Sea ice phenology and timing of primary production pulses in the Arctic Ocean

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Abstract

Arctic organisms are adapted to the strong seasonality of environmental forcing. A small timing mismatch between biological processes and the environment could potentially have significant consequences for the entire food web. Climate warming causes shrinking ice coverage and earlier ice retreat in the Arctic, which is likely to change the timing of primary production. In this study, we test predictions on the interactions among sea ice phenology and production timing of ice algae and pelagic phytoplankton. We do so using the following (1) a synthesis of available satellite observation data; and (2) the application of a coupled ice-ocean ecosystem model. The data and model results suggest that, over a large portion of the Arctic marginal seas, the timing variability in ice retreat at a specific location has a strong impact on the timing variability in pelagic phytoplankton peaks, but weak or no impact on the timing of ice-algae peaks in those regions. The model predicts latitudinal and regional differences in the timing of ice algae biomass peak (varying from April to May) and the time lags between ice algae and pelagic phytoplankton peaks (varying from 45 to 90 days). The correlation between the time lag and ice retreat is significant in areas where ice retreat has no significant impact on ice-algae peak timing, suggesting that changes in pelagic phytoplankton peak timing control the variability in time lags. Phenological variability in primary production is likely to have consequences for higher trophic levels, particularly for the zooplankton grazers, whose main food source is composed of the dually pulsed algae production of the Arctic.

Keywords: Arctic, bloom, ecosystem model, ice algae, phenology, phytoplankton

Received 23 July 2012 and accepted 2 October 2012

Introduction

Across ecosystems, climate change is frequently linked to the timing variability (phenology) of seasonal events for plants and animals (e.g. Edwards & Richardson, 2004; Winder & Schindler, 2004; Amano *et al.*, 2010). Marine biota is no exception, and the observed changes in seasonal timing have prompted increased attention to the phenology of both phytoplankton and zooplankton in a variety of marine ecosystems, although mostly from midlatitude and near-shore ecosystems (see a recent review by Ji *et al.*, 2010). Phenology in the Arctic Ocean deserves particular attention for at least three reasons: (1) The Arctic system features strong seasonality in environmental conditions such as light, temperature, sea ice, snow cover, and nutrients. (2) Arctic organisms are adapted to the narrow time window for growth defined by the strong seasonality of environmental forcing; a small timing mismatch between

organisms' life strategy and their physical environment could have a substantial consequence for the entire food web (e.g. Gradinger, 1995). (3) Climate change is observed and predicted to be particularly marked in high-latitude ecosystems –first and foremost in the Arctic (Arctic Climate Impact Assessment, 2005; Wassmann *et al.*, 2011). The study of phenology can identify particularly sensitive indicators of ecosystem responses to major external disturbances such as changes in water temperature and ice coverage, and it proves extremely valuable for better understanding the phenological coupling and trophic interactions in pelagic food webs (Edwards & Richardson, 2004; Winder & Schindler, 2004).

There is large spatial and temporal variation in the primary production of the Arctic Ocean, as is evident from ice and water samples (Gosselin *et al.*, 1997; Hill & Cota, 2005; Joo *et al.*, 2012) and satellite-based measurements (Qu *et al.*, 2005; Arrigo *et al.*, 2008; Pabi *et al.*, 2008; Kahru *et al.*, 2011), and as is predicted by numerical models (Popova *et al.*, 2010; Zhang *et al.*, 2010; Jin *et al.*, 2012; Reigstad *et al.*, 2011). Most of the above-mentioned studies focus on the spatial variability but not the timing variability in the primary production

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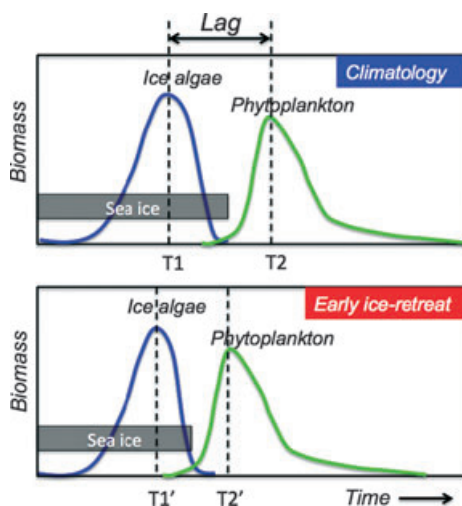Correspondence: Rubao Ji, tel. +508 289 2986, fax +508 457 2134, e-mail: rji@whoi.edu

