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HORIZONS

Marine plankton phenology and life history in a changing climate: current research and future directions

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Increasing availability and extent of biological ocean time series (from both *in situ* and satellite data) have helped reveal significant phenological variability of marine plankton. The extent to which the range of this variability is modified as a result of climate change is of obvious importance. Here we summarize recent research results on phenology of both phytoplankton and zooplankton. We suggest directions to better quantify and monitor future plankton phenology shifts, including (i) examining the main mode of expected future changes (ecological shifts in timing and spatial distribution to accommodate fixed environmental niches vs. evolutionary adaptation of timing controls to maintain fixed biogeography and seasonality), (ii) broader understanding of phenology at the species and community level (e.g. for zooplankton beyond *Calanus* and for phytoplankton beyond chlorophyll), (iii) improving and diversifying statistical metrics for indexing timing and trophic synchrony and (iv) improved consideration of spatio-temporal scales and the Lagrangian nature of plankton assemblages to separate time from space changes.

KEYWORDS: plankton; phenology; life history; climate change

INTRODUCTION

Phenology is defined (Oxford English Dictionary) as "the study of cyclic and seasonal natural phenomena, especially in relation to climate and plant and animal life". In many environments, including the upper water-column of oceans, the seasonal cycle sets much of the total environmental variability experienced by

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individual organisms and populations. The seasonal range of upper ocean environmental conditions is typically greatest at mid and high latitudes, but substantial seasonal variations of environment and plankton biomass also occur in many tropical regions (Sheridan and Landry, 2004; Longhurst, 2007). Many species have evolved elaborate behavioral and life history strategies that exploit favorable periods of the year (those best matching optimal niche requirements) for growth and reproduction, and minimize exposure of sensitive life stages to stressful periods. For marine plankton, the primary modes of phenological variability are expressed as changes in population size, reproductive/developmental status and (for some species) the timing and duration of seasonal dormancy.

Phenological variability occurs because the amplitude and phasing of environmental conditions and individual organism responses are not perfectly repetitive from year to year. In cases when the interannual variability of environmental cycles (e.g. light, temperature and density stratification) and biotic responses (e.g. population densities, dormancy, reproduction and migration) are strong but their covariability is low, potential timing mismatches occur between organisms and their physical environment, or across trophic interconnections. The concept that timing match–mismatch between trophic levels might be an important driver of interannual changes in total population abundance and/or annual reproductive success dates back more than 40 years to papers by Cushing and colleagues (see Cushing, 1990 for an updated summary). However, most of the marine studies of plankton phenology have been completed only within the last decade.

Compared with marine systems, the history of research on freshwater plankton is somewhat longer, especially in Europe and North America (see Sparks and Menzel, 2002; Thackeray *et al.*, 2008, for introductory reviews). In most cases, the functional taxonomy is similar between freshwater and coastal marine systems. However, we can expect differences in ocean responses, due to greater depth, thermal inertia, advective transport and reduced boundary–volume ratios. Perhaps even more important, marine plankton populations are typically numerically larger (by several orders of magnitude) and less genetically isolated than corresponding freshwater populations. This creates important limits on the maximal rate of within-species evolution and genetic adaptation of marine plankton (further discussion below under Future directions).

Climate change is causing significant trends of seasonal timing in a wide variety of biota and environments (see Sparks and Menzel, 2002; Durant *et al.*, 2007). This has stimulated an increased attention to phenological variability of individual "target" marine taxa, and also greater effort to integrate the results across trophic levels and methodological approaches. Three examples of the upsurge in interest were recent conference theme sessions on marine phenological variability and its food web consequences: the November 2007 PICES conference (Sydeman, 2009), the June 2009 GLOBEC Open Science Meeting (Mackas, Ji and Edwards, convenors; this paper), and the February 2010 AGU/ASLO Ocean Sciences Meeting (Bograd and Sydeman, convenors). The purpose of this paper was to summarize the recent results and interpretations and to consider and propose directions for future study.

CURRENT STATUS

Locations and general characterizations of the existing studies

There is a large literature quantifying the aspects of phytoplankton phenology from observational data. Commonalities are that (i) most analyses have focused on the spring bloom, with a strong northern hemisphere bias, (ii) with the exception of analyses of the Continuous Plankton Recorder (CPR) data and measurements at few open ocean sites [e.g. Hawaii Ocean Time series (HOT) and Bermuda Atlantic Time Series (BATS)], most analyses of open ocean phytoplankton phenology are based on satellite-measured chlorophyll data (obtained since 1978) and (iii) a large number of *in situ*, but largely coastal, phytoplankton time series, potentially suitable for analysis of phenology, are available but have not been fully analyzed. Many of the latter were identified at the recent Chapman conference on phytoplankton time series (http://www.agu.org/meetings/chapman/2007/bcall/).

