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## Changing zooplankton seasonality in a changing ocean: Comparing time series of zooplankton phenology

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### ARTICLE INFO

#### Article history:

Available online 22 November 2011

### ABSTRACT

Marine zooplankton must deal with seasonal variations of the upper-ocean environment that are both intense and prolonged compared to their life spans. This leads to large seasonal fluctuations of population size, and strong evolutionary tuning of demographic processes (e.g. reproduction, somatic and population growth, and dormancy) for optimal match with the average annual alternation between good and poor growing conditions. However, neither environmental nor zooplankton seasonal cycles are exactly repetitive year-to-year. Recent analyses of several long zooplankton time series have found large (1–3 months) interannual variability of seasonal timing. In this paper, we compare and synthesize results from these studies. Variability in zooplankton phenology is often correlated with anomalies of one or more environmental variables. The most common phenology correlate is water temperature during and before the growing season, and the most common phenologic response to temperature is “earlier when and where warmer”. But several species with seasonal maxima in late summer or autumn have a clear “later when warmer” response. Covariance of seasonal timing with temperature must therefore involve more than thermal acceleration of physiological rates. We suggest that water temperature (relatively slowly and smoothly varying in aquatic environments) is also used by zooplankton as a timing cue, much as terrestrial biota uses day-length. During recent warming trends, temperature-linked changes in seasonal timing may have moved some species outside their locally-optimal seasonal windows (e.g. *Calanus finmarchicus* in the North Sea, and *Pseudocalanus elongatus* in the Adriatic), and have been a major contributor to changes in community composition. Between-location similarities of zooplankton phenology and temperature anomaly time series decay with increasing site-to-site spatial separation. The decorrelation scale is several thousand kilometers in the subarctic Pacific, but a thousand kilometers or less in marginal seas of the NE Atlantic.

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## 1. Introduction

### 1.1. Importance and intensity of seasonal variability

Zooplankton populations are variable at temporal scales ranging from hours to many decades (Haury et al., 1978). A standard strategy for analysis of long zooplankton and environmental time

series is to filter out variability at annual and shorter time scales to reveal multi-year fluctuations and trends (Mackas and Beaugrand, 2010). However, in most ocean regions, the annual cycles of zooplankton amount and composition, and also of key environmental variables (e.g. surface temperature, mixed layer depth, insolation, nutrient availability, chlorophyll concentration and daily primary productivity) are among the strongest contributors to total temporal variance. Concise summaries by region of these strong annual cycles are available in Longhurst (1998). In most regions, zooplankton must survive and adapt to seasonal variations

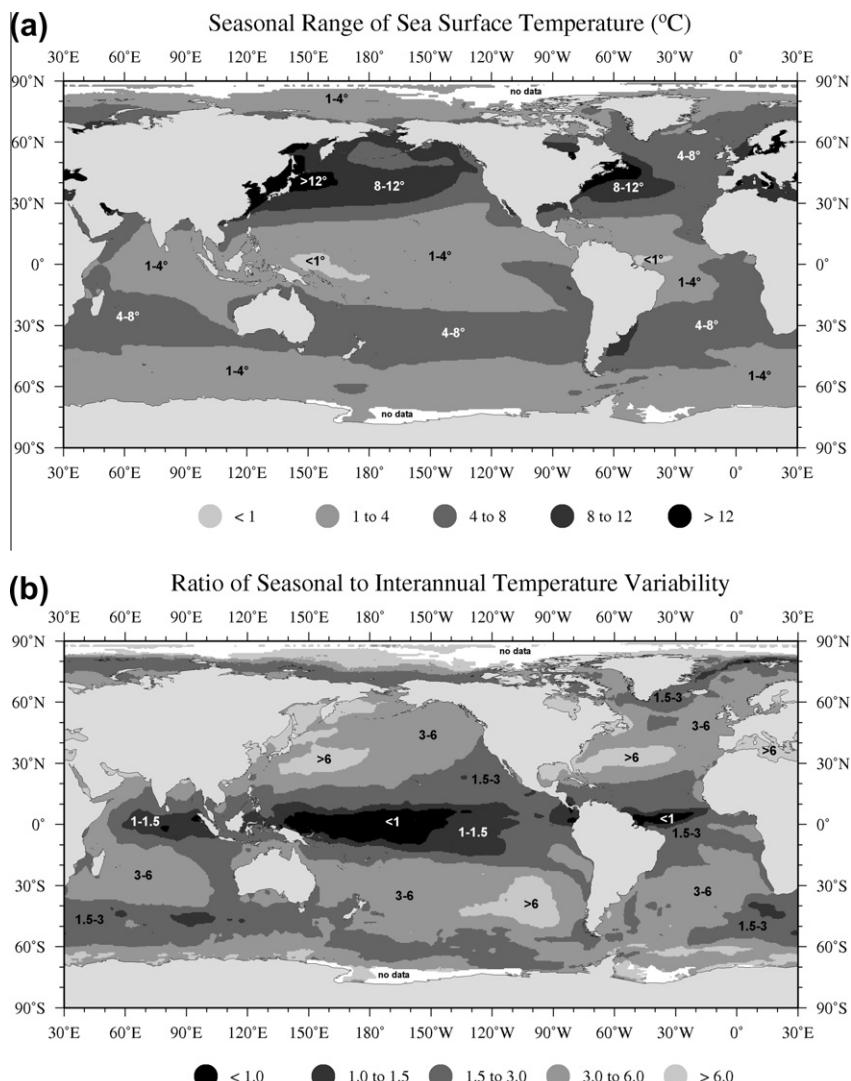
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of upper-ocean environmental conditions that are both intense and prolonged compared to zooplankton generation lengths (a few weeks to a year). Although annual ranges of environmental and zooplankton variability are greatest at northern mid-latitudes, few ocean regions have annual ranges that are smaller than interannual-decadal deviations from climatologies. To illustrate this we compare the spatial distributions of seasonal vs. interannual variability of monthly-average sea surface temperature using data from the HadISST  $1^\circ \times 1^\circ$  grid. As expected, seasonal temperature variation (Fig. 1a) is greatest in enclosed seas and along mid-latitude western ocean boundaries, where continental influence is largest. Globally, the seasonal temperature variation is more intense than the interannual variation (Fig. 1b). Seasonal range is more than 3-fold larger than the extreme multi-year anomalies in 56% of the grid, and more than 6-fold larger in 12%. By contrast, interannual variability is  $\geq$  average seasonal range in only 3%. All locations where interannual exceeds seasonal variation are in places where seasonal temperature variation is small – either near the equator (mostly in the Pacific), or at high latitudes where much of the annual change in heat content occurs as formation/melting of sea ice, rather than change in water temperature.

## 1.2. Adaptive mechanisms available to zooplankton

Large regional interannual anomalies/trends of zooplankton biomass and composition often accompany interannual temperature anomalies/trends as small as one to a few degrees (McGowan et al., 1998; Mackas and Beaugrand, 2010; Mackas et al., 2001, 2007; Beaugrand, 2003, 2004; Beaugrand et al., 2002, 2003; Hays et al., 2005; Chiba et al., 2006; Valdés et al., 2006). We know (Fig. 1) that most zooplankton populations encounter and survive larger seasonal ranges of water temperature. Many species also vertically migrate across the thermocline each day and thereby encounter a daily temperature range of  $10^\circ\text{C}$  or more. How are zooplankton able to cope with intense seasonal and diel environmental variability when their sensitivity to similar or smaller interannual variability is so great? One reason is that the seasonal and daily variation is repetitive, and therefore to a considerable degree predictable. This has allowed zooplankton (and most other upper-ocean biota) to make large investments in evolved life history, behavioral, physiological, and distributional strategies that are tuned to the annual and daily periodicities. In general, these strategies maximize the abundance/exposure of vulnerable life stages during time windows that are optimal for reproduction, growth,



**Fig. 1.** Maps comparing the intensity of seasonal and interannual sea surface temperature variability (derived courtesy Todd O'Brien from the Hadley Centre SST data set (a) Annual seasonal temperature range, and (b) the ratio of seasonal variability (indexed by the range of the average seasonal cycle, as shown above) to interannual variability (indexed by  $4 \times [\text{root-mean-square annual anomaly}]$ ).

**Table 1**

Examples of physiological, developmental, and behavioral responses by which zooplankton can adapt to strongly seasonal environments.

Response	Mechanism	Controls and cues	
		(Environmental)	(Internal)
Reproductive timing	Maturation + Behavior	Photoperiod, temperature, chemical signals, etc.	Ripeness
Dormancy as adult or late juvenile (onset and duration)	Physiological 'switch', phenotype	(As above)	'Condition' (e.g. lipid accumulation), 'clock'
Dormancy as resting egg (production and emergence)	(As above)	(As above)	(As above)
Seasonal migration	Behavioral switch, but often tied to dormancy	(As above)	(As above)
Developmental rate	Physiological	Temperature (mostly) + nutrition	'Condition'
Generation length (#/year)	Development rate and dormancy (physiology + phenotype)	T°C + nutrition	'Condition'
Date-dependent survivorship and net rate of population increase/decrease	Population dynamics	Predation, nutrition	'Condition'??

and survival, while minimizing exposure during times when conditions are unfavorable for growth and/or survival.

Our focus in the remainder of this section will be on how zooplankton optimize their seasonal exposure. Processes and mechanisms that can alter zooplankton seasonal timing are summarized in Table 1. Their relative importance varies among taxa and ocean regions. It is important to note that many of the adaptation mechanisms involve lag times: days to weeks of physiological or developmental "preparation time" elapse between the triggering cue and effective adaptive response. Important generalizations are that:

- Seasonal focusing of reproductive output is almost universal, not only for zooplankton, but also for higher trophic level taxa with multi-year life spans.
- Seasonal dormancy of pre-reproductive stages is less common, but is prominent among many mid- and high-latitude zooplankton (Miller et al., 1991) and terrestrial arthropods (Tauber et al., 1986).
- Resting eggs are produced by some copepods and cladocerans (Marcus, 1996; Madhupratap et al., 1996; Miller et al., 1991). Nearly all of these taxa are neritic, but in these environments they are often dominant. An analogous strategy (cyst production) plays an equivalent role for seasonal timing of neritic diatoms and dinoflagellates.
- Seasonal migrations by zooplankton (often associated with start and end of a dormant life stage) are primarily vertical. By moving deeper, the zooplankton avoid for part of each year the intense environmental variability and higher predation pressure of the near-surface layers.
- Generation length and number, and seasonally-variable growth and development rates affect both the duration of the active growth season, and also the rise and fall rates of annual abundance and biomass curves.

- Within-year variations in rate of mortality rate affect rise and fall rates of population numbers, but can also be considered an outcome and evolutionary driver of the preceding adaptive strategies.

Collectively, these adaptations are highly effective for maintaining population persistence and resilience, provided that environmental seasonality remains within previously-encountered bounds and that seasonal timing remains 'predictable' (either by maintaining fixed periodicity, or by providing clear precursor signals of variations in amplitude and/or phase). But the same adaptations have neutral-to-negative fitness consequences if environmental seasonality changes unpredictably. Fitness consequences are especially likely to be negative if environmental cues become misleading, causing the organism to target the wrong seasonal window. Perturbations to average seasonal cycles of environmental conditions, and the ability (or inability) of biota to track these perturbations, are therefore potentially very important drivers of interannual variability in growth, survival, and population size. This is likely to be especially true for organisms (including most zooplankton) that complete their life span within a single year, because if they miss the window of best growing conditions in that year, they do not get another chance the following year.

### 1.3. Historical antecedents – the "match–mismatch" hypothesis

Recognition of the ecological importance of phenology (the relationship between annually recurring biological phenomena and climate conditions) is not new. Some of the earliest and most influential ideas are marine in origin and derive from papers by David Cushing and colleagues in the 1960s and 1970s. The "match–mismatch hypothesis" (see Cushing (1990) for a comprehensive history and complete list of citations) argues that much of the interannual recruitment variability of marine fish is caused by variation in the extent of timing overlap between the annual peak(s) of larval fish abundance and the seasonal peak(s) of planktonic production. The hypothesis is built up from several observational and logical elements that are also very relevant to the interpretation of zooplankton phenology (for additional detail, see Cushing, 1990; Durant et al., 2007):

- Spawning of mid- and high-latitude fish is strongly seasonal. Although the total duration of the spawning seasons can be moderately long (2–3 months), annual modal timing is often nearly constant (standard deviation ~1 week).
- In the same ecosystems, peaks of phytoplankton productivity and biomass are also strongly seasonal, and are associated with the spring increase in density stratification and light availability, and sometimes also with the fall breakdown of stratification and increase in nutrient availability.
- Young fish (larvae and/or early juvenile stages) need plentiful planktonic food for good growth and survival.
- Peak larval/juvenile abundance (and their peak requirement for abundant planktonic food) lags spawning by up to 1–2 months. This means that optimal timing of fish spawning (and prior ripening) must anticipate future, rather than respond to current, plankton availability.
- In contrast to the regularity of fish reproductive seasonality, there is large year-to-year variability in the seasonal timing of wind events, stratification, and resulting peaks of primary and secondary production.
- In some years, seasonal peaks of food demand and food availability overlap strongly (a timing "match" leading to good fish growth, survival, and year class strength). In other years, food availability is low during peak food demand (a "mismatch")

- leading to poor growth, survival, and subsequent recruitment). Because the requirement of the juvenile fish is for adequate food availability rather than modal timing match *per se*, the “match” window is broader in years when the duration of adequate food supply is longer (see Durant et al., 2007; Kristiansen et al., 2011) either because total food biomass is larger (peak amplitude) or because the plankton peak is broader (peak duration).
- Cushing suggested that fixed spawning timing of mid- and high-latitude fish is a generalist bet-hedging strategy evolved because they are unable to anticipate the exact optimal timing in any given year. In a temporal analogue to how animals adapt to “fine grained” vs. “coarse grained” environmental spatial heterogeneity (Levins, 1968; Yamazaki et al., 2002), the fish experience within-season differences in food availability as unpredictable = “fine grained”. Selective pressure for reproductive timing can therefore target only the long-term average of the dates of annual optima. This strategy succeeds reasonably well in many years. And because of their long reproductive life span, spawners can “try again next year” after one or a few successive years of mis-match.
  - However, “try again next year” is much less likely to ensure eventual reproductive success for fish that have short total (or reproductive) life spans. Cushing (1990) also notes that in low latitude upwelling regions, fish spawning is episodic rather than seasonal. Match-mismatch still applies, but the window of “match” is less defined by annual periodicity. Adaptive response can be “coarse grained” if the fish are able to identify and exploit individual productive events and locations. It is “fine grained” if the fish are unable to target specific optima but instead spread their reproductive output over a large fraction of the year.
  - The original match-mismatch hypothesis tacitly assumed that changes of the plankton timing lack year-to-year serial autocorrelation. However, Cushing subsequently noted that the spawning date of Arcto-Norwegian cod has changed gradually over time, presumably in response to prolonged climate-driven change in the average optimal date. Recent research on marine climate trends and decadal ‘regimes’ (including examples in this paper) shows that prolonged changes in the environmental conditions that affect phenology have occurred and will continue. Durant et al. (2007) and Ji et al. (2010) provide examples and a theoretical discussion of obstacles to rapid evolutionary adaptation.

#### 1.4. Interannual variability in zooplankton phenology – expectations and early observations

Despite the marine origin and long history of the seasonal match-mismatch hypothesis (and despite how rapidly match-mismatch concepts stimulated research on terrestrial and freshwater systems), Cushing (1984) and Ellertsen et al. (1987) and subsequent republication of their data in Cushing (1990) were the first and only observational analyses of interannual variability of marine zooplankton phenology to be completed before the late 1990s. What did their pioneering studies tell us about both the causes of variability in zooplankton seasonality, and their consequences for zooplankton population dynamics?

First, that there is large interannual and among-region variability of spring-season weather, timing of seasonal warming and stratification, and timing/availability of phytoplankton (note that most of the observations of plankton phenology cited by Cushing were of phytoplankton ‘greenness’, not zooplankton amount). All of these modes of environmental variability are likely to strongly affect zooplankton seasonal timing.

Second, that interannual variability of timing is large for one dominant North Atlantic zooplankton species (*Calanus finmarchicus*). Its relatively narrow (1–2 month wide) seasonal peak of abundance shifted by at least 1–2 months both in the northeastern North Sea (Cushing, 1984) and in the coastal Norwegian Sea (Ellertsen et al., 1987). In both regions, changes in zooplankton timing altered the seasonal overlap with larval gadoid fishes, thereby affecting the year-class strength of the fishes. However, the sign of the correlation between zooplankton timing and fish recruitment differed between the two regions. In the northeastern North Sea (58–63°N), delay of *Calanus* seasonal timing improved the match with cod and several other cod-like fishes, although intermediate *Calanus* timing (a peak in April) appeared to be most favorable for haddock. Further north (68°N), earlier seasonal timing of *Calanus* improved trophic match with Arctic-Norwegian cod larvae.

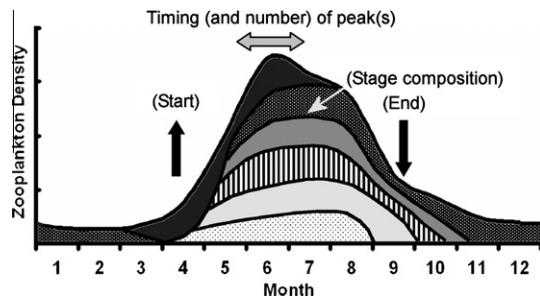
Third, individual lifespan/fecundity of most mesozooplankton is much shorter/lower than the mid- and high-latitude fish examined by Cushing. The entire zooplankton population must replace itself at least annually. Any reproductive and developmental timing mechanism that leads to a fixed and narrow seasonal timing window is risky, because a backup strategy of “try again next year” is unavailable. Miller et al. (1991) note that genetic controls on zooplankton phenology are relatively simple. Because zooplankton generation times are short, and the fitness payoff for each generation of a match in timing is very strong, the rate and magnitude (both in absolute number of days, and relative to their life span) of selection for interannual/decadal plasticity in zooplankton phenology is probably larger than for fish. Such a contrast across trophic levels has been shown for terrestrial and marine avian predators, which change their seasonal reproductive timing less and more slowly than their insect (Durant et al., 2007; Visser et al., 1998) or zooplankton prey (Bertram et al., 2001; Hipfner, 2008).

## 2. Methods

### 2.1. Goals for analyses

Analyses of variability of marine zooplankton phenology became more common during the past decade (as did the number and length of zooplankton time series), but nearly all have been confined to a single site or ocean region. Richardson (2008), Mackas and Beaugrand (2010), and Ji et al. (2010) provide brief summaries of some of the phenology results, as part of broader reviews of zooplankton-climate interactions and plankton phenology. Our goal in this paper is an update, plus a more extensive comparison and synthesis of the regional analyses.

Sampling designs (especially sampling interval, but also depth range and the presence/absence of within-time-period spatial averaging of multiple samples) differ considerably among the phenology time series. Data processing and analysis methods also differ, usually because they were selected by the original investigator to be appropriate for the temporal and taxonomic resolution of each individual sampling design. However, all zooplankton phenology analyses have attempted to measure rather similar attributes of zooplankton seasonality. Input data can be viewed as annual plots of “amount” vs. date-within-year (Fig. 2). Differences among data sets are in the number and regularity of data points each year (temporal resolution); the number of years sampled (time series duration); and whether or not there has been further classification of species abundance or biomass into within-species size or stage categories (composition resolution). Key attributes to be derived from these plots include the annual dates of the population maxima, and when and if there are multiple peaks per year. Ideally, we would also like information about year-to-year variability of



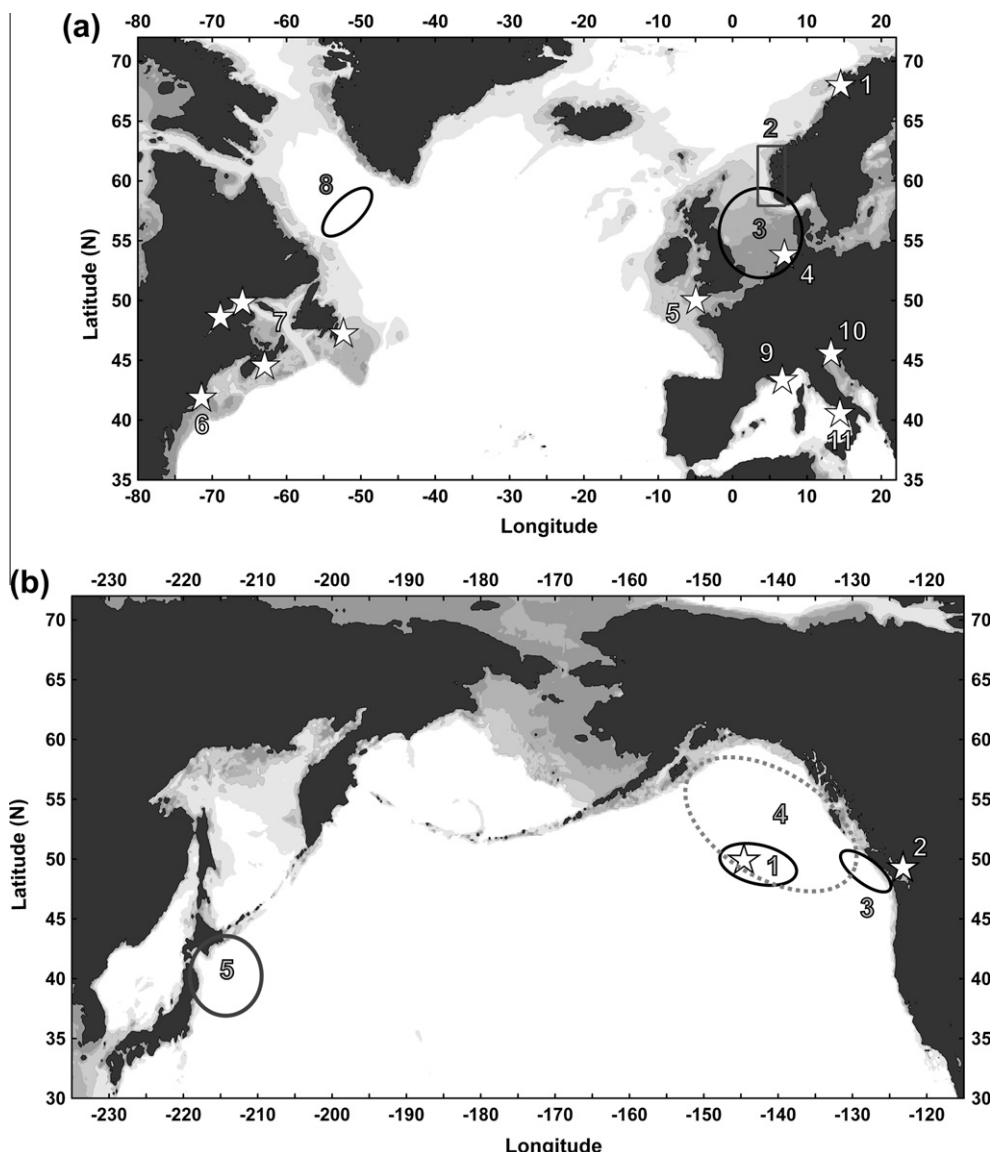
**Fig. 2.** Schematic annual cycle for a copepod population. The primary timing attribute is the year-to-year variability of the central date of population peak(s) (gray double headed arrow). Other useful attributes include the “start” and “end” of the peak (black arrows); “season duration” (the time span between the start and end dates), and cohort age-stage composition (shading).

peak amplitude (annual range), the duration and start/end dates of the peak(s), and the size/stage structure within the overall species total. All of these are relatively easy to identify and quantify if the amount vs. date curve is fully resolved and smoothly varying (as in

the idealized graph shown in Fig. 2). The estimation process is more difficult if (as is typical) there are large gaps between observations, or if the data sequence is noisy due to patchiness, advective gains/losses, or sampling errors. In Section 2.2, we describe the important sampling design and environmental attributes of the zooplankton phenology time series. In Section 2.3 we discuss the variety of indexing methods that have been applied, and their strengths and limitations. Section 2.4 describes how we quantified and tested strength of association between phenology and environmental time series.

## 2.2. Data sources and sampling methods

Locations of available time series of zooplankton phenology are mapped in Fig. 3a (North Pacific) and b (North Atlantic and Mediterranean). All are from the Northern Hemisphere. Most (compare Fig. 1) are from mid-latitude regions in which seasonality of surface water temperature is intense. Tables 2a–2c provide details of sampling design and sampling and analytical methodology for each time series (Atlantic/Arctic, Pacific, and Mediterranean



**Fig. 3.** Locations of historic and ongoing zooplankton phenology time series. Numbers correspond to time series in Tables 2a–2c. Stars and white numbers indicate single-location time series. Ovals/rectangles indicate approximate perimeters for regional time series (multi-sample averages), also identified by dark numbers. (a) North Atlantic and Western Mediterranean, (b) North Pacific.

**Table 2a**

North Atlantic zooplankton time series used to examine timing and forcing of changes in zooplankton phenology. Numbers correspond to site labels in Fig. 3a. The current paper provides initial or significant additional phenology analyses in North Atlantic regions 1–5 and 8.