Fig. 1 Schematic algal bloom timing under climatological and early ice-retreat conditions in the Arctic Ocean. The *x* and *y* axes denote time and biomass, respectively. T1(T1′) and T2(T2′) denote bloom peak timing for ice algae and pelagic phytoplankton, respectively, under climatological (early ice-retreat) conditions. The 'Lag' is defined as the timing difference between the peaks of ice algae and pelagic phytoplankton blooms. Note that ice algae peak concentration could be much higher/lower than that of pelagic phytoplankton. Since peak time varies by latitude and location, figures are only intended to denote relative changes in bloom timing between different environmental conditions.

process. This is largely due to the difficulty in obtaining long-term, high-frequency time series data across the Arctic Ocean. Furthermore, the unique ice algae component of Arctic primary production cannot be studied using the satellite-based measurements. However, the ice algae component must be included for a complete picture, including the time lag between the ice algae and pelagic phytoplankton production peaks, given the ecological importance of the intricate match or mismatch scenarios resulting from a dually pulsed primary production (Tourangeau & Runge, 1991; Søreide *et al.*, 2010; Varpe, 2012). The combination of satellite and model data used in this study allow us to examine the timing variability in the entire Arctic, for both the ice algae and pelagic phytoplankton components of the primary production, and thus to test phenology-related hypotheses, as described below.

Conceptually, the timing of both the ice algae and the pelagic phytoplankton production is depicted as taking place progressively later in the year, with increasing latitude (increased ice cover and stronger seasonality in irradiance), and with the ice algae component increasing in abundance relative to pelagic phytoplankton (Leu *et al.*, 2011; Wassmann, 2011). The time gap between peak ice algae and peak pelagic phytoplankton abundance is depicted as relatively constant with increasing latitude. As illustrated in Fig. 1, the timing

of pelagic phytoplankton blooms is likely controlled by the timing of ice retreat caused either by ice melting or drifting, and earlier ice retreat is directly responsible for earlier pelagic phytoplankton blooms; whereas the timing of ice algae blooms is influenced by the timing of snow melt and ice melt. Consequently, the time lag between ice algae and pelagic phytoplankton blooms could become narrower under an early-season ice-retreat scenario.

Despite a seemingly well-established conceptual understanding, there are few large scale and quantitative representations of the major phenological variables for Arctic primary production. Here we attempt to reduce this shortcoming. With a combination of model results and satellite-derived chlorophyll-a (Chla) observations, we estimate the timing (of peak abundance) of the ice algae and the pelagic phytoplankton blooms across the entire Arctic Ocean. These results are then used to test whether (1) the blooms of both ice algae and pelagic phytoplankton occur later at higher latitudes; (2) the timing variability in pelagic phytoplankton peaks is governed by the sea ice retreat; and (3) the lag between the ice algae and pelagic phytoplankton peaks is independent of latitude and its variability is mainly controlled by the timing of pelagic phytoplankton peaks.

Materials and methods

Satellite analyses

Satellite remote sensing is crucial to understanding biological and physical processes in the Arctic Ocean. Ocean color data have been used to examine the open-ocean primary production process (e.g. Qu *et al.*, 2005; Arrigo *et al.*, 2008; Pabi *et al.*, 2008; Kahru *et al.*, 2011). In this study, we use the Level-3 8-day composite data sets of chlorophyll-a concentration obtained from NASA's Ocean Color website (http://oceancolor.gsfc.nasa.gov/), with a spatial resolution of 9 km and a time span of 1998–2007. We focus our analysis from 1998 to 2007 due to the lack of SeaWiFS data for an extended period in 2008 and 2009. The data were interpolated into a regular grid with a 25 km resolution (similar to Kahru *et al.*, 2011) followed by a three-point moving average for the time series in each grid. The midday of the 8-day period when the maximum Chla occurred is considered as the peak day. It is well recognized that, compared to the lower latitude ocean, ocean color remote sensing at higher latitude suffers from more cloud cover and sensor sensitivity (Arrigo *et al.*, 1998; Moore & Abbott, 2000; Qu *et al.*, 2005), so a cautious approach must be taken when interpreting data and comparing them with the model results. As the focus of this study is on the timing of the annual Chla maximum, rather than absolute values, we adopted the same assumption as Kahru *et al.* (2011)–that small errors in Chla estimates are expected to have a minor effect on the phenology assessment.

