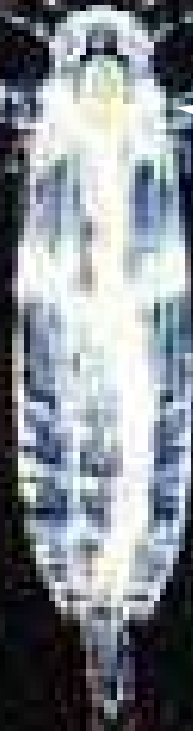
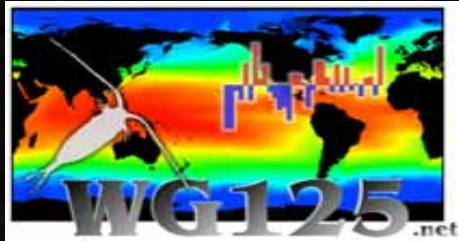


Changing seasonal timing of zooplankton populations, and their link to ocean climate

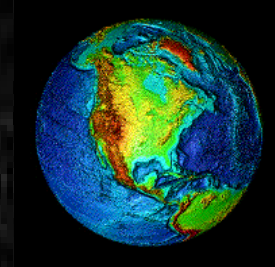


A year can
feel like
forever



D. Mackas, M. Edwards,
S. Chiba, A. Arashkevich,
A. Richardson

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W. Greve, G. Beaugrand,
D. Eloire, S. Batten,
K. Tadokoro, C. Johnson

('Data Partners')

Photo: H. Saito

Presentation Outline

1. Ocean seasonality (intense but 'predictable')
2. Zooplankton seasonal timing mechanisms + Environmental controls/cues
3. Methods for quantifying zooplankton phenology
4. Examples of timing variability:
 - NE Pacific
 - NW Pacific
 - North Sea & NE Atlantic
 - NW Atlantic
 - Mediterranean
5. Conclusions & shared themes

Ocean Weather: Strong seasonality at mid-high latitudes

Photo by M. Clemons

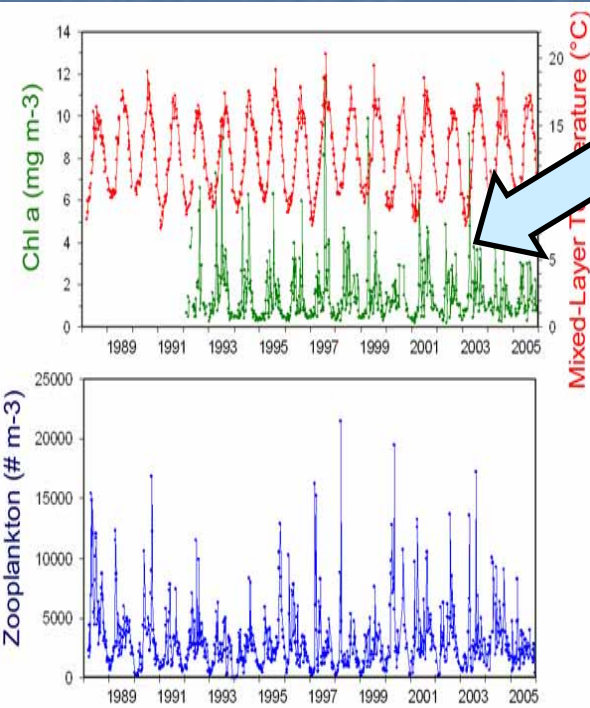


*Photo by Fisheries
& Oceans Canada*

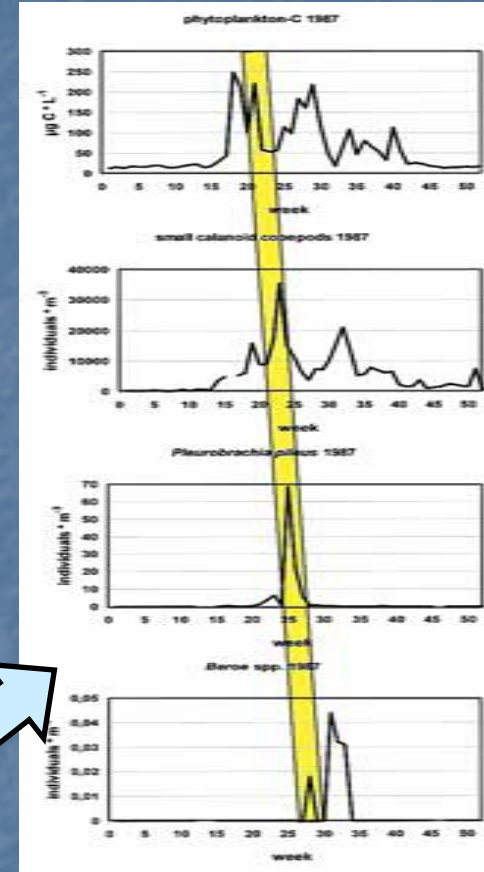


Winter days (left) are short, dim, cold, and often stormy.
Summer days (right) are long, sometimes bright & calm.

Seasonal weather drives large annual cycles of ocean physics & lower trophic level biology



- Annual amplitudes often 2-5x larger than interannual differences
- The big (but predictable) environmental signal selects for large investment in seasonal adaptations
- 'Match-mismatch' is not only with food & physics (predator & competitor timing also matter)



Prey-predator succession at Helgoland (Greve et al. 2004)

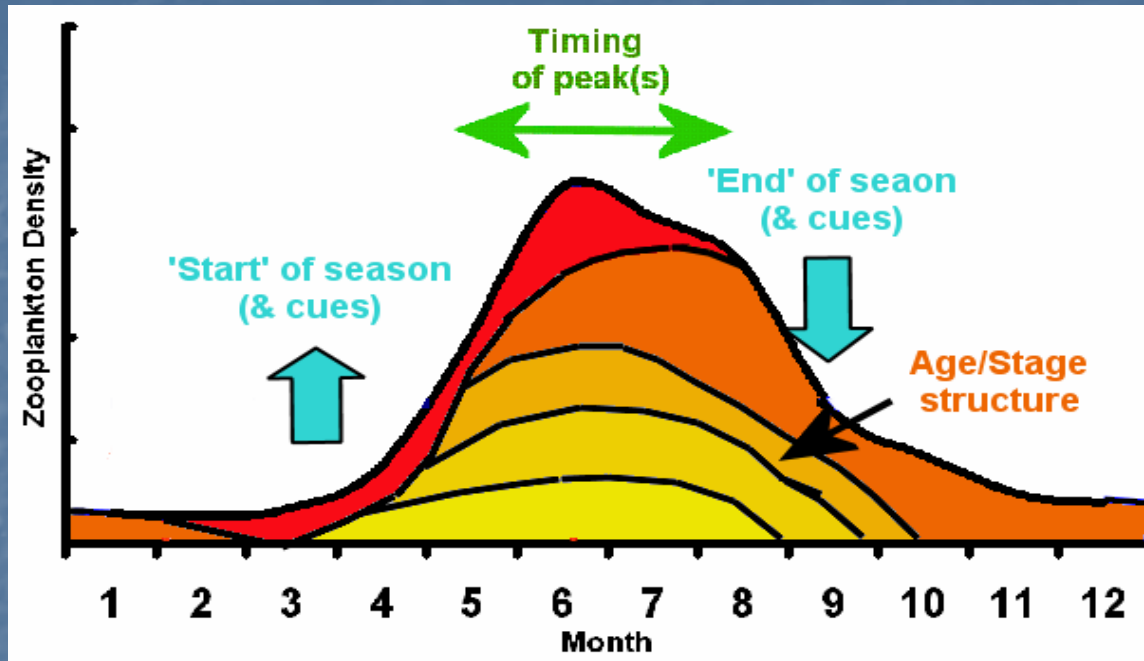
Plymouth L4 time series (from Valdes et al. 2006)

How do zooplankton respond to seasonal stress?