To date, time series of marine zooplankton phenology have been analyzed from fewer than 20 locations (see reviews by Richardson, 2008; Mackas and Beaugrand, 2010). All of these are from northern hemisphere, most are from mid-latitude and nearshore, and most have focused on a limited range of taxa (primarily calanoid copepods). Several additional time series are, or will soon be, sufficiently long and taxonomically resolved for similar analysis, including regions in the Baltic, the western Mediterranean, the Spanish coast, the coastal NW Atlantic, parts of the Benguela and Humboldt Current systems, central Oregon, Hawaii, and parts of the Southern Ocean.

In the next sections, although we do not attempt to review all the available literature, we point to specific examples to highlight approaches and understanding.

Highlights of published results

Phytoplankton phenology: observation and modeling

Phytoplankton seasonality is controlled primarily by light and nutrient availability (Sverdrup, 1953; Legendre, 1990). Two bloom events dominate phytoplankton phenology in temperate pelagic environments. The spring phytoplankton bloom starts when seasonal increases in daily irradiance and thermal stratification remove light limitation, and allow phytoplankton to grow rapidly on nutrients supplied by prior turbulent and convective mixing. The spring bloom ends by combined effects of nutrient depletion, grazing mortality and in many cases viral control (Brussaard *et al.*, 1996; Larsen *et al.*, 2004). The fall bloom, on the other hand, occurs when and if seasonally increasing vertical mixing (convective cooling and winds) renews the nutrient supply in the euphotic zone before light availability becomes fully limiting (Findlay *et al.*, 2006). Phytoplankton bloom dynamics can differ strongly in polar, tropical/subtropical and coastal regions where additional factors such as ice, wind-driven upwelling, a shallow bottom, tidal mixing and/or freshwater runoff significantly modify the seasonality of stratification and light/nutrient availability (Legendre, 1990), forming different ecological domains (Longhurst, 1995; Cloern and Jassby, 2008).

In the coastal zone, phytoplankton seasonal cycles are readily apparent in both satellite and *in situ* time series. However, connections between local phytoplankton timing and large-scale forcing are often masked by local effects such as those listed above, and also by short spatial and temporal decorrelation scales of "stochastic" variability (Cloern and Jassby, 2008). Empirical regression analyses can sometimes link the phenological shift of phytoplankton dynamics (bloom timing and strength, and species composition) to changes in environment factors such as sea surface temperature (SST), cloudiness and wind mixing (Li and Harrison, 2008; Nixon *et al.*, 2009), but not always (Kim *et al.*, 2009). This underscores the complexity of coastal ecosystems driven by nonlinear interaction of multiple physical and biological processes.

Our most geographically complete views of phytoplankton phenology are from satellite ocean color data. Climatological averages of seasonality provide a background against which future changes can be compared (Thomas *et al.*, 2001; Kahru *et al.*, 2004; Yoo *et al.*, 2008). Over the Northwest Atlantic shelf, Ji *et al.* (Ji *et al.*, 2007) showed spatial pattern in the onset of the spring bloom imposed by the varying influence of freshwater on stratification. Similarly, satellite data effectively delimit cross-shelf and latitudinal regions of the California Current where the spring increase of chlorophyll was delayed by over a month in 2005; a shift that could be linked to delays in the onset of upwelling-favorable wind forcing (Kudela *et al.*, 2006; Thomas and Brickley, 2006). On basin scales, satellite data show the latitudinal progression of the spring bloom and interannual differences over the North Atlantic (Henson *et al.*, 2009). Despite daily orbits, cloud cover introduces data gaps of regionally and temporally varying severity in satellite time series. Given the rapid physiological response times of phytoplankton, it is clear that satellite time series may miss or mask details of phytoplankton interannual variability, potentially biasing our view of phenology. The best views will emerge from careful integration of satellite data with high temporal resolution *in situ* time series and models.

Species-level phytoplankton time series can contain information about details of seasonal succession that are embedded (or hidden) in time series of more aggregated variables such as chlorophyll, "greenness", or particulate carbon. The North Sea CPR time series (Edwards and Richardson, 2004) shows large taxon-dependent differences in the range and temperature dependence of timing variability. This means that the changes in the timing of the main chlorophyll peak may also involve in the changes in the identity (and perhaps food quality) of the species responsible for the main peak. This is elaborated further below in the "Beyond chlorophyll for phytoplankton" section.

Biological–physical coupled models have been used to understand how environmental forcing affects the timing, duration and magnitude of phytoplankton blooms. Most bloom-related modeling studies focus on identifying what physical processes control stability of the water column (e.g. mixed layer depth) and thereby average light availability, a key parameter in the classic Sverdrup critical depth hypothesis (Sverdrup, 1953). These studies have been conducted for coastal/shelf (Sharples *et al.*, 2006; Ji *et al.*, 2008) and open ocean systems (Lancelot *et al.*, 2000; Hashioka *et al.*, 2009; Henson *et al.*, 2009). The spatial domain of coupled models varies from one-dimension (1D, vertical) to regional and global three-dimension (3D, horizontal and vertical), depending on the temporal and spatial scale of the phenological questions to be addressed.

