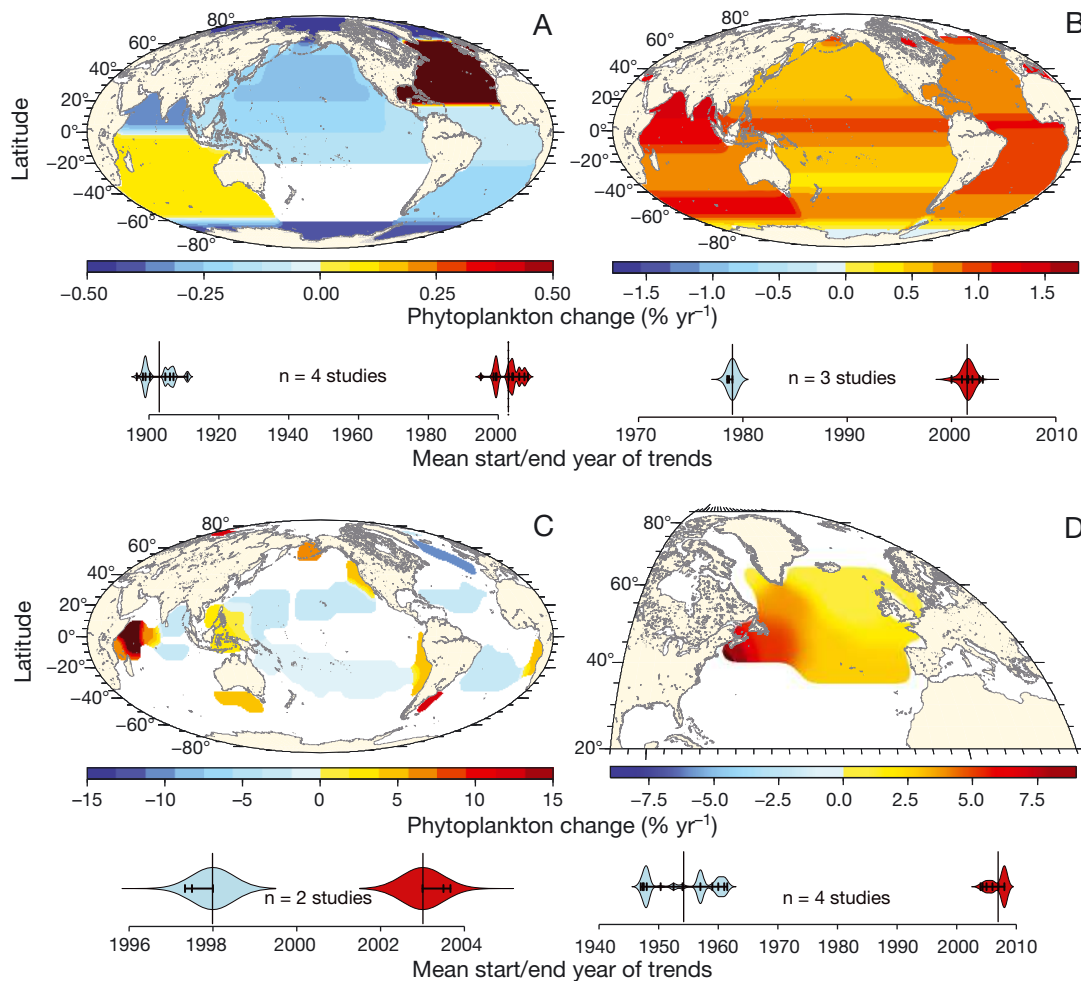


Fig. 4. Average phytoplankton change over different time scales and sampling instruments. Average rate of phytoplankton change from (A) direct oceanographic measurements of chlorophyll, ocean color, and transparency since 1890; (B) satellite observations since 1975; (C) contemporary satellite observations since 1995; and (D) continuous plankton recorder measurements since 1945. Colors within the maps depict the average rate of phytoplankton change within each 5° × 5° cell and are spatially interpolated; white depicts no data. The plots below each map are the distributions of the start (blue) and end (red) years for all trends. The long vertical lines represent the averages, and the marine vertical ticks are the actual start and end values for each trend
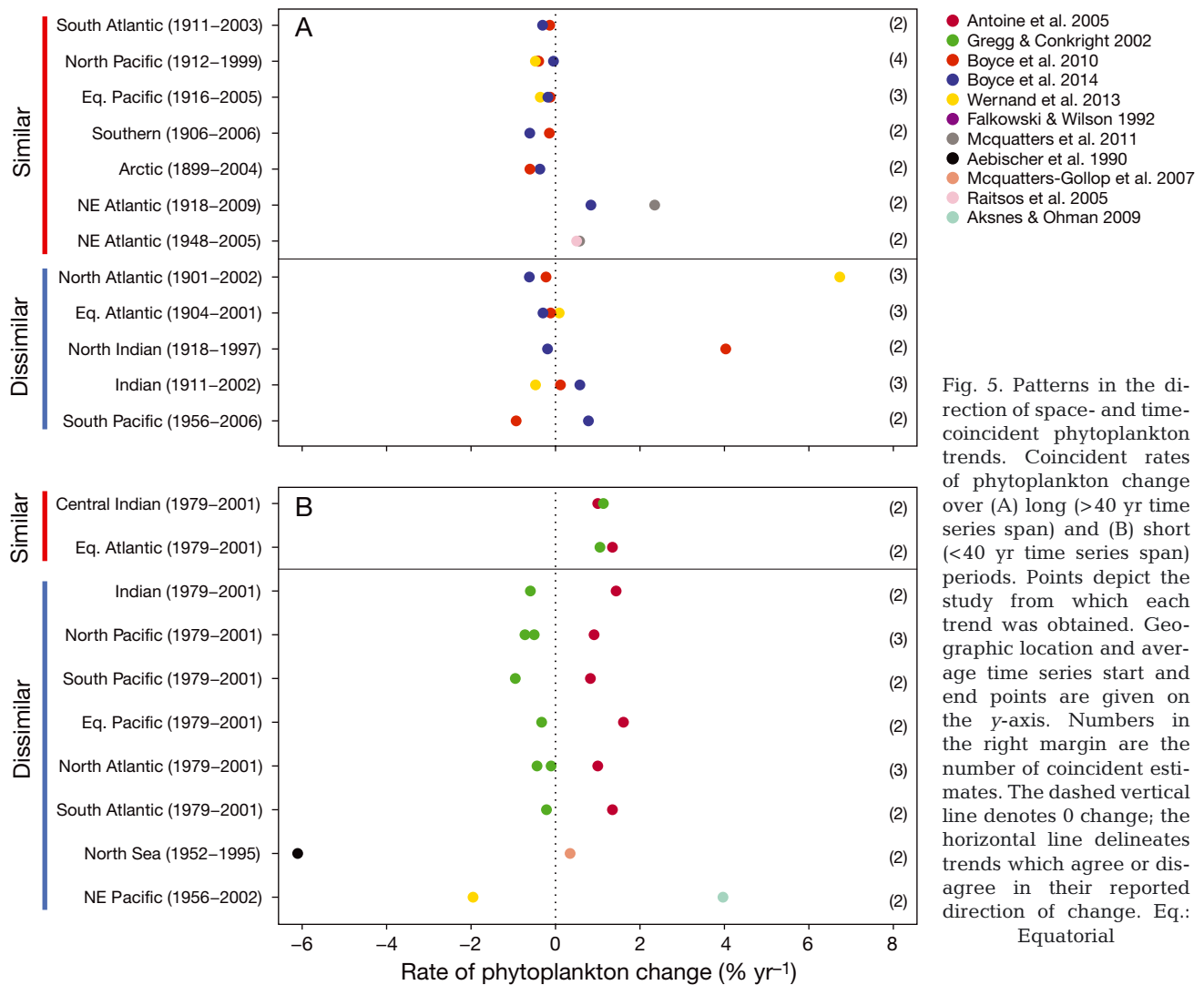
Fig. 5. Patterns in the direction of space- and time-coincident phytoplankton trends. Coincident rates of phytoplankton change over (A) long (>40 yr time series span) and (B) short (<40 yr time series span) periods. Points depict the study from which each trend was obtained. Geographic location and average time series start and end points are given on the y-axis. Numbers in the right margin are the number of coincident estimates. The dashed vertical line denotes 0 change; the horizontal line delineates trends which agree or disagree in their reported direction of change. Eq.: Equatorial