Regions	Sampling (interval, depth range, duration)	Phenology index	Taxa included	Environmental data included	Reference
1. Coastal Norwegian Sea – Lofoten (68°10'N, 14°35'E)	~Weekly, z ~ 0–300 m, spring of various years between 1960 and 1984	Date of peak abundance of first copepodite stage	<i>Calanus finmarchicus</i>	Temperature in mixed layer	Ellertsen et al. (1987) and Cushing (1990)
2. Northeastern North Sea – Continuous Plankton Recorder area B1 (58–63°N, 3–8°E)	Monthly averages in B1, z ~ 10 m, January–July, 1949–1978	'Index of delay' = # of months after March for peak abundance of fifth copepodite + adults	<i>Calanus finmarchicus</i>	March surface temperature, 53–55N, 1W–2E	Cushing (1984), this paper
3. Central North Sea – Continuous Plankton Recorder (55–58°N)	Monthly averages of CPR statistical areas, z ~ 10 m, 1958–2002	'Center of gravity' of annual (single mode) or semiannual (bimodal) population histograms ("center-of-gravity" hereafter)	36 zooplankton taxa (16 copepods, 12 'other holoplankton', 8 meroplankton), 10 dinoflagellates, 36 diatoms	Spring SST anomaly	Edwards and Richardson (2004); this paper
4. North Sea – Helgoland Roads (54°11.3'N, 7°54'E)	Weekly averages, z ~ 0–6 m, 1974–2006, using two nets (17 cm mouth, 0.15 mm mesh and 100 cm mouth 0.5 mm mesh)	'Start', 'middle', 'end', and 'duration of season' from cumulative abundance percentiles ("cumulative percentiles" hereafter)	70 + taxa (mostly holozooplankton, some larval meroplankton and fish)	Temperature in mixed-layer	Greve et al. (2004), Greve (2001), and this paper
5. Western English Channel – Plymouth L4 (50°15'N, 04°13'W)	~Weekly, z = 0–55 m, 1988–2007	"Cumulative percentiles"	4 copepods, 1 cladoceran, chaetognaths, appendicularians, echinoderm larvae (more to follow)	Temperature, chlorophyll	D. Eloire (pers. comm. Based on data in Eloire et al. (2010)); this paper
6. Narragansett Bay (three nearby stations ~41.5°30'N, 71.3'W)	~Weekly, z = 0–3, 6 or 14 m, 1951, 1958, 1973, 1976, 1982–1983, 2000–2004	Dates for annual appearance/rise and disappearance/decline of populations	2 copepods ( <i>Acartia hudsonica</i> , <i>A. tonsa</i> ), 1 ctenophore ( <i>Mnemiopsis leidyi</i> )	Temperature	Costello et al. (2006), Sullivan et al. (2007)
7. Canadian coastal monitoring stations, NW Atlantic (4 sites), (44.27–49.72 N, 52.59–68.58°W)	~Biweekly, mid-late 1990s–2005	Dates of dormancy onset and exit indexed by stage composition ratios (% fifth copepodite and % adult respectively)	<i>Calanus finmarchicus</i>	Photoperiod, temperature, and chlorophyll	Johnson et al. (2008)
8. Labrador Sea, NW Atlantic	Annual, variable timing from late May to late July, z = 0–100 m	"Population Development Index" = sum (first through third copepodite stage)/sum (all stages)	<i>Calanus finmarchicus</i>	Temperature and chlorophyll time series from satellite	Head et al. (2003) (field sampling); Head (2009 presentation) & this paper for PDI

respectively). For the majority of the time series, the raw data are vertically-integrated abundance and/or biomass resolved to species, or to developmental stage within species, obtained from conventional vertical or oblique plankton net tows. Continuous Plankton Recorder (CPR) data come from a specialized sampler towed at high speed behind commercial ships at a depth of about 10 m. Individual CPR samples are sequential along the ship track (each has filtered about 3 m<sup>3</sup> of water along about 18.5 km horizontal distance) and their data are grouped/averaged into larger spatial regions.

The zooplankton data sets can be grouped into three broad classes, each with characteristic advantages and disadvantages for analysis as time series:

- Frequent (weekly to monthly) sampling at a single fixed site. Advantages are good temporal resolution, and (often) a strong commitment to continuity by local scientists and institutions. Disadvantages are potentially large "noise" variance added by spatial patchiness, and that such time series are usually available only for nearshore locations. Important examples include Helgoland Roads and Plymouth L4 from the NE Atlantic, Canadian coastal monitoring stations in the NW Atlantic, the three Mediterranean time series listed in Table 2c. Early years (1958–1980) of the open ocean Stn P time series (subarctic NE Pacific) also had very frequent sampling.
- Less frequent (monthly to seasonal, occasionally less often) sampling of multiple sites within a mesoscale-or-larger region. Advantages of this design are that within-time-period spatial averaging can greatly reduce patchiness noise. Disadvantages

are lower temporal resolution, and often some variation in how many and which sites are included per survey. Examples that have been examined for phenologic variability include the Oyashio, Vancouver Island, and recent Line P time series in the Pacific. Several other long zooplankton time series share this design (e.g. CalCOFI and Korean NFRDI time series in the North Pacific, IMARPE collections off Peru in the SE Pacific, NMFS Georges Bank in the NW Atlantic, Latvian and Finnish time series in the Baltic, Benguela Current in the SE Atlantic) and can/should be exploited in future analyses.

- Rare to frequent (~monthly to annual) CPR line transects. Advantages include long term and very broad spatial coverage by a single method, and good temporal resolution in regions such as the North Sea where multiple survey lines intersect. Disadvantages include small individual sample volume, sensitivity to day-night differences in capture rate, sampling restricted to near-surface, difficulty of detailed taxonomic identification of squashed zooplankton, and an enumeration method that is semi-quantitative (see Richardson et al. (2006) for additional discussion of CPR data processing).

### 2.3. Methods for indexing seasonal timing

There has also been a wide range of data analysis and indexing methods. Because time series of both zooplankton and environmental variables often include a strong annual periodicity, one potential approach is to fit data within each year as a sum of annual mean, plus a sinusoid at annual frequency (plus, perhaps, sinusoids at one or two higher harmonics). Time series of the amplitude and

**Table 2b**

As for Table 2a except for North Pacific zooplankton phenology time series. The current paper provides initial or significant additional phenology analyses in North Pacific regions 1 and 3–5.

1. NE Pacific – Southern Alaska Gyre (Stn P and vicinity, 50°N, 145°W)	~2 per week, z ~ 0–150 m, 1957–1981 (biomass), intermittent 1984–1996 (biomass + abundance by species and stage); 3 per year 1997–present (biomass + species and stage)	Date of annual biomass peak from: Biomass vs. Date (1957–1981, 1984, 1987) Copepod developmental stage ratio C5:total (1971, 1973, 1980, 1984, 1987, 1988, 1993, 1994 and 1996–2008) ("stage ratio" hereafter)	<i>Neocalanus plumchrus</i> (the dominant copepod) and total upper ocean wet weight biomass	Temperature in mixed layer and at depth of dormancy (400–1000 m); Pacific Decadal Oscillation (PDO, Mantua et al., 1997)	Mackas et al. (1998, 2007), this paper
2. NE Pacific – Strait of Georgia (49–50°N, 123–124°W)	1–2 per month in 16 years from the past 4 decades, z ~ 0–50 m?	"Stage ratio" and/or "abundance and biomass vs. date"	<i>Neocalanus plumchrus</i> (formerly the dominant copepod, strong decrease in the past decade) and total upper ocean dry weight biomass	Temperature, chlorophyll and phytoplankton lipid composition	Bornhold (2000), El-Sabaawi (2009)
3. NE Pacific – Vancouver Island continental margin (48–52°N, 125–130°W)	3–6 surveys/year (multiple stations, mostly z = 0–250 m), 1979–2008	"Stage ratio" cross-referenced to abundance and biomass	<i>Neocalanus plumchrus</i> (the dominant copepod) and total upper ocean dry weight biomass	Temperature in mixed layer	Mackas et al. (2007), this paper
4. Southern and central Alaska Gyre – Continuous Plankton Recorder (48–55°N, 130–145°W)	~Monthly from late winter through summer, z ~ 10 m, 2000–2008	"Stage ratio" and "cumulative percentile" methods	<i>Neocalanus plumchrus</i> (the dominant copepod) and total upper ocean wet weight biomass	Temperature and chlorophyll fluorescence in mixed layer	Batten et al. (2003), Mackas et al. (2007), Batten and Mackas (2009)
5. NW Pacific – "Oyashio Water" (37–43 N, 142–150°E and 100 m temperature $\leq 5^{\circ}\text{C}$ )	~Monthly, 1960–2002	Month of peak abundance (tried "stage ratio" method but found that cohort width was too great)	<i>Neocalanus cristatus</i> , <i>N. flemingeri</i> , <i>N. plumchrus</i> , plus composites of "spring", "spring–summer", and "summer" copepod communities	Monthly average surface temperature, phosphate concentration	Chiba et al. (2006, 2008), Tadokoro et al. (2007), and Chiba and Tadokoro (pers. comm.)

**Table 2c**

As for Tables 2a and 2b except for Western Mediterranean zooplankton phenology time series. The current paper provides the initial phenology analyses for Mediterranean site 3 and an extended analysis for site 2.

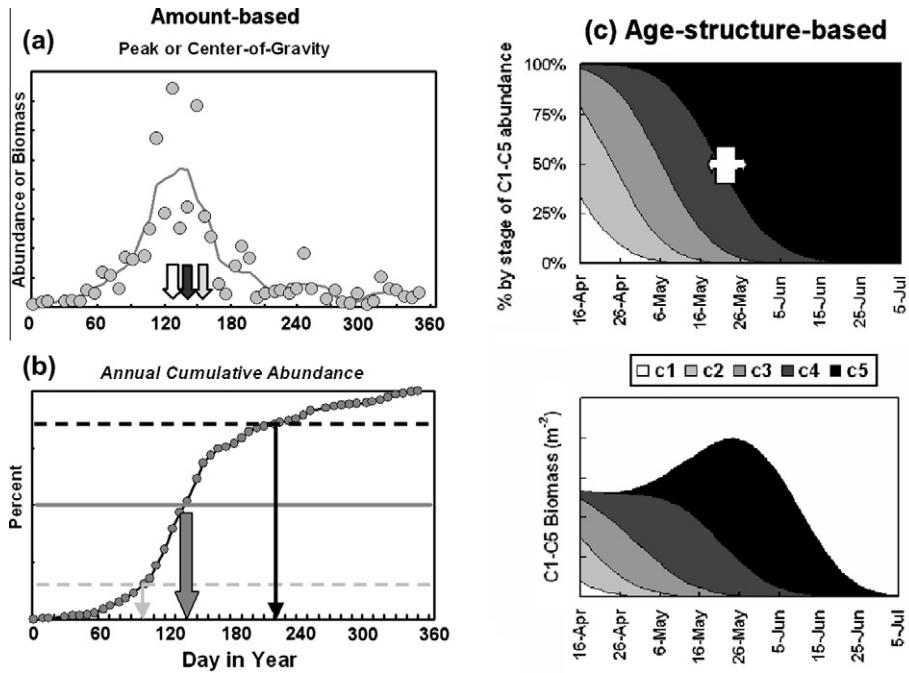
9. Mediterranean – Ville Franche (43°41'N, 7°19'E)	~Weekly, 0–75 m, 1966–1993 (for published analysis; sampling is ongoing)	Between decades/regimes comparison of average seasonal cycles, timing indexed as the middle of the month with highest abundance	<i>Centropages typicus</i> , <i>Temora stylifera</i> , plus various gelatinous and chaetognath predators	Mean monthly hydrography plus empirical composite of large-scale climate indices	Molinero et al. (2005)
Adriatic – Trieste (45°42'N, 13°42.5'E)	~Monthly, 0–18 m, 1970–1981 and 1986–2005	"Center-of-gravity" method, averages compared 1970–87 vs. 1988–2005	13 copepod taxa	Seasonal averages of surface temperature; circulation and salinity changes linked to 'Eastern Mediterranean Transient'	Conversi et al. (2009)
Mediterranean – Gulf of Naples (40°49'N, 14°15'E)	~Biweekly, 0–50 m, 1984–1990 and 1995–2006	"Cumulative percentile" method	4 dominant copepods ( <i>Acartia clausi</i> , <i>Centropages typicus</i> , <i>Paracalanus parvus</i> , <i>Temora stylifera</i> )	Sea surface temperature	Mazzocchi et al. (2012) and this paper

phase angle estimates can then be used to describe among-year differences in phenology (Dowd et al., 2004). In practice, although this method described the average seasonal cycle well, its ability to detect interannual differences was very vulnerable to the "patchiness" noise of individual data points, and probably has limited usefulness for sparse and noisy zooplankton time series. A new and more flexible approach to annual curve-fitting (Weibull function "Cardinal Dates", Rolinski et al., 2007) allows non-sinusoidal "shapes" for annual (or seasonal) peaks. It has been applied to densely-sampled phytoplankton time series, but not yet to zooplankton time series.

The remaining methods are variants of the types shown in Fig. 4. Four of these examine within-year changes in amount (either abundance or biomass). In the first (Fig. 4a), the annual amount-at-date curve is inspected to find the timing (day, week, or month) of the maximum data point (used by Cushing (1984)

for the northeastern North Sea, and for the Japanese ODATE time series, Chiba et al., 2006, 2008; Tadokoro, unpublished; this paper). Cushing originally reported his data as an "index of delay", which he defined as the difference (in months) between the month of peak C5 abundance and March (month = 3). For ease of comparison with other time series, we back-convert index of delay to month of peak C5 abundance. The Japanese data are reported as the month of peak biomass for each species analyzed (and also as within-group sums of species classified as usually having "spring", "spring–summer", or "summer" maxima). Although not necessarily a characteristic of this indexing method, both of the above examples were quantized only to monthly resolution, and their time series therefore consist of only a few discrete integer values.

A second index is similar but chooses the maximum of a running-mean smoother of adjoining within-year data points (applied to the early Stn P biomass time series, Mackas et al., 1998). Both of



**Fig. 4.** Alternative indexing methods for zooplankton seasonal timing. The “Amount-based” indices (illustrated in 4a and 4b) examine changes in total abundance or biomass vs. date within year. All of the amount-based examples are applied to the same input data: abundance of *Pseudocalanus elongatus* in 1996 at the Plymouth L4 site. In (a) white arrow shows the date with maximum observed abundance, black arrow shows the date of the maximum of a five point running mean smoother. Gray arrow shows the “center-of-gravity” for the full annual histogram. (b) Illustrates the cumulative-percentile method. Light gray arrow/dashed line is the 15th percentile “start-of-season”, medium gray arrow/solid line the 50th percentile “middle of season”, and (b) black arrow/dashed line the 85th percentile “end-of-season”. “Age-structure-based” indices (example in (c)) examine changes in the percentage contribution of one or more developmental stages to the species total, smoothed or interpolated between observations. “Age-structure-based” methods require a simple cohort structure, but are more tolerant of longer sampling intervals. The example shown is an idealized model of *Neocalanus plumchrus* biomass-at-stage, forced by temperature and size-dependent development, growth and mortality rates. Upper panel shows percentage of abundance at each stage vs. date, lower panel shows biomass by stage and date. White bar and arrow indicates the date of 50% C5. See Mackas et al. (1998) for graphical examples of the method applied to field data, and Batten and Mackas (2009) for graphical examples of how cohort width affects the conversion from stage composition to biomass peak.

these peak-identification approaches are targeting only a subset of the annual observations. They are therefore sensitive to positive spikes in the data record (patchiness), and are most reliable if the reported amount-at-date is a spatial average of multiple individual samples.

A third indexing method (“center-of-gravity”, originally developed by Colebrook and Robinson (1963) to describe average seasonal cycles, and used more recently by Edwards and Richardson (2004) and Conversi et al. (2009) to describe variability of phenology) calculates the date of the weighted mean of the entire population curve using the formula:

$$\Sigma N_D * D / \Sigma N_D \text{ (where } N_D \text{ is the estimated or observed amount at time period } D\text{).}$$

If the annual curve is unimodal but asymmetric, the center-of-gravity estimate is shifted slightly from the modal peak in the direction of the skew. If the annual curve of population abundance is bimodal, the method divides each year into two segments, and centers-of-gravity are calculated separately within each segment. Note that this choice effectively assumes that there is no overlap between the two modes. If there is overlap, the timing estimates of both modes are biased toward mid-summer or mid-winter (whichever season has the stronger overlap). Conversi et al. (2009) noted that timing estimates of smaller secondary peaks can be severely biased, especially if secondary peaks are present only in a subset of years.

A fourth set of indices (“cumulative percentile”, Fig. 4b) also uses all data points, but sums  $N_D$  through the year (or potentially through the duration of a single seasonal mode), and compares the cumulative sum at each date to the final total. This method was originally used by Greve et al. (2001, 2004, 2005) for the

Helgoland Roads time series, and subsequently for North Pacific CPR (Batten and Mackas, 2009) and for Naples Bay and Plymouth L4 time series (this paper). “Middle of season” is defined as the date at which the 50th cumulative percentile is crossed. The cumulative percentiles also provide additional descriptions of the seasonal curve. Higher and lower percentiles (typically 15th or 25th and 75th or 85th) are defined as the “start” and “end” of growing season, and the time span between “start” and “end” dates gives an estimate of growth season duration.

For input time series that have short and reasonably uniform sampling interval (e.g. the Plymouth L4 time series for *Pseudocalanus*; source for the data plotted in both Fig. 4a and b), all of the previous methods perform well. Within-year differences among “peak” vs. “center of gravity” vs. “mid-season” dates are small (~10 days or less) and match in direction the expected differences noted above (compare arrows in Fig. 4a and b). However, adjustments to both methods are useful if the input data are less regularly spaced. Note that the goal is to describe the shape of the entire annual curve (not just the dates at which samples were collected). If input data are evenly spaced through the year (equal width cells in the amount vs. date histogram; ~true for both the monthly North Sea CPR averages, and the biweekly Helgoland Roads samples), simple summation of samples is a good approximation to the desired annual integration for both center of gravity and cumulative percentile methods. However if sampling interval is irregular, or there are occasional large unsampled gaps, the summation/integration calculations should take account of varying time spans between observations. This can be done in various ways: unevenly spaced data can be interpolated to a regular spacing (e.g. the subset of Plymouth L4 results reported in this paper), or each sample can be weighted by the date span that it represents (a rectangular integration of a histogram, but with varying width

cells), or the annual integration can be trapezoidal (modified cumulative percentile method, used here for the Naples time series, and by Batten and Mackas (2009), for NE Pacific CPR data).

The precision of any amount-based index of zooplankton phenology degrades rapidly if the sampling interval approaches or exceeds the doubling time for the species of interest. The likelihood of mis-identification of primary or secondary seasonal peaks also increases. Because development rates are faster for smaller organisms and at warmer water temperature (Hirst et al., 2003), the necessary sampling frequency is greatest for small tropical zooplankton, and for zooplankton taxa (e.g. planktonic tunicates, Aldredge and Madin, 1982) that have fast developmental and reproductive rates. However, even for large copepods living in cold water environments, the maximum interval between samples is  $\leq$  monthly during the growing season. Several of our time series have sampling intervals longer than this. For these time series, alternative indexing methods based on sequential changes in species stage composition may still be feasible. If there is a single annual cohort or a clear time separation between successive reproductive cohorts (a relatively common pattern in polar and cool temperate regions), stage composition changes monotonically and often rather smoothly through the cohort developmental cycle. Stage composition ratios therefore can be used to index biomass phenology, and assessment of cohort timing may require only one or two sampling periods per cohort. The biomass maximum of the cohort occurs when gains from growth and recruitment begin to be exceeded by losses to mortality, or to seasonal migration (if present) into an unsampled deep dormancy. Fig. 4c shows a schematic example of this approach: the relationship between the ratio of C5:total copepodite abundance and timing of the annual biomass maximum of *Neocalanus plumchrus* in the NE Pacific (applied by Mackas et al. (1998, 2007), Batten et al. (2003), and Batten and Mackas (2009)). For this species, the biomass maximum occurs some time during the ~15–25 day interval when pre-dormant C5 are the most abundant stage. During the 1980s in the NE Pacific, the biomass maximum occurred at ~50–65% C5; (Mackas et al., 1998). However, the stage-to-biomass timing conversion is dependent on cohort width and on C5 stage duration, and can vary from ~35% to 90% (Batten and Mackas, 2009). In the Oyashio region (NW Pacific), *Neocalanus* peaks are broader and local populations often never reach 50% C5 before declining steeply (Tadokoro, 2005, unpublished). For this reason, Japanese researchers have chosen to report the month of the observed biomass maximum. Prolonged annual peaks of *Neocalanus* spp. in the Oyashio region are perhaps a consequence of very strong alongshore advection and environmental gradients in this region (Tatebe et al., 2010), which together lead to a within-species mixture of source populations that have had widely differing environmental and growth histories. Other places such as the NW Atlantic probably face similar complications. Ji et al. (2010) have recently discussed the challenges of interpreting Lagrangian processes (phenology of plankton advected from distant source populations) from Eulerian time series (observations of the outcome at a single and sometimes distant and dissimilar downstream site). But we will show below that, despite these complications, correlations between zooplankton phenology and local environmental signals often remain strong and locally predictive.

Other stage composition approaches have alternatively focused on the timing of peak abundance (not biomass) within one or a few developmental stages. In the two earliest studies of zooplankton timing variability, Ellertsen et al. (1987) estimated the date of maximum abundance of C1 *C. finmarchicus* off northern Norway, while Cushing (1984) estimated the month of maximum abundance of C5 and adult *C. finmarchicus* in the northeastern North Sea. More recently, Head (pers. comm.) has developed a “Population Development Index” PDI based on the ratio of early-stage abundance to total abundance, and calculated using the formula:

$$PDI = 100 * \sum_{i=1}^3 C_i / \sum_{i=1}^6 C_i$$

(where  $C_i$  is the abundance of copepodite stage  $i$ ; the numerator is summed over stages 1–3, the denominator over all six stages, and their ratio is converted to a percent scale). Head is applying this index of *C. finmarchicus* timing at several NW Atlantic locations; her Labrador Sea example is included in Section 3.2.6 below.

#### 2.4. Statistical association of zooplankton phenology with environmental controls and cues

We examine the degree of association between zooplankton timing (estimated by one or more of the phenology indices described in Section 2.3) and various potential environmental drivers/cues using a combination of paired time series plots, scatter plots, and regression, correlation, and ordination analyses. For significance tests for regressions and correlations, we account for year-to-year temporal autocorrelation by using estimated number of effective degrees of freedom (typically ~10–20% smaller than the number of years in the time series). However, we have chosen not to apply Bonferroni multiple comparisons correction to threshold significance levels. The reason is that large fractions (far more than the 5% or 10% that would be expected by chance) of the observed pairwise correlations between timing and key environmental variables (such as temperature) exceed the  $p = 0.05$  or 0.10 significance threshold for individual comparison. In this situation, we suggest that the risk of imposing large Type II error (failing to detect 70–80% of ‘real’ associations) exceeds the benefit of minimizing Type I error (accepting as significant an extra 5–10% of pairwise comparisons). For the scatterplots describing association between phenology response and environmental variables, linear associations significant at  $p < 0.10$  are indicated by solid regression lines. Scatterplots with weak or no association are summarized by dashed lines. Scatterplots also show the coefficient of determination ( $R^2$  = fraction of variance accounted for by the fit). Note that the significance threshold for  $R^2$  varies among our time series due to differences in their durations. For the longest (Central North Sea, Oyashio, and Stn P; 40+ year duration, and 30–35 d.f.)  $p < 0.05$  for  $R^2 > 0.1$ . For ~30 year time series (Vancouver Island, Helgoland Roads, Ville-Franche),  $p < 0.1$  for  $R^2 > 0.1$ . For the ~20 year time series (Plymouth, Trieste, Naples)  $p < 0.1$  for  $R^2 > 0.16$ .

### 3. Results (past and new), comparison, and discussion

#### 3.1. Section organization

In the following subsections, we briefly review results of already-published analyses of zooplankton phenology time series. We also present (as additional text plus graphs) some new and/or updated analyses of these and of several previously-unanalyzed time series. Many of the analyses (both published and new) show a strong association between seasonal timing and water temperature before and during the growing season. To explore this association further and facilitate comparison, many of our graphs from the individual time series will be provided in a standard format:

- Time series plots of within-year zooplankton timing and seasonal temperature anomalies vs. year, paired with
- Scatterplots of within-year zooplankton timing vs. ‘recent’ time-averaged temperature anomalies. As noted above, solid regression lines indicate relationships that are significant at  $p < 0.10$ . Dashed lines indicate  $p \geq 0.1$ , although many of these are non-significant due more to brevity of the time series than to low  $R^2$ .

Between-site comparisons of the time series will allow us to identify places and species for which interannual variability of phenology is to some degree synchronous. Comparisons of the timing vs. environmental scatterplots will help us identify cross-taxa similarities and differences in control mechanism (and in probable response to future climate warming). The presentation sequence for the individual time series will be by region (North Atlantic/Barents, North Pacific, Mediterranean), and then by publication chronology within region.

### 3.2. North Atlantic

#### 3.2.1. Vestfjorden, Norway

Although several studies had previously examined multi-year records of marine zooplankton abundance to describe the spatial pattern of average seasonal timing for various species (e.g. Colebrook, 1979), the first analyses to focus on interannual variability of marine zooplankton seasonality were the northern Norway study by Ellertsen et al. (1987) and the northeast North Sea study by Cushing (1984); results from both were discussed in Cushing (1990). Ellertsen et al. examined 13 years spread over a 25-year time span, and indexed start-of-season timing for the annual *C. finmarchicus* cohort using the date of peak abundance of the first copepodite stage. Despite the modest number of years, they detected large (~2 month) variations in timing that were strongly and negatively correlated with April water temperature (Fig. 5a). A time series plot of their data (Fig. 5b) shows that the earliest year (1960) was the warmest and had the earliest timing, while one of the last years (1984) was the coolest and had the latest *Calanus* timing. However, the association between temperature and *Calanus* timing is much stronger than the 25 year trend for either variable. Ellertsen et al. (1987) also made the important interpretation that, although warmer water would be expected to shift timing earlier by shortening the duration of egg and naupliar stages, a 2-month change in phenology is much larger than can be explained by temperature dependence of development rate. Unlike the northern fish species of the match-mismatch hypothesis, the parental copepod generation must have adjusted its dates of diapause emergence and/or spawning in response to local temperature conditions (or perhaps in response to some other environmental condition(s) very strongly associated with April temperature).