Annual periodicity makes stress predictable. 'Wired' adaptations can evolve (but can also fail disastrously if the annual forcing changes)

<i>Response</i>	<i>Mechanism</i>	<i>Environmental controls/cues</i>
Dormancy onset & duration (egg or pre-adult)	Physiological 'switch', Phenotype	'Condition', 'Clock', Photoperiod, T°C, Chemical signals, ...
Seasonal Migration	Behavioral switch	(As above)
Reproductive timing	Maturation + Behavior	(As above)
Developmental rate	Physiological	T°C (mostly) + Nutrition
Date-dependent survivorship	Population dynamics	Predation, Nutrition
Generation length (#/year)	Physiology + Phenotype	Development vs. Dormancy

What among-year comparisons might we want?



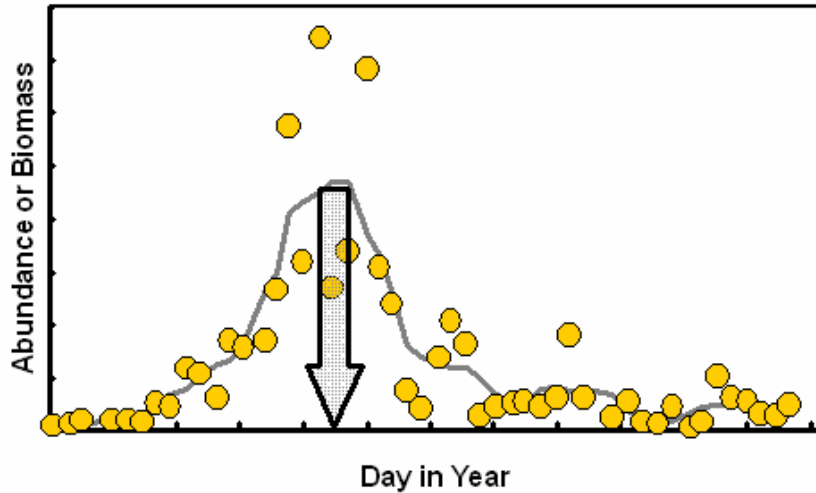
Desirable Data Characteristics:

- Taxonomically-resolved (because timing parameters differ species-by-species)
- Good within-year temporal resolution (because some changes happen quickly)

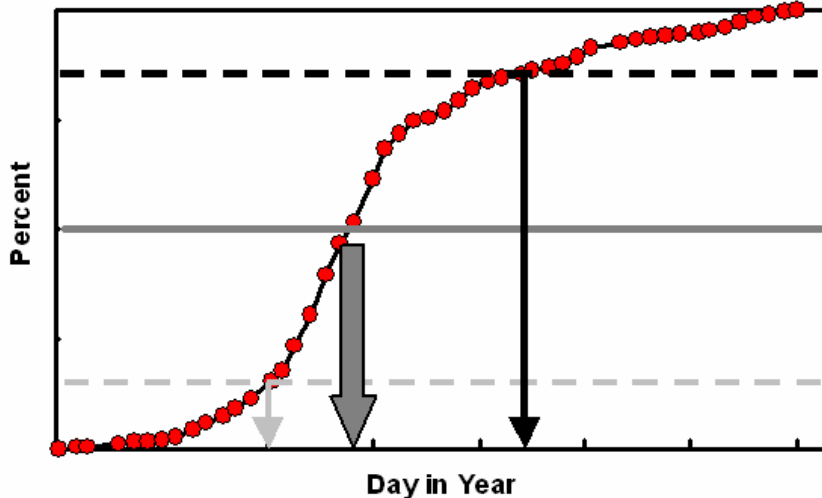
Potential Timing Indices:

Amount-based

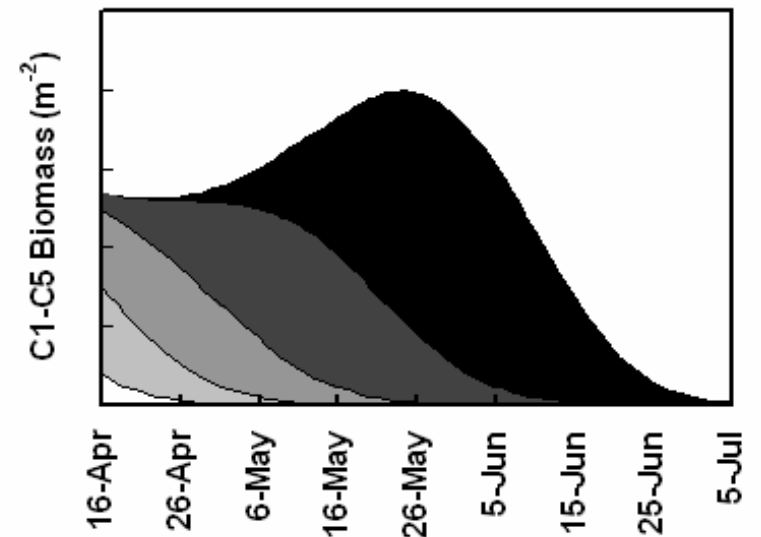
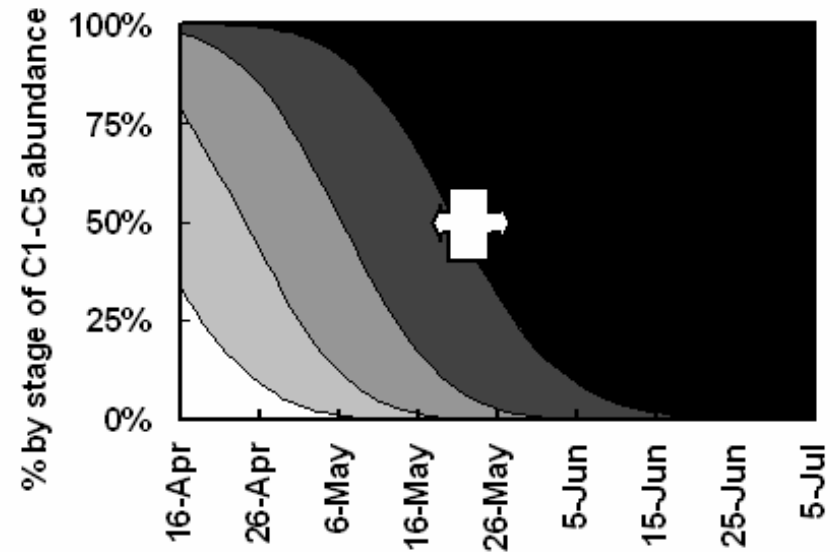
Peak or Center-of-Gravity