## Patterns of phytoplankton change

Although the average phytoplankton trends were generally variable (Fig. 4), examining only those reported trends which were coincident in space and time enabled us to identify instances where the direction and magnitude of change were in agreement. Long-term phytoplankton trends in the North and equatorial Pacific Oceans all indicated declining trends (Fig. 5A). Phytoplankton trends in the North and equatorial Pacific Oceans were estimated from measurements of Secchi depth, water colour, or *in situ* chlorophyll between ~1911 and ~2003 and suggested that phytoplankton had declined at rates of between −0.48 (Wernand et al. 2013) and −0.05% yr⁻¹ (Boyce et al. 2014). Three phytoplankton trends in the Northeast Atlantic Ocean also showed good

agreement and suggested an increase between ~1918 and ~2009 at a rate of change between 0.5 (Raitsos et al. 2005) and 2.4% yr⁻¹ (McQuatters-Gollop et al. 2011). Long-term trends in the Arctic and Southern Oceans also agreed, but this is perhaps unsurprising, since they were estimated using similar data sources and methods (Boyce et al. 2010, 2014).

Phytoplankton trends in the North Atlantic Ocean appeared to be particularly variable, and both long- and short-term phytoplankton trends there disagreed widely in terms of sign and magnitude of change (Fig. 5). While limited data availability may contribute variability and disagreement among trends in the Indian, South Atlantic, and South Pacific Oceans, this is not the case in the North Atlantic (Boyce et al. 2012). To some extent, the high trend variability there is driven by unrealistic rates of

change (6.7% yr$^{-1}$) estimated from semi-quantitative ocean color measurements (Wernand et al. 2013). However, even after removing this outlier, variability in the North Atlantic Ocean remained high. Interestingly, similar variability has been predicted for future estimates of phytoplankton change derived from ocean circulation models, which are also highly divergent in the North Atlantic Ocean (Henson et al. 2010). As the North Atlantic is subject to strong variability on seasonal, decadal, and multi-decadal time scales (Martinez et al. 2009, Boyce et al. 2010), it is likely that high natural variability masks smaller inter-annual changes that are occurring (Henson et al. 2010).

Again, we observed that coincident trends available over shorter time periods tended to be more variable and less similar in the direction of change (Fig. 5B). This likely reflects quasi-periodic climate variability, which may strongly influence shorter-term (less than ~27 to ~40 yr) trends (Behrenfeld et al. 2006, Martinez et al. 2009, Boyce et al. 2010, Henson et al. 2010, Chavez et al. 2011, Beaulieu et al. 2013). As such, some of the trends reported here, particularly those estimated from contemporary remote sensing estimates of ocean color (Fig. 4B,C), may reflect climate-driven variability rather than sustained long-term changes. Phytoplankton trend estimates were observed to switch from negative to positive through time and with proximity to the nearest coastline (Fig. S2 in the Supplement), similar to the findings of other long-term studies (Boyce et al. 2010,

2014). Phytoplankton declines in the open oceans have also been observed previously (Gregg & Conkright 2002, McClain & Signorini 2004, Polovina et al. 2008) and are predicted to continue into the future (Polovina et al. 2011). Increases in nearshore waters are well documented in many regions and are likely related to increasing coastal eutrophication there (see 'Environmental conditioning' for further details).

## Phytoplankton trends in the 21st century

Similar to our results from observational measurements, predicted patterns of future phytoplankton change from process-based ocean models are variable (Table 3). Despite this variability, 15 of 18 studies (83%) predict a global phytoplankton decline over the next century. Most predictions suggested phytoplankton increases at high latitudes and declines at low and middle latitudes (Schmittner et al. 2008, Henson et al. 2010, Steinacher et al. 2010, Hofmann et al. 2011, Mora et al. 2013). Some of the largest and most variable declines are predicted to occur in the North Atlantic Ocean (Henson et al. 2010, Steinacher et al. 2010, Mora et al. 2013), where published empirical estimates are also highly variable. This suggests that temporal phytoplankton dynamics in the North Atlantic are particularly difficult to constrain from both empirical estimates (Boyce et al. 2014) and process-based models (Table 3).