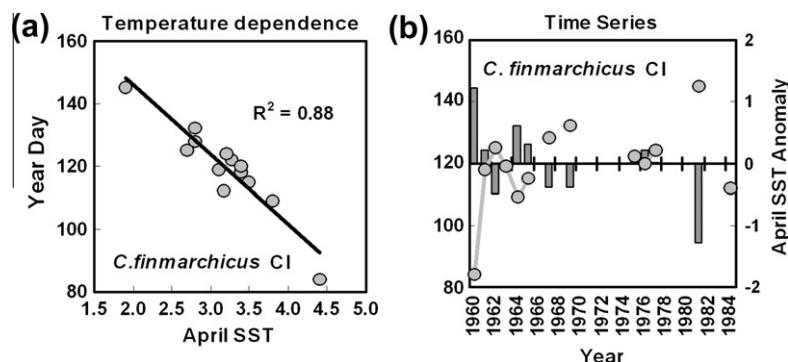
#### 3.2.2. CPR zone B1, northeastern North Sea

Cushing (1984) examined 30 years of CPR data from the northeastern North Sea, and compared mean seasonal abundance curves for 1949–1961 (on average “earlier” and warmer) vs. 1962–1978 (on average “later” and cooler). He showed graphs of annual cod

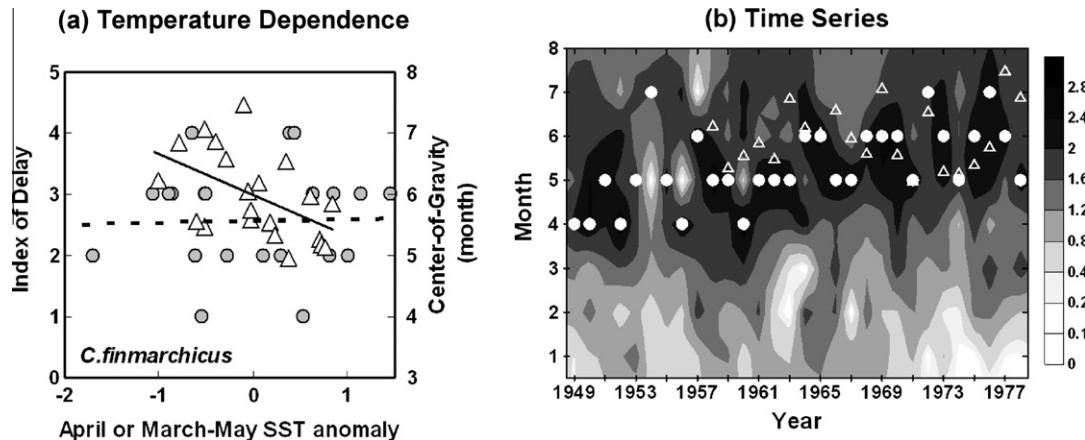
and haddock year class strength vs. annual “index of delay”, but did not plot the detailed “index of delay” time series nor scatter plots of delay vs. annual ocean temperature. We provide these here (Fig. 6b, “index of delay” back converted to “peak month” to facilitate comparison with other data sets, and overlaid on a contour plot of log abundance vs. month and year). The data show a clear trend to later timing but, unlike the overlapping Norwegian (Section 3.2.1) and Central North Sea (Section 3.2.3) time series, Cushing reported no association of delay index with March temperature ( $r = 0.03$ , filled circles and dashed trend line Fig. 6a). It is unclear why this association is absent in Cushing's data. Edwards and Richardson (2004; additional results in Section 3.2.3) analyzed a larger but overlapping set of CPR data (1958–2002 and four North Sea CPR statistical areas, vs. 1949–1978 and one statistical area in the Cushing analysis), and found much stronger association of *C. finmarchicus* timing with spring temperature ( $r = -0.34$ ). We have subsequently compared the Edwards and Richardson (2004) “center-of-gravity” time series for the years of overlap (1958–1978, triangles in Fig. 6b) to time series of spring sea surface temperature anomalies (ERSSTv3 data set, Smith et al., 2008) in various North Sea CPR sub-regions and obtain an even stronger negative correlation between timing and spring temperature ( $r = -0.47 \pm 0.08$ , triangles and solid trend line in Fig. 6a). Possible explanations for the discrepancy include noise and pooled identification of *C. finmarchicus* and *Calanus helgolandicus* in the early (1949–1957) years of the Cushing CPR data, coarse quantization of his “delay index” (see Fig. 6b), or errors in his original temperature time series (although these correlate strongly with the Edwards and Richardson and ERSSTv3 temperature time series).

#### 3.2.3. CPR, Central North Sea (CNS)

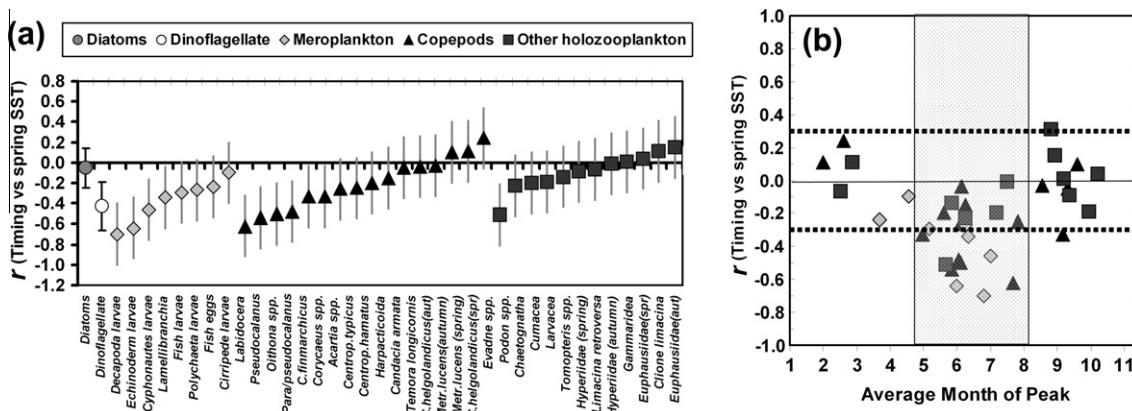
As noted in the previous section, a much broader and longer North Sea CPR data set (1958–2002, 55–58°N) was analyzed by Edwards and Richardson (2004). This time series is the longest continuous sequence that has been examined for variability in phenology of marine zooplankton. Data are monthly averages from CPR transects covering much of the North Sea (see Vezzulli et al. (2007) and [www.sahfos.org/WinCPR.htm](http://www.sahfos.org/WinCPR.htm) for details of spatial coverage vs. year). Spatial and temporal averaging of the CPR data is extensive (a large number of individual CPR samples covering a large fraction of the North Sea and a date span of 1 month) to reduce noise that would otherwise be introduced by small-volume samples, and small-scale patchiness. The CNS is bathymetrically smooth and relatively homogeneous: bottom depths are mostly between 50 and 150 m (Fig. 3a), with a narrow deeper trough (>200 m) entering from the north near the Norwegian coast. Most of the CNS is also vertically stratified in summer by surface warming. However, there is systematic within-region variation of water



**Fig. 5.** Pioneering study of interannual variability of *Calanus finmarchicus* phenology by Ellertsen et al. (1987), one of two zooplankton data sets used by Cushing to develop the “timing match–mismatch” hypothesis for variability in fish recruitment. (a) Temperature dependence of early season abundance: date of peak abundance of first copepodite stage vs. April temperature. (b) Time series of *Calanus* timing (circles/lines) and April temperature anomaly (columns).



**Fig. 6.** Comparison of Cushing (1984) and Edwards and Richardson (2004) estimates of *Calanus finmarchicus* phenology, both based on North Sea CPR data. (a) Scatterplots showing temperature dependence of *C. finmarchicus* timing. Filled circles (dashed non-significant trendline,  $R^2 = 0.00$ ) are Cushing's estimates of month of peak C5-adult abundance vs. 1954–1977 March sea temperature anomaly in the North Sea (the data tabulated in Cushing (1984)), open triangles/solid trend line ( $R^2 = 0.26$ ) are Edwards' and Richardson's 1958–1978 annual "center of gravity" vs. March-May temperature anomaly (b) Time series of the peak timing estimates of Cushing (circles) and of Edwards-Richardson (triangles) overlaid on a contour plot of monthly log abundance in CPR region B1 (as tabulated in Cushing (1984)).



**Fig. 7.** Differences in the strength of temperature dependence of Central North Sea zooplankton phenology among taxa and seasons, based on data from Edwards and Richardson (2004). (a) Correlation between timing and spring temperature for individual zooplankton taxa, and multi-taxa averages for diatoms and dinoflagellates. Error bars are the approximate 95% confidence interval for individual pairwise correlations (i.e. without Bonferroni correction for multiple comparisons). Many taxa show negative correlation, implying a shift to earlier timing after warmer springs. (b) Interannual timing-temperature correlation vs. mean timing of the zooplankton taxa. The strongest shifts to earlier timing in warm years are by taxa that peak during the summer stratified season (indicated by shading).

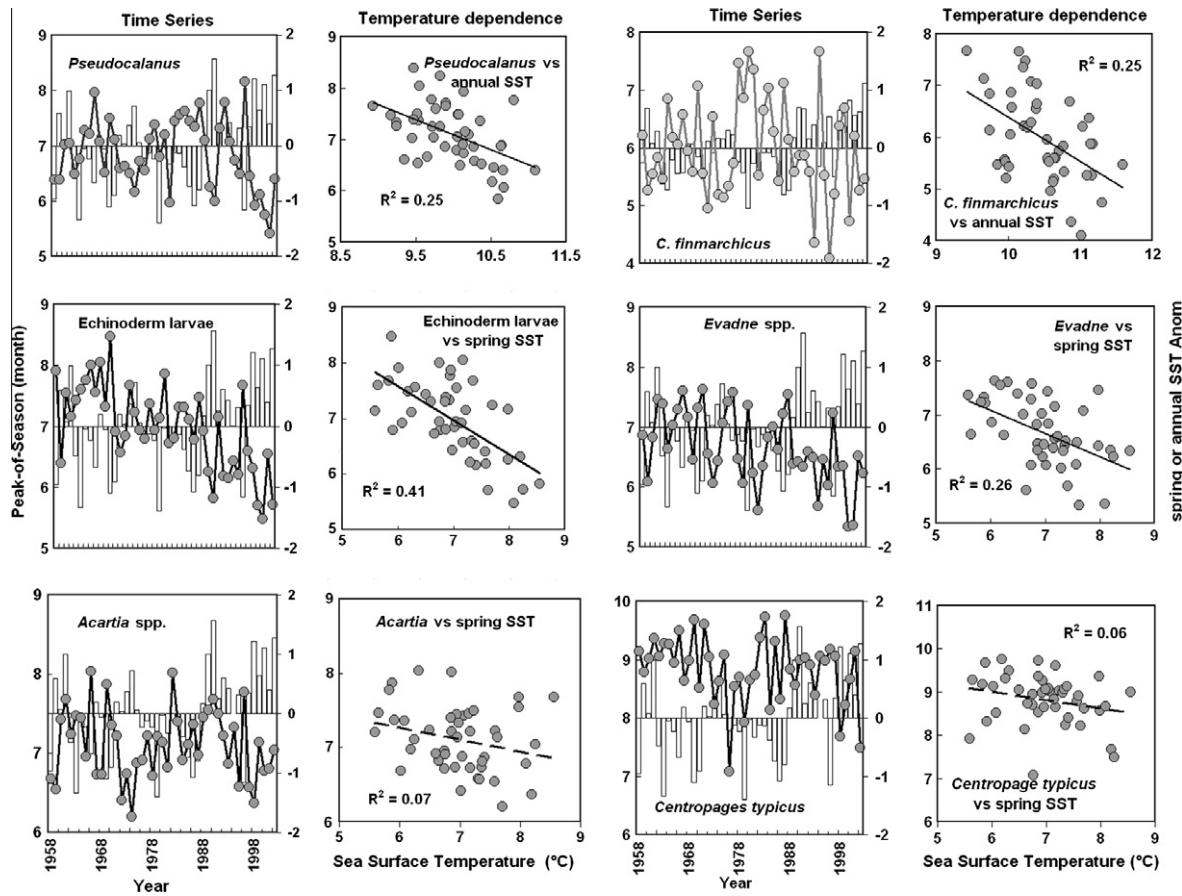
properties and advective source. The large scale mean circulation in the North Sea is U-shaped and cyclonic: North Atlantic water enters north of Scotland, mixes with freshwater inputs along the eastern margin, and then exits northeastward along the Norwegian coast.

The Edwards and Richardson (2004) phenology analysis was multi-species, covering "phytoplankton" (46 diatoms and dinoflagellates), holozooplankton (28 taxa) and meroplankton (8 taxa). Seasonal timing was estimated as the center-of-gravity of annual abundance for taxa with unimodal seasonal abundance curves, and of January–June and July–December abundances for taxa with bimodal annual sequences. Their findings included:

- Long-term trends to earlier seasonal peak timing for many species (67% of all changes and 78% of the changes that were significant after conservative corrections for multiple comparisons and autocorrelation).
- Negative correlation of seasonal peak with sea surface temperature (earlier when warmer), also for many species (Figs. 7 and 8). Because Edwards and Richardson applied a very conservative multiple comparisons correction, the number of taxa with real associations between timing and temperature almost certainly exceeds the number they reported as significant.

- Both the magnitude of the timing change trend (plotted in Edwards and Richardson (2004)), and the strength of the correlation between timing and temperature (Fig. 7a and b, this paper) varied systematically among taxa and seasons. Ranked by taxa (Fig. 7a), the largest trends in phenology and the strongest correlation with spring season temperature were by meroplanktonic larvae (nearly all have shifted 1–2 months earlier, vs. an average of ~0.7 months earlier for dinoflagellates, ~0.3 for diatoms, ~0.15 for copepods, and ~0.2 for "other holozooplankton"). Ranked by season (Fig. 7b), the largest shifts to earlier timing and the strongest negative correlation of timing with temperature were for taxa that have annual peak abundances during the stratified season (~late April–August, indicated by stippled zone along date axis). Nearly all taxa peaking during the stratified season had negative correlations of timing with temperature (warmer = earlier), and about half exceeded our estimated 5% significance threshold ( $R^2 \sim 0.1$ ) for individual pairwise comparisons. Only one zooplankton category (the fall peak of euphausiids) showed a significant shift to later timing in years with warmer temperatures.

Fig. 8 shows CNS phenology and temperature anomaly time series paired with phenology-temperature scatterplots for six of the



**Fig. 8.** Covariability of zooplankton phenology and ocean temperature for six of the central North Sea zooplankton taxa (background data from Edwards and Richardson (2004)). Taxa were selected because of their ecological importance but also for their co-occurrence in other time series. For each taxon, data are shown as paired plots. Left hand graph shows time series of annual “center-of-gravity” phenology index (lines and circles) and seasonal temperature anomaly (bars). Right hand graph is scatter-plot of phenology index vs. average surface temperature (either March–May or annual). Note the interannual covariance of timing among several of the zooplankton time series (see also Table 3).

dominant zooplankton taxa (spring temperature vs. phenology correlations for all zooplankton taxa are shown in Fig. 7a). The variability in timing for most taxa has some long-term trend but also considerable shorter-term (but often multi-year duration) fluctuations. Both the trend and fluctuations are associated with temperature anomalies in the North Sea. Edwards and Richardson (2004) focused on the relationship between timing shifts and spring (March–May) sea surface temperature. For most of the taxa, spring temperature was the most explanatory. But for some of the taxa (e.g. *Pseudocalanus*, *Calanus finmarchicus* in Fig. 8) correlations with winter or annual temperature anomalies were as strong or stronger, although the differences in  $R^2$  are too small to support interpretation of significance or cause of between-season differences in forcing.

The North Sea CPR data also provide clear evidence of cross-taxa similarities ( $r = 0.4\text{--}0.8$ ) of the timing variability and trends (Table 3), especially among the small-to-medium size copepods and cladocerans that peak during the stratified season (*Acartia*, *Centropages hamatus*, *Centropages typicus*, *Oithona*, *Pseudocalanus*, *Evdne*, *Podon*). All of these have among-taxa correlations that are positive. Many are as strong or stronger than their individual correlations (all negative) with spring water temperature. Similarity of mean timing (shown in the upper diagonal of Table 3) appears to be a contributory but not sufficient condition for strong ( $r > 0.4$ ) interannual covariability among taxa. Another important point (noted by Edwards and Richardson (2004) and Mackas et al. (1998); discussed at greater length by Richardson (2008)) is the

magnitude of observed timing changes of marine plankton. Compared to phenology changes by terrestrial taxa, the changes in zooplankton seasonal timing are large in absolute time span (range in months is often 2–3 months), and very large relative to the developmental/reproductive turnover time scale for the species (cf. the within-year peak durations of 2–3 months shown in Fig. 4).

Edwards and Richardson (2004) did not test for links between timing of zooplankton, and timing and amount of their phytoplankton food source. We do so in this paper using pairwise comparisons of timing (peak month) of individual zooplankton taxa with individual and taxonomically-grouped phytoplankton species (using data reported in Edwards and Richardson (2004)). We also compare zooplankton timing to the amount and seasonality of total phytoplankton biomass, as indexed by the Continuous Plankton Recorder “Phytoplankton Color Index” (PCI hereafter, using CNS monthly PCI averages (D. Johns, SAHFOS Laboratory). Although we know that microzooplankton are important additional food sources for mesozooplankton in many systems, comparable data for microzooplankton phenology are very scarce. However, growth rates of heterotrophic microplankton are as fast as the growth rates of their autotrophic prey (Fenchel, 1982). We expect that their seasonal cycles will be closely coupled and similar, especially in locations where average phytoplankton cell size is very small and the importance to mesozooplankton of larger microzooplankton prey is therefore high.

Both the phytoplankton species abundance and the PCI time series reveal substantial long-term changes in the North Sea phyto-

**Table 3**

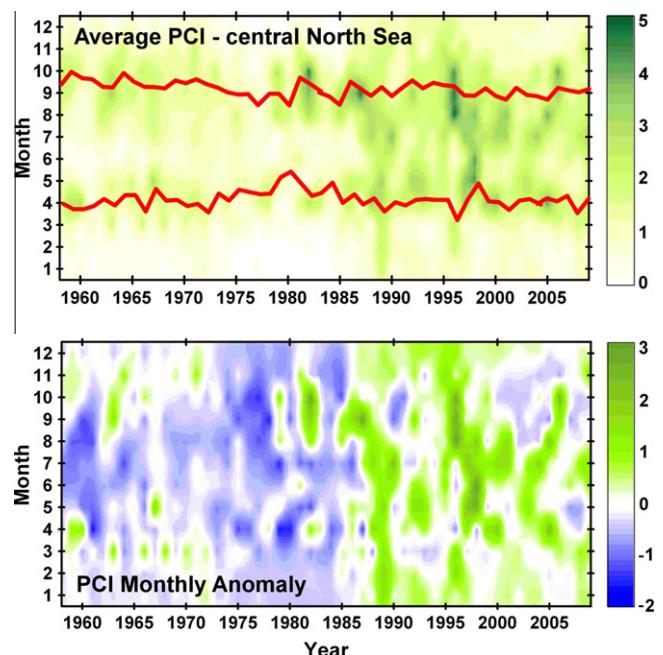
Similarity of interannual variability in phenology vs. similarity of mean seasonal timing among small crustacean zooplankton in the central North Sea (calculated from data of Edwards and Richardson (2004)). Lower diagonal of the matrix shows correlation of timing variability across years, shading highlights taxa pairs with the highest correlation ( $\geq 0.4$ ). Note that among these taxa, all of the correlation estimates are positive. Significance threshold for an individual pairwise comparison is  $\sim 0.3$ . All taxa have their annual peak during the stratified season (although *C. typicus* is late here compared to the others), and all show negative correlation between timing and spring water temperature (see Figs. 7 and 8). Upper diagonal shows between-taxa differences in mean timing (in months), shading indicates differences in average timing  $< 0.5$  month.

Taxon (mean center-of-gravity month)	<i>Acartia</i>	<i>C. hamatus</i>	<i>C. typicus</i>	<i>Oithona</i>	<i>P. elongatus</i>	<i>Evadne</i>	<i>Podon</i>
<i>Acartia</i> spp. (7.1)	–	0.5	1.7	0.0	0.3	0.4	0.1
<i>Centropages hamatus</i> (6.6)	0.59	–	2.2	0.5	0.2	0.1	0.6
<i>Centropages typicus</i> (8.8)	0.37	0.12	–	1.7	2.0	2.2	1.6
<i>Oithona</i> spp. (7.1)	0.40	0.22	0.14	–	0.2	0.4	0.1
<i>Pseudocalanus elongatus</i> [adult] (6.9)	0.52	0.35	0.34	0.43	–	0.2	0.4
<i>Evadne</i> spp. (6.7)	0.32	0.51	0.15	0.11	0.47	–	0.6
<i>Podon</i> spp. (7.3)	0.35	0.30	0.20	0.02	0.39	0.65	–

plankton. These changes were most rapid during the mid-late 1980s, and included:

- shifting phenology of a subset of the phytoplankton taxa (primarily dinoflagellates, but also a few diatoms, Edwards and Richardson (2004) and Fig. 7);
- large increases in annual and summer average PCI (Reid et al., 1998; Edwards et al., 2001; McQuatters-Gollop et al., 2007; Fig. 9a), and
- more frequent occurrences of anomalously low PCI (Fig. 9b) in late autumn (October–November).

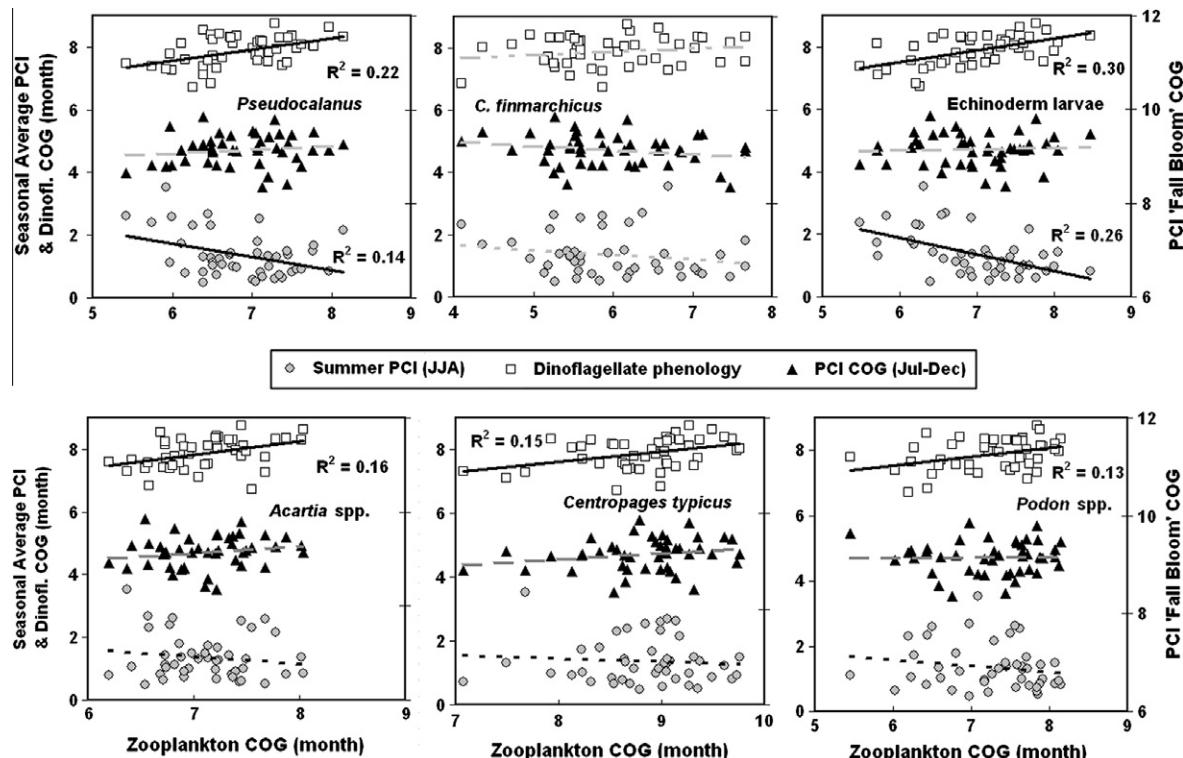
However, these changes in phytoplankton amount and timing do not appear to have driven the species level changes in CNS zooplankton phenology. Fig. 10 shows scatterplots of CNS zooplankton timing (same zooplankton taxa as Fig. 8) vs. three indices of phytoplankton availability (total summer-season phytoplankton biomass, timing of total phytoplankton biomass, and mean peak timing of ten dinoflagellate taxa). As noted earlier, most of the North Sea zooplankton taxa that have seasonal peaks in late spring to early summer also have strong “earlier when warmer” dependence on spring season temperature (Figs. 7 and 8). Given the well-established causal link between thermal stratification of the water column and onset of the spring bloom in mid-and high-latitude deep ocean regions, and the importance of food supply to zooplankton growth and reproduction, we might hypothesize that seasonality of warming is a proxy for seasonality of food availability (as assumed, e.g. by the mismatch-mismatch model of Kristiansen et al. (2011)) and expect similarly strong associations of zooplankton phenology spring or summer phytoplankton. By and large, we do not find them in the CNS data. The correlations of zooplankton timing with phytoplankton (Fig. 10) are on average (and in almost all cases) weaker than the correlations of zooplankton timing with temperature. Of the various phytoplankton indices, dinoflagellate timing (open squares) has by far the strongest correlation with zooplankton timing, but these are no stronger than the correlations between zooplankton and spring water temperature (compare Fig. 7). Note also that changes in dinoflagellate phenology cannot be a precursor cause of changes in zooplankton phenology, because the dinoflagellate peaks occur 1–2 months after the zooplankton peak for most pairwise comparisons. All other statistical associations between phytoplankton and zooplankton phenology were weak in the CNS data. Many (75%) zooplankton taxa showed earlier seasonal timing in years when summer PCI/phytoplankton biomass (gray circles) was larger, but this correlation exceeded the significance threshold for only about 12%. Association of zooplankton timing with spring bloom intensity, indexed by March–May average PCI, was absent-to-marginal ( $r = -0.15 \pm 0.15$ ). Note that all pairwise associations of zooplankton phenology with PCI are confounded by shared covariance with temperature: years



**Fig. 9.** Changing amount and seasonal timing of phytoplankton biomass in the CNS (updated from Edwards et al. (2001)). Upper panel contour plot shows month vs. year time series of average Phytoplankton Color Index (PCI), an index of phytoplankton biomass. Red lines show changes in ‘spring bloom’ and ‘fall bloom’ timing (PCI ‘center of gravity’ within January–June and July–December date windows). Lower contour plot shows monthly PCI anomalies, relative to 1958–2009 average seasonal cycle (stronger anomalies have darker shading (green = positive, blue = negative), near-zero anomalies are indicated by white). Annual and summer average phytoplankton biomass increased strongly after the mid 1980s, while February–March and October–November have tended to be lower. PCI time series data courtesy of D. Johns (SAHFOS).

with warm spring temperatures have not only earlier zooplankton timing, but also higher North Sea phytoplankton biomass in both spring (March–May,  $r = 0.31$ ) and summer (June–August,  $r = 0.45$ ). Correlations of zooplankton timing with fall bloom timing (black triangles) are often positive (i.e. zooplankton earlier when fall bloom earlier), but all pairwise correlations are individually non-significant. Correlations with spring bloom timing ( $-0.07 \pm 0.21$ ), and diatom timing ( $0.06 \pm 0.19$ ) are even weaker.