Annual Cumulative Abundance

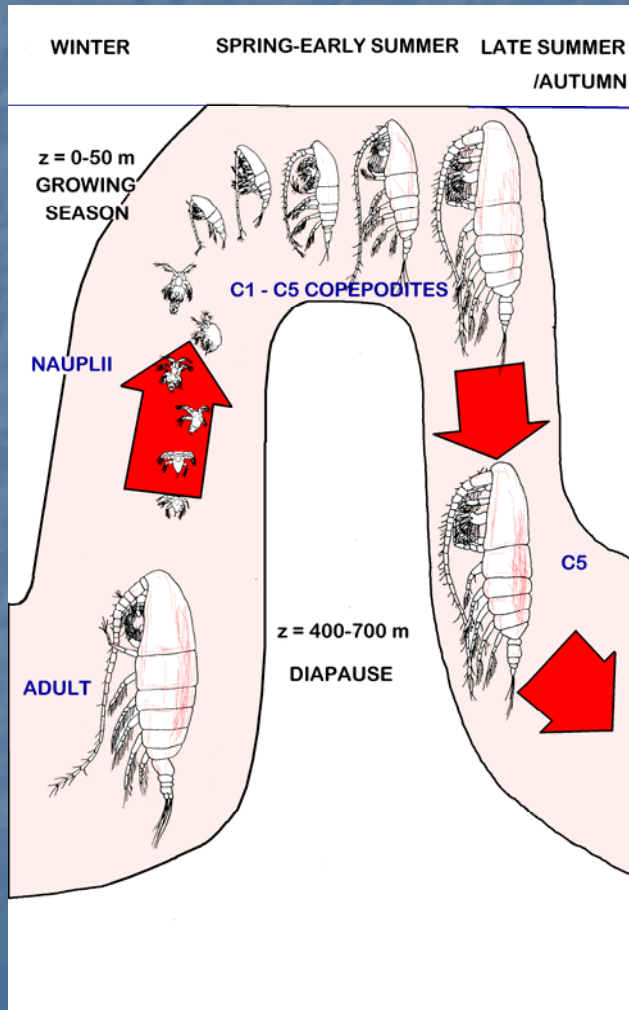


Age-structure-based

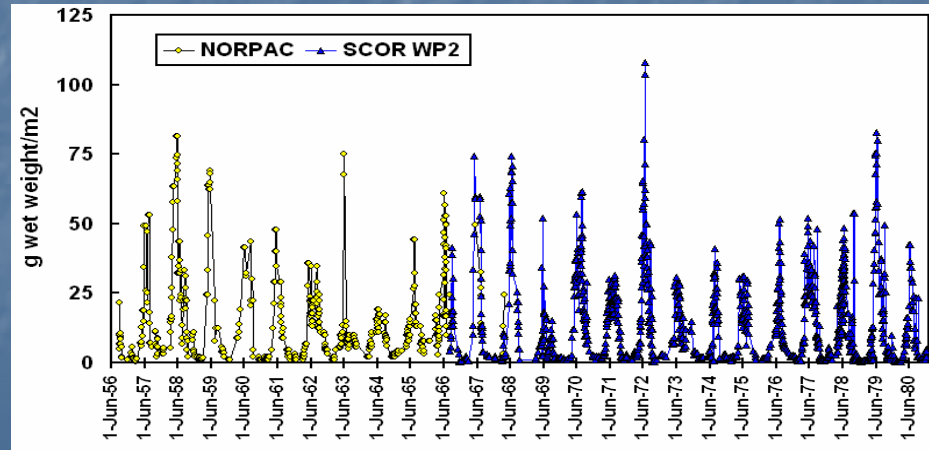


Phenology Observations (Various Regions)

1. *Neocalanus plumchrus* in the NE Pacific

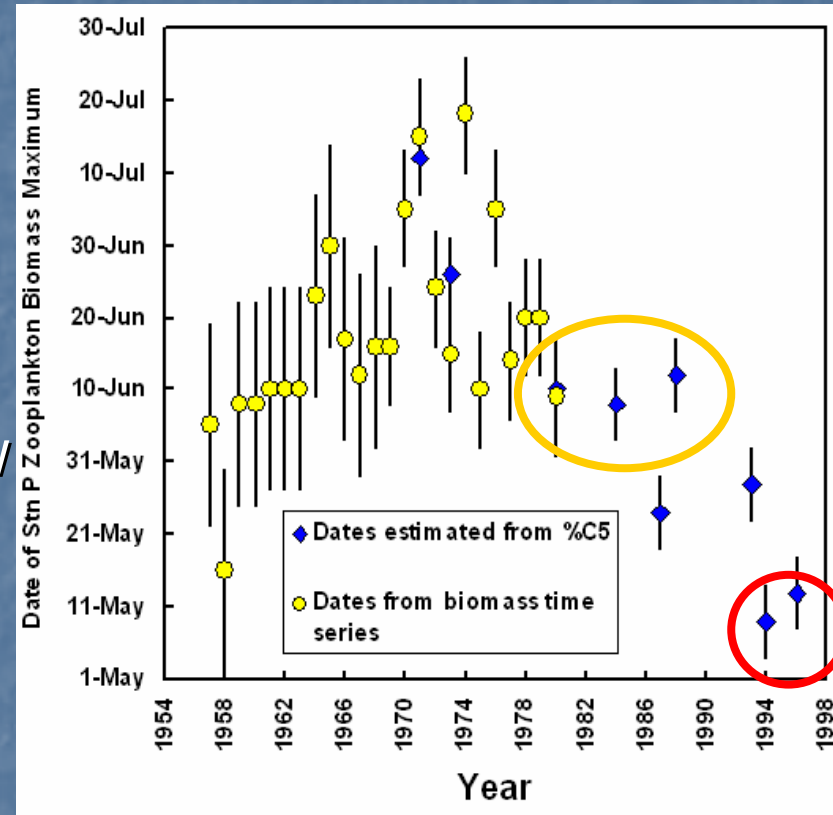


- Dominant copepod in Alaska Gyre & its deep marginal seas
- Prolonged & deep dormancy as C5
- Mates & spawns at depth (no feeding)
- Brief growing season in surface layer, culminates in intense spring biomass peak (well-resolved by the Stn P weather-ship time series)