Table 3. Published projections of future changes in phytoplankton chlorophyll (Chl), carbon biomass (C), or primary production (PP). $CO_2$: carbon dioxide

| Reference | Simulation range (yr AD) | Span (yr) | Response | Change | Unit | Forcing |
|---|---|---|---|---|---|---|
| Hofmann et al. 2011 | 2000–2200 | 200 | Chl | −50 | % | $CO_2$ |
| Schmittner et al. 2008 | 2000–4000 | 2000 | Chl | +5 | % | $CO_2$ |
| Henson et al. 2010 | 2001–2100 | 99 | Chl | −0.0002 | mg m$^{-3}$ yr$^{-1}$ | Temperature |
| Boyd & Doney 2002 | 2000–2080 | 80 | Chl | −8.5 | % | $CO_2$ |
| Beaulieu et al. 2013 | 2001–2100 | 99 | Chl | $-1.53 \times 10^{-4}$ | mg m$^{-3}$ yr$^{-1}$ | $CO_2$ |
| Olonscheck et al. 2013 | 2000–2100 | 100 | Chl | −50 | % | $CO_2$ |
| Mora et al. 2013 | 2014–2100 | 86 | C | −4 | % | $CO_2$ |
| Mora et al. 2013 | 2014–2100 | 86 | C | −10 | % | $CO_2$ |
| Henson et al. 2010 | 2001–2100 | 99 | PP | −0.15 | mg C m$^{-2}$ d$^{-1}$/yr | Temperature |
| Sarmiento et al. 2004 | 2040–2060 | 20 | PP | +4.4 | % | Temperature |
| Taucher & Oschlies 2011 | 2000–2100 | 100 | PP | −5.3 | % | Temperature |
| Bopp et al. 2001 | 2000–2080 | 80 | PP | −8.9 | % | $CO_2$ |
| Bopp et al. 2001 | 2000–2080 | 80 | PP | −8.5 | % | $CO_2$ |
| Boyd & Doney 2002 | 2060–2070 | 10 | PP | −5.5 | % | $CO_2$ |
| Steinacher et al. 2010 | 1860–2099 | 239 | PP | −11 | % | $CO_2$ |
| Schmittner et al. 2008 | 2000–4000 | 2000 | PP | +100 | % | $CO_2$ |
| Cermeño et al. 2008 | 2000–2100 | 100 | PP | −14 | % | $CO_2$ |
| Cox et al. 2000 | 2000–2100 | 100 | PP | −5 | % | $CO_2$ |

### Drivers of phytoplankton change

To the first order, phytoplankton cell growth is determined by the availability of sunlight and macronutrients (bottom-up processes) as well as grazing, viral infection, auto-catalyzed programmed cell death (PCD; Agusti et al. 1998, Bidle & Falkowski 2004), pathogenic bacteria, and fungi (top-down processes). Based on this, we discuss drivers of plankton change in the context of changes in (1) physical forcing and (2) biological forcing, which may alter the strength of bottom-up and top-down processes on marine phytoplankton.

#### Physical forcing

Particularly in the open oceans, which account for 90% of the ocean surface, studies have observed phytoplankton growth and productivity to be strongly driven by physical processes, such as mixing and upwelling, which control nutrient flux (Oschlies & Garcon 1998, McGillicuddy et al. 2007). Passive diffusion across the thermocline (Chavez & Toggweiler 1995), biological nitrogen fixation (Capone et al. 1997), and the atmospheric deposition of iron are also of regional importance (Behrenfeld et al. 1996). Hence, it is likely that the observed chlorophyll declines in open ocean regions (Figs. 4C & 5) are driven by factors affecting these processes. Primary among these is increasing sea surface temperature, which generally leads to reduced mixing depth, enhanced stratification, and reduced nutrient flux from deeper waters. Studies using observational measurements have reported strong temperature-driven stratification (TDS) effects on phytoplankton concentration at seasonal (Lozier et al. 2011), inter-annual (Behrenfeld et al. 2006), multi-decadal (Martinez et al. 2009), and geological time scales (Romero et al. 2011, Vermeij 2011). Analyses of satellite observations suggest that TDS may also be leading to an expansion of the low-chlorophyll gyres of the open oceans (McClain & Signorini 2004, Polovina et al. 2008); bio-physical models also predict this expansion to continue over the coming century (Polovina et al. 2011). Studies using empirical observations (Behrenfeld et al. 2006, Boyce et al. 2010, Boyce 2013) and process-based models (Henson et al. 2010) have provided strong empirical evidence that TDS effects on phytoplankton also vary by latitude, with strong negative effects at low and middle latitudes but positive effects at high latitudes. This pattern of change is partly at odds with observations, which suggest declining trends at high latitudes (>70°N or S; Fig. 4A,B). In well-mixed high-latitude oceans, increasing TDS may positively influence phytoplankton growth by retaining phytoplankton cells above the critical depth (Sverdrup 1953, Jacobs et al. 2002, Montes-Hugo et al. 2009, Arrigo et al. 2012) or by modifying phytoplankton–grazer interactions (Behrenfeld 2010). Process-based models also predict that over the coming century, rising temperatures may lead to reduced ice cover and increased light availability; combined with a longer growing season, this may lead to increased phytoplankton biomass and productivity at high latitudes (Schmittner et al. 2008, Henson et al. 2010, Steinacher et al. 2010, Mora et al. 2013). Large-scale phytoplankton trend estimates are generally less available at these high latitudes (Fig. 2B), likely contributing to the variability of the empirical estimates of change there.

Experimental, field, and modeling studies suggest that TDS may also lead to declines in the concentration of larger phytoplankton species such as diatoms and increases in smaller species such as small flagellates and cyanobacteria (Li et al. 2009, Morán et al. 2010, Barnes et al. 2011, Boyce et al. 2015a). These effects may be related to different nutrient uptake strategies between large and small phytoplankton species (Bopp et al. 2005, Cermeño et al. 2008, Li et al. 2009), the temperature-size rule (Atkinson 1994, Atkinson et al. 2003, Morán et al. 2010), or increased sinking rates of larger phytoplankton species (Rodríguez et al. 2001).