Given the strong association of zooplankton timing with spring temperature, the weakness/absence of association with spring season phytoplankton is surprising. One possible explanation is that the North Sea spring phytoplankton community is strongly dominated by diatoms, and that neither diatom phenology nor overall spring bloom timing show much correlation with annual or sea-



**Fig. 10.** Covariability of North Sea zooplankton phenology (same six taxa as Fig. 7) with interannual changes in phytoplankton biomass (June–August PCI) and in phytoplankton phenology (average 'center of gravity' bloom timing estimates for the dinoflagellate species reported in Edwards and Richardson (2004), and for July–December PCI). Zooplankton phenology is shown on horizontal axes, phytoplankton amount and phenology on vertical axes (open squares = dinoflagellate phenology, triangles = fall bloom PCI phenology, gray circles = June–August average PCI). Trendlines are shown for each scatter plot, but are significant only if solid lines.

sonal temperature anomalies. This is perhaps because many of the dominant diatom species in mid-latitude continental shelf systems form resting spores. Recent studies (see review by Ji et al. (2010) for a more detailed discussion) have found that timing of diatom spore germination is controlled primarily by photoperiod (fixed seasonality) rather than by temperature (larger interannual variability).

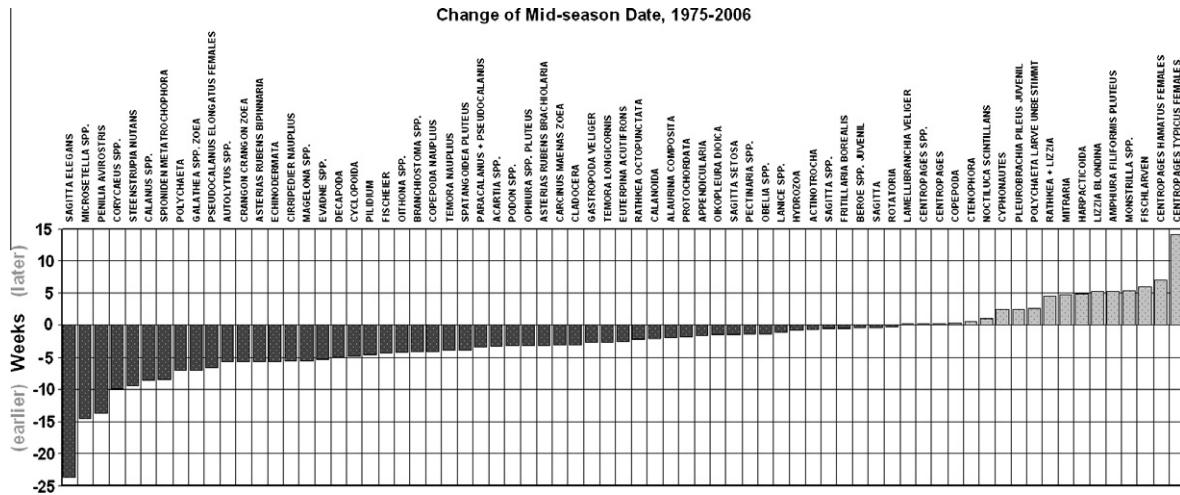
### 3.2.4. Helgoland Roads, southeastern North Sea

Another long and taxonomically rich North Sea time series is from Helgoland Roads (HR hereafter, see Greve et al. (2004, 2005) for details of site and methods). This site was the first to develop operational forecasts of local zooplankton phenology from hindcast fits of observed timing to local hydrography (Greve et al., 2001, 2014; [www.senckenberg.de/dzmb/plankton](http://www.senckenberg.de/dzmb/plankton)). The HR time series differs from the CPR data set in many ways, but is similar in design and site characteristics to many other coastal time series in the Atlantic and Mediterranean. The HR sampling site is a shallow (6–8 m) channel between two islands located 50 km offshore in a shallow (30–50 m deep) and tidally-mixed part of the North Sea. Strong continental influence on local weather plus a shallow water column lead to a large annual temperature range (12–14 °C). HR sampling is frequent and regular (3–7 per week using both large and small nets, and subsequently analyzed at weekly resolution), and detailed taxonomic/age resolution has been possible. Because of the shallow water column and rich benthos, many of the taxa examined are meroplanktonic (including many fish larvae). Seasonal timing has been assessed by the cumulative percentile method to produce annual estimates of start, middle, end, and duration of season for each taxon. For larger-bodied taxa (e.g. *Calanus*, *Sagitta*, most medusae) that were sampled in

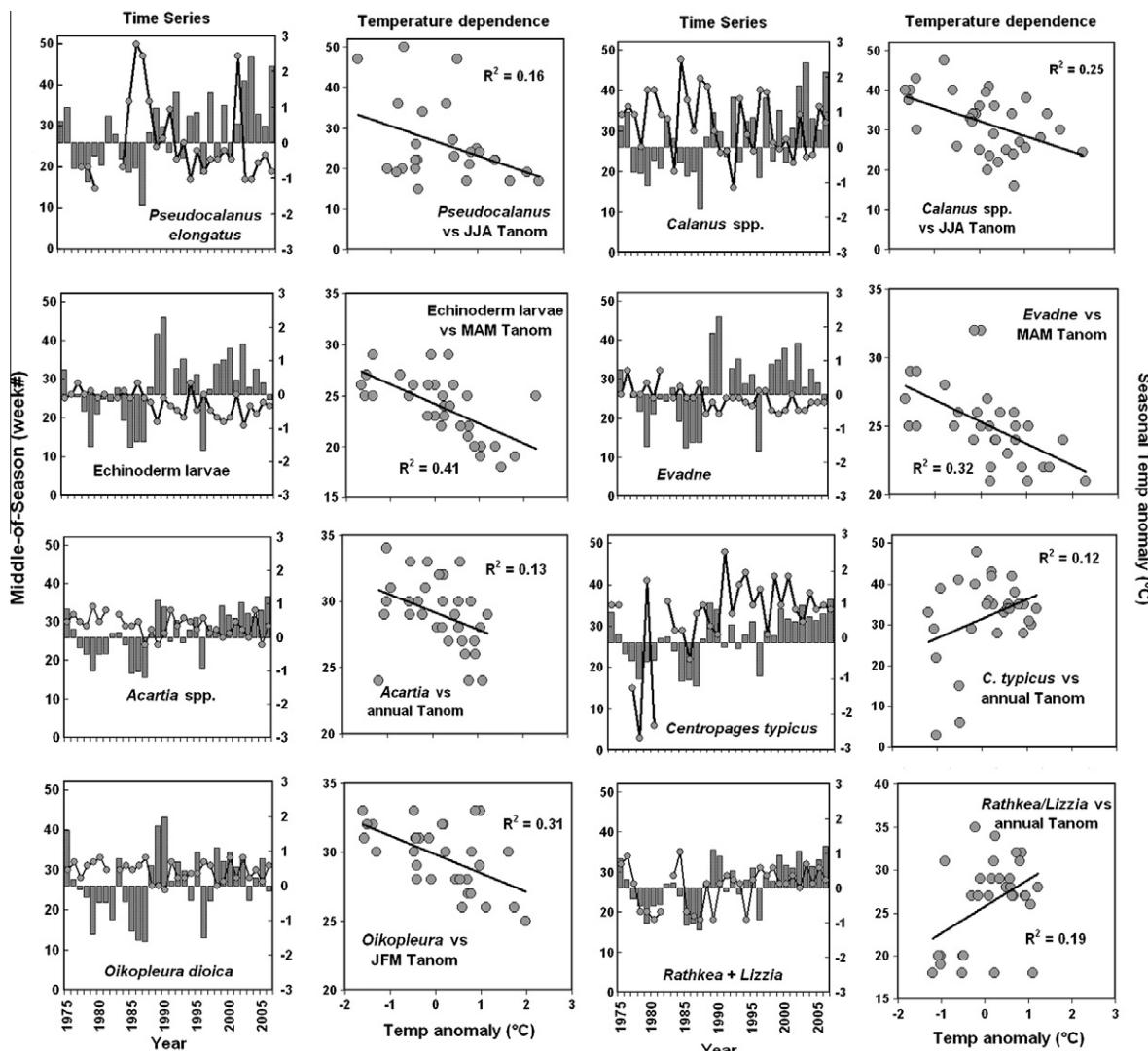
both net types, we have averaged the annual timing indices from the two data sets.

Despite the differences in site and sampling design, several results from HR are similar to the North Sea CPR results described above. The majority of HR taxa have shifted to earlier timing over the past three decades (Fig. 11); the within-time series range of timing variability is typically ~2–3-fold larger than the long-term trend (Fig. 12); and both trend and shorter-term fluctuations covary with water temperature variability (a ~2 °C range and ~1.2 °C upward linear trend over 30 years for the annual temperature anomalies). Of the HR trends to earlier zooplankton timing, 34% are by >4 weeks and 10% by >8 weeks. Largest movements were by the cool-water chaetognath *Sagitta elegans* (24 weeks) and the harpacticoid copepod *Microsetella* sp. (15 weeks). A smaller number of taxa have trends to later timing (12% by more than 4 weeks). However, there were two important differences between the HR and CPR North Sea time series results. One is that, for the same taxa, trends (change per year) and the total ranges of timing variation were on average about 2-fold larger at HR than in the CNS (compare Figs. 8 and 12). Second, two *Centropages* species had the largest trends toward later timing at HR (*C. typicus* 14 weeks, and *C. hamatus* 7 weeks) and their timing–temperature correlations were positive (later when warmer). In contrast, within the CPR CNS time series, the same species shifted earlier by about 2 weeks (0.4–0.6 month) and had weak but negative timing–temperature correlation.

Zooplankton phenology at HR also appears to be unrelated to local phytoplankton timing. This part of the North Sea is kept unstratified by strong tidal-mixing of a shallow water column. Consequently, phytoplankton biomass is high for much of the year (~early March–November, e.g. Edwards et al., 2001). Wiltshire et al. (2008) recently analyzed spring bloom dynamics at HR. They



**Fig. 11.** Trends in seasonal timing observed at Helgoland Roads (southeastern North Sea), 1975–2006. The majority of taxa have shifted to earlier timing, but several important taxa have shifted to later timing.



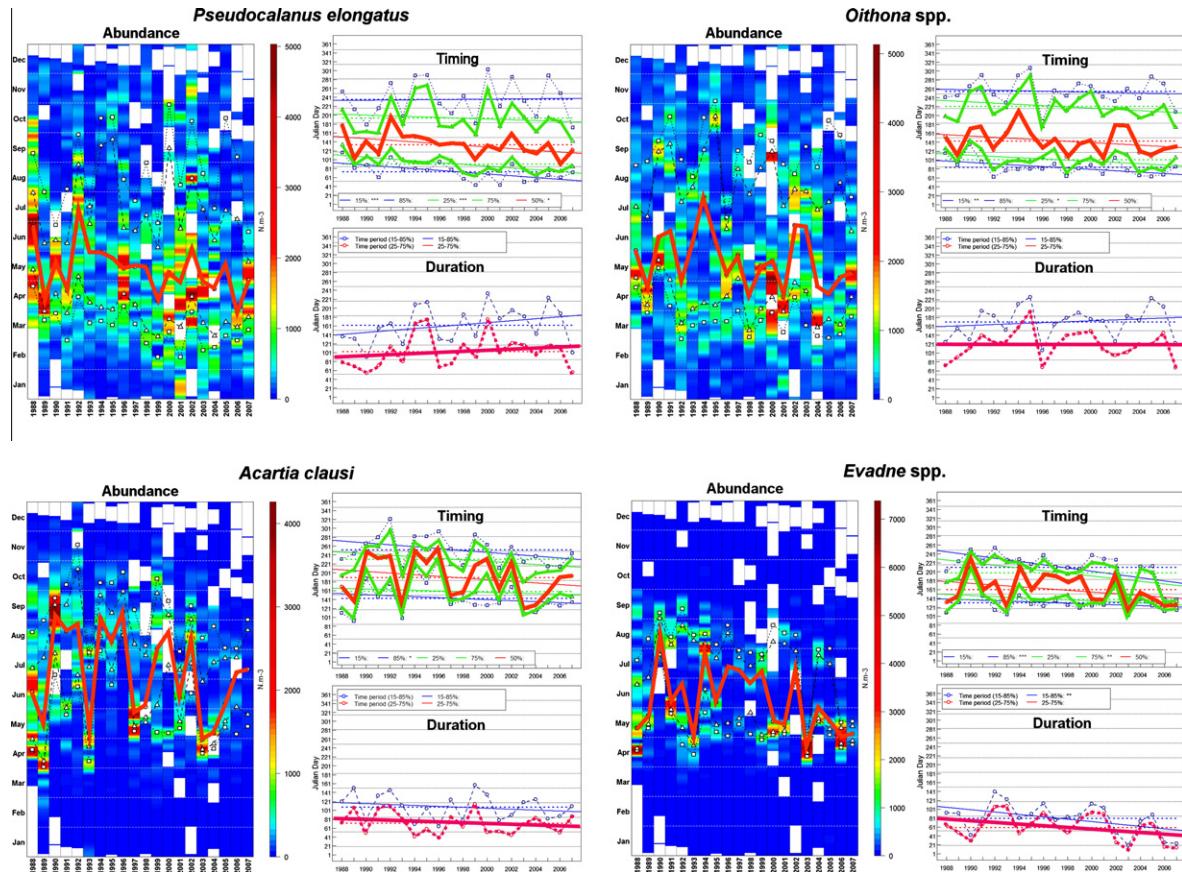
**Fig. 12.** Zooplankton phenology and ocean temperature for eight Helgoland Roads zooplankton taxa. Taxa were selected for their ecological importance but also for their co-occurrence in other time series. For each taxon, data are shown as paired plots. Left hand graphs are time series of annual “middle-of-season” (50th cumulative abundance percentile, lines and circles) and seasonal temperature anomaly (bars). Right hand graphs are scatterplots of the phenology index vs. seasonal or surface temperature anomaly. Compare ranges and slopes of phenology changes vs. Fig. 8 (the top three rows of Fig. 10 correspond to the same rows in Fig. 8, except that *Calanus* at Helgoland Roads is mostly *C. helgolandicus*).

found that a small diatom-dominated bloom begins in late January or February of most years (peak timing estimated by their MDD = “mean diatom day” index), and is followed by a second larger bloom in March–April (start timing indexed by their FEBD = “first exponential bloom day”; see Wiltshire et al. (2008) for detailed explanation of these indices). Year-to-year variability of phytoplankton bloom timing is relatively small (interannual std. dev. of their two timing indices was ~10–20 days, vs. 30–60 days for the mid-season dates of the dominant holozooplankton, Fig. 11). Warm temperature during the previous autumn is the best predictor of the intensity (but not the timing) of the spring bloom. For this paper, we compared their MDD and FEBD time series with 50th percentile “middle-of-season” date estimates from the HR zooplankton time series, and also with seasonal and annual temperature anomalies. We found that although the correlations of zooplankton timing with phytoplankton timing had a preferred sign (positive with MDD, negative with FEBD), their strengths were almost always weaker ( $R^2$  always <0.1 and often near zero) than the associations of timing of either phytoplankton or zooplankton with temperature ( $R^2$  typically ~0.1 and occasionally ~0.2). The only zooplankton taxa for which correlations with spring bloom phenology were stronger than with temperature were the autumn-season cladoceran *Penilia avirostris* (FEBD  $r = -0.6$ , but present in only 11 years) and the spring-season larvacean *Fritillaria borealis* (MDD  $r = 0.4$ ). Although the long phytoplankton productive season at HR can support a wide range of zooplankton seasonal timing within taxa, and also an among-taxa diversity of life history strategies (Halsband-Lenk et al., 2004), the interannual var-

iability and trends of phytoplankton biomass and phenology do not appear to be dominant local controls on zooplankton timing.

### 3.2.5. Plymouth L4, western English Channel

The present Plymouth zooplankton time series (L4 hereafter) began in 1988 as a supplement/successor to time series observations at slightly more distant English Channel locations. Like HR, L4 is a single sampling site, and has had frequent (usually weekly) sampling, and good taxonomic resolution. The location at the western end of the English Channel exposes it to strong and time-varying advective influence from both the North Sea/English Channel, and from the open North Atlantic (Russell, 1939). Zooplankton data from L4 are supported by a broad accompanying suite of physical and chemical observations (see Harris (2010) and [www.westernchannelobservatory.org.uk](http://www.westernchannelobservatory.org.uk)). Analysis of the zooplankton time series is currently a work in progress (e.g. Eloire et al., 2010). We provide here only some examples of how the L4 data can be examined for phenology. Fig. 13 shows examples of indices for the start-, middle-, and end-of season time series, overlaid on contours plots of abundance vs. month and year. All four of these taxa have strong trends toward earlier timing (by ~20–25 days over 20 years) overlaid by larger amplitude interannual variability (timing range ~120 days). *Acartia* and *Evdne* also show trends to briefer growth-season duration, while the *Pseudocalanus* growth season has become slightly longer. Date vs. year contour plots such as those in Fig. 13 are very useful for exploratory analysis, and can help identify potential outliers or ‘blind spots’ of the various phenology metrics. For example, it is clear from Fig. 13 that



**Fig. 13.** Zooplankton abundance and phenology time series at the Plymouth L4 site for four taxa. For each taxon, the left plot shows contours of abundance vs. month (y-axis) and year (x-axis) overlaid by 50th percentile “middle of season” (red line). White blocks are data gaps. Right hand plots show the full range of phenology time series. Top graphs show timing: middle-of-season (red line), start and end of season as 25th and 75th percentiles (green lines). Bottom graphs show season duration estimates (days between 25th and 75th percentiles – time series as magenta dotted line, trend as solid line). Many of the taxa suggest trends to earlier and shorter seasons, although significance levels are as yet low due to the relatively small number of years.

taxa with seasonal cycles that switch between unimodal and bimodal (e.g. *Oithona* and *Evadne* in Fig. 13) are difficult to analyze with any of the indices described in Section 2.2. If early and late modes are of similar amplitude, the 50th cumulative percentile will tend to fall between the two peaks. But if the modes are very different in amplitude, the timing estimate for the smaller mode can be dominated by leakage from the early or late margins of the larger mode.

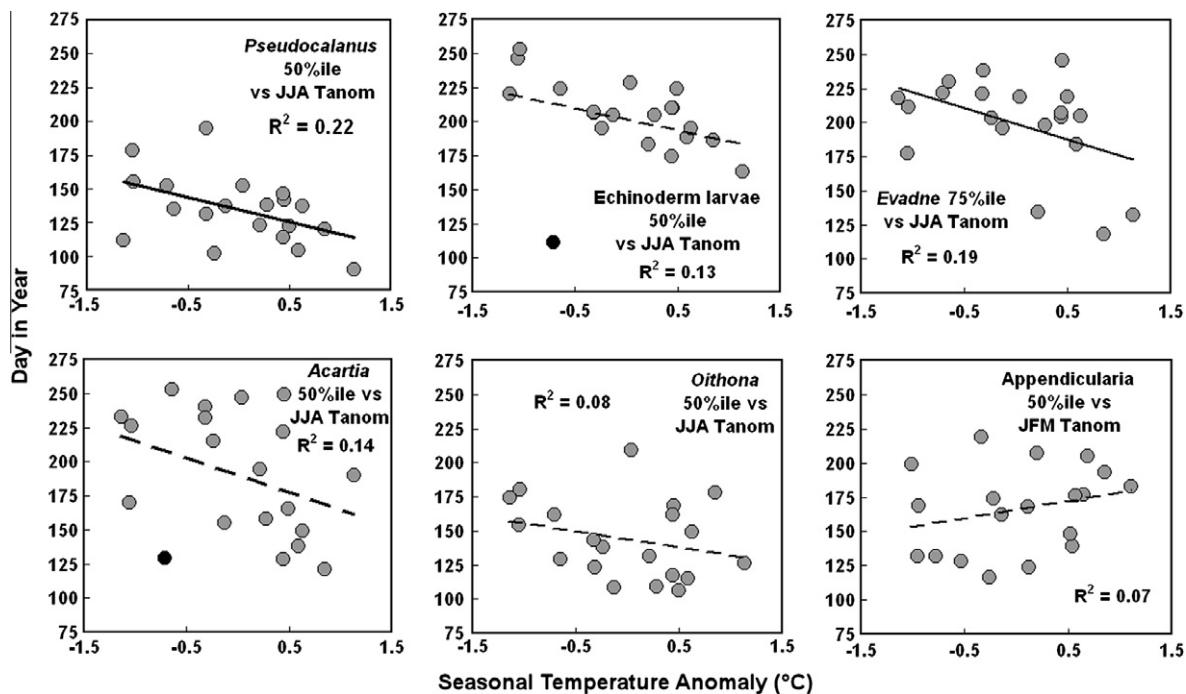
Most zooplankton taxa at L4 show earlier timing under warmer conditions (Fig. 14). But unlike the North Sea and Norwegian time series, the strongest correlations between timing and water temperature at L4 were usually in summer (June–August, year-days 121–243) rather than spring (March–May). Because many of the population peaks occur during or before summer, this suggests the local effect of water temperature may act mostly through altering timing of the end of the growing season. Because the L4 time series is still relatively short (20 years, ~15 d.f.), timing vs. temperature regressions are to date statistically significant only for *Pseudocalanus* mid-season and *Evadne* end-of-season. However, regressions for several other L4 taxa are marginally significant ( $R^2 \sim 0.1$ –0.15) and will cross  $p = 0.1$  or 0.05 thresholds if similar strength-of-association persists for another 10 years. Strength-of-association at L4 between zooplankton phenology and phytoplankton seasonality and abundance has not yet been fully examined, but visual inspection of monthly-averaged data (see figures in Eloire et al. (2010)) suggest that although climatological seasonal patterns (spring and fall peaks of zooplankton abundance and phytoplankton biomass) are closely aligned, the interannual deviations of zooplankton and phytoplankton from their respective climatologies are independent.

### 3.2.6. Northwest Atlantic – Narragansett Bay, Canadian coast, and Labrador Sea

Several Northwest Atlantic time series have been examined for changes in zooplankton phenology, but the analyses all cover fewer

years and narrower sets of species than the NE Atlantic time series described above. In this paper, we will not extend the NW Atlantic analyses, but will briefly review the setting and results for each data set, so that we can compare the results with other studies.

The Narragansett Bay time series (Costello et al., 2006; Sullivan et al., 2007) has been built up from several shorter collections. Although intermittent, it extends over 50+ years, with ~weekly resolution in the 10 years sampled. Most of Narragansett Bay (NB hereafter) is shallow and tidally-mixed, and has experienced a 1.2 °C increase in annual average temperature, much of which is due to increase in the winter minimum temperature. Zooplankton data were examined for changes in timing of the annual abundance maxima of two copepod congeners (*Acartia hudsonica* and *Acartia tonsa*) and a predatory ctenophore (*Mnemiopsis*). All three have relatively narrow seasonal maxima and zoogeographic ranges that differ but overlap near NB. *Acartia hudsonica* is a temperate–boreal species, and historically has been the dominant spring season copepod in NB. *Acartia tonsa* is a subtropical–temperate species, but is at the poleward end of its range; where its annual population maxima are in summer. In NB, it is historically the mid-late summer dominant. Seasonality of both *Acartia* species is linked to production and hatch timing of their resting eggs; both of which are strongly controlled by temperature (see references in Sullivan et al. (2007)). The ctenophore *Mnemiopsis leidyi* is a subtropical–temperate species. Its highest abundance in NB was historically during the warmest late summer months (about a month later than the summer maximum of *A. tonsa*). One plausible scenario for the ecological response of NB zooplankton to warming would be earlier seasonal timing of all three species, plus an increase in the relative dominance of the warmer water *A. tonsa*. However, the NB time series show substantial shifts to earlier timing (1–2 months) by only two species (*A. hudsonica* and *Mnemiopsis*). In contrast, *A. tonsa* showed little change in timing, but a 4–5-fold decline of summer abundance. Costello, Sullivan and their coau-



**Fig. 14.** Plymouth L4 scatterplots of zooplankton seasonal timing (from cumulative percentiles of abundance) vs. seasonal temperature anomalies. Most of the dominant L4 taxa show weak-to-moderate association of earlier timing with warmer temperature. However, unlike the North Sea and Norwegian time series, the season with the strongest influence on all taxa is summer rather than spring. Interannual ranges of timing are ~3 months – similar to the CPR data from the Central North Sea, but smaller than at Helgoland Roads. Outlier points in the L4 Echinoderm and *Acartia* plots (black circles) are both from 1993 (retained in the correlation analysis, but an anomalous year in which a warm spring was followed by a cool summer, and abundance of echinoderm larvae was the lowest in the entire time series).

thors deduced that the cause was differing exposure to the long term surface warming trend, in part because of the seasonality and local fine-scale spatial pattern of the warming (greater during winter, and at the landward end of NB) and in part because the taxa differ in their spatial location during winter-early spring (*A. hudsonica* are already hatching from the dormant eggs, *Mnemiopsis* are in the shallow inner estuary, but *A. tonsa* remain as benthic resting eggs in the deeper parts of the outer estuary). The lack of timing shift by *A. tonsa* has resulted in much stronger seasonal overlap with the population peak of *Mnemiopsis* and presumably also in large increases in predation mortality for the copepod. As in the NE Atlantic studies by Cushing and Ellertsen, we are seeing species-specific change in trophic match-mismatch caused by differential shifts in phenology. But in NB, the larger survival consequences have been for the prey rather than for the predator species.