Surface forcing (e.g. wind stress and heat flux) is commonly considered the major driver of changes in water column stability and hence of variability of phytoplankton bloom phenology. One-dimensional models have proved helpful in revealing the underlying mechanisms driving the phenological shift when local forcing controls the mixing/stratification dynamics (Sharples *et al.*, 2006). In

cases where water column stability is influenced by advection-related environmental factors, such as changes in surface salinity, a spatially explicit 3D model can be useful (Ji *et al.*, 2008). With the advent of computational capability and the improved skill of hydrodynamics modeling in simulating vertical mixing and horizontal circulation, the long-term simulation of biological–physical interactions over a large spatial domain becomes possible. Recent work by Henson *et al.* (Henson *et al.*, 2009) in the North Atlantic shows clearly the value of this type of multi-year 3-D simulation. Regional differences in forcing driving decadal-scale bloom timing variability can now be analyzed more mechanistically than was possible with empirical regression-based studies.

Zooplankton phenology: observation and modeling

Despite the relatively small number of studies of zooplankton phenology (see above), several consistent and important generalizations can be made based on the results so far with the caveat that nearly all of these results come from mid- and high-latitude continental margin regions. First, zooplankton phenological variability can be adequately indexed by within-year changes in abundance, if the temporal resolution of the time series is bi-weekly to monthly (Ellertsen *et al.*, 1987; Edwards and Richardson, 2004; Greve *et al.*, 2005; Chiba *et al.*, 2006; Sullivan *et al.*, 2007; Johnson *et al.*, 2008; Conversi *et al.*, 2009), and sometimes by within-year changes in developmental stage composition or reproductive status for lower resolution time series (Mackas *et al.*, 1998, 2007; Batten and Mackas, 2009). Second, interannual timing variability as great as 1–2 months (of abundance peaks or life history events that have approximately a month long duration) is common (see all references listed in the previous sentence). Third, the proximal biological mechanisms controlling the observed timing variability include reproductive timing of the parent generation (Ellertsen *et al.*, 1987), onset/emergence from dormancy (Sullivan *et al.*, 2007; Johnson *et al.*, 2008), and/or strong within-year variability of mortality rate (Mackas *et al.*, 1998). It is worth noting that forcing-to-response time lags of weeks to a few months are likely with all of these, especially for biological processes such as dormancy and reproduction that require considerable advanced physiological preparation. Fourth, the zooplankton timing variability is often correlated with environmental temperature and/or with phytoplankton biomass (or species composition) during the preceding weeks to months. For zooplankton taxa that have their maximum abundance and activity in spring/summer, the usual pattern is "earlier when warmer" (Mackas *et al.*, 1998, 2007; Edwards and Richardson, 2004; Greve *et al.*, 2005; Chiba *et al.*, 2006). However, the magnitude of the timing change is often much larger than can be explained solely by acceleration of physiological rates by high temperature or good nutritional state (Ellertsen *et al.*, 1987; Mackas *et al.*, 1998), and taxa that have maximum abundance in late summer or autumn often show a "later when warmer" pattern (Edwards and Richardson, 2004; Conversi *et al.*, 2009; Mackas and Beaugrand, 2010). Fifth, in some systems that are highly advective and/or have strong horizontal zoogeographic distributional gradients, seasonal changes in flow pattern also have a strong association with observed changes in abundance and composition (Hooff and Peterson, 2006). Sixth, the long-term phenology trends of zooplankton (vs. temperature or year) are often steeper than the same trends for vertebrate planktivores that depend on zooplankton (Bertram *et al.*, 2001). There are several evolutionarily plausible reasons why seasonal timing of marine zooplankton is highly variable, including (i) high incidence/importance of a dormant life stage; (ii) generation time almost always less than a year (largely eliminating any fitness advantage of fixed-calendar response because individual and year-class reproductive success cannot be deferred to subsequent years); (iii) apparent reliance on timing cues/controls (thresholds of temperature, food supply, internal body condition) that also have large interannual variability and (iv) little capability for long range horizontal migration to seek optimal conditions elsewhere. Whatever the cause, trophic-level discrepancy of response increases the likelihood of trophic mismatch under progressive global warming.

Most of the completed species-level modeling studies have targeted calanoid copepods. Recent advances in modeling technique and skill (review in Runge *et al.*, 2005; Stegert *et al.*, 2007; Gentleman *et al.*, 2008; Hu *et al.*, 2008; Record and Pershing, 2008; Neuheimer *et al.*, 2009; Ji *et al.*, 2009) have opened opportunities to investigate variability in seasonal demographic cycles under different scenarios of environmental forcing. Computational capacity and modeling skill now allow coupling of multi-stage, concentration-based copepod life cycle models to three-dimensional, high-resolution hydrodynamic models, for example, to populations of *Pseudocalanus* and *Centropages* in the Gulf of Maine (Ji *et al.*, 2009), *Pseudocalanus elongatus* in the southern North Sea (Stegert *et al.*, 2007) and *Calanus finmarchicus* in the North Atlantic Ocean (Speirs *et al.*, 2006) and Norwegian Sea (Slagstad and Tande, 2007). The copepod life cycle and hydrodynamic model can also be linked to an NPμZD model, providing mechanistic insight into effects of timing variability in microplankton prey fields (Fennel and Neumann, 2003). These advances provide an emerging capability of forecasting the relative roles of environmental forcing (e.g. temperature and food) and advection in determining

distribution and abundance. For example, Ji *et al.* (Ji *et al.*, 2009) have predicted that (i) warmer temperatures in the Gulf of Maine are likely to cause the seasonal growth of *Centropages typicus* to occur earlier and extend longer into the autumn and (ii) that a connection between Arctic melting and the freshening of the late winter surface layer in the Gulf of Maine will alter the timing of the spring increase of *Pseudocalanus* spp.