Changes in a range of additional physical variables such as wind intensity or salinity may modify the influence of temperature on stratification and nutrient flux in some locations. For instance, observations of changing wind intensity over the past century will have large effects on upwelling intensity, including highly productive Eastern Boundary Current systems (Bakun 1990, Vecchi et al. 2006). In the Indian Ocean, warming of the Eurasian land mass has been linked to intensifying monsoon winds and upwelling, leading to reported phytoplankton increases of 300 to 350% (Goes et al. 2005; Fig. 4B,C; Table 1). Wind-driven atmospheric deposition of iron is of regional importance to phytoplankton growth (Behrenfeld et al. 1996). In polar oceans, melting sea ice has been linked to increased upper-ocean irradiance and reduced surface salinity, which may have stronger effects on phytoplankton than TDS (Lee et al. 2012, Post et al. 2013). Increasing ocean acidification may also alter phytoplankton community structure, benefiting smaller species and possibly hindering calcifying ones (Orr et al. 2005, Iglesias-Rodríguez et al.

2008, Beaufort et al. 2011, Riebesell et al. 2013). Acidification-driven reductions in the bioavailability of iron could also lead to phytoplankton declines in expansive high-nutrient, low-chlorophyll regions of the ocean (Shi et al. 2010).

### Biological forcing

*Trophic control.* Consumers may drive changes in phytoplankton biomass and species composition through their trophic (feeding) behaviour. These effects may be caused by modified grazing pressure (direct) or by changes to other consumers which may propagate across multiple trophic links, ultimately modifying grazing pressure (indirect). For instance, the removal of a top predator from the Northwest Atlantic ecosystem led to cascading trophic effects which may have contributed to a long-term (~40 yr) increase in phytoplankton there (Frank et al. 2005, 2011). Such trophic cascades have been observed across diverse ecosystems but often weaken at the plankton level (McQueen et al. 1986, Micheli 1999, Shurin et al. 2002, Baum & Worm 2009, Boyce et al. 2015b). While it is unclear what factors determine the occurrence and strength of such cascades, the intensity of fisheries exploitation is likely a contributing factor (Frank et al. 2005, 2006, Myers et al. 2007, Baum & Worm 2009). It is also possible that short food chains with fewer trophic transfers between predators and producers may be more susceptible to cascading effects, with reduced diversity and lower functional redundancy rendering the systems generally less stable (Frank et al. 2006, Worm et al. 2006, Casini et al. 2008). Grazing pressure (Loeb et al. 1997, Sommer et al. 2007), heterotrophic bacterial activity (Llewellyn et al. 2008), and viral infection (Suttle 1994) can all be influential in controlling phytoplankton concentrations. Experimental and modeling studies also show that ocean warming induces a more rapid metabolic response in heterotrophs as compared to autotrophs, which leads to increased grazer control and reduced standing biomass of phytoplankton (O'Connor et al. 2009, Lewandowska et al. 2014), although this effect also appears to be context-specific (Lewandowska et al. 2014).

*Environmental conditioning.* Marine organisms modify their environment through a range of non-trophic activities, thereby promoting or inhibiting phytoplankton growth in a process termed environmental conditioning (Smetacek 2008). For instance, whales and seals forage at depth and excrete fecal plumes in surface waters. In this manner, essential macronutrients such as nitrogen and iron are transported from deeper to surface waters, promoting phytoplankton growth. Changes in this so-called whale pump have been suggested as a possible driver of phytoplankton change in some regions (Smetacek 2008, Lavery et al. 2010, 2014, Roman & McCarthy 2010). Particularly, long-term reductions in whale biomass in the Northwest Atlantic (Roman & Palumbi 2003) and Southern (Smetacek 2008) Oceans may have led to reduced efficiency of the whale pump and could contribute to observed long-term phytoplankton declines there (Boyce et al. 2010, 2014).

The activities of biological organisms may also influence phytoplankton through their effects on ocean mixing (Munk 1966). Kinetic energy generated by swimming organisms could account for 33% of global ocean mixing; this is comparable to wind- or tidal-driven mixing (Dewar et al. 2006). Observational studies have also reported that the swimming activities of krill may induce 4 orders of magnitude increases in turbulence in nearshore waters (Kunze et al. 2006). Given the global distribution and large biomass of vertically migrating marine organisms (Gjosaeter & Kawaguchi 1980, Irigoien et al. 2014), biologically generated turbulence may have larger impacts on the global flux of nutrients to phytoplankton in surface waters than previously recognized. The harvesting of large-bodied consumers (Estes et al. 2011) may have disproportionately reduced nutrient cycling and physical mixing, with possible effects on phytoplankton (Behrenfeld et al. 2006, Polovina et al. 2008, Boyce et al. 2010). This mechanism could have contributed to part of the observed phytoplankton declines in the open oceans (Fig. S2 in the Supplement), where vertical mixing is a particularly strong driver of phytoplankton change.

By accounting for 20% of all marine microorganism mortality, viruses may have large effects on nutrient fluxes in the oceans, with consequences for phytoplankton (Suttle 2007). Viruses negatively influence phytoplankton directly via cell lysis, or their presence may trigger phytoplankton PCD, likely as an antiviral defence mechanism (Bidle & Falkowski 2004). Viruses may also infect consumers ranging from bacteria to whales, thereby increasing the amount of dissolved and particulate organic matter available for phytoplankton growth (Suttle 2007).

The activities of humans provide perhaps the clearest examples of environmental conditioning. Some examples concern strong effects on coastal nutrient inputs stemming from soil erosion, agricultural prac-

tises, and industrial activities. For instance, anthropogenic activity has led to global increases in the river-borne deposition of nitrate and phosphate to nearshore waters by up to 300% (Duce et al. 1991) or more in some regions (Howarth et al. 1996), while atmospheric deposition of nitrate has increased by up to 50% in some regions (Brimblecombe & Pitman 1980). Such large-scale environmental conditioning by humans in nearshore oceans is almost certainly contributing to the large phytoplankton increases observed there (Figs. 4 & 5).