In addition, we extracted satellite-derived ice information from the National Snow and Ice Data Center. Ice coverage is obtained from the Scanning Multichannel Microwave Radiometer and Special Sensor Microwave/Imager data, available daily from 1987 to the present with a resolution of 25 × 25 km (gridded) over the Arctic Ocean. The day-of-year when the ice concentration at each grid point drops below 50% is used as a proxy for ice-retreat timing (this includes both thermo-dynamically- and hydro-dynamically-induced change in ice concentration).

The spatial geography of the above timing metrics for both pelagic phytoplankton blooms and ice retreat is analyzed and used mainly for comparison with the model results. A similar analysis is conducted for the results from the coupled model (see the following subsection for a brief description of the model). For the model results, the spatial distribution of correlation coefficient and slopes between ice-retreat timing and (1) pelagic phytoplankton peak timing; (2) ice-algae peak timing; and (3) lag between ice-algae and pelagic phytoplankton peak timing. The correlation analysis is conducted based on 16-year (1992–2007) time series of above timing variables at each spatial grid. It is worth noting that the observation data time series contains some spatio-temporal gaps due to clouds and ice coverage; whereas the model results have full spatio-temporal coverage and thus allow us to examine links between the variability in ice-retreat timing and the phenology of primary production.

Coupled ice-ocean-ecosystem model

An ecosystem model is fully coupled with the POP-CICE (Parallel Ocean Program-Los Alamos Sea Ice Model) global physical model, allowing nutrients and biomass to be exchanged between the pelagic and ice algal components (Jin *et al.*, 2012).

The pelagic ecosystem model is a medium-complexity nutrients-phytoplankton-zooplankton-detritus model. This model has evolved from the models by Moore *et al.* (2001, 2004), in which multiple types of pelagic phytoplankton and nutrients were included to accommodate diverse ecological regimes around the globe. The advantages of this model are the following: (1) it is coupled with a state-of-the-art coupled ice–ocean physical model with continuous updates and large community support; (2) the global domain avoids the long open-boundary settings around the Arctic Ocean; and (3) the ecosystem model has proved its ability to model biogeochemical cycles across diverse regimes. The model includes 24 state variables: nitrate, ammonium, iron, silicate, phosphate, three types of pelagic phytoplankton (explicit C, Fe, and chlorophyll pools for each phytoplankton group, and an explicit Si pool for diatoms and $CaCO_3$ pool for small phytoplankton, with a total of 11 state variables), zooplankton, dissolved organic carbon, dissolved organic nitrogen, dissolved organic iron, dissolved organic phosphate, oxygen, dissolved inorganic carbon, alkalinity, dimethyl sulfide (DMS), and dimethylsulfoniopropionate (DMSP).

The ice algal model was first developed based on ice-cored data from the fast-ice offshore Barros (Jin *et al.*, 2006) and then tested and validated by coupling it with a vertically 1-D pelagic ecosystem model (Jin *et al.*, 2007), a global CICE with a simple two-layer ocean model (Deal *et al.*, 2011), and the fully coupled POP-CICE and 3-D pelagic ecosystem model (Jin *et al.*, 2012). It includes seven components: ice algae, NO_3, NH_4, Si, DMS, and dissolved and particulate forms (DMSP).

The POP-CICE-ecosystem model runs on a global domain with nominal one-degree resolution and a displaced North Pole in Greenland (Danabasoglu *et al.*, 2006). The grid spacing ranges between 20 and 85 km, averaging 40 km north of 70°N. There are 40 vertical layers in the ocean, and the layer thickness ranges from 10 m on the surface to 250 m at 2000 m below. CICE partitions the ice pack in each grid cell into a 5-category ice thickness distribution, with four ice layers and one snow layer in each category. The thickness category ranges are 0–0.64, 0.64–1.39, 1.39–2.47, 2.47–4.57 m, and greater than 4.57 m (Hunke & Bitz, 2009).

Atmospheric forcing data include 6-hourly air temperature, specific humidity, and wind velocity components from the Common Ocean Reference Experiments, version 2 (1958–2007, Large & Yeager, 2009), along with monthly 'normal year' precipitation from version 1 (Large & Yeager, 2004), as described by Hunke & Holland (2007).