An additional recent set of NW Atlantic time series are located 100–400 km NE of Narragansett Bay. During the 1990s, Fisheries and Oceans Canada established biweekly monitoring of several sites located near east coast DFO laboratories (Atlantic Zonal Monitoring Program; <http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/index-eng.html>). These time series are all still young, but offer good taxonomic and within-year temporal resolution. Johnson et al. (2008) used them to examine correlates of diapause onset and emergence of *Calanus finmarchicus* at four nearshore sites (Fig. 3 for locations). Timing of diapause onset in autumn was estimated by the ratio of stage C5 to total copepodite abundance, timing of spring diapause emergence by the ratio of adults to total, and also by hind-cast modeling of development rates of young copepodites sampled later in the growing season. Dormancy onset and emergence dates differed by nearly 150 days among sites, and varied interannually by ~50–100 days within sites. The study compared/evaluated several mechanistically-plausible environmental controls (year-day, daylength, surface temperature, deep temperature, and surface chlorophyll). Effects of chlorophyll and deep temperature were non-significant. Year-day, daylength, and surface temperature had significant effects on the timing of the onset of local dormancy, year-day and daylength had significant effect on timing of local emergence, but none had threshold or trigger values that were consistent across all four sites. Johnson et al. (2008) concluded that internal controls on dormancy timing (accumulated lipid reserves and/or an internal clock) are probably additional and important modulators of responses to environmental cues.

Frequent *in situ* sampling of high seas locations is often difficult or impossible, especially at high latitudes (due to a combination of distance, weather and ice) and in the tropics (owing to distance to the few and widely-separated oceanographic laboratories). Nevertheless, several sites in different ocean regions are being sampled one or two times per year (see Valdés et al., 2007). Are there analytical methods that can exploit these very sparse time series?

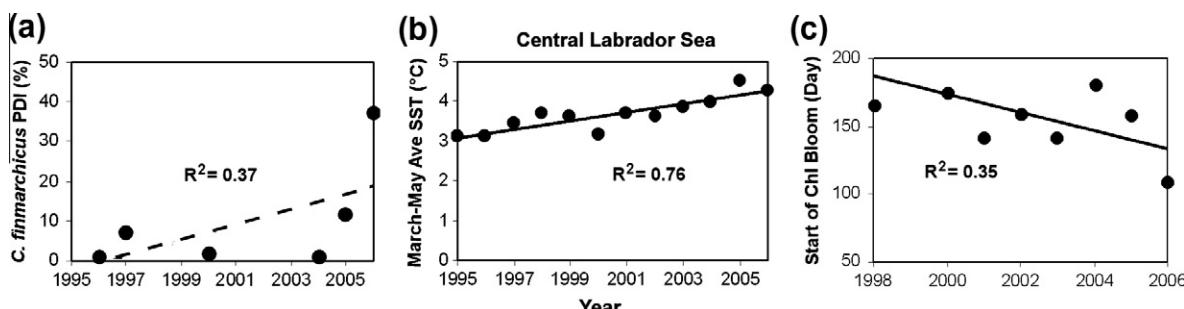
Perhaps yes, if the annual cycle is sufficiently simple (often true at high latitudes). Erica Head (Pers. comm.) recently developed a “proportional development index” (PDI, see Section 2.3 for formula) that is applicable to once-per-year data. To date, she has applied this index to *Calanus finmarchicus* at locations/transects in the NE Atlantic (off Norway), the NW Atlantic (off Newfoundland), and in the Labrador Sea (see Fig. 3 for location). One interpretive caution is that the PDI index is not monotonic – it reaches an annual maximum early in the post-hatch development of the annual cohort. Earlier in the season, the population is entirely made up of post-dormant C5 and adults of the parent generation (low PDI). Later in the season, C4 and C5 of the offspring generation become dominant (again reducing the PDI). Year-to-year differences in PDI must therefore be interpreted based on knowledge of when within each year the sampling has occurred, combined with prior knowledge of the expected annual cycle at that location. Fig. 15 shows examples of the PDI index from the Labrador Sea. There has been a recent trend to earlier zooplankton timing (indexed by local PDI in Fig. 15a; in this season a high PDI implies early cohort timing), associated with a warming trend of spring temperatures (Fig. 15b), and also with an earlier start of the phytoplankton spring bloom (Fig. 15c). Similar trends and associations (not shown) are present in the eastern Labrador Sea, off Newfoundland, and off Norway. The time series are as yet too short to identify if temperature or chlorophyll is a better predictor of zooplankton timing (results to date from this comparison differ among sites).

### 3.3. North Pacific

Time series from several North Pacific sub-regions have been analyzed for zooplankton phenology, but the taxonomic range is narrower than in the Atlantic (to date analyses have focused entirely on subarctic copepods). Most of the North Pacific data also lack the detailed temporal resolution of the North Atlantic and Mediterranean coastal time series (but benefit from more within-region spatial averaging). Two exceptions are the first two decades of the Ocean Station P time series (~weekly or better at a single site), and the NH5 time series off Newport Oregon (biweekly/monthly at a small number of cross-shelf sites). However, zooplankton seasonality on the Oregon continental shelf appears to be dominated by very strong advective seasonality, rather than by local reproductive and developmental processes (Hooff and Peterson, 2006).

#### 3.3.1. Northeast Pacific

Zooplankton phenology time series in the NE Pacific (Tables 2a–2c and Fig. 3b) cover six decades for Ocean Station P (50°N 145°W) in the southern Alaska Gyre, fragments of five decades for the Strait of Georgia, three decades for the Vancouver Island continental margin, and slightly less than a decade for other parts of the Alaska Gyre that have been sampled by the North Pacific CPR program. In



**Fig. 15.** Shared decadal trends of seasonal timing and environmental conditions in the Labrador Sea: (a) *Calanus finmarchicus* phenology as indexed by PDI in late May, (b) average sea surface temperature (March–May) from satellite data, (c) phenology of the phytoplankton bloom (year-day when satellite chl a first exceeds 1 mg m<sup>-3</sup>).

all of these areas, analyses to date have focused on timing of the interzonal migrant copepod *Neocalanus plumchrus*. Reproductive strategies of this (and other *Neocalanus*) species differ greatly from the Atlantic-dominant *C. finmarchicus*: emergence from dormancy, oocyte production, mating, spawning and hatch of nauplii all occur at or near the dormancy depth (Miller and Clemons, 1988), without a need (or opportunity) for the parents to feed in the surface layer as does *C. finmarchicus*. The parent generation therefore relies entirely on lipid reserves accumulated during the previous growing season (“capital spawning”) rather than on recent feeding (“income spawning”, see Fiksen (2000) and Varpe et al. (2009) for additional definition and discussion of fitness tradeoffs). Early stage copepodites are also usually the first stages to be detected in spring surface-layer samples, partly because the eggs hatch at depth and perhaps also because nets used for time series sampling have had relatively coarse mesh (0.2–0.35 mm).

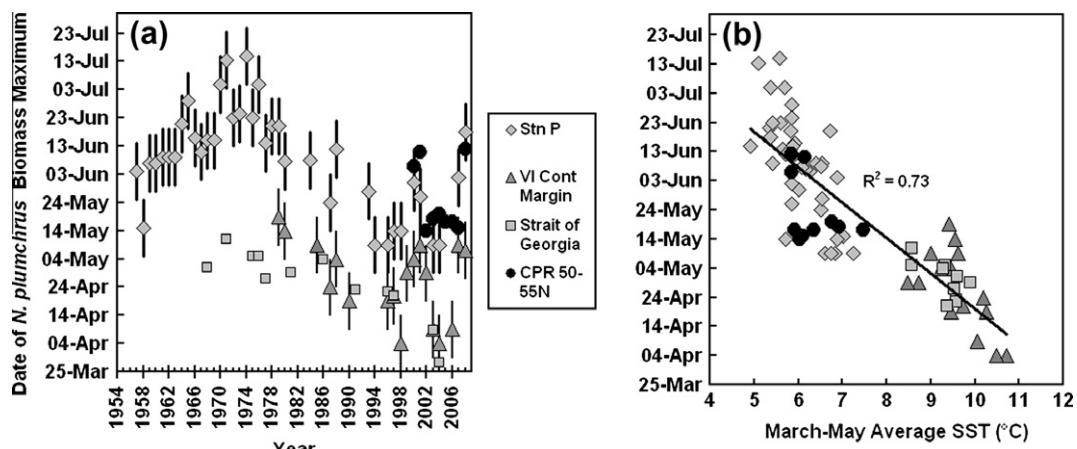
Although samples have been collected for several decades, much of the detailed knowledge of *Neocalanus* life history is based on samples from only a few years at each location (Miller and Clemons (1988) for the Alaska Gyre, Fulton (1973) for the Strait of Georgia, and Tsuda et al. (1999, 2004) for the NW Pacific). The large interannual variability of *Neocalanus* phenology was not recognized until the mid-late 1990s, when the mid-1990s Canadian JGOFS program encountered only very few and near-dormant C5 at Stn P during the same months that the 1980s Project SUPER samples had contained high abundance of C3–C5. A subsequent retrospective analysis (Mackas et al., 1998) revealed strong decadal fluctuations of *N. plumchrus* timing that had been present throughout the time series (Fig. 16a), and also showed that timing variation at Stn P is strongly and ~linearly correlated with spring surface temperature anomalies (Fig. 16b), but has no correlation with the (smaller amplitude) temperature anomalies at the dormancy depth. Mackas et al. (1998) discussed potential mechanisms that could produce earlier cohort timing when/where spring surface temperature is anomalously warm. They noted that although direct physiological effects of temperature on stage duration act in the right direction, the observed 2 °C range of spring season surface temperature anomalies at Stn P could account (at most) for only about a 20 day range of timing (vs. an observed timing range of >60 days).

Both the ranges of NE Pacific temperature and timing variability, and the conclusion that developmental acceleration cannot be the primary linking mechanism, are similar to those by Ellertsen et al. (1987) for *Calanus finmarchicus* in the Norwegian Sea (com-

pare Figs. 5 and 16). However, because *Neocalanus* mature and spawn at their dormancy depth, it is unlikely that variability of the date of maturation and spawning by the parent generation (plausible for *Calanus finmarchicus* in the Norwegian Sea) is the cause for variability of timing of late-stage *Neocalanus* copepodites in the NE Pacific. Mackas et al. (1998) suggested that the most probable mechanism in the NE Pacific was a narrow and temperature dependent window for survival of the developing nauplii and copepodites (we will revisit this topic later in this sub-section, as part of our discussion of variable cohort width).

The time series of NE Pacific *Neocalanus* timing (Fig. 16a) show that a major change in the direction of the timing trend occurred in the mid-1970s, more-or-less coincident with the 1976 “regime change” of the Pacific Decadal Oscillation pattern of sea surface temperature anomalies (PDO, Hare and Mantua, 2000). *Neocalanus plumchrus* timing at Stn P continued to become earlier from the mid 1970s until ~1997–1998. We and colleagues have subsequently examined *N. plumchrus* seasonal timing in adjoining parts of the NE Pacific and for additional years (Bornhold, 2000; Batten et al., 2003; Mackas et al., 2007; El-Sabaawi et al., 2009; Batten and Mackas, 2009). Large and persistent latitudinal and onshore-offshore offsets in timing are present (~1–2 months earlier timing at more coastal and more southerly locations, compare Figs. 16a and 3b). But the spatial differences in timing are well-explained by corresponding among-region differences in spring-season surface temperature, acting on a common shared-or-very-similar temperature-timing relationship (Fig. 16b). Since 1997–1998, timing in all NE Pacific regions has oscillated in approximate synchrony between short (2–4 year) episodes of cool-late (1999–2002; 2007–2008) and warm-early (~2003–2006, 2009–2010) conditions. Overlying the changes in timing, we have observed fluctuations and trends in population size. The most extreme change has been in the Strait of Georgia, where the abundance of *N. plumchrus* has decreased by about an order of magnitude since 2000 (El-Sabaawi et al., 2009; we will revisit this observation in Section 3.8)

NE Pacific phenology estimates have been based on one of three alternative indexing methods: either direct observation of the date of the maximum abundance/biomass (the early Stn P time series, and some years within the Strait of Georgia time series), or on developmental stage-ratios from species-level enumerations (the sparser post-1981 Stn P time series, all of the Vancouver Island continental margin time series, and some years in the Strait of Georgia), or on cumulative percentiles (used for some analyses of



**Fig. 16.** (a) Time series and (b) temperature dependence of *Neocalanus plumchrus* timing in four adjoining sub-regions of the eastern Subarctic Pacific (Fig. 3 for locations). Timing is later at more oceanic and more northerly locations, but interannual-decadal variability is strongly coherent among locations, and all regions share a similar temperature dependence (updated from Mackas et al. (1998, 2007)).

the N Pacific CPR time series). Data suitable for cross-comparison of the first two indexing methods were available at Stn P for a few years in the 1970s and 1980s. In these years, the biomass maxima occurred when ratios of C5:total copepodites were between 35% and 65% (The explanation for this is simple. At lower % of C5, total abundance is high but average body size is low; at later dates the abundance and biomass drop off steeply because large numbers of C5 leave the upper ocean to enter dormancy). The stage ratio “50% C5” was therefore adopted by Mackas et al. (1998) as an empirical estimator of the date of the upper ocean biomass maximum, as well as being its own independent and self-consistent phenology index. However, the exact equivalence point between total biomass and stage ratio depends on several factors: (1) the balance between stage-dependent rates of individual somatic growth and population mortality; (2) the degree of uniformity of stage durations; and (3) especially important, the degree of cohort synchrony (Batten and Mackas, 2009; Mackas et al., 2007). Note that in the extreme (and unrealistic) case of a cohort that is entirely synchronous, the annual *Neocalanus* biomass maximum would occur at 100% C5 (when the entire population has synchronously accumulated maximum body weight, but just before it begins the downward ontogenetic migration to enter dormancy).

Additional NE Pacific time series (with more frequent sampling) were started/resumed in the late 1990s (Alaska Gyre and Strait of Georgia respectively). The North Pacific CPR program has provided monthly-resolution Alaska Gyre data suitable for both amount-based and stage-based indices of timing, as has the recent sampling in the Strait of Georgia. Batten and Mackas (2009) compared timing estimates from these newer data. They found that in recent years (when peak timing has mostly been early compared to the 1970s and 1980s) the biomass maximum corresponds more closely to a stage ratio of ~80–85% C5, and that the cause of this change has been a narrowing (greater synchronization) of the annual cohort of late stage *N. plumchrus* copepodites. Peak duration estimates (mean ± standard error) have declined after 1996, from 55 ± 4 days beforehand to 35 ± 5 days afterwards in the Alaska Gyre, and from 38 ± 5 to 11 ± 3 days in the Strait of Georgia. The cohort-narrowing has accompanied the shift to earlier timing shown in Fig. 16. The combination could have important match-mismatch consequences for predators that rely on these copepods, because the prey-availability timing window has become narrower by about 20 days, earlier by 1–2 months, and also lower amplitude in the Strait of Georgia. Even the early, broader maxima represent a substantial narrowing of the annual cohort between egg and late copepodite stage. Lab incubations by Saito and Tsuda (2000) showed that individual *Neocalanus* females produce sequential clutches of eggs at regular intervals; at 2 °C (4 °C) the durations of the individual egg-laying period were 47 (42) days for *Neocalanus flemingeri*, 60 (56) days for *N. plumchrus*, and 91 (67) days for *Neocalanus cristatus*. Unless all individuals spawn in synchrony, the spread for an entire local population is necessarily broader, and observations support this. Fulton (1973) found a population spread of >65 day in the Strait of Georgia (where spawning temperature are much warmer: 8.5–9.5 °C); Miller and Clemons (1988) observed active spawning for 150–200 days at Stn P/eastern subarctic Pacific (spawning temperature 3.4–3.8 °C); Tsuda et al. (1999) report similar or longer spawning in the western subarctic Pacific (spawning temperature 0.0–4.0 °C). Progressive narrowing of the annual cohort as it develops implies either a very narrow survival window (Miller and Clemons, 1988; Mackas et al., 1998), or that duration of an intervening early stage becomes prolonged if growing conditions are not yet suitable (Miller and Clemons, 1988; Saito and Tsuda, 2000; L.M. Slater and R.R. Hopcroft, pers. comm.; and H. Fujioka and A. Tsuda, pers. comm.).

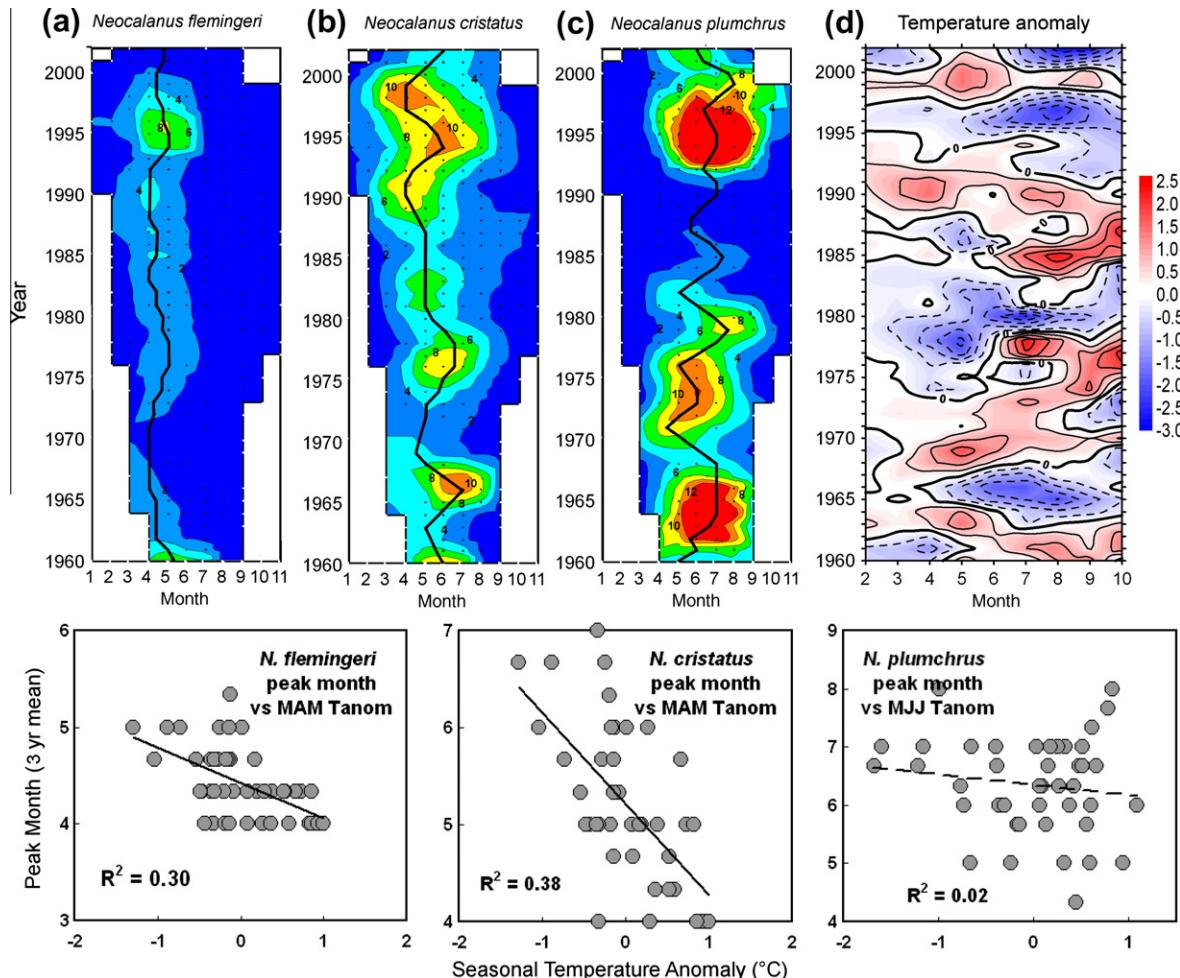
Compared to the strong temperature correlation, none of the NE Pacific regions has much association of *Neocalanus* phenology with

year-to-year differences in seasonality of local phytoplankton concentration (and chl concentration is itself only loosely coupled to seasonal warming of the upper ocean). In the Alaska Gyre, there is no spring chlorophyll peak. Along the Vancouver Island continental margin and in the Strait of Georgia, a sequence of phytoplankton bloom events extends from ~March to September. In these more nearshore regions, bloom timing is controlled mostly by recent wind history, and/or by the tidally-and-seasonally-modulated mixing/entrainment of coastal river discharge with nutrient-rich deep water (see Mackas, 1992; Mackas and Harrison, 1997). However, the intense spring peak of *Neocalanus* in the Strait of Georgia often coincides with a minimum of phytoplankton biomass, presumably due to strong top-down grazing pressure by the copepods (Bornhold, 2000).

### 3.3.2. Northwest Pacific

The analyses of variability of zooplankton phenology in the NW Pacific have been based mostly on the very extensive “ODATE” collections (1960–2002) from Pacific waters off Japan. About 18,000 samples had originally been processed only for wet-weight biomass (Odate, 1994), but had been archived in good condition. A consortium of Japanese scientists recognized the value of the species-level “data in jars”, and in 2003 began taxonomic reprocessing of a subset of the samples (see Chiba et al., 2006, 2009). Interpretation of the zooplankton species data set is still ongoing, but phenology results are becoming available. Initial focus has been on the boreal–subarctic Oyashio Current (OY) region, and on the locally-dominant cool-water copepods (*Neocalanus plumchrus*, *N. cristatus*, *N. flemingeri*, *Eucalanus bungii*, *Metridia pacifica*, and *Pseudocalanus* spp.). The two major boundary current systems off Japan (Kuroshio and Oyashio) are both very strong, but ecologically very different, and also highly variable among years in their latitudinal position off northern Japan. To deal with this variability, ODATE samples have been classified as representative of the OY region by a combination of criteria: location (bounded between 37–43°N and 142–150°E) and water mass (temperature <5 °C at 100 m). The dominant cool-water copepod species are the same as in the NE Pacific, but differ in details of life history strategy and average seasonal timing compared to the same taxa in the NE Pacific. Differences include a biennial life cycle of *N. flemingeri* at some of the coldest NW Pacific locations, later growth/development of *N. plumchrus*, prolonged growing season of *N. cristatus*, and alternating annual–biennial life cycles of *Eucalanus bungii* (Tsuda et al., 1999, 2004). Interpretation of zooplankton phenology in the NW Pacific is complicated by very strong advection (0.5–1+ m s<sup>-1</sup>) and along-flow mixing of multiple source water masses. Both processes are more evident off Japan than in other ocean regions discussed in this paper (although the Newfoundland Shelf, outer English Channel, northern Norway, and NW Mediterranean regions also have time-varying inputs of contrasting source waters). Copepod populations that are sampled off Japan as late juveniles or adults are a mixture of individuals that have developed along multiple drift trajectories. Some of the source regions are >2000 km from the sampling region (Tatebe et al., 2010). Their growth and survival will reflect integration along similarly diverse and large spatial gradients of environmental conditions (see Ji et al., 2010 for additional discussion of Eulerian observations of Lagrangian processes, and how these might be better reconciled using a mix of observations and models).

Phenology analyses of the ODATE data set that have been published/presented to date include Chiba et al. (2006, 2008, 2009, 2012) and Tadokoro et al. (unpublished). The “50% C5” index of *Neocalanus* cohort timing used in the NE Pacific does not work in the OY region because the spread of age-within-cohort is sufficiently broad that the population declines before the 50% threshold is reached. Instead, Japanese scientists have selected as their index



**Fig. 17.** Oyashio region copepod phenology and temperature time series. Top row: Biomass (contour plots, lighter shading indicates higher biomass) and timing of annual abundance peak (heavy black line) for *Neocalanus flemingeri* (a), *N. cristatus* (b), and *N. plumchrus* (c), plus time series of monthly temperature anomalies ((d), darker shades are stronger anomalies, solid contours are warm, dashed are cool) [from Tadokoro, unpublished 2005 and 2007 conference presentations]. Bottom row: Scatterplots of peak month (3 yr running mean) vs. seasonal temperature anomaly for (e) *N. flemingeri*, (f) *N. cristatus* (both dominant members of the spring community, tracking March–May temperature), and (g) *N. plumchrus* (spring–summer community, weakly tracking May–July temperature). The range of timing variability differs among species (~1.5 month for *N. flemingeri*, ~3–4 months for *N. cristatus* and *N. plumchrus*) but all three species have an “earlier when warmer” response to interannual temperature variability.

of annual timing the month in which average abundance of C5 is maximal. This index is the same as was used by Cushing (1984), and in raw form shows similarly large year-to-year quantization noise. However, variability of the OY time series appears to be dominated by time scales of several years-to-decades. Most analyses have smoothed the phenology time series by applying a 3–10 year running mean filter to the annual zooplankton timing estimates. Chiba et al. (2006) used cluster analysis to classify individual copepod species into seasonal communities based on their within-group similarity of timing. Membership in these seasonal groups corresponds closely with an earlier classification (Chihara and Murano, 1997) based on thermal preference. The “spring” community peaks between March and May and is dominated by the cold-water species *Neocalanus flemingeri* and *N. cristatus*. The “spring–summer” community (May–July peak) is dominated by *N. plumchrus*, *Eucalanus bungii*, *Metridia pacifica*, *Pseudocalanus minutus* and *Pseudocalanus newmani*, and *Oithona similis* and *Oithona atlantica*. Fig. 17a–c shows biomass time series for the three *Neocalanus* species overlaid by smoothed (3-year running mean) estimates of their “peak month” timing. Fig. 17d shows the corresponding time series of monthly temperature anomalies, and Fig. 17e–g shows temperature vs. timing scatterplots. For all three *Neocalanus* species (and also for the overall “spring” and “spring–

summer” communities, Chiba et al., 2006), the temperature dependence follows a “warmer = earlier” pattern, but the strength and season of the temperature association differs among taxa. For the spring species, the phenology variations (for both group and individual taxa, as well as annual and smoothed) track local March through May temperature anomalies closely. The time series of the spring–summer community (and of *N. plumchrus* individually) contain more variability among adjoining years, which is poorly explained by temperature anomalies in the same year. The weak negative correlation with summer-season temperature anomalies does strengthen as temporal smoothing gets longer (e.g.  $r \sim -0.46$  for a 5-year running mean of peak timing). However, it is possible that seasonal development of near-surface thermal stratification makes SST a weak proxy for the depth-averaged temperature experienced by the summer copepods or that other (or non-local) environmental variables are contributing more strongly to control of local zooplankton timing. For example, *N. plumchrus* timing in the Oyashio region has a strongly negative covariance with timing of the same species in the eastern Pacific (Section 3.5.3 below). Model analyses by Chiba et al. (2008) suggest that local phytoplankton bloom timing is not an important control. They showed interannual variability of the start-of-bloom phytoplankton bloom

timing (~20 days) and correlations with the zooplankton phenology ( $\pm 0.2$ ) are both small. Tadokoro et al. (2005, 2012) found strong positive associations of timing and abundance of all three *Neocalanus* species vs. spring/summer phosphate concentration (a later zooplankton peak when phosphate higher). They hypothesized that high nutrient supply might increase the magnitude and duration of the spring bloom, with prolonged food availability allowing a broader, later-at-end-date, and larger zooplankton cohort. However, we suggest that interannual change in phosphate concentration might also be in part a proxy for large interannual differences in advective history and/or source population (as described by Tatsumi et al. (2010)) and that later timing might be a consequence of greater contribution from colder upstream source regions such as the Okhotsk Sea.