### Synergistic and context-dependent forcing

Individual physical and biological drivers of phytoplankton change might reinforce or counteract each other. For instance, ocean warming generally increases phytoplankton growth rates (Sarmiento et al. 2004) and microbial metabolism (Taucher & Oschlies 2011), which could counteract negative TDS effects on phytoplankton. However, the metabolic theory of ecology (MTE; Brown et al. 2004) and experimental results (Sommer & Lengfellner 2008, O'Connor et al. 2009) suggest that rising temperature increases grazer metabolic rates faster than phytoplankton metabolic rates, leading to reduced phytoplankton via increased grazing pressure. Hence, it is important to distinguish clearly between the physically mediated temperature effects on phytoplankton via changes in stratification and nutrient delivery and the biologically mediated temperature effects on phytoplankton via altered phytoplankton and consumer metabolism. One experimental study compared the relative importance of these processes and found that this varied depending on average nutrient availability in the ecosystem (Lewandowska et al. 2014). In nutrient-limited systems, the effect of rising temperature on nutrient delivery was dominant, while in nutrient-replete systems, the effect of rising temperature on grazing pressure was stronger. However, under both nutrient regimes, the net effect of increasing temperature on phytoplankton was negative. Such context-dependent forcing has also been revealed in a recent synthesis of published studies which found that trophic control in marine ecosystems scaled unimodally with temperature: strong resource control occurred between 5 and 15°C, and consumer control occurred at the cold and warm extremes of this range (Boyce et al. 2015b). Such context-dependent physical–biological effects on phytoplankton are an important frontier for further research.

### Case study 1: Global patterns of phytoplankton, nutrients, and grazers

To quantitatively explore primary controls on phytoplankton biomass across the seascape, we examined spatial gradients in chlorophyll (mg m$^{-3}$) in conjunction with spatial data for nitrate concentration (µmol l$^{-1}$) and total zooplankton carbon biomass (mg m$^{-3}$) at global scales (Fig. 6A–C). This approach has been used to show the strong positive relationship between phytoplankton and zooplankton concentration across the Atlantic Ocean (Irigoien et al. 2004) but to our knowledge had not yet been applied globally. All data were extracted from publicly available sources (see Supplement at www.int-res.com/articles/suppl/m534p251_supp.pdf). Based on this simple approach, global patterns in chlorophyll appeared similar to those of nitrate and zooplankton (Fig. 5A–C). Elevated levels in nearshore, high-latitude, and upwelling regions were well delineated, as are the oligotrophic gyres of the major ocean basins, where lower nitrate and phytoplankton concentrations prevail. Ordinary least-squares (OLS) regressions of log-transformed mean nitrate or zooplankton on phytoplankton measurements for each 1° × 1° cell statistically confirmed this relationship, a result suggestive of bottom-up control of both phytoplankton and zooplankton concentrations by nitrate (Fig. 5D,F). The relationship between nitrate and chlorophyll was strongly positive (r = 0.51, p < 0.0001) and was best approximated by a polynomial regression ($r^2$ = 0.39; p < 0.0001; Fig. 6D). The nonlinearity of the relationship likely relates to the phytoplankton requirement for additional resources such as phosphate, silicate, carbon, and iron but may also be driven by a nutrient saturation. For example, despite high available nitrate concentrations in some regions, phytoplankton biomass is limited by, and responds strongly to, the addition of iron across 20 to 40% of ocean surface waters (Behrenfeld et al. 1996, Boyd et al. 2000, Moore et al. 2009). It is therefore possible that changes in physically or biologically driven iron deposition may have influenced the observed phytoplankton trends, particularly in the Pacific, Atlantic, and Southern oceans (Fig. 4).

## Ecological consequences of phytoplankton change

### Consequences of phytoplankton change globally

Globally, spatial variation in phytoplankton concentration is strongly and positively related to varia-
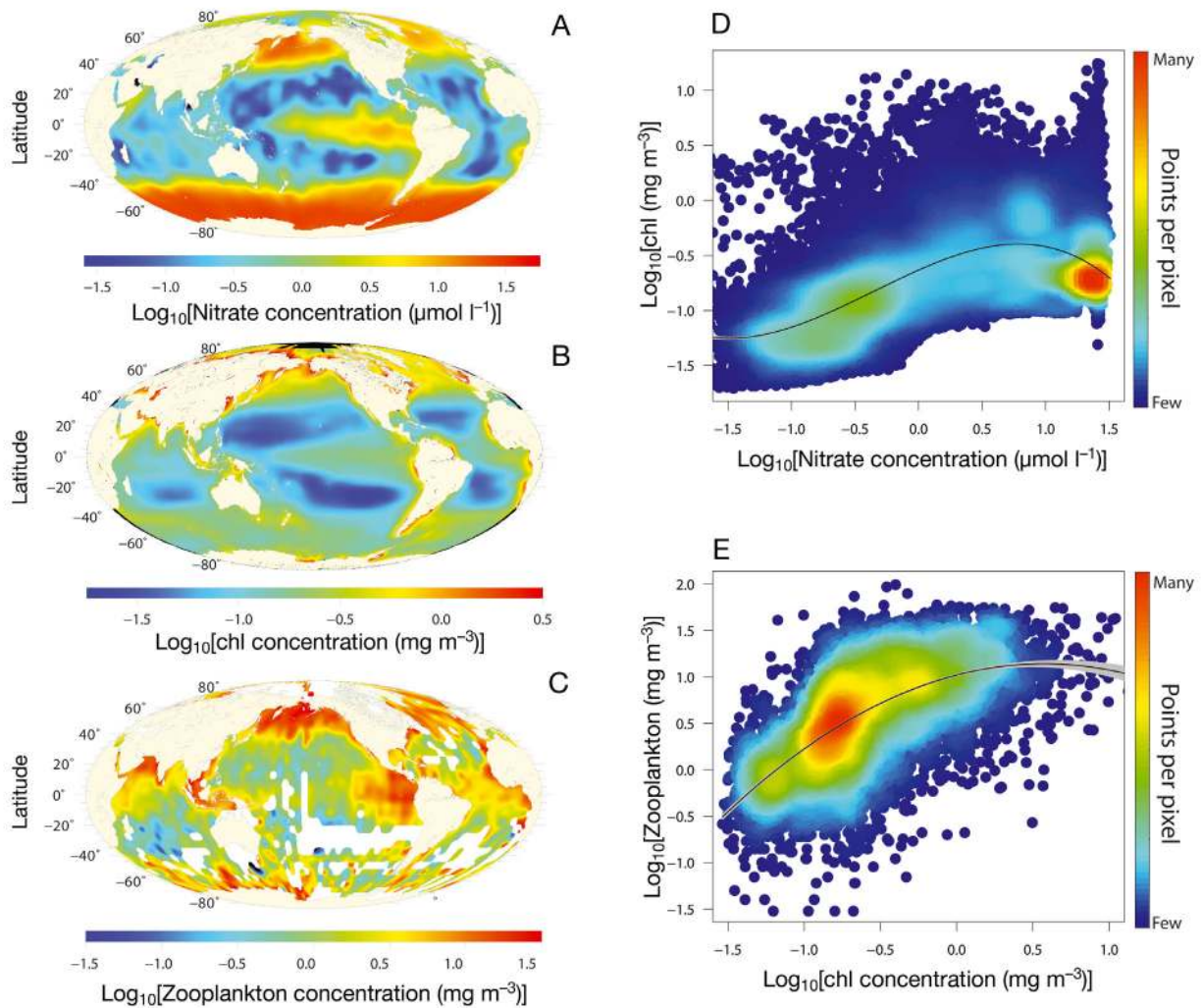
Fig. 6. Global climatology of phytoplankton, zooplankton, and nutrient concentrations. Averaged (A) nitrate, (B) chlorophyll, and (C) zooplankton concentration per $1° \times 1°$ cell depicted as colors. White represents areas with no data. (D) Chlorophyll as a function of nitrate, and (E) zooplankton as a function of chlorophyll. All variables are $\log_{10}$-transformed average concentrations per $1° \times 1°$ cell. Colors depict the number of measurements per pixel. Relationship in (D) was best approximated by a polynomial function, and relationship in (E) was best approximated by a quadratic function. Shading represents the 95% confidence limits around the fitted curve