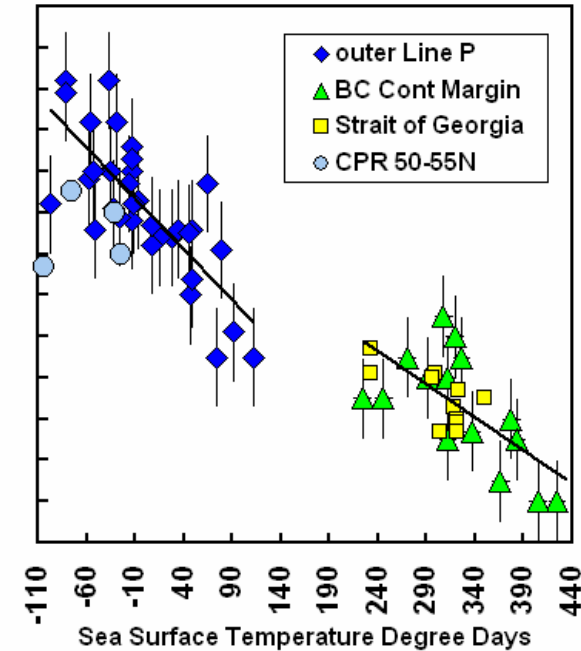
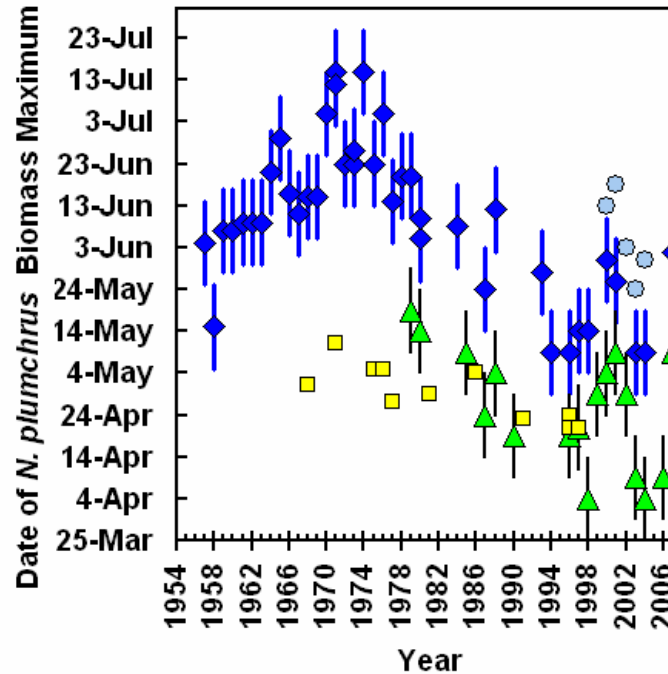
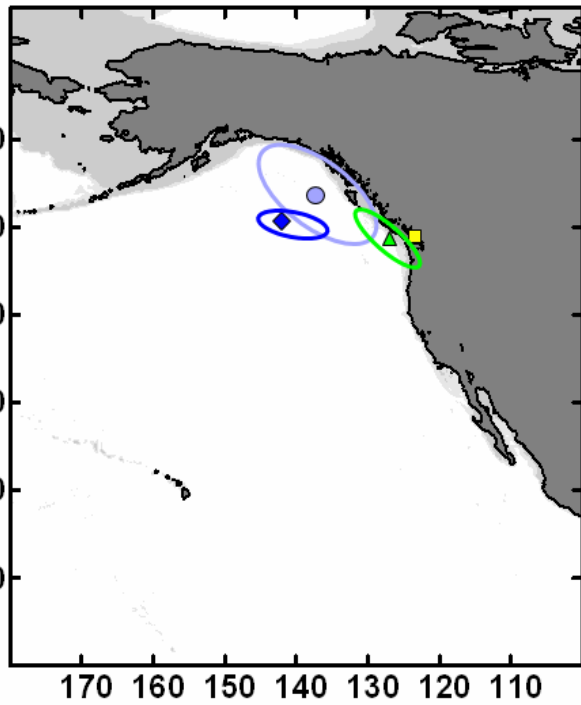
An educational surprise!!

- In the mid-1990s, we resumed intensive 'spring' sampling of the Alaska Gyre.
- Mid 1980s data ○ led us to expect peak copepod biomass in June
- In Mid-1990s June, we caught few (and elderly) *N.plumchrus*.
- *WHY??*
- Not gone, but EARLY ○
- Retrospective analysis documented showed a timing range from May to July.



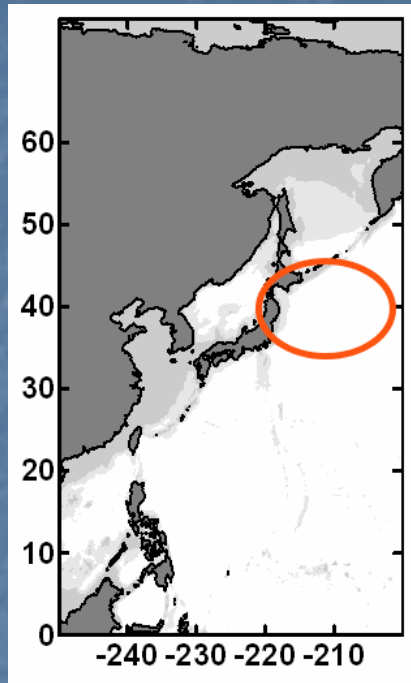
Mackas, Goldblatt & Lewis 1997

We subsequently looked more broadly (and for more years) in the NE Pacific



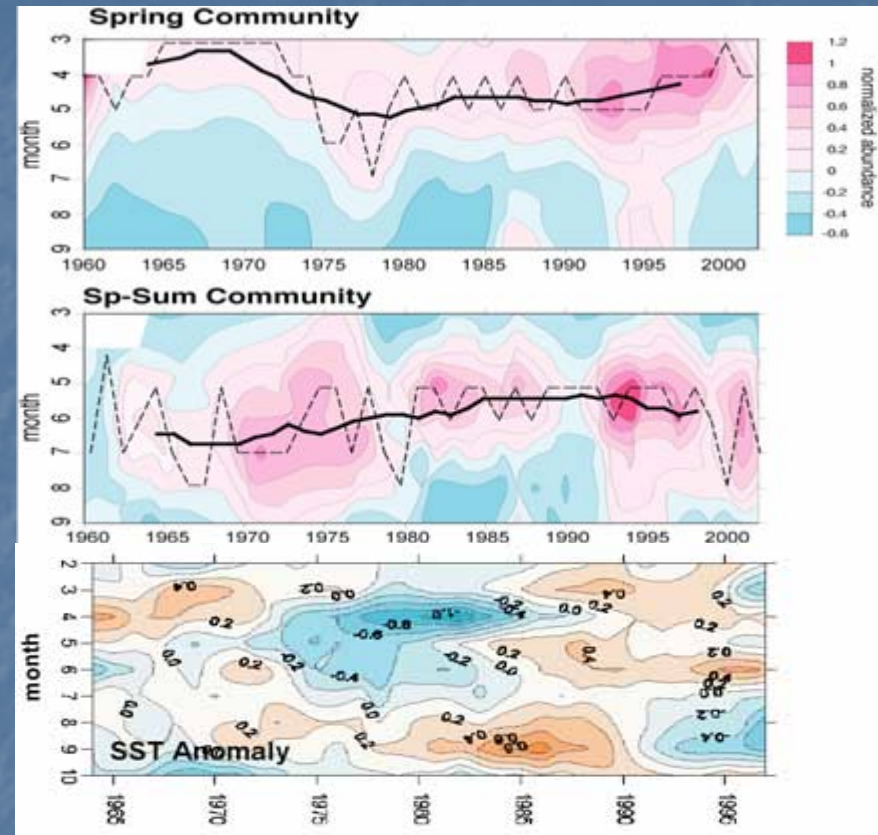
- *N. plumchrus* timing varies with latitude, but interannual variability is correlated across regions (middle)
- Timing in all regions shares similar temperature dependence (right)
- But the magnitude of the timing range, and difference in regression between oceanic and nearshore suggest that $T^{\circ}\text{C}$ dependence may also be a proxy for stratification and/or survival rate.