For copepods that undergo diapause, like *Calanus finmarchicus*, individual development (and consequently population growth) is seasonally interrupted. Models of life cycle seasonality must build on an understanding of the environmental or physiological cues that control timing of entry into and exit from diapause. Observed patterns of within- and between-region variability of the onset timing of *C. finmarchicus* diapause in the coastal northwest Atlantic are consistent with a hypothesis that control of diapause entry is associated with lipid accumulation during the growing copepodite stages (Johnson *et al.*, 2008). Timing of exit from diapause is hypothesized to be a function of the development time–temperature relationship (Hind *et al.*, 2000), but may also be influenced by the temperature-dependent rate of lipid utilization during diapause (Saumweber and Durbin, 2006), such that the individual becomes active if its lipid reserves fall too low. Quantitative depiction of how lipid accumulation affects *Calanus* diapause timing can be achieved using an individual-based model (IBM), in which the development, growth and lipid accumulation rates of individuals can be followed, and the sum of the individual responses yields the population demography. Overall, IBM models provide a powerful tool to track individual and population variability in response to environmental forcing, laying the foundation for prediction of phenological responses to scenarios of climate change.

Timing of life history events in a seasonal cycle has important fitness consequence. Life history models have been used to explore links between timing of those events (such as diapause and reproduction) with individual fitness, and thereby predict and better understand phenological changes from a life-cycle perspective (Fiksen, 2000; Varpe *et al.*, 2007, 2009). For example, Varpe *et al.* (Varpe *et al.*, 2009) use a state-dependent life history model and dynamic programming to evaluate the seasonal variability in offspring fitness as a function of how alternative genetically programmed developmental "choices" cope with imposed seasonal cycles in food availability, mortality due to predation and temperature effects on physiological rates. The results provide insight into within-population shifts in life history strategies (in this instance the timing and source of energy for reproduction) that may occur in a changing environment. The main mode of adaptive response to environment changes, either through ecological shifts in timing and spatial distribution to accommodate fixed environmental niches or possibly through evolutionary adaptation of timing controls to maintain fixed biogeography and seasonality, remains to be further explored through laboratory and modeling studies.

Trophic phenological match–mismatch

Temperate and high-latitude pelagic ecosystems may be particularly vulnerable to phenological changes caused by climatic warming. Recruitment success of higher trophic levels is highly dependant on synchronization with seasonally pulsed primary production and the response to regional warming varies among functional groups. Changes in any of these can lead to mismatch in timing between trophic levels (Edwards and Richardson, 2004). For example, the changes in the North Sea planktonic assemblage and copepod phenology were correlated with warming of the North Sea over the last few decades, and have resulted in a poor food environment for cod larvae and hence an eventual decline in overall recruitment success (Beaugrand *et al.* 2003). Similar evidence linking plankton phenology and higher trophic levels has been found elsewhere, e.g. phenology of shrimps and phytoplankton in the North Atlantic (Koeller *et al.*, 2009) and seasonality of zooplankton abundance and energy propagation up to fish and seabird predators in the Northeast Pacific (Mackas *et al.*, 2007). For some copepod species like *Calanus glacialis* in the Arctic, a match between its reproductive cycle with two algal blooms is probably necessary for a successful population development: an ice algal bloom to fuel females' early maturation and reproduction, and a subsequent phytoplankton bloom to support a fast development of their offspring (Søreide *et al.*, 2010). In this sense, the phenological mismatch between two trophic levels can be more important than phenological variability of individual species, leading to the concept of relative phenological shift that uses the phenology of the lower trophic level (or food) as a "yard-stick" against which phenological shifts of higher trophic levels can be measured (Visser and Both, 2005).

Shifts in timing of copepod reproduction and seasonal growth patterns also have ramifications for the seasonal timing of energy-rich lipids available to higher trophic levels. The energy content and timing of availability of copepodite stage CV for forage fish in coastal feeding areas depends in large part on environmental factors (food and temperature) that determine lipid accumulation rates. The actual accumulation rate in forage fish also depends on the seasonal light field

needed for visual feeding, which may mitigate or exaggerate phenological shifts in copepod prey availability (Varpe and Fiksen, 2010). Long-term climate warming may lead to dramatic reduction in abundance of lipid-rich copepod species in ecosystems at the southern edge of the range of subarctic *Calanus* species, with no identifiable prospects for replacement (Beaugrand, 2009; Kattner and Hagen, 2009). Such scenarios can be explored with new modeling tools that couple life histories and lipid content to physical circulation and hydrographic models as well as ecophysiological niche-based models as the skill of these models improves.