tion in zooplankton ($r = 0.63$; $p < 0.0001$) (Fig. 6E), suggesting that phytoplankton biomass strongly influences zooplankton via resource control (Fig. 6B,C). The well-established positive relationship between zooplankton and fish for both the larval and adult stages (Lasker 1975, Cushing 1990, Beaugrand et al. 2003) suggests that these observed relationships (Fig. 6B,C) likely propagate to higher trophic levels. Additionally, bottom-up linkages between phytoplankton primary production, zooplankton, mesopelagic fishes biomass, and total fisheries landings have been observed at regional scales (Ware & Thomson 2005, Chassot et al. 2007) and globally (Chassot et al. 2010, Irigoien et al. 2014). These cor-

relations between spatial gradients of primary and secondary productivity do not necessarily imply causation but support the hypothesis that phytoplankton productivity sets the carrying capacity of marine ecosystems through resource control (Fig. 6B,C). It needs to be observed, however, that such variation across ecosystems only captures order of magnitude changes in the abundance of different trophic groups on a log–log scale. Within individual ecosystems, there is ample evidence for top-down effects of grazers on phytoplankton that may interact with the bottom-up forcing discussed in the previous subsection (Verity & Smetacek 1996, Micheli 1999, Frank et al. 2006, Baum & Worm 2009, Estes et al. 2011).

In addition to the spatial approaches discussed above, temporal approaches have also revealed resource regulation of the grazer food web by phytoplankton affecting such taxonomically distant organisms as leatherback turtles (Saba et al. 2008), octopuses (Otero et al. 2008), seabirds (Frederiksen et al. 2006), and fishes (Richardson & Schoeman 2004). Phytoplankton concentrations also influence higher trophic levels via changes in the timing and magnitude of phenological cycles (Hjort 1914, Cushing 1990). Observational studies have demonstrated that the amount, species composition, and timing of phytoplankton blooms can strongly influence the survival of larvae and the subsequent population size of fish (Lasker 1975, Platt et al. 2003). Such phenological changes in the concentration and quality of phytoplankton may be manifest as temporal changes in overall biomass and can also affect ecosystem structure from the bottom up (Edwards & Richardson 2004).

Apart from the effects operating within pelagic waters, the observed changes in plankton abundance may also affect deep-sea ecosystems, which are almost entirely sustained by the rain of particulate organic matter (POM) from surface waters, the majority of which is produced by phytoplankton (Ruhl et al. 2008). The downward flux of particulate organic carbon (POC) accounts for up to 67% of deep-sea benthic biomass in some regions (Johnson et al. 2007). Studies have also documented positive relationships between spatial gradients of surface chlorophyll, POC flux, and deep-sea macro-faunal abundance (Johnson et al. 2007, Ruhl et al. 2008). Phytoplankton-derived POC flux may also influence inter-specific body size distributions of deep-sea macrofauna (Ruhl et al. 2008) and diversity of deep-sea ecosystems. There is broad consensus among physically based models, which predict declining export production over the coming century to be driven in part by rising temperature and changes in phytoplankton biomass and community composition (Steinacher et al. 2010). The strong dependence of food-stressed deep-water ecosystems on export production would likely render them particularly sensitive to changes in phytoplankton concentration and community composition.

## Consequences of phytoplankton change across ecosystems

The evidence reviewed thus far suggests that phytoplankton biomass and productivity place first-order constraints on the carrying capacity of pelagic and deep-sea ecosystems. Additional factors such as the structure of the ecosystem, the degree to which productivity is affected, altered phenology, and changes in species composition and size structure will likely further modify the ecological response to phytoplankton biomass changes across ecosystems.

In the open ocean oligotrophic gyres, phytoplankton biomass is low and comprised mainly of pico- and nanophytoplankton (<0.2 to 20 μm diameter). Due to the small primary producer cell size and the constraints of size-based predation (Barnes et al. 2010, Wirtz 2012, 2013, Boyce et al. 2015a), primary production in the open ocean is inefficiently channelled to higher trophic levels through a microbial food chain, or microbial loop, consisting of picophytoplankton, viruses, bacteria, and small heterotrophic protists (Ryther 1969, Azam et al. 1983, Azam & Worden 2004, Azam & Malfatti 2007). The prevalence of the microbial loop in open ocean ecosystems (Pomeroy et al. 2007) results in long, complex flows of primary production from producers to grazers and highly efficient recycling of organic matter (Ryther 1969). Ultimately, the microbial loop increases the recycling efficiency of phytoplankton and other dissolved organic matter but reduces the amount of primary production available to both the grazer and deep-sea ecosystems (Iverson 1990). This, in combination with the low phytoplankton biomass, contributes to the low fishery landings per unit area and export production of open ocean ecosystems (Ryther 1969); hence, they are sometimes referred to as biological deserts (Polovina et al. 2008).