Initial conditions for some physical variables (temperature and salinity) and biological variables (NO_3, Si) are from the gridded World Ocean Atlas (WOA 2005). Other initial conditions for the biological model are from a global model simulation by Moore *et al.* (2004). Initial sea ice conditions for the physical model are from earlier runs (1958–2006), without the biological model (Hunke & Bitz, 2009).

Results

Both satellite data (Fig. 2a) and model results (Fig. 2b) show a clear latitudinal shift in the timing of ice-retreat across the Arctic, with a general pattern of earlier retreat in the lower latitude coastal regions and later retreat in areas closer to the central Arctic. This latitudinal gradient is stronger on the Atlantic side of the Arctic, resulting primarily from the intrusion of the warm Atlantic waters into the Barents Sea, which accelerates the melting process during early summer.

The latitudinal shift of pelagic phytoplankton peak timing is detectable from both observation (Fig. 2c) and model (Fig. 2d) in some portions of the Arctic marginal seas, including the eastern portion (0–60°E) and western portion (120–180°W). However, the peak timing is similar at different latitudes for the marginal seas on the eastern side of the Arctic (from 60 to 180°E). It is worth noting that Fig. 2 seems to show peak pelagic phytoplankton timing frequently occurred earlier than ice-retreat timing. This is because the definition of ice-retreat timing in this study is the day-of-year when the ice concentration drops below 50%. This suggests that the pelagic phytoplankton may often reach its peak timing before half of the ice has retreated. Recent observations (Arrigo *et al.*, 2012) even showed that significant phytoplankton blooms are possible under fully
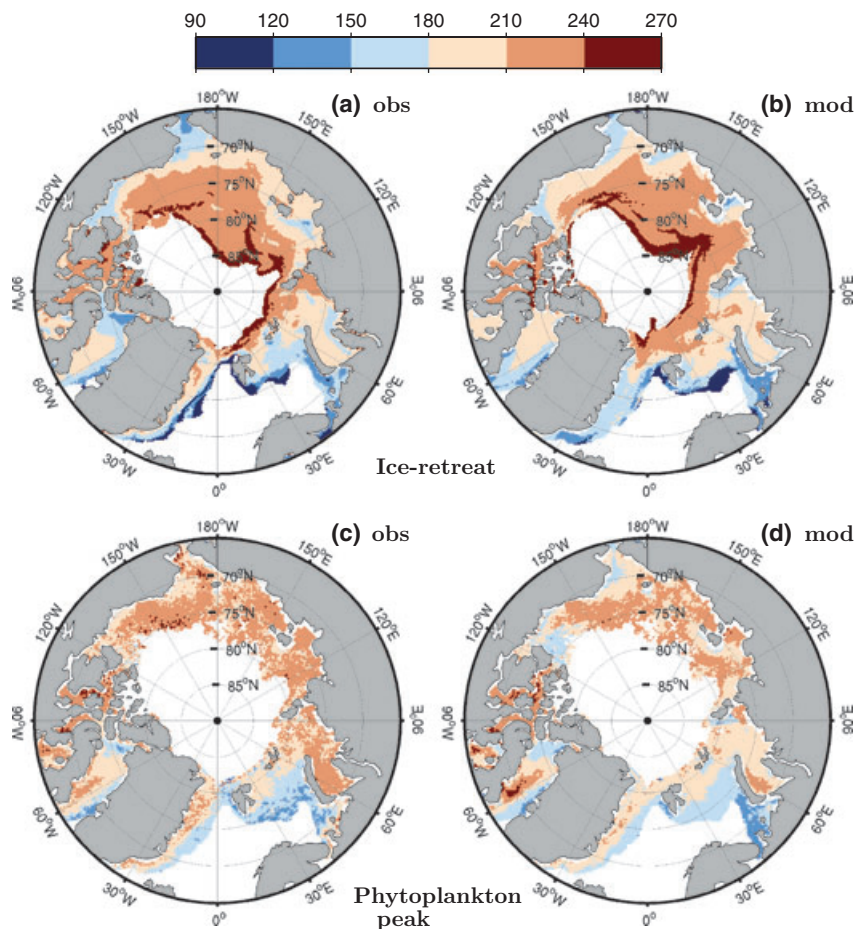
Fig. 2 Model-data comparison for the timing of ice retreat and pelagic phytoplankton bloom peaks (10-year average for years from 1998 to 2007). Timing of ice retreat: (a) satellite- derived and (b) model-computed; Timing of pelagic phytoplankton peak: (c) satellite-derived and (d) model-computed. Color bar unit: day-of-year.

consolidated first-year ice pack. These type of blooms are not visible to satellite remote sensing, but can be detected by our model. This may partially explain the relatively earlier peak timing in the model (Fig. 2d) than that seen from remote sensing (Fig. 2c).