2. Timing of copepod species groups in the NW Pacific (ODATE project: S. Chiba, K. Tadokoro)



Spring dominants:
N. flemingeri,
N. cristatus

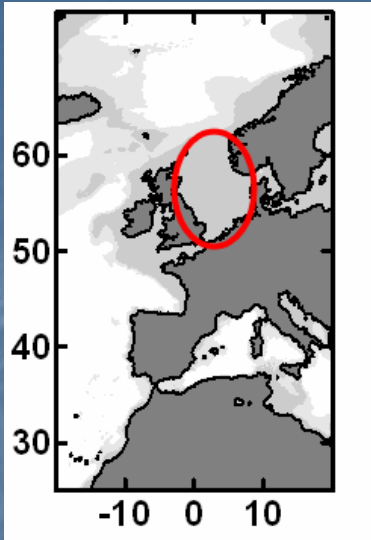
Spring-Summer:
N. plumchrus,
Eucalanus bungii,
Metridia pacifica,
Pseudocalanus spp.



Within seasonal species groups, peak timing (and abundance) covary with corresponding seasonal temperature/stratification anomalies

Between seasonal species groups, no sustained synchrony of phenologic variability

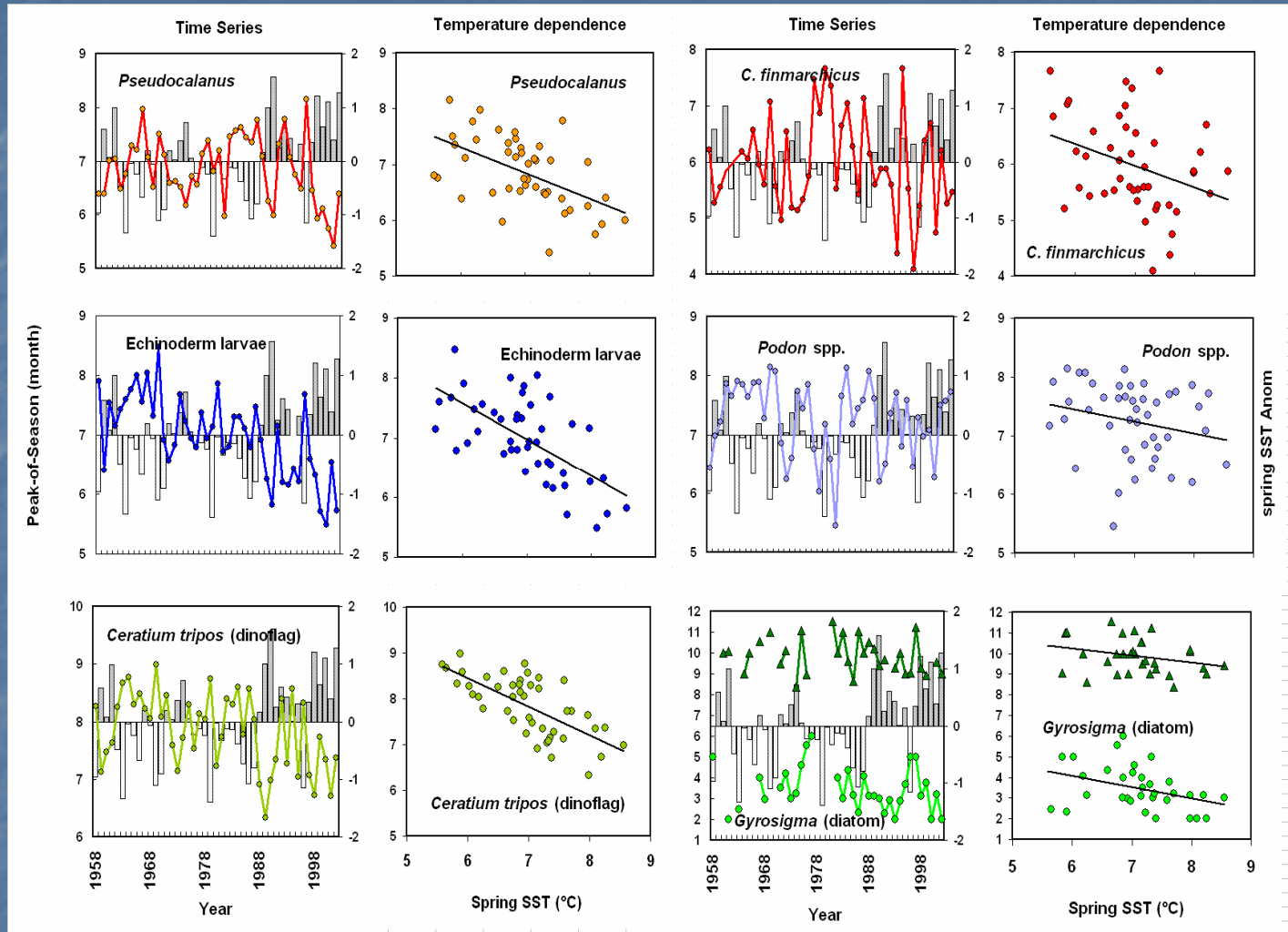
3. North Sea CPR surveys



50+ years

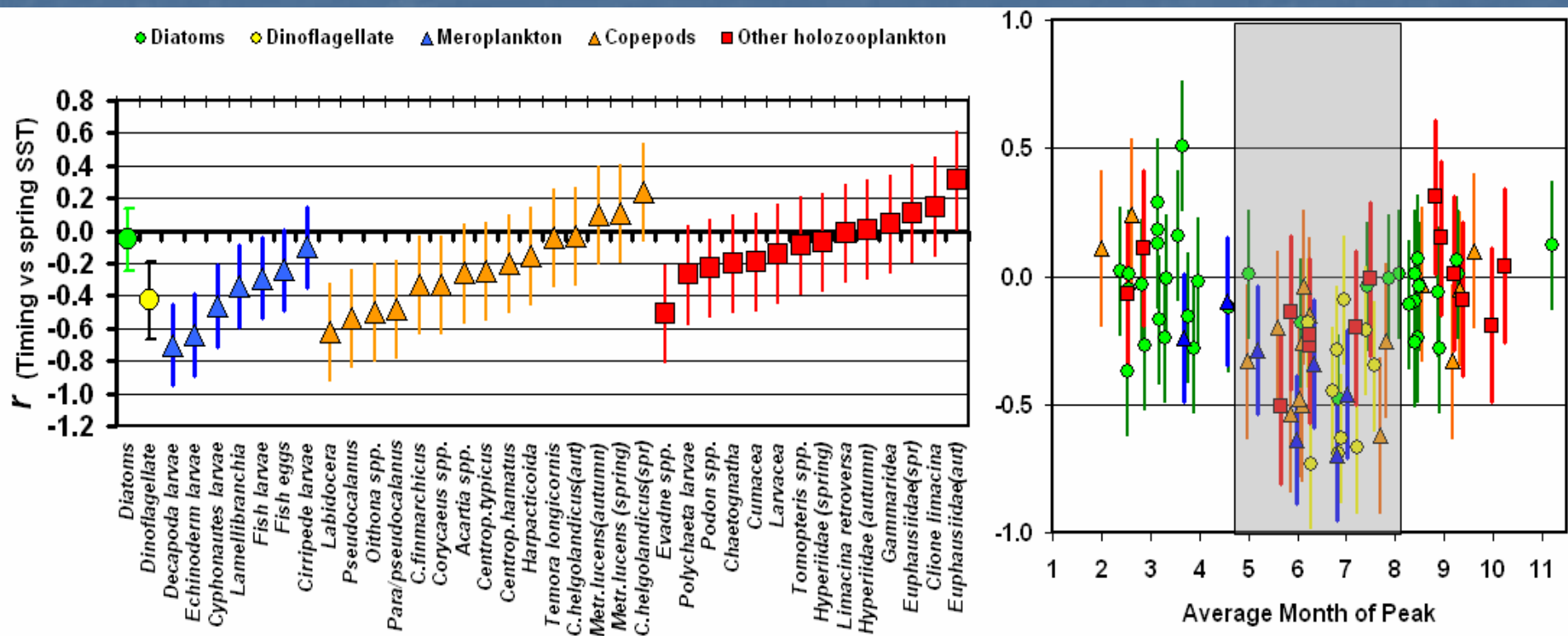
Many species exhibit trend to earlier timing