FUTURE DIRECTIONS

Main mode of change: ecological vs. evolutionary

Species and population responses to environmental change are conventionally classified into either ecological or evolutionary responses. Ecological responses include physiological acceleration/deceleration, phenotypic plasticity and dispersal in space or time. Evolutionary responses involve direct genetic change. It has been suggested by Parmesan (Parmesan, 2006) that species are more likely to shift their seasonal cycles and distributions in response to climate change, rather than evolve *in situ*. Currently, the biogeographical and phenological patterns observed for marine plankton support this view. For example, at the species level, some of the first consequences of climate warming and global change are often seen in altered species phenology (i.e. timing of annual life-cycle events) and in altered geographical distribution limits. This is mainly because environmental changes continually impact the life cycle of the species and naturally the population will respond over time, providing it is not biotically restrained or spatially restricted, to its optimum position within its bioclimatic envelope. Marine planktonic organisms, with short life cycles and largely free of geographical barriers, are capable of quickly tracking changing bioclimatic envelopes, whether this is within a temporal niche as in seasonal succession (observed as a phenological response) or in its overall spatial niche (observed as a geographical movement in a population).

Current evidence for plankton points to phenotypic plasticity and movement both spatially and temporally (at the decadal time-scale at least) as opposed to evolutionary change. However, this is not to say that direct genetic change at an ecological scale is not possible. Organisms may adapt to extreme environment fluctuations through rapid evolution, especially in geographically restricted areas (Lee and Gelembiuk, 2008; Lande, 2009). This is evident in many isolated freshwater systems (Hairston and Dillon, 1990; Latta *et al.*, 2007; Van Doorslaer *et al.*, 2007). The underlying genetic mechanisms, such as co-adapted gene complexes (Burton *et al.*, 2006; Edmands *et al.*, 2009) and gene rearrangement (Machida *et al.*, 2005) have been explored. There is a need to further synthesize the interaction between ecological and evolutionary responses to global change for marine plankton and also to understand the genetic basis for phenotypic responses. A potentially interesting case study of these responses could be the spatially isolated population of *Pseudocalanus elongatus* in the northern Adriatic. This population is considered to be an ice-age relic cut-off by warm Mediterranean waters from contact with larger populations in the North Atlantic. However, the species has recently shown some rapid and dramatic phenological changes (Conversi *et al.*, 2009). While this species can temporally shift in its succession cycle within a finite window, it is also spatially constrained and therefore cannot shift its distribution northward. If climate continues to warm, this population, in the absence of any genetic adaptation, could face extinction.

Broadened understanding of phenology: additional taxa and response indices

Beyond calanus for zooplankton

The number of zooplankton taxa for which there are long phenology time series is high in the North Sea (over 50 in the North Sea CPR time series, ~60 at Helgoland Roads), moderate in the Mediterranean (Naples and Trieste) and much lower (1–5 species) elsewhere in the Atlantic and in the Pacific. Nevertheless, more taxa and with a much broader range of life history strategies and seasonal preferences have been observed than have been examined in numerical models. Copepod taxa (other than *Calanus*) for which both future data analysis and numerical modeling studies of phenology hold promise include:

- *Neocalanus*: Strong diapause phase similar to "*Calanus finmarchicus*", but spring reproduction relies on remaining over-winter lipid reserves, without precursor feeding by the parent (Miller and Clemons, 1988).
- *Calanoides carinatus*: A subtropical species found in upwelling systems in the Atlantic and Indian Oceans, notably the Benguela upwelling system; strong diapause phase, but dormancy timed to upwelling cycles rather than to calendar season (Verheye *et al.*, 1991).

- *Centropages* and/or *Acartia*: These copepod taxa have multiple generations per year, no pre-adult dormancy, little lipid accumulation, "current income" reproduction, often a summer or autumn abundance maximum, dormant eggs for several species, and are also amenable to stage-based coupled physical biological modeling (Halsband-Lenk *et al.*, 2004; Sullivan *et al.*, 2007).

While time series and physiological data are available for many species within these and other taxa, at some point parameterization of life history models will require more extensive measurements of vital rate parameters, similar to the pioneering work on *Calanus* by Vidal (Vidal, 1980a, b). In addition, demographically detailed observations must be made at sufficient frequency to resolve seasonal timing and to estimate seasonal variations in stage specific mortality.

Other meso- and macro-zooplankton taxa that play key roles in marine ecosystems are also candidates for modeling studies. Euphausiids (differing from the copepods listed above by having much larger body size, multistage indirect development; potential for multi-year life span, absence of seasonal dormancy, winter "shrinkage", and iteroparous reproduction that is either season-locked or triggered at higher frequency by episodic phytoplankton blooms) are increasingly recognized for their important roles as both predators and prey in high-latitude and upwelling ecosystems. Quantitative analysis of the life histories of several species of euphausiids is advancing (Tanasichuk, 1998a, b; Hofmann and Lascara, 2000; Cuzin-Roudy *et al.*, 2004; Fach *et al.*, 2008; Pinchuka *et al.*, 2008; Wiedenmann *et al.*, 2008; 2009; Feinberg *et al.*, 2009). Additional candidate groups include meroplankton (Koeller *et al.*, 2009), pteropods, ctenophores (Costello *et al.*, 2006), appendicularians (Greve, 2005) and fish larvae (of particular interest for trophic match-mismatch analysis). As the resources required to conduct studies of phenology are substantial, judicious selection of species and locations is needed, guided by understanding of trophic roles of key zooplankton species in mid- to upper-latitude ecosystems.