### 3.4. Mediterranean Sea

Relatively long zooplankton and hydrographic time series have been collected at six coastal stations in the Mediterranean Sea (see Berline et al., 2012). The Mediterranean Sea is warmer and more oligotrophic than the Atlantic and Pacific regions discussed in previous subsections, and seasonalities of water properties are strongly influenced by surrounding land masses. In addition, annual chlorophyll maxima are usually earlier (February or March, Berline et al., 2012). However, the Mediterranean Sea has many zooplankton taxa in common with the NE Atlantic, and therefore offers a range of useful comparisons. To date, zooplankton phenology has been investigated at three sites (Ville-Franche and Trieste in earlier publications, the Gulf of Naples in this paper. See Fig. 3 for locations, and Table 2c for meta-data summary). These sites have strong covariance of winter and annual temperature anomalies, and strong response to the North Atlantic Oscillation climate mode (NAO hereafter). One of the most striking results from the Mediterranean zooplankton data, shared to some degree by all three sites, is that the “earlier when warmer” response in phenology seen in most of the Atlantic and Pacific time series is less frequent in the Mediterranean, and is replaced in many species by a strong “later when warmer” pattern.

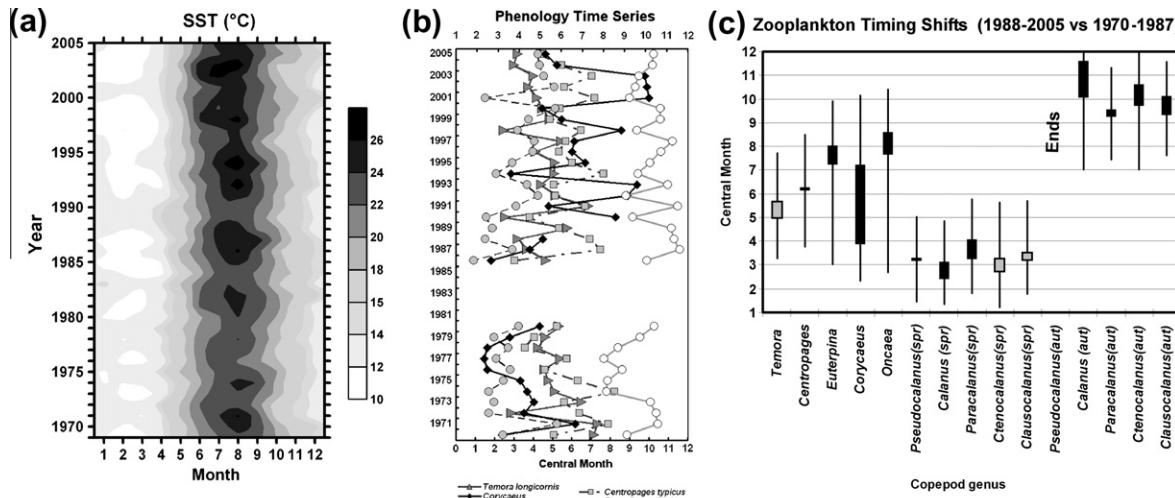
#### 3.4.1. Ville-Franche – Northwestern Mediterranean

The Ville Franche sampling site is the westernmost, deepest, and most oligotrophic and “oceanic” of the three Mediterranean sites. Species-level zooplankton time series from this site extend from 1966 to 1993 at weekly intervals. Molinero et al. (2005) used these data to examine variability in abundance and seasonal timing of *C. typicus* and *Temora stylifera* and their association with the winter NAO. Although there are several ways to index and classify the NAO (see Hurrell and Deser, 2009), all are based on the atmospheric pressure difference between the subarctic and temperate/subtropical NE Atlantic (often but not always Iceland and the Azores respectively). At the basin scale, a larger-than-average pressure difference (positive phase of the NAO) is associated with stronger-than-average surface westerly winds across the middle latitudes of the Atlantic, and intensified winter storms that follow a more northerly track into Europe. Conversely, negative NAO is associated with weaker zonal winds but more southerly storm tracks. For the Mediterranean region, Molinero et al. (2005) reported that positive winter NAO is associated with higher local atmospheric pressure, warmer ocean surface temperature, and reduced precipitation. They also found that positive NAO was associated with earlier and higher peak abundance of the dominant spring copepod *C. typicus* but later and lower peak abundance of the dominant fall copepod *T. stylifera*. Observed timing changes were substantial for both species: ~2 month differences between means of “high NAO” vs. “low NAO” years. The mechanism(s) responsible for the phenology changes are less certain. Molinero

et al. (2005) concluded that warmer ocean temperature during positive NAO had contributed to earlier reproduction (probably by both species) and better recruitment/trophic match for *C. typicus*, but that additional ecological interactions affecting the seasonal distribution of mortality rates were probably responsible for both the decrease and delay of *T. stylifera*. They note that both salps and medusae were very abundant during summers of the 1980s (coincident with a period of high NAO). They suggest that gelatinous zooplankton may have strongly depressed the seasonally-overlapping summer population of *T. stylifera* through increased competition and predation (see also Halsband-Lenk et al., 2004), but had relatively little effect on the (seasonally-earlier) *C. typicus*. However, a recent update/review of Mediterranean time series (Berline et al., 2012) examines abundance summed within composite taxonomic groups (copepods, cladocerans, medusae, salps) and finds little evidence of top down control of total copepod abundances by gelatinous zooplankton.

#### 3.4.2. Trieste – Northern Adriatic

The Trieste site is at the northernmost tip of the Adriatic Sea. The region is both shallow and strongly influenced by the surrounding land and rivers. The annual temperature range is large (Fig. 18a), and nutrient supply and annual phytoplankton productivity and biomass are all among the highest in the Mediterranean. The Trieste zooplankton time series consists of two segments (1970–1980 and 1986–2005) interrupted by a gap of five unsampled years. Conversi et al. (2009) examined decadal variability of the zooplankton and hydrographic time series. Both types of data show differences centered near the 1987 NAO shift described by Molinero et al. (2005). Contour plots of ERSST temperature data (Fig. 18a) show 30-year trends of strong summer warming, and a slight winter cooling. Zooplankton data show major differences in abundance, composition, and phenology between the early and recent segments of the Trieste time series. Although total copepod abundance approximately doubled after 1987, three cool-water copepods (*Pseudocalanus elongatus*, *Clausocalanus* spp., *Ctenocalanus vanus*) declined sharply in absolute abundance between the late 1980s and early 1990s, and a fourth (*Acartia clausi*) showed a large decline in relative abundance. Conversely, four taxa (*Paracalanus parvus*, *Oncaea* spp., *Oithona* spp., *Euterpinina acutifrons*) increased 4–7-fold. The southern Adriatic species *Diaixis pygmoea* appeared for the first time in 1990 and has subsequently remained moderately abundant. Conversi et al. (2009) then tested for temporal trends in phenology of the different taxa. They used the Edwards and Richardson (2004) center-of-gravity indexing method, with annual summation for seven unimodal taxa, and January–June plus July–December summations for the six taxa with bimodal cycles. Detailed time series (examples in Fig. 18b) show very large year-to-year variability superimposed on longer-term trends and fluctuations. Short-term fluctuations in the Trieste time series have little correlation with temperature or among taxa. It is unclear to what extent the short term variability reflects real temporal changes of the sampled populations, vs. noise resulting from patchiness and absence of within-month spatial/temporal averaging. The longer-term signal is much clearer, and was the focus of the analysis in Conversi et al. (2009). They quantified changes in phenology by the difference in months between the start (1970) and end (2005) of the fitted trendlines. Eight of the taxa showed significant ( $p < 0.10$ ) trends in timing, of which six were to later timing. Of the nine remaining taxa ( $p > 0.10$ ), eight also had best fit trends to later timing. Similar to the Ville-Franche contrast between spring (*C. typicus*) and autumn (*T. stylifera*) species, all Trieste trends to earlier timing were by taxa that peak early in the year. All fall or winter taxa and seasonal modes shifted later. However, as noted by Conversi et al. (2009) and in Section 2.2 (above), leakage between population modes can produce artifacts in the timing



**Fig. 18.** Trends in surface temperature and copepod phenology in the northern Adriatic (plotted from background data for Conversi et al. (2009)). (a) Year vs. month sea surface temperature contour plot. Post 1987 years showed a large (3–4 °C) increase in summer temperature accompanied by a small winter temperature decrease. Note also the large (>15 °C) annual range. (b) Examples of detailed phenology time series. Most show large year-to-year noise (see text) superimposed on longer-term trends. (c) Box and whisker plots comparing average zooplankton phenology, 1970–1987 vs. 1988–2005. Box shading indicates the direction of the timing change for each taxon (black = later, gray = earlier) and box height shows the magnitude of the mean timing difference. Whiskers show the overall range of timing. The majority of taxa, and all of the taxa that peak in fall, have shifted to later timing as the Adriatic has warmed. For the *Pseudocalanus* fall mode, the dominant signal is a disappearance of this mode when July–September became very warm.

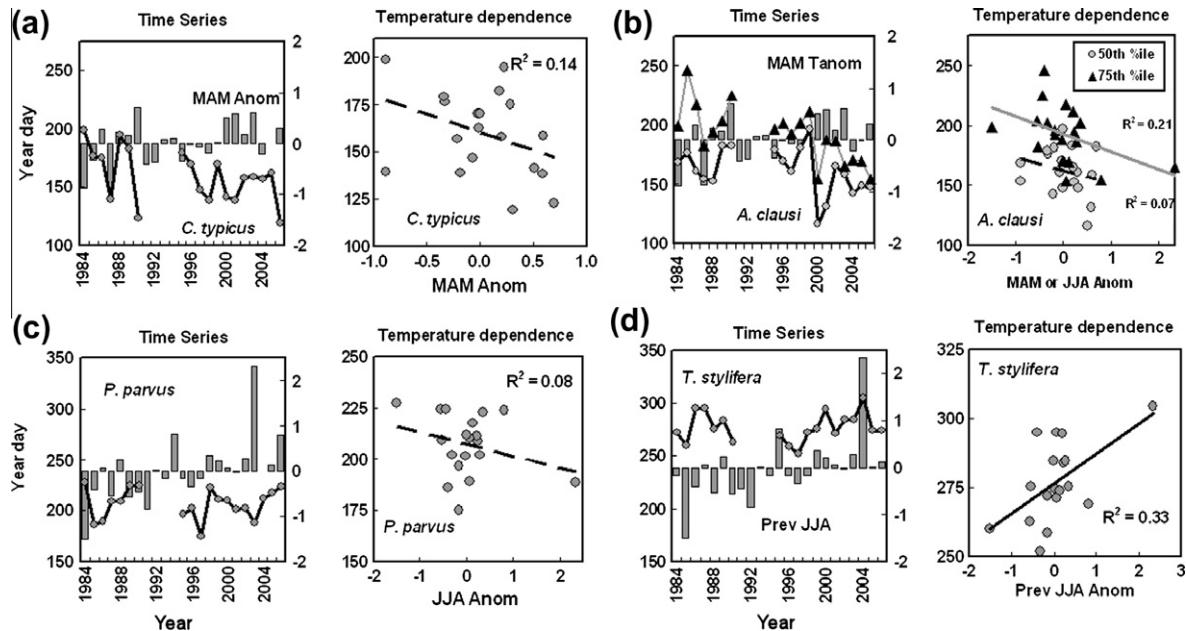
index for the weaker mode. In this data set, the species most likely to have been affected is *P. elongatus*. The COG index indicates an apparent shift to late (December) timing by the autumn mode of *Pseudocalanus*. But the main underlying change is a large post-1987 decline of abundance in the months from August to October (see Fig. 7 in Conversi et al. (2009)). The low numbers present in November and December could perhaps be the result of a delay of the fall mode (this cause is assumed by the summation boundaries for the COG index), but are more likely to be early members of the spring mode for the following year.

An additional view of the Trieste zooplankton timing data is provided here as Fig. 18c, which shows the overall range of timing, and differences in mean timing between the 1970–1987 and 1988–2005 time blocks. Boxes shaded in black indicate taxa that have shifted to later mean date (box height indicates the magnitude of the difference in mean dates), gray boxes indicate shifts to earlier timing.

#### 3.4.3. Gulf of Naples – Western Mediterranean

The third Mediterranean zooplankton phenology time series is from the Gulf of Naples. This site is intermediate between Ville Franche and Trieste in water depth, chlorophyll concentration, and annual temperature range (see Berline et al., 2012), but is located further south (Fig. 3a) and has a warmer annual mean temperature. As at Trieste, the time series at Naples consists of two segments separated by a gap of several unsampled years (1984–1990 and 1995–2006 at Naples). Compared to most of the zooplankton time series in Tables 2a–c, the Naples time series is young, and analyses are recent and ongoing. Mazzocchi et al. (2007) compared seasonal and interannual variability of *Centropages typicus* among several Mediterranean sites including Naples. Mazzocchi et al. (2012) discuss many additional aspects of interannual species-level zooplankton variability at the Naples site, while Berline et al. (2012) make a broad comparison with other Mediterranean zooplankton time series but with less taxonomic detail. Variability in phenology of several Naples zooplankton species are examined for the first time in this paper; a more complete comparative analysis is planned by Mazzocchi and Eloire.

Although it contains fewer years, the Gulf of Naples time series is similar in temporal and taxonomic resolution to Helgoland Roads and Plymouth L4. We therefore chose to index seasonal timing using the same (cumulative percentile) method, with a modified (trapezoidal) time-integration scheme to deal with occasional within-year data gaps. The analysis was carried out for the four seasonally-dominant copepods in this system: *A. clausi*, *C. typicus* (both usually peaking April–June), *P. parvus* (July–August), and *T. stylifera* (September–October). Results for each species are shown as paired time series and timing–temperature scatterplots in Fig. 19. Spring (March–May) and summer (June–August) seasonal temperature anomalies show warming trends (0.5–1 °C) overlaid by larger (1–2 °C) shorter-term variability. Temperature trends and year-to-year variations are both larger for the summer season. Phenology responses differed between spring and summer species. Both of the spring–early summer species (*Centropages* and *Acartia*, Fig. 19a and b) show significant temporal trends to earlier middle-of-season (50th percentile) timing, associated with negative correlation (stronger for *C. typicus*) between mid-season timing and spring temperature anomalies. For *A. clausi* the correlation between timing and temperature was stronger for the end-of-season date (75th percentile) and summer temperature anomalies, suggesting (as at L4) that one important effect of warming has been to truncate the duration of the annual population peak. The late summer–autumn species (*P. parvus* and *T. stylifera*) had no temporal trend of seasonal timing, despite overall upward trends of summer temperatures. But *T. stylifera* did have a significant positive correlation between timing and the year-to-year variation of summer temperature (later when warmer). Interestingly, the *T. stylifera* timing correlation was stronger with temperature anomalies in the preceding summer (Fig. 19d), suggesting some connection of outcome to the previous year's cohort. One possibility is a fixed-duration internal clock for a prolonged over-wintering dormant stage. We know of no alternative mechanism that could account for a stronger association to temperature at a 1-year time lag. However, nearby (Ville-Franche) populations of *T. stylifera* spawn year round (Halsband-Lenk et al., 2004) and are not known to produce diapause eggs. In other respects, the phenology responses of *C. typicus* and *T. stylifera* in the Gulf of Naples between



**Fig. 19.** Zooplankton phenology and seasonal temperature anomalies in the Gulf of Naples (paired time series and timing–temperature scatterplots). Species in top row are spring dominants, bottom row are autumn dominants. (a) *Centropages typicus* middle-of-season and March–May temperature anomalies (b) *Acartia clausi* middle-of-season (circles, black line) and March–May temperature; end-of-season (triangles, gray line) and June–August temperature (c) *Paracalanus parvus* and June–August temperature, (d) *Temora stylifera* and temperature in June–August of previous year.

1984 and 2006 are very similar in sign and magnitude to those reported by Molinero et al. (2005) for Ville-Franche between 1966 and 1993. In particular, the timing separation between the spring and fall dominants has increased in both locations.

### 3.5. Between-region comparisons

There are several ways that zooplankton phenology could be considered “similar” across sampling locations. The most basic is similarity of aggregate univariate statistics of phenology such as mean date of annual maximum, and total or root-mean-square (RMS) range of timing variation across years. A second is the extent to which signs and magnitudes of correlation with environmental drivers (such as temperature, photoperiod, or food supply) are similar across locations. A third form of similarity (for which the second is a necessary but not sufficient prerequisite) is between-region synchrony of the trends and fluctuations in the phenology time series. The following subsections will examine these in sequence.

#### 3.5.1. Comparison of mean and variance of species timing

With few exceptions, within-species means and variances of seasonal timing are similar across regions. Species that have strong trends or multiyear fluctuations at one site have strong timing variability (often up to 1–2 months) at most or all other sites where they occur (examples: *C. finmarchicus*, *Neocalanus* spp., *Pseudocalanus* spp., *Centropages* spp.). Taxa that peak in the first (vs. second) half of the year usually peak in spring-to-early-summer (vs. late-summer-to-winter) throughout their zoogeographic range. However, one well-documented exception is *C. typicus*, which has spring maxima in the warm oligotrophic Mediterranean, but late summer–autumn maxima in the cooler, more mesotrophic NE and NW Atlantic (Mazzocchi et al., 2007). Some taxa usually or occasionally have bimodal seasonal cycles (examples: *C. finmarchicus* and *C. helgolandicus* in the North Sea; *Oithona* and *Evdad* at L4; *Calanus*, *Clausocalanus*, *Ctenocalanus*, *Paracalanus* and *Pseudocalanus* in the Adriatic). For most zooplankton taxa with bimodal sea-

sonality, one of the peaks is much larger and its time series tends to be relatively smoothly varying in both amplitude and timing. The smaller peaks tend to be more erratic in both amplitude (see Conversi et al., 2009 and Fig. 23 below) and timing (although the latter may be in part an artifact of indexing method, see Sections 3.2.3, 3.2.5 and 3.4.2).

#### 3.5.2. Comparison of environmental correlates and controls

Upper-ocean temperature has been our most commonly-observed correlate of zooplankton timing variability. Is this because temperature is the dominant proximate control or because tests-of-association with alternative environmental controls lack statistical power as a result of insufficient data? Or is this simply because (owing to great interest in consequences of global warming) temperature association has been the most likely to be examined? For the longer time series, the range of available environmental correlates (other than SST and atmospheric pressure) is severely limited by the diversity, duration, and/or frequency of *in situ* oceanographic observations. In circumstances when and where multiple environmental time series are available for sufficient duration at sufficient seasonal resolution, we have often found correlation of zooplankton timing with two or more environmental signals. Of these, temperature remains not only the most often observed correlate, but also (usually) the correlate with the largest  $R^2$ .

Other plausible environmental controls on zooplankton timing (both statistically and mechanistically) include dominant wind patterns (e.g. the AO in the NE Atlantic and Mediterranean), water column stratification, prior food availability (chlorophyll or phytoplankton abundance), and the intensity and timing of predation mortality (to be discussed in Section 3.7). Unfortunately, these environmental signals are often themselves inter-correlated at about the same level as they are associated with zooplankton timing, making difficult the identification of ultimate and proximate causes. For average seasonal cycles, and sometimes also for inter-annual deviations from climatology, observed correlates of zooplankton seasonal timing make sense when interpreted in terms

of food supply and growth/survival opportunities (although as noted repeatedly above, the statistical association is usually stronger for temperature-based indices than for food-availability indices). In many regions (but clearest at high latitudes), “spring” and “early summer” species have an “earlier where and when warmer” association that tracks (usually with a 1–2 month lag) the spring onset of warming, thermal stratification, and primary production. Conversely, “fall” species (especially in oligotrophic and sub-tropical environments such as the Mediterranean) often have an “earlier where and when cooler” that coincides with (or tracks after a short lag) autumn cooling, breakdown of thermal stratification, and temporary fall increase of phytoplankton productivity and biomass.

### 3.5.3. ‘Synchrony’ and spatial autocorrelation of phenology time series

The number of available zooplankton phenology time series is relatively small at present. Nevertheless, we think an initial quantification of their between-site similarity, and of how far observed timing changes at one location can be extrapolated to surrounding regions, is useful. There are two possible approaches. The first is to combine pair-wise comparisons of separation vs. temporal correlation from the present suite of phenology time series, and fit these observations with one or more spatial correlograms. The advantage of this approach is that it is direct. The disadvantage is that large numbers of time series are needed to give a reliable description of the correlogram shape because of the noise in individual estimates of local timing, and the short duration of overlap (10–30 years) between most of the time series (see Batchelder et al. (2012) for examples of correlograms estimated from the much more numerous time series of zooplankton biomass and abundance).

A second approach is to make use of strong temporal covariance between zooplankton phenology and environmental drivers that are more completely sampled. If one or a few environmental variables (e.g. temperature, and/or horizontal currents) have a large influence on zooplankton seasonal timing, we can reasonably expect spatial maps of zooplankton phenology and maps of environmental anomalies to be similar. Fortunately, the spatial structure of sea-surface temperature covariance is well described. A common and useful approach by climatologists and physical oceanographers has been to partition SST variability into multiple and asynchronous “modes” operating at different time and space scales. The modes can be separated and quantified using principal components analysis or empirical orthogonal functions (EOFs, Figs. 20b and 21). A given pair of locations will have similar annual anomalies if they share the same sign and similar amplitudes for dominant (i.e. large eigenvalue) EOF loadings, and these EOFs also have large amplitudes during the period of interest.

On average, we expect eigenvectors (and time series) at nearby locations to covary positively, and distant locations to vary independently or inversely. However, nearby locations can sometimes have negative (or weak) correlation if the locations are on opposite sides of a sign change of eigenvector loadings, or if local responses are dominated by different components, or if amplitudes of the dominant EOFs are weak during the observation period. We will show below that Atlantic vs. Pacific differences in the spatial scale of EOF patterns for SST (and in locations of our zooplankton time series relative to these patterns) are consistent with between-ocean differences in the zooplankton phenology correlograms.

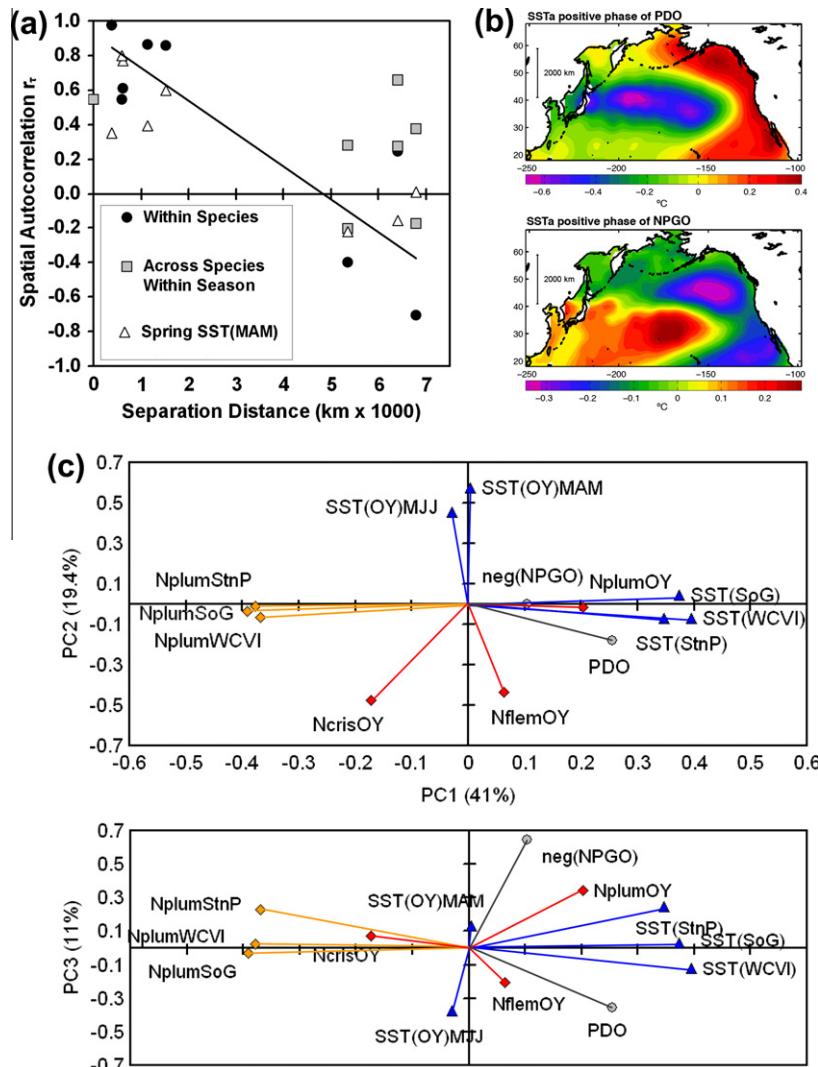
In the North Pacific, about half of the interannual variability of SST is accounted for by three spatial/temporal climate modes, all of which have very large scale spatial covariance, and all of which are routinely indexed by climatologists:

- The Pacific Decadal Oscillation (PDO; Mantua et al., 1997; Hare and Mantua, 2000). This is the leading EOF of detrended SST anomalies. East-to-west gradients of PDO spatial loadings (shown in the upper panel of Fig. 20b) are very similar to those for ENSO (not shown) but operate at longer time scales.
- The “Victoria Pattern” (2nd EOF of SST variability, Bond et al., 2003). This has the same spatial and temporal signatures as the North Pacific Gyre Oscillation (NPGO; DiLorenzo et al., 2008, defined as the 2nd EOF of sea surface elevation anomalies, and shown in the lower panel of Fig. 20b).