Many species have timing correlated with sea surface temperature



Plots for individual taxa from supplementary data provided by Edwards and Richardson (2004)

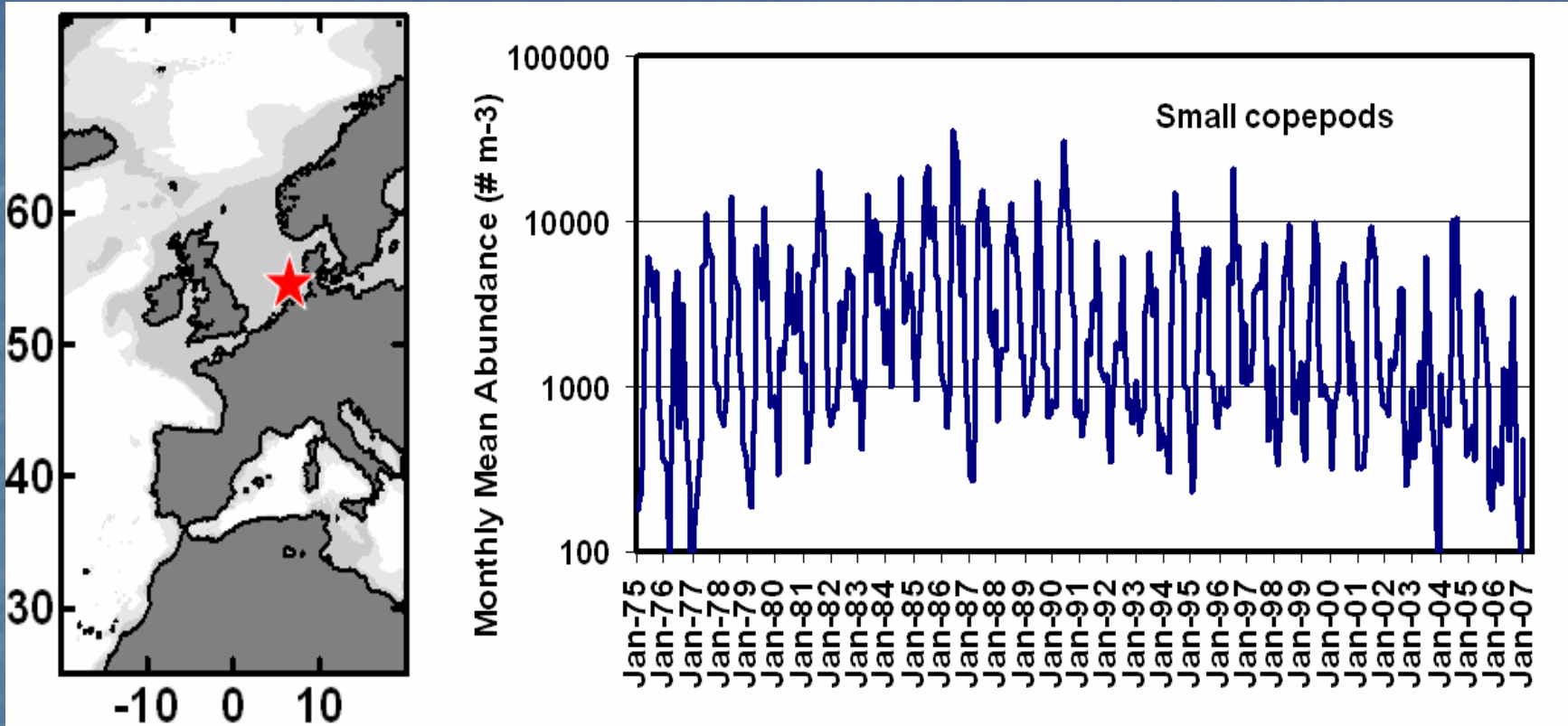
North Sea CPR surveys continued



Temperature dependence varies widely among species:

- By taxa, strongest for meroplankton and dinoflagellates (left)
- By month, strongest for species whose annual maxima are during the stratified season (shaded, right)