Since the open oceans are already food stressed, ecosystems there may be particularly sensitive to any reductions in phytoplankton biomass. Process-based models and field and experimental studies suggest that continued warming will lead to increases in the abundance of picophytoplankton (Cermeño et al. 2008, Polovina & Woodworth 2012), expansions of the oligotrophic oceans (Polovina et al. 2008, 2011), and increased microbial metabolism (Taucher & Oschlies 2011). Such changes may increase the relative importance and turnover rate of the microbial loop both in the oligotrophic gyres and elsewhere, thereby increasing primary production, but may reduce the channeling of primary production to the grazer and deep-sea food chains. These changes in the oligotrophic open oceans may be exacerbated by predicted temperature-driven reductions in phytoplankton diversity over the coming century (Thomas et al. 2012). Such diversity losses may alter the structure (Hooper et al. 2012) and stability (Worm et al. 2006) of open ocean ecosystems and may further reduce primary

productivity in these ecosystems through the loss of productive species (Tilman et al. 1996), reduced complementarity (Reich et al. 2012), or increased grazer pressure (Hillebrand & Cardinale 2004).

In contrast to the open oceans, nearshore ecosystems are supported by an abundance of large microphytoplankton species (~20 to 1000 µm in diameter; Cermeño et al. 2008). These ecosystems often have shorter food chains and are thought to be more efficient, with fewer trophic transfers between phytoplankton and predators. Large blooms of rapidly sinking diatoms, slower turnover, and sloppy grazing by large zooplankton result in large fluxes of POC to benthic ecosystems (Ryther 1969, Cermeño et al. 2008, Guidi et al. 2009, Chavez et al. 2011, Norris et al. 2013). There is evidence for phytoplankton increases in most nearshore waters (Fig. S2 in the Supplement), likely due to human-derived nutrient input (Jickells 1998). Increasing phytoplankton in these nearshore systems is hypothesized to have a positive effect on global fishery landings, ~50% of which derive from nearshore and shelf systems (FAO 2010), but may also trigger negative effects in some regions. For instance, large phytoplankton blooms are known to increase heterotrophic bacterial activity and can lead to large subsurface anoxic regions known as dead zones (Grantham et al. 2004). Such effects have been linked with decreased secondary biomass and fishery yield (Diaz & Rosenberg 2008), particularly in nearshore waters. Additionally, some phytoplankton species can form harmful algal blooms, which negatively affect secondary production and fisheries (Nixon & Pilson 1983).

Upwelling ecosystems occur in both nearshore and oceanic waters and contain characteristics of both systems. These ecosystems are predominantly influenced by the wind-driven upwelling of nutrient-rich waters, resulting in large blooms of microphytoplankton, which support large fisheries and export large amounts of POM to the deep sea. Contrary to nearshore systems, phytoplankton trends in upwelling systems are mostly related by changes in upwelling intensity as driven by changes in wind, temperature, and stratification. Any increases in TDS here would reduce total phytoplankton biomass but may have disproportionate negative effects on larger phytoplankton, which are outcompeted by picophytoplankton under conditions of warming, stratification, or prolonged nutrient limitation (Atkinson et al. 2003, Cermeño et al. 2008, Li et al. 2009, Morán et al. 2010). Since large grazers in these systems are often incapable of consuming picophytoplankton (Hansen et al. 1994, Sommer & Stibor 2002, Sommer

& Sommer 2006), a shift towards smaller phytoplankton may decrease the transfer efficiency of primary production through the grazer food chain (Ryther 1969, Barnes et al. 2010, Chavez et al. 2011). These size-selective negative effects are predicted to be strongest in the North Atlantic and tropical upwelling systems, possibly due to the proportionally larger contribution of microphytoplankton to phytoplankton standing stock (Cermeño et al. 2008). Studies of the relationship between phytoplankton changes and fisheries landings confirm these observations, with the average effect of changing chlorophyll on fish yield being strongest in upwelling, temperate, and nearshore marine ecosystems (Ware & Thomson 2005, Chassot et al. 2007, 2010). Although model predictions for upwelling systems are variable and uncertain (Wang et al. 2010), many predict temperature-driven future declines in phytoplankton biomass and size (i.e. Henson et al. 2010, Steinacher et al. 2010). Such changes are hypothesized to have strong and negative effects on productivity.

## Case study 2: Ecological effects of climate-driven phytoplankton variability

Some of the clearest examples of the drivers and ecological consequences of marine phytoplankton change derive from studies of the effects of quasi-periodic climate fluctuations, for example from the El Nino Southern Oscillation or North Atlantic Oscillation (NAO; Barber & Chavez 1986, Chavez et al. 1999, Behrenfeld et al. 2006, Martinez et al. 2009). Such climate fluctuations represent natural experiments which can shed light on the drivers and consequences of longer-term trends in phytoplankton change.

A well-known example of the effects of climate variability propagating up the food web comes from the North Sea (Aebischer et al. 1990). Here, the positive correspondence between standardized long-term (1955 to 1987) time series of westerly weather, phytoplankton, zooplankton, herring *Clupea harengus* abundance, and breeding success of kittiwakes *Rissa tridactyla* suggests that environmental effects on phytoplankton abundance are transmitted up the food chain. Although the study accounted for the influence of weather patterns, the potential effects of periodic climate variability were not realized at the time. The NAO is a major mode of climate variability in the region and is negatively related to the average concentration of phytoplankton (Boyce et al. 2010) and zooplankton (Fromentin & Planque 1996) in the

North Atlantic. On longer time scales, the Atlantic Multidecadal Oscillation (AMO) may be the dominant mode of climate variability (Martinez et al. 2009, Chavez et al. 2011) and is positively related to marine phytoplankton concentration in the region (Martinez et al. 2009). To examine the interplay between decadal climate fluctuations, plankton abundance, and ecosystem structure, we extracted time series of westerly weather, phytoplankton, zooplankton, herring, and kittiwake chicks (Aebischer et al. 1990) as well as time series for the NAO and AMO. All series were filtered to remove any high-frequency variability and re-scaled such that they ranged over the same interval (see the Supplement for data sources and full methods). Westerly weather had a low explanatory power and was thus removed from the analysis. All series were positively related (Fig. 7), yet the AMO emerged as the dominant climate driver of observed ecological change, showing a much stronger correlation than the NAO or westerly weather. However, it is unclear if the AMO alters ecosystem dynamics directly through physical processes or indirectly by modifying the trophic state of the environment.