The coupled model shows reasonable skill capturing the general spatial patterns of ice retreat and pelagic phytoplankton peak timing when compared to remote sensing data. The quantitative skill assessment for each individual year is summarized in a Taylor diagram (1) for both ice-retreat timing and pelagic phytoplankton peak timing (Fig. 3). The model shows slightly better skill at simulating the timing of ice retreat than at the timing of pelagic phytoplankton peaks, with correlation coefficients generally higher than 0.6 (except in 2001) for ice-retreat timing and 0.4–0.65 for pelagic phytoplankton peak timing. Correspondingly, the difference in the normalized, centered root-mean-square (Fig. 3) between model and observation is smaller for ice-retreat timing than that for

pelagic phytoplankton peak timing. The normalized standard deviation of the model-computed fields of both ice-retreat and pelagic phytoplankton peak timing are very close to 1.0, suggesting that the variance of computed fields match well with observations. The validation of the ice-algae model results is difficult due to the poor availability of observations. The modeled ice-algae bloom timing was initially compared against observations off Barrow in a 1-D model (Jin *et al.*, 2006) that was then adopted for the 3-D simulation in this study, and achieved a good model-data fit at the same site. Ice algae blooms peak during April to May in most of the Arctic, with a general (but weak) trend of earlier peaks at lower latitudes (see Fig. 4a, and notice that only timing in the seasonal ice zone is plotted in accordance with where remote sensing data are available). A small proportion of spatial variability in ice-algae bloom timing can be explained by the ice-melt timing ($r = 0.54$, $P < 0.01$), but likely be affected more by processes that have a stronger impact on light availability
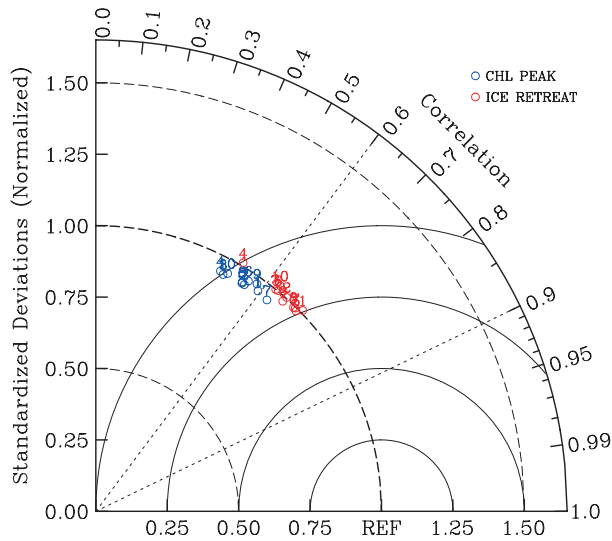
Fig. 3 Taylor diagram (Taylor, 2001), showing the model's skill at simulating the timing of ice retreat (red circles) and pelagic phytoplankton peak (blue circles) for 10 years. The numbers from 1 to 10 near each circle (representing years from 1998 to 2007) are not distinguishable as they are tightly clustered, suggesting that the model has a similar skill during each year. Three statistical quantities are summarized in this Taylor diagram: (1) the correlation coefficient between the data and simulation indicated on the azimuthal axis; (2) the normalized standard deviation (normalized to the standard deviation of observational data), shown as the distance from the origin of the plot; and (3) the normalized, centered root-mean-square (RMS) (normalized to the RMS of observational data), shown as the distance from the 'REF' point.

(e.g. latitude, snow melt or ice thickness). The time lag between ice algae and pelagic phytoplankton peaks are in the range 45–90 days in most of the seasonal ice zones, and there is no obvious latitudinal gradient in the time lag (Fig. 4b). The time lag across the Arctic marginal seas appears to be negatively related to the timing of ice-algae bloom ($r = -0.67$, $P < 0.01$), suggesting that in areas with earlier ice-algae bloom, the duration between ice-algae and pelagic phytoplankton peaks is longer.