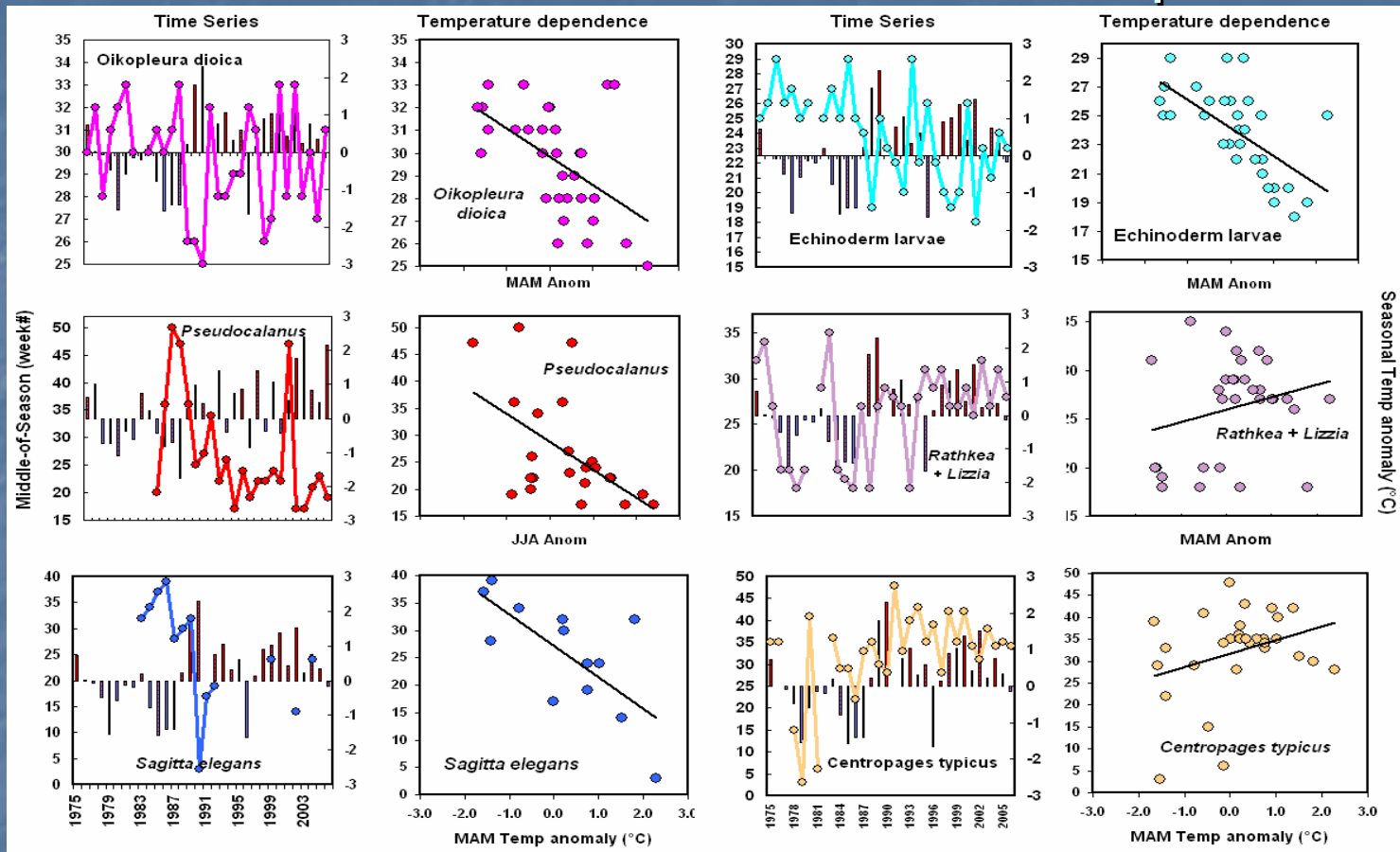
4. North Sea: Helgoland Roads Time Series



30+ years, excellent temporal and taxonomic resolution

'Start', 'Middle', 'End', and 'Length-of-season' estimated from cumulative abundance percentiles for ~100 taxa (W. Greve)

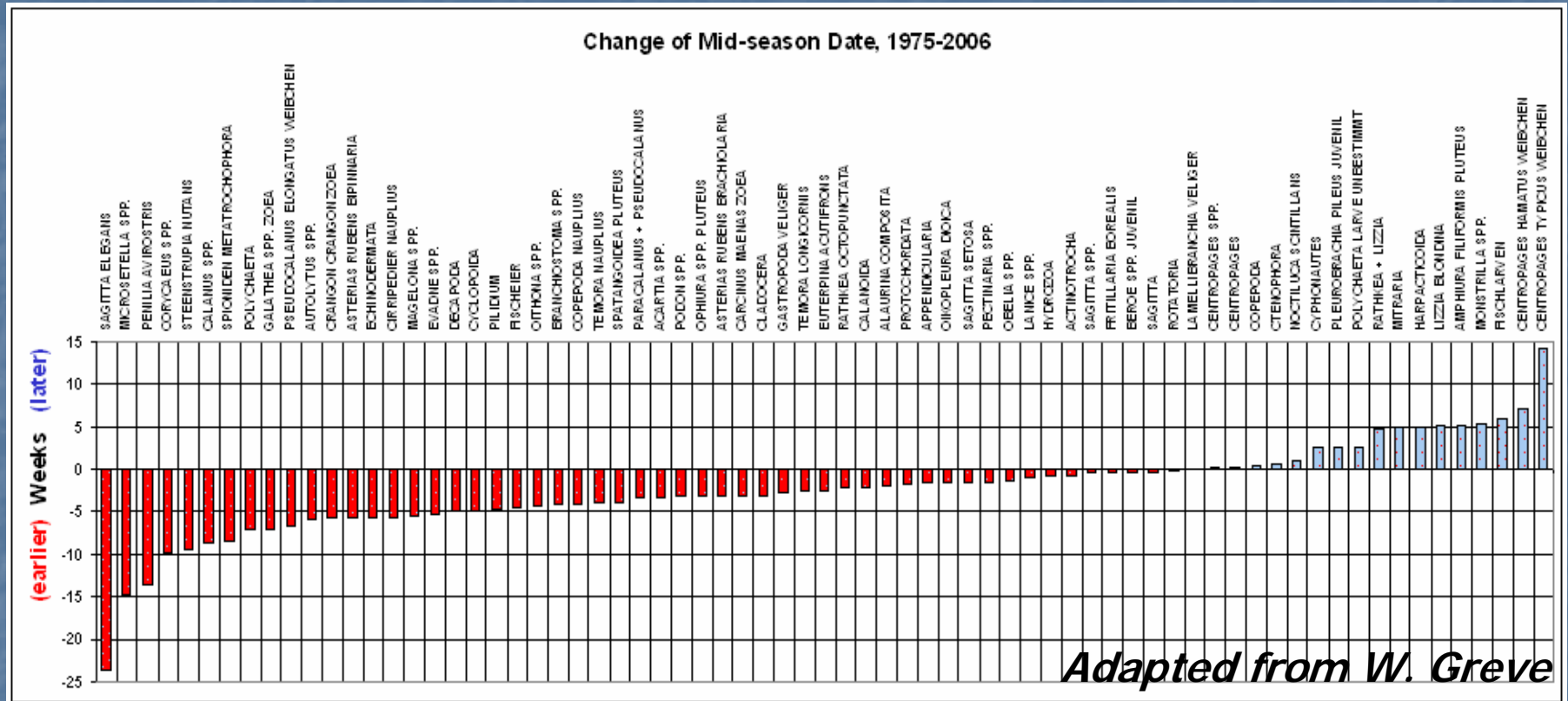
Helgoland Roads continued: Mid-season Date vs. Year & Temperature



Correlations of temperature anomaly and phenophase are significant for about half the taxa.

r is again usually (but not always) negative

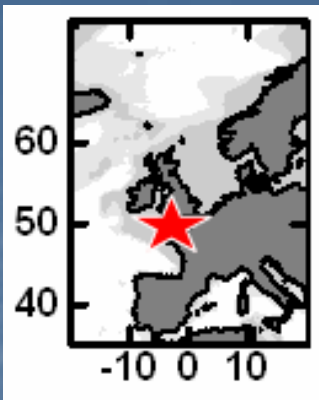
Helgoland Roads continued: Temporal trend of 'start', 'mid' and 'end' dates