Beyond chlorophyll for phytoplankton

Species-specific responses to changing environmental phenology probably differ from biomass responses, offering insight into mechanisms and trophic implications not possible with measurements of chlorophyll alone. For instance, previous studies suggested that photoperiodic control of diatom spore growth and germination could be an important factor in the development of the spring bloom and that critical light levels are more important than direct physiological temperature effects in initiating the spring phytoplankton bloom (Eilertsen *et al.*, 1995; McQuoid and Hobson, 1996; Eilertsen and Wyatt, 2000). This is not the scenario for all spring diatom blooms, however. Blooms initiated by *Skeletonema costatum* begin much earlier in the season and are not limited by day-length (Erga and Heimdal, 1984). After the initial start of the bloom, which appears to be community dependant and in some circumstances triggered by photoperiod, variations in its amplitude are still regulated by classical forcing by following the Sverdrup model (Eilertsen and Wyatt, 2000). On the other hand, dinoflagellates species showed a strong temperature-dependant response (higher seasonal temperatures leading to earlier blooms and vice versa). It is not yet known whether the movement in dinoflagellates is a physiological response to temperature or whether it is a response to the seasonal adjustment to prey items (as many dinoflagellates are mixotrophic and/or heterotrophic). It must be noted, however, that the North Sea study was conducted in the relatively shallow central North Sea and the same hypothesis may not be applicable in deep oceanic environments where the degree of deep winter mixing, and other environmental controls (e.g. indirect temperature effects such as thermal stratification and wind energy input) that dictate critical light levels, may play a more dominant role in controlling the onset of the spring diatom bloom.

While CPR surveys cover ocean-basin scales with records on 170 phytoplankton species, synoptic quantification of basin-scale phytoplankton phenology depends primarily on satellite (bio-optical) estimates. One developing path for application of the satellite data is coupling these with vertically profiling autonomous buoys and gliders (Boss *et al.*, 2008; Perry *et al.*, 2008) that better constrain the surface view afforded by the satellite. Many metrics of phytoplankton phenology are possible from satellite data [e.g. timing of initiation and maxima/minima, magnitude and duration of events (Platt and Sathyendranath, 2008)]. In addition, analyses of time series of other bio-optical signals derived from satellite data afford new views of phytoplankton dynamics. Some examples are beam attenuation (Behrenfeld and Boss, 2006), backscatter-based estimates of phytoplankton carbon (Behrenfeld *et al.*, 2005), fluorescence (Behrenfeld *et al.*, 2009), primary production (Kahru *et al.*, 2009), and shifts in multispectral radiance (Martin-Trayovski and Sosik, 2003) or estimates of community structure (Alvain *et al.*, 2005). Such metrics of phytoplankton phenology likely offer satellite-based ecological insight previously masked by considering chlorophyll concentration alone.

Table I: Examples of timing indices for quantifying plankton phenology

Index	Description	Advantage/disadvantage	Published examples
Start of seasonal increase	Year day when biomass rise above certain threshold value; often used for indexing phytoplankton.	Based on biomass; easy to estimate; may use raw data; less robust if data are noisy; results vary with the choice of threshold.	Siegel *et al.* (2002), Platt *et al.* (2008), Wiltshire and Manly (2004), Wiltshire *et al.* (2008), Vargas *et al.* (2009)
	Year day when a lower threshold percentile (e.g. 25th percentile) of annual or seasonal cumulative biomass or abundance is reached; used for indexing zooplankton.	Based on cumulative biomass or abundance; relatively insensitive to noisy individual data points; results vary with the choice of threshold.	Greve *et al.* (2005)
	Year day of maximum instantaneous growth rate within a defined period; used for indexing phytoplankton.	Based on rate of change; less dependent on threshold; less straightforward; gap-filling or smoothing is needed especially when data points are sparse.	Sharples *et al.* (2006), Rolinski *et al.* (2007)
Seasonal peak	Year day with highest biomass at a defined period; Used for indexing phytoplankton and zooplankton.	Straightforward; easy to estimate; Less robust if data are noisy; more bio-physical factors (compared to start of bloom) involved in controlling peak timing. Smoothing is needed to mitigate the effect of outliers.	Mackas *et al.* (1998), Chiba *et al.* (2006), Platt *et al.* (2009), Wiltshire *et al.* (2008)
Middle of Season	Date of center-of-gravity for the entire annual amount vs. date curve. Used for indexing phytoplankton and zooplankton.	Based on integrative property; less affected by outliers; may have low sensitivity if timing shift is small; multi-modal cases require splitting the year into two or more segments (problematic if modes differ greatly in amplitude, or are present only in a subset of years)	Edwards and Richardson (2004), Wiltshire and Manly (2004), Wiltshire *et al.* (2008), Conversi *et al.* (2009)
	Date of 50th percentile of cumulative abundance. Used for indexing zooplankton.	Based on cumulative biomass; easy to estimate; sensitive to small change; problematic in multi-modal cases.	Greve *et al.* (2005), Batten and Mackas (2009)
End of season	Year day when an upper threshold percentile (e.g. 75th percentile) of annual or seasonal cumulative amount is reached; used for indexing zooplankton.	(as for "start of seasonal increase")	Greve *et al.* (2005)
Duration of season	Number of days between "start" and "end" of season percentile thresholds.	(as for "start of seasonal increase")	Greve *et al.* (2005), Batten and Mackas (2009)
"Cardinal Dates"	Produces date estimates for start, middle and end of season, based on parameters of a Weibull function fitted to annual or seasonal time series. Applied (so far) only to phytoplankton data.	Provides flexible fit to a variety of peak shapes; can deal with multiple modes; but requires a prior within-year fitting step to estimate number of peaks and their separation dates.	Rolinski *et al.* (2007)