The model results show a varying degree of impact from ice-retreat on the phenology of primary production. For a large portion of the Arctic seasonal ice zone, the timing variability in pelagic phytoplankton peaks at a specific location is strongly affected by the timing variability in ice retreat (Fig. 5a, b). For all grid points over which the correlation was computed, more than 54% show significant correlation ($P < 0.05$) between the timing of ice retreat and pelagic phytoplankton peak; only 17% of these points, however, distributed sporadically in various Arctic regions, show significant correlation between the timing of ice retreat and ice algae peak (Fig. 5d, e). In some eastern Arctic regions (on the

(a) Ice-algae peak timing (day-of-year)
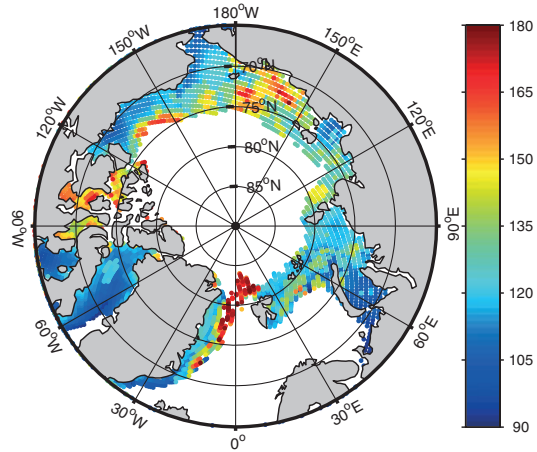
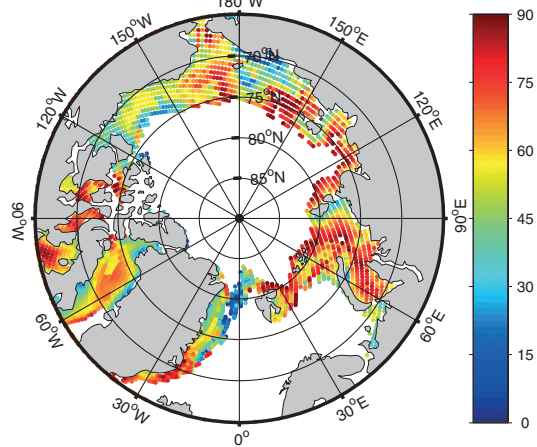**(b) Time lag between ice-algae and pelagic phytoplankton peak timing (days)**

Fig. 4 Model-computed (a) ice-algae bloom peak timing and (b) time lag between ice-algae and pelagic phytoplankton peak timing. Model output represents 16-year average for the years 1992–2007. Notice that only the timing in the seasonal ice zone is plotted, as this is the region with available satellite-derived pelagic phytoplankton observations.