To more quantitatively address this issue, we examined the linear correlation between all series. If climate is driving consumer abundance via changes in phytoplankton, the correlation between adjacent, trophically coupled trophic levels should be stronger than the correlation between individual trophic levels and climate. Using this simple approach, we observed strong evidence of bottom-up effects mediated by the influence of climate on phyto-

plankton (Fig. S3 in the Supplement). Climate indices were the strongest predictors of phytoplankton concentration. For example, the AMO shows almost perfect positive correlation (NAO: $r = -0.596$; AMO: $r = 0.998$; Fig. S3). Zooplankton and herring were best predicted by the concentration of phytoplankton on which they graze (zooplankton: $r = 0.961$; herring: $r = 0.781$). Also, the number of kittiwake chicks was most strongly predicted by their primary food source, herring ($r = 0.989$). While these correlations do not imply causation, they do provide observational support for the hypothesis of climate-induced control of the ecosystem and suggest that long-term changes in phytoplankton could cascade up the food web, ultimately influencing apex predators and humans. The strong influence of the AMO particularly highlights the importance of decadal-scale temperature variation in determining phytoplankton concentration in the upper ocean.

## SUMMARY AND OUTLOOK

Our analysis suggests that the high variability among estimated changes in marine phytoplankton over the past century likely relates to a larger number of local and regional factors that cannot be easily identified in a global overview. However, when we compiled published trend estimates from throughout the global ocean, we tended to observe declining phytoplankton concentrations more commonly in studies conducted over longer time scales and in the open oceans. Conversely, phytoplankton increases were observed more frequently over recent time periods and closer to shore. Regionally, our analysis suggests that phytoplankton concentrations have declined across the North and equatorial Pacific Oceans and at high latitudes and increased in the South Indian Ocean and in the Northeast Atlantic. Estimates of change in the North Atlantic Ocean and in the Southern Hemisphere appeared particularly variable. Continued monitoring of phytoplankton levels using standardized methods, such as *in situ*, remote sensing, Secchi disk, and CPR, will lead to improved inter-calibration and more accurate estimates of long-term phytoplankton changes.
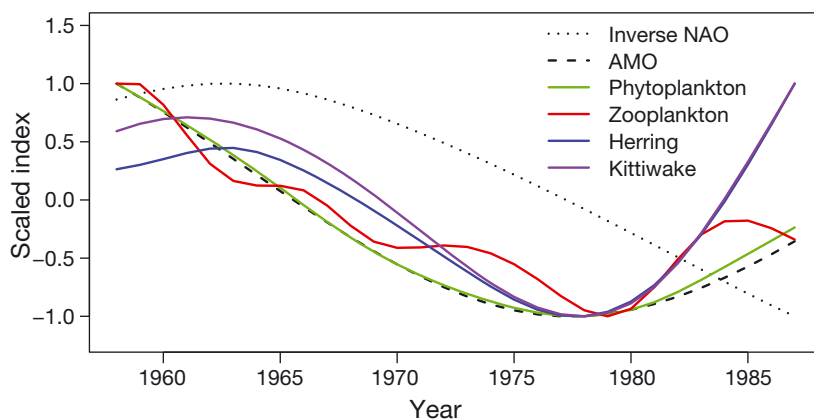


Fig. 7. Bottom-up cascade driven by low-frequency climate effects on phytoplankton. Time series of climate and abundance across multiple trophic levels in the North Sea. Dashed lines represent climate indices, and colors depict different trophic levels within the food web. Biological time series were extracted from Aebischer et al. (1990). Series were smoothed with a moving average and normalized between −1 and 1 (see Supplement for full details). NAO: North Atlantic Oscillation; AMO: Atlantic Multidecadal Oscillation

While empirical estimates vary widely, most predictive models suggest that globally averaged phytoplankton concentrations will gradually decline over the coming century (Table 3). Although increases are predicted at high latitudes and in nearshore waters, global trends will likely be dominated by phytoplankton declines across the low- and mid-latitude oceans and in the open oceans, where ~82% of annual global ocean primary production occurs (Ryther 1969).

Multiple lines of evidence point towards changes in temperature as an important (but certainly not exclusive) driver of observed phytoplankton trends, particularly in the open oceans. Increasing temperatures are predicted to induce shifts in phytoplankton biomass concentration (Behrenfeld et al. 2006), diversity (Thomas et al. 2012), phenology (D'Ortenzio et al. 2012), species composition (Cermeño et al. 2008, Li et al. 2009), size structure (Polovina & Woodworth 2012), and zooplankton grazing pressure (O'Connor et al. 2009, Sommer et al. 2012, Boyce et al. 2015b). The pathways by which temperature changes influence phytoplankton are multifarious, but TDS has emerged as an important mechanism over geological (Schmittner 2005), historical (Boyce et al. 2010, 2014, Boyce 2013), contemporary (Behrenfeld et al. 2006), and future (Henson et al. 2010, Hofmann et al. 2011, Olonscheck et al. 2013) time horizons. Experiments and process models further suggest that warming is shifting the balance of autotrophic to heterotrophic metabolism, which may exacerbate (O'Connor et al. 2009, Sommer et al. 2012, Olonscheck et al. 2013) or counterbalance (Taucher & Oschlies 2011) any declines in biomass driven by TDS.

Such changes in plankton abundance, composition, and diversity, variable as they may be, will likely have effects on the wider ocean food web. For example, progressive declines in phytoplankton biomass would likely reduce the carrying capacity of marine ecosystems if not counterbalanced by increases in biomass-specific productivity. A robust examination of future phytoplankton change and its ecological consequences will depend on better resolving critical uncertainties, such as the influence of consumers on marine phytoplankton, the net effect of changing metabolic rates on productivity, and the effects of size-restructured phytoplankton communities on ecosystem functioning. Further, the scarcity of consistent, long-term measurements of consumer abundance across trophic levels limits any rigorous analysis of their relevance as drivers of long-term phytoplankton change. Such challenges and limitations may explain why relatively few studies have

considered the importance of top-down effects at global scales. Further investigation may be facilitated by combining process-based models with experimentation and field observation and through the formation of coordinated working groups (i.e. ICES and Scientific Committee on Oceanic Research working groups and the International Group for Marine Ecological Time Series) aimed at integrating, sharing, and validating phytoplankton time series.

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