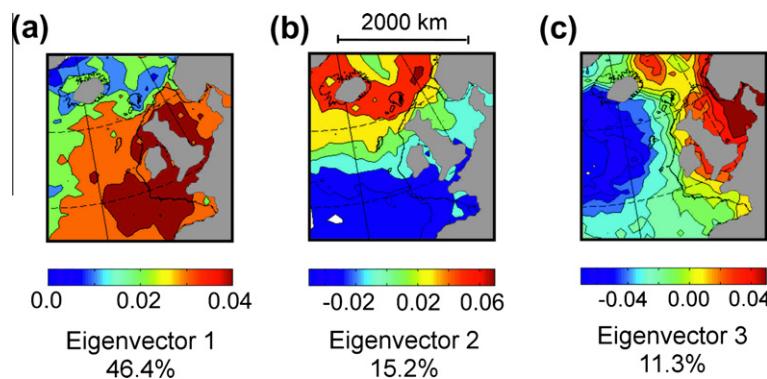
An important feature for our comparison of zooplankton phenology is the east vs. west sign reversal of PDO spatial loadings. The NE Pacific and Oyashio regions also differ considerably in loadings for the NPGO/Victoria mode. Although separated by up to 1500 km, the four time series located within the NE Pacific all share similar eigenvector coefficients for both PDO and Victoria/NPGO modes of SST variability (Fig. 20b). In contrast, the Oyashio region in the NW Pacific is located in/near stronger eigenvector gradients, and has opposite PDO sign from all of the NE Pacific sites. PDO and NPGO loadings also change considerably along the ~1000–2000 km NE-to-SW advective trajectories traced by the subarctic copepods in the course of their 2–3 month development to C5.

Fig. 20a shows North Pacific spatial correlograms for *Neocalanus* seasonal timing and locally-observed SST anomalies. Throughout the eastern subarctic Pacific, between-site correlations are strongly positive ( $r_\tau = +0.8 \pm 0.2$  for zooplankton timing,  $+0.7 \pm 0.2$  for SST). Within the western subarctic Pacific (a single sampling region, the Oyashio), cross-species timing similarity is moderately strong ( $r_\tau = +0.5$ ) between the two spring-dominant taxa (*N. flemingeri* and *N. cristatus*) but weak ( $r_\tau \sim 0 \pm 0.02$ ) between the spring species and the spring–summer dominant (*N. plumchrus*). Between eastern and western Pacific, between-site correlations are weakly negative for temperature and weakly positive to strongly negative for *N. plumchrus* timing. When we combine temperature and phenology time series from the eastern and western subarctic Pacific into a single PCA (Fig. 20c), we find that the dominant axis is aligned with spring temperatures in the eastern subarctic Pacific and *Neocalanus* timing throughout the subarctic Pacific. Timing of *N. plumchrus* (early in the east and late in the west) is very strongly associated with warm spring temperatures in all three NE Pacific subregions. Somewhat surprisingly, the timing variability of *N. plumchrus* in the Oyashio region is more strongly correlated with spring SST anomalies in the eastern subarctic Pacific ( $r_\tau = +0.25$  to  $+0.45$ ) than with more local spring or early summer SST anomalies within the Oyashio region ( $r_\tau = -0.14$  to  $-0.15$ ). Oyashio-region temperature anomalies, and the phenology of the spring species *N. flemingeri* and *N. cristatus*, all project more strongly on the 2nd component axis. The third component captures most of the NPGO variability, and an additional relatively large fraction of the May–July SST anomalies. Because east and west project onto different component axes, the cross-Pacific correlation of local SST variability is also relatively weak ( $r_\tau \sim -0.1$ ). Local temperature anomalies in the Oyashio are only weakly synchronized with the PDO. Both temperature and phenology may instead be influenced more by variability of advection and mixing in this region of strong horizontal gradients, than by local air-sea exchange. However, the strong association of OY region *N. plumchrus* phenology with NE Pacific phenology, temperature, and PDO suggests that there must be an important and rather strong and rapid mechanism providing trans-Pacific connection. Although details of the correlogram fits are uncertain, we are confident that the North Pacific basin scale decorrelation lengths exceed 2000 km for both phenology and temperature, and probably lie somewhere between 3000–5000 km.

- The El Niño Southern Oscillation (ENSO).



**Fig. 20.** Spatial autocorrelation/synchrony of zooplankton phenology and temperature in the subarctic North Pacific. (a) Between-region correlation vs. spatial separation. All variables show strong within-gyre correlation (separations <1000 km); many show negative correlation east vs. west. Black circles compare *N. plumchrus* timing throughout the N. Pacific, and blackline shows the trend of similarity in *N. plumchrus* phenology vs spatial separation. Gray squares compare cross-Pacific timing of spring dominants (*N. plumchrus* in east vs. *N. flemingeri* and *N. cristatus* in west). Triangles compare spring sea surface temperature at all sites. (b) Maps of spatial correlations ( $^{\circ}\text{C}$  per unit EOF anomaly) for the Pacific Decadal Oscillation (top) and the North Pacific Gyre Oscillation (bottom). Both patterns are dominated by very large spatial scales (>2000 km). The PDO pattern has an east vs west sign reversal (negative correlation between Alaska Gyre and Oyashio region). The NPGO has a north-south reversal; eastern and western subarctic Pacific share the same sign, but NPGO response is stronger in the east. Maps courtesy E. Di Lorenzo (website <http://www.o3d.org/nngo/>). (c) Principal component projections of normalized time series of: *Neocalanus* phenology (orange = eastern N. Pacific, red = western N. Pacific), season-averaged sea-surface temperatures (blue), and PDO and NPGO climate indices (gray). Top graph is PCs 1&2, bottom graph is PCs 1&3. Arrow labels identify variable, followed by location. Axis scaling is proportional to % of normalized variance accounted for. The strongly dominant first component (40%) is associated with a “warm in east, *plumchrus* timing early in east, late in west” pattern. As expected from (b), “warm in east” is also associated with +PDO and -NPGO.



**Fig. 21.** NE Atlantic spatial loading patterns (eigenvalues) for EOFs of sea-surface temperature variability 1960–2005 (adapted with permission from Beaugrand et al., 2009). The NE Atlantic patterns have considerable variation at scales smaller than 1000 km, in contrast to the N. Pacific EOFs shown in Fig. 20. (a) EOF 1 is correlated with the Northern Hemisphere warming trend. Loadings vary in intensity but have the same sign throughout the region. (b) EOF 2 is correlated with the Subarctic Gyre Index, and has a north-to-south sign reversal. © EOF 3 is correlated with the NAO, and has a west-to-east sign reversal.

The correlation structure of the dominant climate modes in the NE Atlantic and Mediterranean have a smaller scale, at least for the portion of these oceans surrounding our time series sites. Beaugrand et al. (2009) showed that nearly 75% of the post-1960 temperature variability in the NE Atlantic and North Sea projects onto three components. As expected for an orthogonal partitioning of variance, each component's eigenvector has a distinctive pattern of spatial expression (Fig. 21a–c). Their component time series are correlated respectively with:

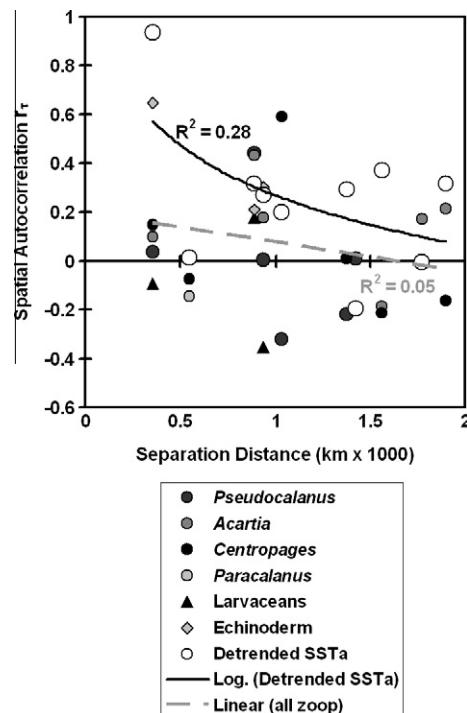
- (1) The overall Northern Hemisphere warming trend (~46%; this trend has the same sign at nearly all locations, but magnitude within the NE Atlantic increases toward the SE).
- (2) The strength of the oceanic circulation in the N. Atlantic subpolar gyre (~15%, NS gradient of spatial eigenvector, sign reversal at ~52°N, largest amplitudes 60–70°N).
- (3) The North Atlantic Oscillation of atmospheric pressure and wind patterns (~11%, NW–SE gradient of spatial eigenvector, strongest regional expression of the NAO is in the Mediterranean and Baltic. Oceanic waters SW of Iceland have the opposite sign of temperature response).

Compared to the NE Pacific, the dominant NE Atlantic and Mediterranean ocean climate signals are more localized and have steeper spatial gradients. They also often include between-site sign reversals for two of the three leading EOFs. The expected (and observed) consequence is that spatial autocorrelations of zooplankton phenology and SST time series are weaker at all separation distances, and the autocorrelations decay more rapidly (Fig. 22) with increasing spatial separation. For SST, the spatial autocorrelation in both the NE Atlantic (three sites) and Mediterranean (two sites) drops below 0.5 at separations between 500 and 1000 km, and is near zero at 2000 km. For zooplankton phenology, the decorrelation length is even shorter. Many species had no correlation of their time series between the closest-spaced NE Atlantic [central North Sea vs. Helgoland,  $\tau \sim 350$  km] or Mediterranean [Naples vs. Trieste,  $\tau \sim 550$  km] site pairs. The only pair of sites for which phenology correlations were consistently positive was central North Sea vs. Plymouth L4 ( $\tau \sim 900$  km), but even for this pair the similarity was not strong ( $r_\tau = 0.18$ –0.44 for phenology, 0.3 for SST).

Because of the small number of phenology time series, and the resulting uncertainty of the underlying phenology autocorrelation function, we can make only a preliminary and rough comparison between the zooplankton phenology correlograms (Figs. 20 and 22) and the better-resolved correlograms for zooplankton biomass/abundance anomalies (Batchelder et al., 2012). However, our results suggest that the two modes of zooplankton response, although very different, nevertheless have autocorrelation functions that are similar in shape and scale (linear to negative exponential decay, and differing by no more than a factor of two in decorrelation length). Similarity at short-to-medium separations (0–1000 km) does appear to be considerably stronger for phenology than for than biomass time series in the Pacific, but this may be due to the positions of the phenology sampling sites relative to the overall PDO footprint.

### 3.6. The role of temperature in zooplankton phenology

Our combined observations suggest that upper-ocean temperature anomalies are frequently very good (and in many locations the best) environmental predictors of variations in zooplankton phenology. But why this is so, and how temperature affects zooplankton seasonal timing, is less obvious. Is temperature a direct physiological control; an easily- and frequently-measured proxy



**Fig. 22.** Spatial autocorrelation/synchrony of zooplankton phenology and temperature in the NE Atlantic and Mediterranean. Both the maximum correlation, and the distance to zero crossing are smaller than in the North Pacific (compare Fig. 20a). Shaded symbols compare zooplankton taxa. Dashed trendline is fit to within-taxon comparisons. White symbols and solid regression line are detrended sea-surface temperature anomalies (correlations are slightly weaker if regional trends in SST are retained).

for the real control (perhaps food supply or predator abundance); a sensory cue that the zooplankton use to trigger various developmental and behavioral activities; or some mix of all of the above? We have partially addressed these questions in our discussion of individual regions (Sections 3.2–3.4). Here, we develop an overall synthesis based on the full range of observations.

We start by noting that “temperature as direct physiological control” (operating through thermodynamic acceleration of vital rates) cannot be a complete explanation. This is so for at least two reasons. First, although warmer temperature does indeed shorten development time (McLaren, 1978) and thereby contributes to the “earlier when warmer” response by taxa that peak in spring and/or early summer, our observed changes in timing of these taxa are often much larger than predicted from  $Q_{10}$  or Belehradek temperature functions applied to post-spawning development rates and corresponding temperature anomalies (Ellertsen et al., 1987; Mackas et al., 1998). Second, in some places and seasons (and especially among taxa that peak after the annual temperature maximum) warmer water temperatures are associated with delayed, not advanced, seasonal timing (Molinero et al., 2005; Conversi et al., 2009, and the Naples time series shown in this paper).

A second possibility is that temperature provides both a proximate and an ultimate (adaptive fitness) control on zooplankton distribution and seasonal timing. This is a relatively new hypothesis but is gaining support. López-Urrutia et al. (2006) showed that water temperature strongly affects the allometric balance between growth and respiration in plankton. This selects for an optimal body size spectrum at any given temperature and trophic level, and also affects the local ability to support export production. Helaouët and Beaugrand (2007) have proposed that many zooplankton species have well-defined (although seasonally-varying) “thermal niches”, and that they are more likely to change their

zoogeographic distribution than to occupy a different temperature range. Changes in life history timing may allow a species to track interannual variability of the seasonal timing of its optimal thermal band. This is especially important to adaptive fitness if the annual duration of that temperature band is brief.

A third possibility is that temperature correlation is a statistical proxy for one or more underlying proximate environmental or internal controls of zooplankton phenology (ref Table 1 for the full list of candidate controls). This could happen if the direct proximate control (e.g. food availability, predation mortality, or accumulated internal energy reserves) has a strong seasonal *and* interannual covariance with SST, but the direct control has been either unmeasured or noisily quantified in the available supporting data sets. The main argument in support of this explanation is that we do lack important information – there is a shortage of long-term and seasonally-resolved time series for several of the plausible direct controls. Controls other than temperature may indeed be important, but remain undetected because any comparisons we make with observed phenology lack statistical power. Another argument is that the temperature correlations alone rarely account for >25% of the interannual variability of phenology. Is the remaining 75% of the zooplankton timing variance simply random noise, or is it associated with additional and different controls (as suggested by Johnson et al. (2008))? We also have examples of species with strongly-variable phenology that are correlated with temperature anomalies in some places, but are either uncorrelated or have different temperature-timing dependence at other locations (e.g. *N. plumchrus* in the Oyashio region, *Centropages* and *Temora* in the NE Atlantic and Mediterranean; many of the Adriatic taxa). Conversely, there are two strong arguments against “temperature as statistical proxy”. First, even in places such as the central North Sea where we do have reasonably complete time series of “food availability” (phytoplankton concentration and phenology), we still find that association between zooplankton timing and temperature is stronger than the associations of zooplankton timing with phytoplankton amount or phytoplankton phenology (Fig. 10). Second, we have many additional examples of taxa and locations for which the between-site consistency of the temperature-zooplankton timing relationship is greater the corresponding strength or between-site consistency of the temperature-proxy relationship. Temperature-timing scatterplots have similar signs and slopes in all four NE Atlantic time series (Figs. 5, 8, 12, and 14) but the seasonality and mean level of phytoplankton concentration have large between-site differences (Edwards et al., 2001; McQuatters-Gollop et al., 2007). In particular, strong tidal mixing leads to prolonged spring-autumn phytoplankton productivity in shallow parts of the North Sea where the window of “high food availability” is controlled by the seasonal cycle of irradiance, not temperature and thermal stratification. Within the NE Pacific, the overall temperature-timing relationship for *Neocalanus plumchrus* is very similar for all four time series (Fig. 16), despite very strong between-site differences in phytoplankton bloom phenology (Continental Margin and Strait of Georgia have strong spring blooms and relatively large summer productivity; while the Alaska Gyre (Stn P and CPR) is a bloom-free “High Nutrient Low Chlorophyll” environment) and in *Neocalanus* diet (dominated by microzooplankton at the oceanic sites, and by phytoplankton closer to the coast).

A final possibility is that water temperature correlates with zooplankton timing because SST provides a cue/“leading indicator” that describes/predicts seasonal environmental suitability. Under this explanation, zooplankton tune their seasonal timing using information provided by SST, rather than because direct physiological/demographic advantages are associated with a particular temperature range. We discussed previously (Section 1.3) reasons why year-by-year and leading-indicator prediction of optimal timing is

especially important for organisms with an annual life cycle. For many ocean locations, environmental temperature provides a more reliable leading indicator than on land because water temperatures vary more gradually and within a narrower range than air temperatures. In the language of Section 1.3 and Levins (1968), temperature is a “coarse-grained” signal in many marine environments, despite being a noisy and “fine-grained” signal in many terrestrial environments. Terrestrial organisms that rely on increasing (decreasing) temperature to identify the onset of spring (autumn) run a major risk of being misled by an intense but transient thaw or frost. More conservative additional or alternative cues relied on by terrestrial species include photoperiod, fixed-calendar internal clocks, and time-integrated temperature anomalies (often expressed in degree-days). For example Valtonen et al. (2010) recently examined controls on moth phenology in Finland. They found that only 33% of species were controlled primarily by environmental temperature, vs. 24% primarily by photoperiod, and 18% by a combination of temperature and photoperiod. In contrast, we find that for zooplankton across the Northern Hemisphere, interannual variability of timing is significantly associated with seasonal temperature anomalies in half of our time series, and consistent with between-site differences in average zooplankton timing for most. We have even detected strong temperature dependence in several environments where upper ocean temperature might be expected *a priori* to provide a rather poor leading indicator for seasonality of stratification and primary productivity. Examples include:

- Deep estuaries such as the Strait of Georgia and Norwegian coastal fjords (where much of the spring stratification is due to salinity).
- Strongly mixed coastal environments such as Helgoland Roads and Narragansett Bay (where a shallow water column and strong tidal currents prevent vertical stratification throughout the year).
- Regions with seasonal ice cover such as the Labrador Sea and the St Lawrence estuary (where water temperature increase lags behind ice melt and associated salinity stratification). Note however that temperature may not be the only or primary control in these environments; ice melt timing can also exert an additional and direct influence on seasonality of zooplankton reproduction and growth (e.g. Hirche and Kosobokova, 2007; Hunt et al., 2008).

Photoperiod and phytoplankton bloom phenology do offer useful prediction and explanation of many (but not all) between-site spatial differences in average timing (Johnson et al., 2008). However, neither phytoplankton nor photoperiod explains much of the within-site interannual variation (although for different reasons). Photoperiod at a given site is almost entirely a fixed function of local latitude, orbital phase, and the tilt of the earth's axis. Interannual variability of daylength-at-date is therefore necessarily very small (mostly caused by between-year differences in dawn and dusk cloud cover). In contrast, local phytoplankton concentration-at-date is a rapidly varying “fine grained” variable. We know from historical observations and theory that, for many ocean regions, each year will include one or more seasonal blooms that develop and decay within the boundaries of a reasonably well-defined growing season window. But until the satellite era, we had little ability to measure details of year-to-year differences. Even with the dense spatial and temporal resolution now provided by satellite data, advance prediction of bloom events remains difficult in coastal regions (Ji et al., 2010). Although zooplankton experience their local details of phytoplankton phenology directly, they typically get the information too late to prepare an adaptive response: differing demographic time scales (both slope and lag)

make within-year phase-matching of phytoplankton supply and zooplankton response unlikely.

### 3.7. Timing match–mismatch between zooplankton and their predators

Estimation of the consequences of interannual variability of zooplankton seasonal timing for fish feeding success, survival, and recruitment was a strong and early motive for study of phenology of marine zooplankton (Cushing, 1984, 1990; Ellertsen et al., 1987; Section 1.4 above). The scientific questions remain important (but also not yet fully answered). For larval fishes, post-Cushing studies in the NE Atlantic and North Sea continue to show that larval fish abundance in the plankton follows predictably from timing of adult spawning. Most fish species have a rather broad climatological spawning peak (~30–60 day duration) modified by smaller (~10–30 d) interannual variations in phase. Annual peak timing is correlated with water temperatures one-to-several months earlier, and as with many of the spring and early summer zooplankton, this association is usually “earlier-when-warmer” (Russell, 1935; Greve et al., 2005) [Although Genner et al. (2010) recently found that some larval abundance of some early spring spawners peaked early following anomalously cold nearshore winter temperatures, they attributed the timing change to earlier adult migration to and from warm offshore wintering grounds. The response of the fish therefore remains “earlier spawning following exposure to warmer water”].

An important point is that, although temperature-covariance of spawning date and larval fish abundance maxima have the same sign as temperature-timing of their zooplankton prey, changes in fish phenology tend to be smaller by about a factor of two, leading to increasing mismatch as temperature anomalies get larger. A similar temperature-linked timing mismatch has been observed for Cassin's Auklet, a planktivorous seabird that preferentially feeds on large *Neocalanus* at its large NE Pacific breeding colony (Bertram et al., 2001; Hipfner, 2008). Auklet hatch dates vary between 5 and 30 May (earlier in warm springs) but *Neocalanus* peak timing has varied by about 40 days for the same set of years. In terrestrial systems, insectivorous birds (multi-year reproductive life span) also have smaller variation in interannual timing variability than their shorter-lived prey (Durant et al., 2007; Visser et al., 1998).

What are the implications of phenology mismatch for subsequent survival and reproductive success of planktivores? Most recent analyses indicate that timing mismatch is bad for predators, but also that change in phenology is often confounded with additional modes of change of the annual zooplankton productivity and community composition. For example, in the North Sea, Beaugrand et al. (2003) showed that timing match–mismatch between cod larvae and appropriately-sized copepod prey contributed to a large drop in cod recruitment after 1985. But additional important factors included replacement of *C. finmarchicus* by *C. helgolandicus* as the dominant *Calanus* species (Fig. 22), reduced mean body size and total biomass of calanoids, and reduced abundance of euphausiids. Off the Vancouver Island continental margin, Mackas et al. (2007) showed that good (vs. poor) first year growth and marine survival of local coho salmon (*Oncorhynchus kisutch*), high (vs. low) year-class strength of west coast sablefish (*Anoplopoma fimbria*), and good (vs. poor) growth and survival of Cassin's Auklet chicks all had strong correlation with cool (vs. warm) annual anomalies of spring temperatures, late (vs. early) *Neocalanus* peak timing, and high (vs. low) biomass of large lipid-rich copepods.

Recent theoretical, modeling and laboratory studies both illustrate and help us interpret the complexity of these multivariate interactions. It is now clear that trophic match–mismatch is affected by between-year differences in prey abundance as well as

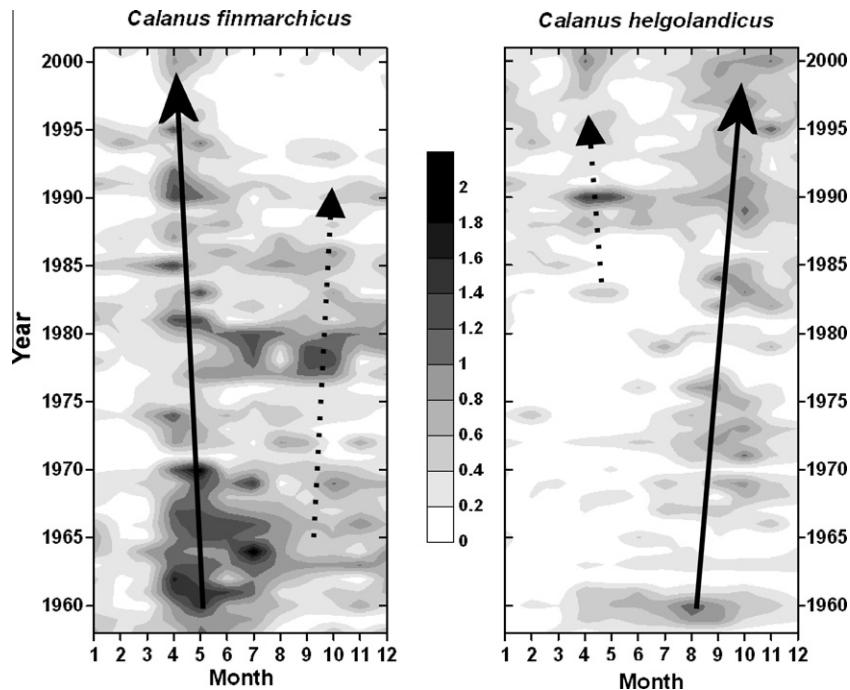
prey timing. Mismatch is more likely and more severe if annual prey abundance is low and/or if the duration of the prey peak is short (Durant et al., 2007; Sydeman and Bograd, 2009; Kristiansen et al., 2011). Seasonal changes and anomalies of the physical environment also modulate match–mismatch between prey and predator abundance curves. For example, Varpe and Fiksen (2010) show that although seasonal peaks of large *C. finmarchicus* (preferred prey of spring-spawning Norwegian herring) occur in March–April (adults of the parent generation) and June–July (C5 of their maturing offspring), the rate of increase in body condition of the herring is maximal in May–June when long bright days allow the fish to forage efficiently despite below-maximum prey concentrations. A modeling study by Kristiansen et al. (2011) used temperature and chlorophyll concentration as a proxy for zooplankton availability and showed that duration of the prey peak is as important as the exact peak date. They predicted that likelihood of mismatch is greater at higher latitudes due to a shorter seasonal window for plankton productivity.

All of the above discussion has been about bottom-up effects of plankton phenology on their predators. We can also ask if large changes in the seasonal timing of a dominant predator could become a top-down driver of changes in the seasonal timing of their zooplankton prey. For two reasons, larval fish are unlikely to provide this top-down forcing: their timing is less variable than their prey, and (due to their low biomass density) they contribute only a small fraction of total zooplankton mortality (e.g. Cushing, 1983; Nielsen and Munk, 1998). Interannual changes in the abundance, migratory timing, and community composition of adult and older juvenile fish are likely to have larger top-down impacts, especially if the older fish remain planktivorous. But evidence for top-down control of marine zooplankton by fish is at best mixed (e.g. see the discussion of trophic controls in Moloney et al. (2010)) and studies to date have examined top-down effects on zooplankton abundance and community composition rather than effects on zooplankton seasonal timing. We suggest that the largest top-down drivers of zooplankton phenology are likely to be those caused by invertebrate predator–prey interactions occurring within the zooplankton community (examples: Davis, 1984; Molinero et al., 2005; Costello et al., 2006). The reasons for this are twofold: relatively large phenologic variability of dominant carnivorous zooplankton such as chaetognaths, ctenophores, and medusae (Greve et al., 2001; Edwards and Richardson, 2004; this paper) plus the very rapid population growth potential of many gelatinous predators (see recent reviews by Gibbons, 2010; Richardson et al., 2009; Purcell, 2005).