Note: Various smoothing/curve fitting methods have been used before computing the indices listed above, e.g. shifted Gaussian fitting (e.g. Platt *et al.*, 2009), low pass filtering (Wiltshire *et al.*, 2008), within-year harmonic analysis (Dowd *et al.*, 2004) and generalized linear model (Vargas *et al.*, 2009). Generally speaking, if a time series is in uni-modal and is from densely sampled data with few outliers, all methods perform well. Otherwise, more advanced and flexible approaches with less assumption of distribution pattern might perform better.

Better statistical methods for indexing of timing

Quite a few indices have been used to quantify the timing of plankton phenology (Table I). For phytoplankton, multiple metrics of bloom phenology are possible, including timing of initiation, peak or decline, bloom duration, and bloom magnitude either as maximum concentrations or time-integrated biomass. The most appropriate phytoplankton metric depends on the question being asked, varying as a function of geography and the dominant forcing mechanisms. For instance, for copepod feeding and reproduction the timing of critical concentration thresholds might be more important than seasonal maxima (Runge *et al.*, 2005), and the presence and timing of late winter blooms created by episodic conditions could be as, or more important than spring blooms for controlling the timing and amplitude of the annual zooplankton biomass (Durbin *et al.*, 2003). In terms of identifying ecosystem responses to climate change and links to physical forcing, a wide range of possible metrics should be explored (Vargas *et al.*, 2009). A commonly used metric is the date when chlorophyll concentrations first become 5% greater than the local

annual median (Siegel *et al.*, 2002). Application of this metric has provided insight into physical forcing mechanisms linked to bloom timing (Ueyama and Monger, 2005; Henson *et al.*, 2009). Metrics focused on timing shifts over other aspects of the annual cycle may be important. For example, at lower latitudes, where the dominant annual feature is the autumn/winter biomass peak resulting from surface nutrient renewal from mixing, duration of the summer stratified period likely has important trophic implications.

Seasonal zooplankton timing has been indexed by a variety of methods based on annual curves of amount-at-date, or cumulative amount, or age/stage composition. In general, the cumulative percentile methods give good results for dense data; the stage composition for sparse temporal coverage. All have some problems indexing peak timing in bimodal or polymodal annual cycles (similar to phytoplankton timing), especially if one or both modes has large fluctuations in amplitude. Also because timing match–mismatch is more important than timing alone, we would additionally like new tools to index the extent of overlap among the annual cycles of organisms occupying adjoining trophic levels. One important issue for match–mismatch is the interaction between timing and amplitude of annual peaks of food availability; we want to know not only the mid-point timing of the peak, but also when and for how long food levels meet or exceed the requirements of a consumer population.

An important consideration in quantifying phenology is effective separation of the seasonal component from both underlying variable long-term trends as well as relatively short-term variability. Certainly traditional approaches (e.g. harmonic analysis, treatments of variance such as empirical orthogonal functions) offer insight. A relatively untried approach is the use of state space models. These are a time series modeling methodology (Durbin and Koopman, 2001) based on fitting-constrained functions using a combination of Kalman filter and maximum likelihood, assuming an observed (sampled) signal results from an unobserved dynamic process modulated by one or more unknown functions observed with noise (or error). The observed signal is decomposed into a series of non-stationary, user specified, functions and an error term. The effectiveness of this method has been demonstrated in various oceanographic applications (Schwing and Mendelssohn, 1997; Mendelssohn and Schwing, 2002; Mendelssohn *et al.*, 2005). The non-stationary nature of both the resulting underlying trend and the seasonal components has the potential to provide improved separation of the two and better insight into plankton phenology links to physical forcing (Mendelssohn *et al.*, 2005).