Atlantic side), there is a mixture of positive and negative correlations between the timing of ice retreat and ice algae peak, supporting the conceptual model presented in the Introduction section: the timing of ice-algae bloom is less likely affected by ice-retreat. Furthermore, nearly 35% of the grid points show a significant correlation between the timing of ice retreat and the lag between the timing of ice-algae and pelagic phytoplankton peaks (Fig. 5g, h). Most of these points are located in areas where the correlation between the ice-retreat and ice-algae peak timing is either negative or insignificant (such as the Kara Sea, the northern Barents Sea, and the Greenland coast). This indicates that the variability in the time lag is controlled by the
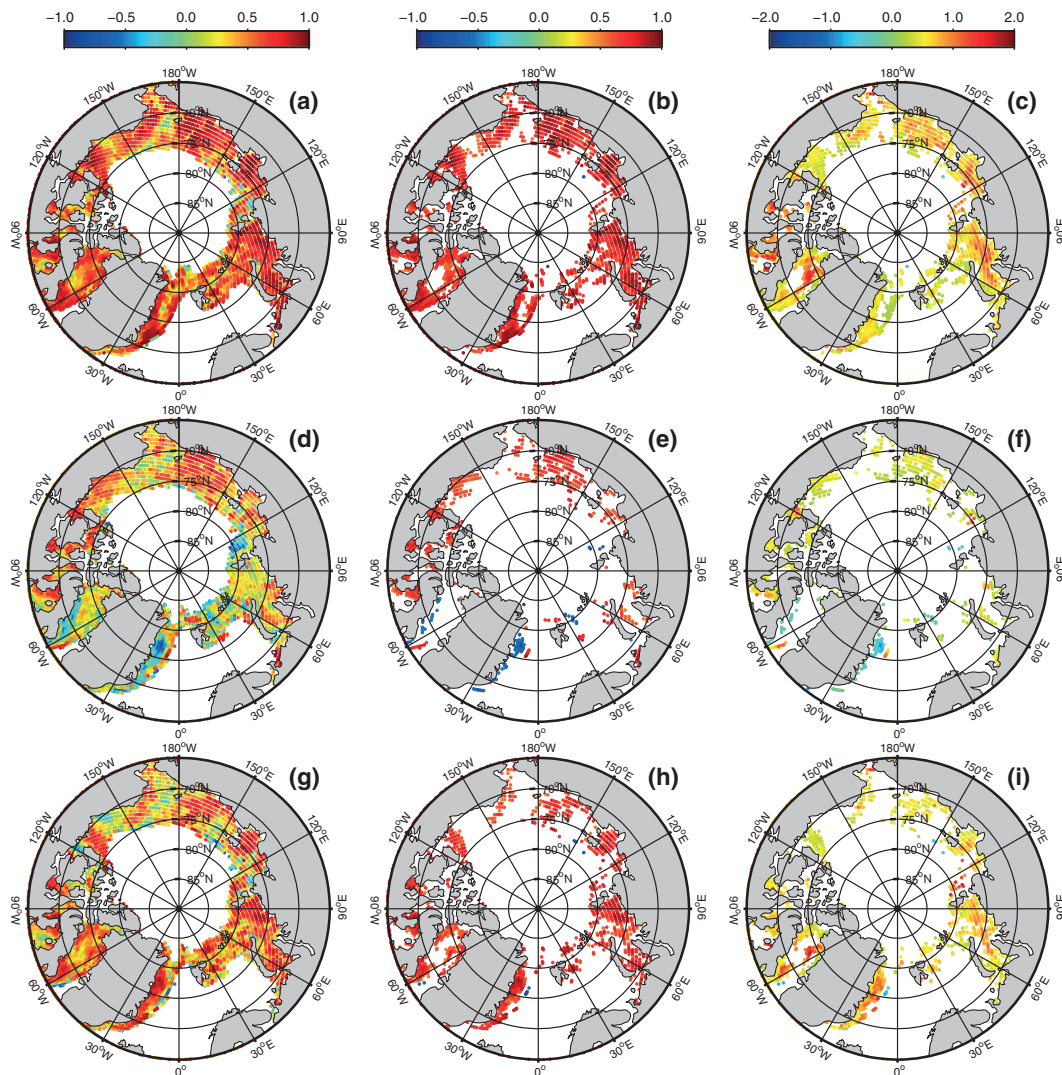
Fig. 5 Spatial distribution of correlation coefficients (*r*) and slopes (*s*) (1) between the model computed ice-retreat timing and pelagic phytoplankton peak timing [top panel, (a) *r* for all data points; (b) *r* for points only with *P* < 0.05; (c) *s* for points only with *P* < 0.05]; (2) between ice-retreat timing and ice-algae peak timing [mid panel, (d) *r* for all data points; (e) *r* for points only with *P* < 0.05; (f) *s* for points only with *P* < 0.05]; (3) between ice-retreat timing and lag between the ice-algae and pelagic phytoplankton peak timing [bottom panel, (g) *r* for all data points; (h) *r* for points only with *P* < 0.05; (i) *s* for points only with *P* < 0.05].

variability in pelagic phytoplankton peak in those regions. The slopes of the regression lines in the correlation analyses (Fig. 5c, f, i) further support the above arguments. The slopes of the regression between ice-retreat and pelagic phytoplankton peak timing are generally in the range 0.5–2.0 (Fig. 5c), which are much greater than the slopes of the regression between ice-retreat and ice-algae peak timing (which vary from −0.5 to 0.5, Fig. 5f). A slope closer to 1.0 indicates that changes in the timing of both events are equivalent; whereas a slope closer to 0, as in the case of ice-retreat vs. ice-algae peak timing, means that ice-algae peak timing does not change much with ice-retreat timing, even though the correlation is significant.