Our overall conclusion is that seasonal match–mismatch between zooplankton and their predators has re-emerged as an important and active research topic. However, we are a long way from a complete set of observations and answers, and probably have not yet formulated a complete set of questions. Given the strong influence of temperature on phenology, global change scenarios add urgency to our search for better understanding.

### 3.8. Community-level vs. species-level phenology

Our final discussion topic will be the consequences of interaction between species-level changes in zooplankton phenology and community-level changes in zooplankton species dominance. We have shown that many zooplankton species exhibit plasticity of seasonal timing, and that within-year timing appears to be linked (by one or several mechanisms) to recent environmental temperature. Our zooplankton time series also provide extensive evidence of large interannual fluctuations and trends in the population density of individual species, and in overall zooplankton community composition (e.g. Beaugrand et al., 2002, 2003; Chiba et al., 2006, 2009; Conversi et al., 2009; Eloire et al., 2010; Helaouët



**Fig. 23.** Year × month contour plots of Central North Sea log abundance of *Calanus finmarchicus* (left) and *C. helgolandicus* (right), showing trends in timing (arrows) and dominance (contour shading). As the region has warmed, the primary (spring) peak of *C. finmarchicus* has shifted earlier and weakened, and the primary (late summer) peak of *C. helgolandicus* has shifted later and strengthened. Secondary peaks for both species also show trends in timing (dashed arrows) and abundance. Both species show similar within-season trends of timing, but the shift in dominance from *C. finmarchicus* to *C. helgolandicus* has led to a large change in total zooplankton community phenology. (Monthly average abundances are from the SAHFOS WinCPR program and database, Vezzulli et al., 2007.)

and Beaugrand, 2007; Mackas et al., 2001, 2007; Molinero et al., 2005; Bode et al., 2012; Mazzocchi et al., 2012). Although species-level plasticity in phenology is almost certainly an evolved adaptation to spatial and interannual variability of environmental seasonality (ref. earlier discussion in Sections 1.2 and 1.3), extreme shifts in timing are likely to expose a species to fitness-limits imposed by the seasonality of other environmental factors such as light, and varying abundance of prey, competitors and/or predators (for additional discussion see Sections 3 and 5.2 in Mackas et al. (2007)). Species-level phenology change could therefore alter “who is most successful”, and become a driver of changes in community composition. Conversely, because zooplankton taxa differ in their mean seasonality and in how they respond to environmental anomalies, changes in community composition are likely to produce changes in the phenology of aggregate variables such as total biomass and size composition. We have already shown/discussed several examples: biomass anomalies of *Neocalanus* spp. in the Oyashio region (Section 3.3.2; Fig. 17); the recent steep decline of *N. plumchrus* in the Strait of Georgia (Section 3.3.1, El-Sabaawi et al., 2009); increase of spring *Centropages* and decline of fall *T. stylifera* in the NW Mediterranean (Section 3.4.1, Molinero et al., 2005); decline/disappearance of cool-water copepods in the Adriatic Sea (Section 3.4.2, Conversi et al., 2009). But our clearest example of interaction between shifts in phenology and shifts in community dominance is the decline of *C. finmarchicus* and rise of *C. helgolandicus* in the North Sea CPR time series (Fig. 23). Before the mid 1980s, the zooplankton community and seasonal cycle was strongly dominated by a spring peak of *C. finmarchicus*, with secondary late-summer peaks of *C. helgolandicus* and (in especially cool years) of *C. finmarchicus*. Accompanying a long-term warming trend in the North Sea (for details of fluctuations around this trend, see Fig. 8), the spring peak of *C. finmarchicus* has shifted earlier by ~2 months. Fall peaks of both species have shifted later by 1–2 months. In addition, spring abundance of *C. finmarchicus* has declined by about an order of magnitude, and its late summer peak

has disappeared. The fall peak of *C. helgolandicus* has strengthened and lengthened, and a small spring secondary peak has appeared. Although the responses in phenology to warming by the two species are rather similar (earlier in spring, later in fall as the North Sea gets warmer), the big change for the ecosystem was that the “abundance/availability of large herbivorous copepods” has shifted from a spring maximum to a fall maximum. As noted by Beaugrand et al. (2003) and in Section 3.7, this appears to have had large consequences for other trophic levels. The recent consequences of combination of shifts in phenology and shifts in community dominance may have been especially strong in the central and northern North Sea (due to its location relative to the thermal niche boundaries of each species, Helaouët and Beaugrand, 2007; Beaugrand et al., 2009). But we suggest that continuing or accelerated global warming will soon lead to similar strong changes in ecosystem structure in other ocean regions, such as along the margins of the NE and NW Pacific, and in parts of the Mediterranean.

## Acknowledgements

This paper is a product of SCOR Working Group 125 “Global comparison of zooplankton time series” and has benefited from support provided to SCOR by NOAA and by the US National Science Foundation to the Scientific Committee on Oceanic Research under Grant OCE-0938349. Salary of the lead author is provided by Fisheries and Oceans Canada. Recent data were contributed by all of the coauthors, and by their respective scientific institutions. Older data (especially valuable in any time series analysis) were gathered through long-term efforts by a host of scientists, field and laboratory technicians, and ship’s crew-members.

## References

- Alldredge, A.L., Madin, L.F., 1982. Pelagic tunicates: unique herbivores in the marine plankton. BioScience 32, 655–663.

- Batchelder, H.P., Mackas, D.L., O'Brien, T.D., 2012. Spatial-temporal scales of synchrony in marine zooplankton biomass and abundance patterns: a worldwide comparison. *Progress in Oceanography* 97–100C, 15–30.
- Batten, S.D., Mackas, D.L., 2009. Shortened duration of the annual *Neocalanus plumchrus* biomass peak in the Northeast Pacific. *Marine Ecology Progress Series* 393, 189–198.
- Batten, S.D., Welch, D.W., Jonas, T., 2003. Latitudinal differences in the duration of development of *Neocalanus plumchrus* copepodites. *Fisheries Oceanography* 12, 201–208.
- Beaugrand, G., 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fisheries Oceanography* 12, 270–283.
- Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography* 60, 245–262.
- Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod diversity and climate. *Science* 296, 1692–1694.
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C., 2003. Plankton effect on cod recruitment in the North Sea. *Nature* 426, 661–664.
- Beaugrand, G., Luczak, C., Edwards, M., 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biology* 15, 1790–1803.
- Berline, L., Siokou-Frangou, I., Marasović, I., Vidjakc, O., Fernández de Puelles, M.L., Mazzocchi, M.G., Assimakopoulou, G., Zervoudaki, S., Umani, S.F., Conversi, A., García-Comas, C., Ibanez, F., Gasparini, S., Stemmann, L., Gorsky, G., 2012. Intercomparison of six Mediterranean zooplankton time series. *Progress in Oceanography* 97–100C, 76–91.
- Bertram, D.F., Mackas, D.L., McKinnell, S.M., 2001. The seasonal cycle revisited: interannual variation and ecosystem consequences. *Progress in Oceanography* 49, 283–307.
- Bode, A., Alvarez-Ossorio, M.T., Miranda, A., 2012. Comparing copepod time series in the north of Spain: spatial autocorrelation of community composition. *Progress in Oceanography* 97–100C, 108–119.
- Bond, N.A., Overland, J.E., Spillane, M., Stabeno, P., 2003. Recent shifts in the state of the North Pacific. *Geophysical Research Letters* 30, 2183. doi:10.1029/2003GL018597.
- Bornhold, E.A., 2000. Interannual and Interdecadal Patterns in Timing and Abundance of Phytoplankton and Zooplankton in the Central Strait of Georgia, with Special Reference to *Neocalanus plumchrus*. MSc Thesis, University of British Columbia, Canada.
- Chiba, S., Tadokoro, K., Sugisaki, H., Saino, T., 2006. Effects of decadal climate change on zooplankton over the last 50 years in the western subarctic North Pacific. *Global Change Biology* 12, 907–920.
- Chiba, S., Aita, M.N., Tadokoro, K., Saino, T., Sugisaki, H., Nakata, K., 2008. From climate regime shifts to lower-trophic level phenology: synthesis of recent progress in retrospective studies of the western North Pacific. *Progress in Oceanography* 77, 112–126.
- Chiba, S., Sugisaki, H., Nonoka, M., Saino, T., 2009. Geographical shift of zooplankton communities and decadal dynamics of the Kuroshio–Oyashio Currents in the western North Pacific. *Global Change Biology* 15, 1846–1858.
- Chihara, M., Murano, M., 1997. An Illustrated Guide to Marine Plankton in Japan. Tokai University Press, Tokyo, 1574 pp.
- Colebrook, J.M., 1979. Continuous Plankton Records: seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. *Marine Biology* 51, 23–32.
- Colebrook, J.M., Robinson, G.A., 1963. Continuous Plankton Recorder Records: seasonal cycles of phyto-plankton and copepods in the north-eastern Atlantic and the North Sea. *Bulletins Marine Ecology* 6, 123–139.
- Conversi, A., Peluso, T., Fonda-Umani, S., 2009. Gulf of Trieste: a changing ecosystem. *Journal of Geophysical Research* 114, C03S90.
- Costello, J.H., Sullivan, B.K., Gifford, D.J., 2006. A physical–biological interaction underlying variable phenological responses to climate change by coastal zooplankton. *Journal of Plankton Research* 28, 1099–1105.
- Cushing, D.H., 1983. Are fish too dilute to affect the density of their food organisms? *Journal of Plankton Research* 5, 847–854.
- Cushing, D.H., 1984. The gadoid outburst in the North Sea. *Journal du Conseil International pour l'Exploration de la Mer* 41, 159–166.
- Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* 26, 249–293.
- Davis, C.S., 1984. Predatory control of copepod seasonal cycles on Georges Bank. *Marine Biology* 82, 31–40.
- DiLorenzo, E. et al., 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters* 35, L08607. doi:10.1029/2007GL032838.
- Dowd, M., Martin, J.L., Legresley, M.M., Hanke, A., Page, F.H., 2004. A statistical method for the robust detection of interannual changes in plankton abundance: analysis of monitoring data from the Bay of Fundy, Canada. *Journal of Plankton Research* 26, 509–523.
- Durant, J.M., Hjermann, D.O., Ottersen, G., Stenseth, N.C., 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33, 271–283.
- Edwards, M., Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430, 881–884.
- Edwards, M., Reid, P., Planque, B., 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960–1995). *ICES Journal of Marine Science* 58, 39–49.
- Ellertsen, B., Fossum, P., Solemdal, P., Sundby, S., Tilseth, S., 1987. The effect of biological and physical factors on the survival of Arcto-Norwegian cod and the influence on recruitment variability. In: Loeng, H. (Ed.), *The Effect of Oceanographic Conditions on Distribution and Population Dynamics of Commercial Fish Stocks in the Barents Sea*. Institute of Marine Research, Bergen, pp. 101–126.
- Eloire, D., Somerfield, P.J., Conway, D.V.P., Halsband-Lenk, C., Harris, R., Bonnet, D., 2010. Temporal variability and community composition of zooplankton at station L4 in the Western Channel: 20 years of sampling. *Journal of Plankton Research* 32, 657–679.
- El-Sabaawi, R., Dower, J.F., Kainz, M., Mazumder, A., 2009. Interannual variability in fatty acid composition of the copepod *Neocalanus plumchrus* in the Strait of Georgia, British Columbia. *Marine Ecology Progress Series* 382, 151–161.
- Fenchel, T., 1982. Ecology of heterotrophic microflagellates – II. Bioenergetics and growth. *Marine Ecology Progress Series* 8, 225–231.
- Fiksen, Ø., 2000. The adaptive timing of diapause – a search for evolutionarily robust strategies in *Calanus finmarchicus*. *ICES Journal of Marine Science* 57, 1825–1833.
- Fulton, J., 1973. Some aspects of the life history of *Calanus plumchrus* in the Strait of Georgia. *Journal of the Fisheries Research Board of Canada* 30, 811–815.
- Gennen, M.J., Halliday, N.C., Simpson, S.D., Southward, A.J., Hawkins, S.J., 2010. Temperature driven phonological changes within a marine larval fish assemblage. *Journal of Plankton Research* 32, 699–708.
- Gibbons, M.J., 2010. Roles of gelatinous zooplankton. In: Barange, M., Field, J.G., Harris, R.P., Hofmann, E.E., Perry, R.I., Werner, F.E. (Eds.), *Global Change and Marine Ecosystems: GLOBEC International Synthesis*. Oxford University Press, Oxford, pp. 181–183.
- Greve, W., Lange, U., Reiners, F., Nast, J., 2001. Predicting the seasonality of North Sea zooplankton. *Senckenbergiana Maritima* 31, 263–268.
- Greve, W., Reiners, F., Nast, J., Hoffmann, S., 2004. Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. *Helgoland Marine Research* 58, 274–288.
- Greve, W., Prinage, S., Zidowitz, H., Nast, J., Reiners, F., 2005. On the phenology of North Sea ichthyoplankton. *ICES Journal of Marine Science* 62, 1216–1223.
- Halsband-Lenk, C., Carlotti, F., Greve, W., 2004. Life-history strategies of calanoid congeners under two different climate regimes: a comparison. *ICES Journal of Marine Science* 61, 709–720.
- Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47, 103–145.
- Harris, R., 2010. The L4 time series: the first 20 years. *Journal of Plankton Research* 32, 577–583.
- Haury, L., McGowan, J.A., Wiebe, P.H., 1978. Patterns and processes in the time-space scales of plankton distributions. In Steele, J.H. (Ed.) *Spatial Pattern in Plankton Communities*, Proceedings of the 3rd NATO Conference on Marine Biology, Plenum Press, pp. 277–327.
- Hays, G.C., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. *Trends in Ecology and Evolution* 20, 337–344.
- Head, E.J.H., Harris, L.R., Yashayaev, I., 2003. Distributions of *Calanus* spp., other mesozooplankton in the Labrador Sea in relation to hydrography in spring, early summer (1995–2000). *Progress in Oceanography* 59, 1–30.
- Heloaët, P., Beaugrand, G., 2007. Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Marine Ecology Progress Series* 345, 147–165.
- Hipfner, J.M., 2008. Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Marine Ecology Progress Series* 368, 295–304.
- Hirche, H.-J., Kosobokova, K., 2007. Distribution of *Calanus finmarchicus* in the northern North Atlantic and Arctic Ocean—expatriation and potential colonization. *Deep-Sea Research II* 54, 2729–2747.
- Hirst, A.G., Roff, J.C., Lampitt, R.S., 2003. A synthesis of growth rates in marine epipelagic invertebrate zooplankton. *Advances in Marine Biology* 44, 1–142.
- Hooff, R.C., Peterson, W.T., 2006. Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem. *Limnology and Oceanography* 51, 2607–2620.
- Hunt, G.L., Stabeno, P., Strom, S., Napp, J.M., 2008. Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain. *Deep-Sea Research II* 55, 1919–1944.
- Hurrell, J.W., Deser, C., 2009. North Atlantic climate variability: the role of the North Atlantic Oscillation. *Journal of Marine Systems* 78, 28–41.
- Ji, R., Edwards, M., Mackas, D., Runge, J., Thomas, A., 2010. Marine plankton phenology and life history in a changing climate: current research and future directions. *Journal of Plankton Research* 32, 1355–1368.
- Johnson, C.L., Leising, A.W., Runge, J.A., Head, E.J.S., Pepin, P., Plourde, S., Durbin, E.G., 2008. Characteristics of *Calanus finmarchicus* dormancy patterns in the Northwest Atlantic. *ICES Journal of Marine Science* 65, 339–350.
- Kristiansen, T., Drinkwater, K.F., Lough, R.G., Sundby, S., 2011. Recruitment variability in North Atlantic cod and match–mismatch dynamics. *PLoS One* 6, e17456. doi:10.1371/journal.pone.0017456.
- Levins, R., 1968. *Evolution in Changing Environments. Some Theoretical Explorations*. Princeton University Press, 115 pp.
- Longhurst, A., 1998. *Ecological Geography of the Sea*. Academic Press, San Diego, 398 pp.
- López-Urrutia, A., San Martin, E., Harris, R.P., Irigoien, X., 2006. Scaling the metabolic balance of the oceans. *Proceedings US National Academy of Science* 103, 8739–8744.

- Mackas, D.L., 1992. The seasonal cycle of zooplankton off southwestern British Columbia: 1979–1989. Canadian Journal of Fisheries Aquatic Science 49, 903–921.
- Mackas, D.L., Beaugrand, G., 2010. Comparisons of zooplankton time series. Journal of Marine Systems 79, 286–304.
- Mackas, D.L., Harrison, P.J., 1997. Nitrogenous nutrient sources and sinks in the Juan de Fuca Strait, Strait of Georgia, Puget Sound estuarine system: assessing the potential for eutrophication. Estuarine Coastal and Shelf Science 44, 1–21.
- Mackas, D.L., Goldblatt, R., Lewis, A.G., 1998. Interdecadal variation in developmental timing of *Neocalanus plumchrus* populations at OSP in the subarctic North Pacific. Canadian Journal of Fisheries and Aquatic Sciences 55, 1878–1893.
- Mackas, D.L., Thomson, R.E., Galbraith, M., 2001. Changes in the zooplankton community of the British Columbia continental margin, 1985–1999, and their covariation with oceanographic conditions. Canadian Journal of Fisheries and Aquatic Sciences 58, 685–702.
- Mackas, D.L., Batten, S., Trudel, M., 2007. Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. Progress in Oceanography 75, 223–252.
- Madhupratap, M., Nehring, S., Lenz, J., 1996. Resting eggs of zooplankton (Copepoda and Cladocera) from the Kiel Bay and adjacent waters (southwestern Baltic). Marine Biology 127, 77–87.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific Decadal Climate Oscillation with impacts on salmon. Bulletin of the American Meteorological Society 78, 1069–1079.
- Marcus, N.H., 1996. Ecological and evolutionary significance of resting eggs in marine copepods: past present and future studies. Hydrobiologia 320, 141–152.
- Mazzocchi, M.G., Christou, E.D., Di Capua, I., Fernández de Puelles, M., Fonda-Umani, S., Molinero, J.C., Nival, P., Siokou-Frangou, I., 2007. Temporal variability of *Centropages typicus* in the Mediterranean Sea over seasonal-to-decadal scales. Progress in Oceanography 72, 214–232.
- Mazzocchi, M.G., Dubroca, L., Garcia-Comas, C., Di Capua, I., d'Alcalà, M.R., 2012. Stability and resilience in coastal copepod assemblages: the case of the Mediterranean long-term ecological research at Station MC (LTER-MC). Progress in Oceanography 97–100C, 135–151.
- McGowan, J.A., Cayan, D.R., Dorman, L.M., 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science 281, 210–217.
- McLaren, I.A., 1978. Generation lengths of some temperate marine copepods: estimation, prediction, and implications. Journal of the Fisheries Research Board Canada 35, 1330–1342.
- McQuatters-Gollop, A., Raitsos, D.E., Edwards, M., Pradhan, Y., Mee, L.D., Lavender, S.J., Attrill, M.J., 2007. A long-term chlorophyll dataset reveals regime shift in North Sea phytoplankton biomass unconnected to increasing nutrient levels. Limnology and Oceanography 52, 635–648.
- Miller, C.B., Clemons, M., 1988. Revised life history analysis for large grazing copepods in the subarctic Pacific Ocean. Progress in Oceanography 20, 293–313.
- Miller, C.B., Cowles, T.J., Wiebe, P.H., Copley, N.J., Grigg, H., 1991. Phenology in *Calanus finmarchicus*: hypotheses about control mechanisms. Marine Ecology Progress Series 72, 79–91.
- Molinero, J.C., Ibanez, F., Souissi, S., Chifflet, M., Nival, P., 2005. Phenological changes in the Northwestern Mediterranean copepods *Centropages typicus* and *Temora stylifera* linked to climate forcing. Oecologia 145, 640–649.
- Moloney, C.L., Jarre, A., Kimura, S., Mackas, D.L., Murphy, E.J., Peterson, W.T., Runge, J.A., Tadokoro, K., 2010. Dynamics of marine ecosystems: ecological processes. In: Barange, M., Field, J.C., Harris, R.P., Hofmann, E.E., Perry, R.I., Werner, F.E. (Eds.), *Marine Ecosystems and Global Change*. Oxford Univ. Press, New York, pp. 179–218.
- Nielsen, T.G., Munk, P., 1998. Zooplankton diversity and the predatory impact by larval and small juvenile fish at the Fishers Bank in the North Sea. Journal of Plankton Research 20, 2313–2332.
- Odate, K., 1994. Zooplankton biomass and its long-term variation in the western North Pacific Ocean. Bulletin Tohoku Regional Fisheries Research Laboratory 56, 115–173.
- Purcell, J.E., 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. Journal of the Marine Biological Association of the United Kingdom 85, 461–476.
- Reid, P.C., Edwards, M., Hunt, H.G., Warner, A.J., 1998. Phytoplankton change in the North Atlantic. Nature 391, 546.
- Richardson, A.J., 2008. In hot water: zooplankton and climate change. ICES Journal of Marine Science 65, 279–295.
- Richardson, A.J., Walne, A.W., John, A.W., Jonas, T.D., Lindley, J.A., Sims, D.W., Stevens, D., Witt, M., 2006. Using Continuous Plankton Recorder data. Progress in Oceanography 68, 27–74.
- Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends in Ecology and Evolution 24, 312–322.
- Rolinski, S., Horn, H., Petzoldt, T., Paul, L., 2007. Identifying cardinal dates in phytoplankton time series to enable the analysis of long-term trends. Oecologia 153, 997–1008.
- Russell, F.S., 1935. The seasonal abundance and distribution of the pelagic young of teleostean fishes caught in the ring trawl in offshore waters in the Plymouth Area. Journal of the Marine Biological Association of the United Kingdom 20, 147–149.
- Russell, F.S., 1939. Hydrographical and biological conditions in the North Sea as indicated by plankton organisms. C.I.E.M. Journal du Conseil 14, 171–192.
- Saito, H., Tsuda, A., 2000. Egg production and early development of the subarctic copepods *Neocalanus cristatus*, *N. plumchrus* and *N. flemingeri*. Deep-Sea Research I 47, 2141–2158.
- Smith, T.M., Reynolds, R.W., Peterson, T.C., Lawrimore, J., 2008. Improvements to NOAA's historical merged land-ocean surface temperature analysis (1880–2006). Journal of Climate 21, 2283–2296.
- Sullivan, B.K., Costello, J.H., Van Keuren, D., 2007. Seasonality of the copepods *Acartia hudsonica* and *Acartia tonsa* in Narragansett Bay, RI, USA during a period of climate change. Estuarine, Coastal and Shelf Science 73, 259–267.
- Sydean, W.J., Bograd, S.J., 2009. Marine ecosystems, climate and phenology: introduction. Marine Ecology Progress Series 393, 185–188.
- Tadokoro, K., Chiba, S., Ono, T., Midorikawa, T., Saino, T., 2005. Interannual variation in *Neocalanus* biomass in the Oyashio waters of the western North Pacific. Fisheries Oceanography 14, 210–222.
- Tatebe, H., Yasuda, I., Saito, H., Shimizu, Y., 2010. Horizontal transport of the calanoid copepod *Neocalanus* in the North Pacific: the influences of the current system and the life history. Deep-Sea Research I 57, 409–419.
- Tauber, M.J., Tauber, C.A., Masaki, S., 1986. *Seasonal Adaptation of Insects*. Oxford University Press, New York, 426 pp.
- Tsuda, A., Saito, H., Kasai, H., 1999. Life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* (Calanoida: Copepoda) in the western subarctic Pacific. Marine Biology 135, 533–544.
- Tsuda, A., Saito, H., Kasai, H., 2004. Life histories of *Eucalanus bungii* and *Neocalanus cristatus* (Calanoida: Copepoda) in the western subarctic Pacific. Fisheries Oceanography 13, 10–20.
- Valdés, L., O'Brien, T., López-Urrutia, A., 2006. Zooplankton Monitoring Results in the ICES Area, Summary Status Report 2004/2005. ICES Cooperative Research Report 281.
- Valdés, L., López-Urrutia, A., Cabal, J., Alvarez-Ossorio, M., Bode, A., Miranda, A., Cabanas, M., Huskin, I., Anadó e, R., Alvarez-Marqués, F., Llorente, M., Rodríguez, N., 2007. A decade of sampling in the Bay of Biscay: What are the zooplankton time series telling us? Progress in Oceanography 74, 98–114.
- Valtonen, A., Ayres, M., Roininen, H., Pöyry, J., Leinonen, R., 2010. Environmental controls on the phenology of moths: predicting plasticity and constraint under climate change. Oecologia 165, 237–248.
- Varpe, Ø., Fiksen, Ø., 2010. Seasonal plankton-fish interactions: light regime, prey phenology, and herring foraging. Ecology 91, 311–318.
- Varpe, Ø., Jørgensen, C., Tarling, G.A., Fiksen, Ø., 2009. The adaptive value of energy storage and capital breeding in seasonal environments. Oikos 118, 363–370.
- Vezzulli, L., Dowland, P.S., Reid, P.C., Hylton, E.K., 2007. Gridded Database Browser of North Sea plankton, Version 1.1: Fifty Four Years (1948–2001) of Monthly Plankton Abundance from the Continuous Plankton Recorder (CPR) Survey. Sir Alister Hardy Foundation, Plymouth, UK. <[www.sahfos.org/WinCPR.htm](http://www.sahfos.org/WinCPR.htm)> (accessed 2008–2009).
- Visser, M.E., van Noorwijk, A.J., Tinbergen, J.M., Lessells, C.M., 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings Royal Society London B 270, 367–372.
- Wiltshire, K.H., Malzahn, A.M., Wirtz, K., Greve, W., Janisch, S., Mangelsdorf, P., Manly, B.F.J., Boersma, M., 2008. Resilience of North Sea phytoplankton spring bloom dynamics: an analysis of long-term data at Helgoland Roads. Limnology and Oceanography 53, 1294–1302.
- Yamazaki, H., Mackas, D., Denman, K., 2002. Coupling small scale physical processes to biology: Lagrangian approaches. In: Robinson, A.R., McCarthy, J.J., Rothschild, B.J. (Eds.), *The Sea*, vol. XII. John Wiley & Sons, Inc., New York, pp. 51–112.