Dealing with advective history

The majority of zooplankton phenology time series are Eulerian (observations at fixed locations, often from single sites). Many of these sites are strongly advective. Analyses to date have compared these observations to environmental time series at the same location. The prior history of the zooplankton would be better described by a Lagrangian reconstruction of environmental conditions along their drift trajectory. In some cases (in and near boundary currents), 1–2 month trajectories may span several thousand kilometers and significant environmental gradients (Tatebe *et al.*, 2010; K. Coyle, personal communication). A Lagrangian approach will require collaboration between modelers, field ecologists and data analysts. However, useful first steps include scaling analyses and mapping differences between Eulerian and Lagrangian histories.

A simple first-order estimation of the importance of advection is through a scaling analysis similar to the one proposed by O'Brien and Wroblewski (O'Brien and Wroblewski, 1973). This compares the time scales of biological process (e.g. nutrient uptake or population growth) vs. advection at certain spatial scales (such as eddy scale or Rossby deformation radius) assuming that the spatial gradient of biological quantities matches those of physical processes. In combination with a spatial coherence analysis (described below), such a scaling analysis can provide a quick assessment of the linkage between the local vs. regional phenological shift.

A second approach could be comparison of lengths of mean-flow advective trajectories with the dominant spatial scale of Empirical Orthogonal Function (EOF)-derived "similarity maps" for environmental forcing and/or response time series (e.g. modes of environmental temporal variability such as NAO or PDO). We can expect upstream and downstream locations (and Eulerian and Lagrangian time series) to have coherent phenology if source and observation locations lie within a region of similar correlation sign and magnitude. Conversely, we can expect heterogeneity of response (and some difficulty interpreting purely Eulerian data) if source regions and observation location are very heterogeneous. Note that the level of spatial homogeneity/heterogeneity may differ depending on the output time scale of interest (year-to-year vs. decade vs. multi-decade). For example, interannual variability of zooplankton seasonal timing is strongly correlated with growing-season SST in many mid- and high-latitude locations. Beaugrand *et al.* (Beaugrand *et al.*, 2009) showed that there are three dominant modes of interannual SST variability in the NE Atlantic. The strongest and slowest mode has the largest

spatial scale (same sign throughout the region). The time series of this mode is well correlated with the long-term upward trend of temperature throughout the northern hemisphere, and with long-term trends to earlier timing and poleward displacement of zooplankton distributions. A second SST mode is zonally homogeneous but shows a strong N vs. S dipole. Its time series is well correlated the Atlantic Subarctic Gyre index. The third SST mode is meridionally homogeneous, but shows an E–W dipole of sign and intensity; it is well correlated with the NAO.

For satellite-derived phytoplankton metrics, and perhaps also in a few regions where taxonomically resolved plankton time series are abundant and closely spaced (such as the NE Atlantic), we may be able to compare the spatio-temporal EOFs of forcing and response variables. However, for most parts of the ocean, zooplankton studies will be limited to comparisons of (i) a single-location response time series with better-resolved maps of potential forcing variables and (ii) widely separated response time series that share only large-scale (but perhaps dominant) modes of environmental forcing. One example of the latter is the spatial covariance of *Neocalanus* peak timing in the subarctic Pacific. All regions show similar strong associations between timing and spring temperature (earlier when warmer). All NE Pacific regions also show coherence of interannual variability, but the NE Pacific time series are negatively correlated with the NW Pacific (Mackas and Beaugrand, 2010). This result is entirely consistent with the pattern of SST variability and covariability captured in the Pacific Decadal Oscillation (Mantua and Hare, 2002).

To better interpolate the phenological signal observed at a fixed station, it will be necessary to identify the year-to-year variability of the source region for the population of interest. Spatially explicit Lagrangian tracking could be used to provide detailed information on the time and space scales of processes related to observed phenology signals. A simple passive particle backtracking shows the variability of advection pathways and source regions (e.g. Batchelder, 2006). To better disentangle the contribution of advection and population dynamics, backtracking for both physical and biological processes will be helpful (Speirs *et al.*, 2004; Christensen *et al.*, 2007). By combining a realistic simulation of the hydrodynamic environment and stage-based demographic model for *Calanus finmarchicus*, Speirs *et al.* (Speirs *et al.*, 2004) inferred the spatial and temporal map of the recruitment history required to reproduce the observed population structure at a fixed station. This type of backward tracking provides a better understanding of demography of copepod populations in an advective system and facilitates estimating the scales of spatial heterogeneity related to an observed phenological signal from a single-station time series.

Compared with marine systems, the advection issue for freshwater systems, especially in small lakes, is probably less of a concern. However, some of the other issues listed above (and therefore future research priorities) are shared by both freshwater and marine systems. For instance, phenology study beyond bulk properties (e.g. biomass) is also needed for freshwater systems when multiple drivers are responsible for species-level phenological shift (Thackeray *et al.*, 2008); and more statistical matrices will be helpful in separating climate vs. non-climate drivers. In terms of identifying evolutionary vs. ecological mode of change, more studies have been conducted for freshwater systems, which usually have much smaller geographic coverage and are much more controlled (isolated) than marine systems, thus providing useful baseline (and/or comparative) information for future marine system studies.

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