Discussion

A satellite data analysis by Markus *et al.* (2009) suggested that many Arctic regions have shown earlier onset of ice retreat over the last three decades, ranging from 1.0 day earlier per decade for the Bering Sea to 7.3 days earlier per decade for the East Greenland Sea. The implication of such changes on the phenology of primary production processes, especially on pelagic phytoplankton blooms, is significant, as we show in this study. A strong connection between ice retreat and pelagic phytoplankton blooms along the ice-edge has also been documented by Perrette *et al.* (2011). From a careful examination of figure 9 in the article by Markus

et al. (2009), the timing trend of ice-retreat onset appears to be discontinued since the early 1990s in most of the Arctic regions. This pattern is similar to our model-based trend analysis on the timing of ice-retreat, based on time series from 1992 to 2007 (results not shown). Kahru *et al.* (2011) have suggested bloom peaks arrived earlier (up to 3–5 days per year) over the last decade in some regions, but the range of those areas are limited, and almost no trends were detected in the Arctic marginal seas (see Fig. 3a in Kahru *et al.*, 2011). It is worth noting that, although no long-term trend is present in this analysis, the timing variability presented in the 1992–2007 time series shows a wide range of ice-retreat timing and different responses from pelagic phytoplankton and ice algae blooms, thus enabling us to assess the correlation between the ice and primary production dynamics; and to project future scenarios using earlier ice retreat associated with shrinking coverage.

Our modeling analyses support much of the conceptual representation of how primary production events of the Arctic respond to changes in warming and ice loss at different latitudes as summarized by Wassmann (2011). Our results further quantify spatial variability in different Arctic marginal seas. The timing differences in either pelagic phytoplankton or ice-algae peaks often vary by a month, even at the same latitude, and especially when comparing between the eastern and western side of the Arctic. In addition, the responses of bloom peak timing to changes in ice-retreat timing vary significantly in different regions. Interestingly, the model results suggest that in areas with earlier (later) ice-algae bloom, the time lag between ice-algae and pelagic phytoplankton bloom is longer (shorter). This is probably because areas with late ice-algae blooms have a narrower time window for pelagic phytoplankton to bloom, and the time lag between the ice-algae and pelagic phytoplankton blooms is thus reduced. It is important to notice that this spatial variability (for multiyear mean) is different from the interannual variability that was examined for specific spatial locations (shown in Fig. 5).

Marine copepods are the main grazers of the marine Arctic ecosystem (e.g. Eilertsen *et al.*, 1989; Hansen *et al.*, 1990). Like other organisms in highly seasonal environments, they have evolved life cycles during which careful scheduling of events and behaviors are vital to maximize individual fitness (e.g. Varpe, 2012). Central in this scheduling is to achieve overlap with conditions beneficial for feeding and reproduction, without jeopardizing survival probability too much (Varpe *et al.*, 2007). Arctic copepods such as *Calanus* spp. have evolved relatively long life cycles with generation times of one to several years, and they often use dormancy strategies for overwintering (e.g. Conover, 1988; Falk-Petersen *et al.*,

2009). Changes in the initiation and duration of the growth season can impact the biogeography of those copepod species in the Arctic Ocean (e.g. Ji *et al.*, 2012). A dually pulsed primary production, with the degree of match also depending on the lag between the ice algae and pelagic phytoplankton, complicates how changes in timing of the food may influence zooplankton grazers (Søreide *et al.*, 2010; Varpe, 2012). In addition, regional differences in the variability in primary production process have been suggested as the cause of life history strategy differentiation for *Calanus* spp. and other zooplankton species (Scott *et al.*, 2000). Despite high interannual and spatial variability in the timing of the food source, systematic shifts in timing have the potential to increase the frequency of mismatch between marine pelagic grazers and their food. If interacting species respond differently to environmental change, ecosystem change through food-web perturbations may follow (Stenseth & Mysterud, 2002; Edwards & Richardson, 2004; Winder & Schindler, 2004).

The earth's primary production, in the ocean as well as on land, displays characteristic seasonality, and generally, the higher the latitude, the more pulsed the production. Factors creating and structuring these pulses must be better understood if we are to realistically predict how climate change and other perturbations may modify primary production. Through a pan-Arctic synthesis of available satellite observation data, and by the application of a coupled ice-ocean-ecosystem model, we have found that the timing of ice retreat has a strong impact on the timing of pelagic phytoplankton peaks over a large portion of the Arctic marginal seas. On the other hand, we have found weak or no impact on the timing of ice-algae blooms in those regions. The correlation between the time lag and ice retreat is noteworthy in areas where ice-retreat has no significant impact on ice-algae peak timing, suggesting that the variability in time lags is mainly controlled by changes in pelagic phytoplankton peak timing in those regions. Higher trophic levels, particularly the abundant copepod species grazing on both ice algae and pelagic phytoplankton, are likely to be sensitive to the timing of the blooms as well as the time lag between them.

Acknowledgements

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