About a third of the taxa have shifted earlier by >1 month

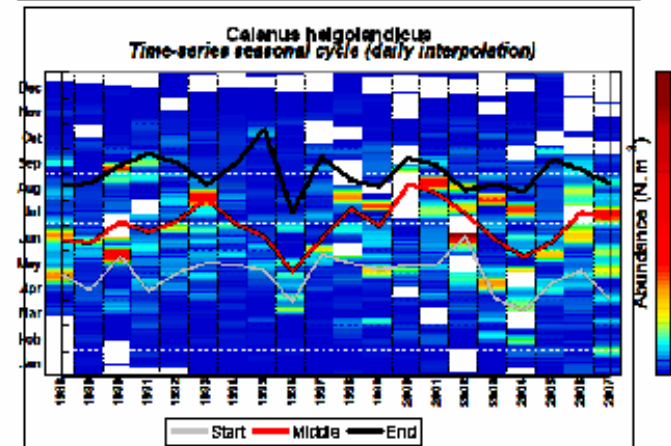
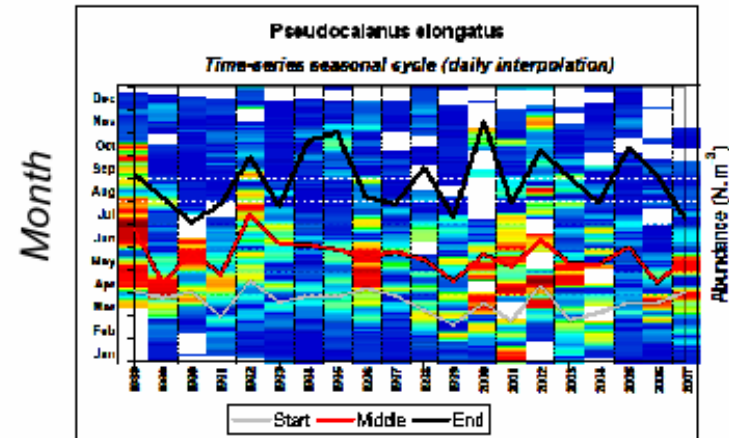
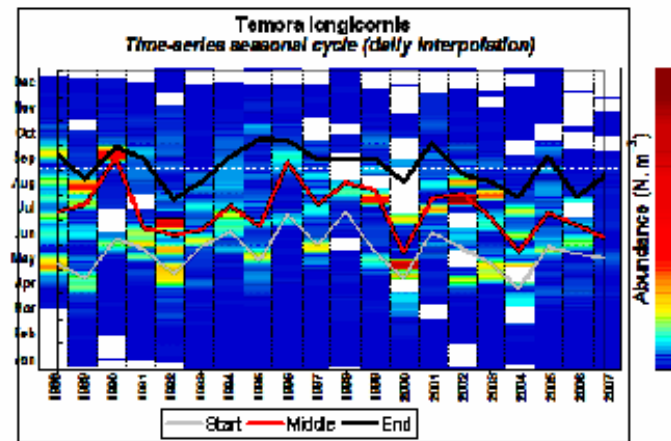
An additional third are earlier by half a month

But 12% have shifted later by > 1 month



5. Plymouth L4 time series

- Adapted the 'cumulative percentile' method for a less regular sampling interval
- Indices of 'start', 'mid' and 'end-of-season' track abundance contour plots
- Interannual synchrony (CPR vs Helgoland vs L4) is present but weaker than in NE Pacific
- L4 is not yet long enough to quantify trends in timing

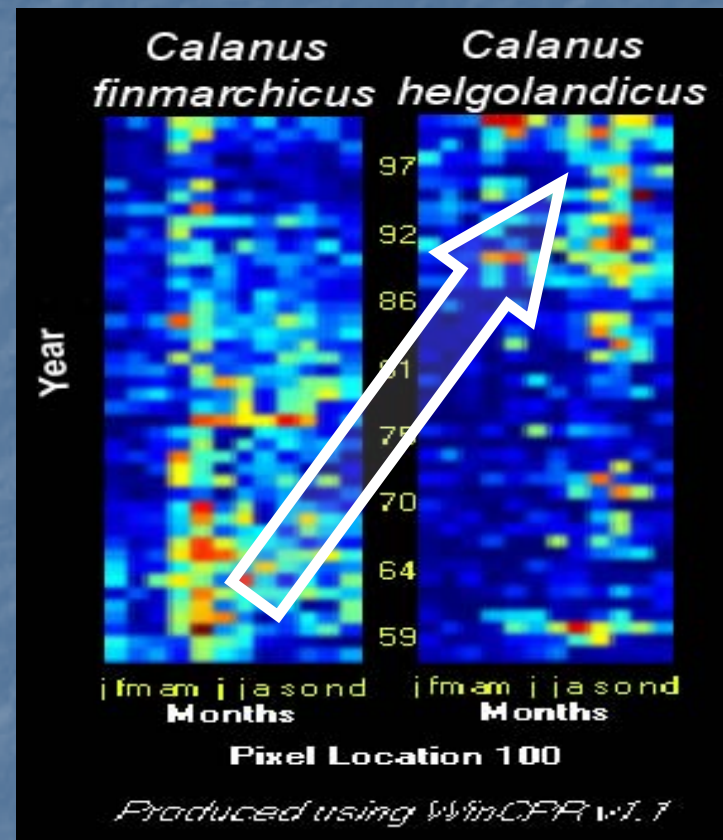
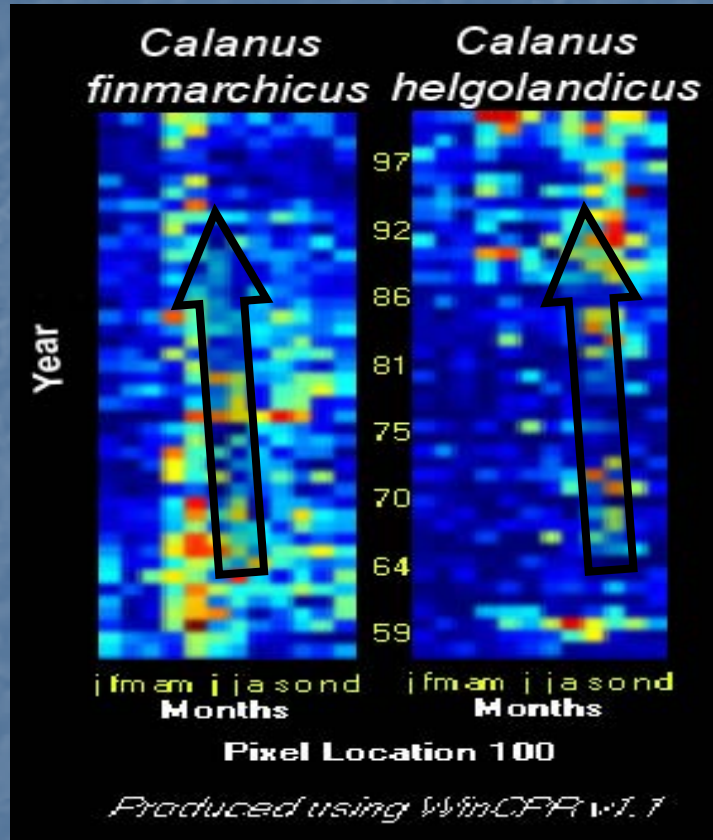


Year

Phenology Summary

- Zooplankton seasonal timing variation by 1-2 months is common (& big for animals with 4-12 month life spans!)
- Within-species timing often correlates with T°C:
'warmer' upper ocean -> 'earlier' timing
(strong link to climate variation/trend)
- But range of timing variability is larger than can be explained by Q10 effects stage duration. Other modes and mechanisms must contribute.
 - Some of these can and do counter the 'warmer = earlier' generalization

Complication #1: At the community level, trends in species dominance (right) may counter trends in phenology of the individual taxa that make up the community (left)

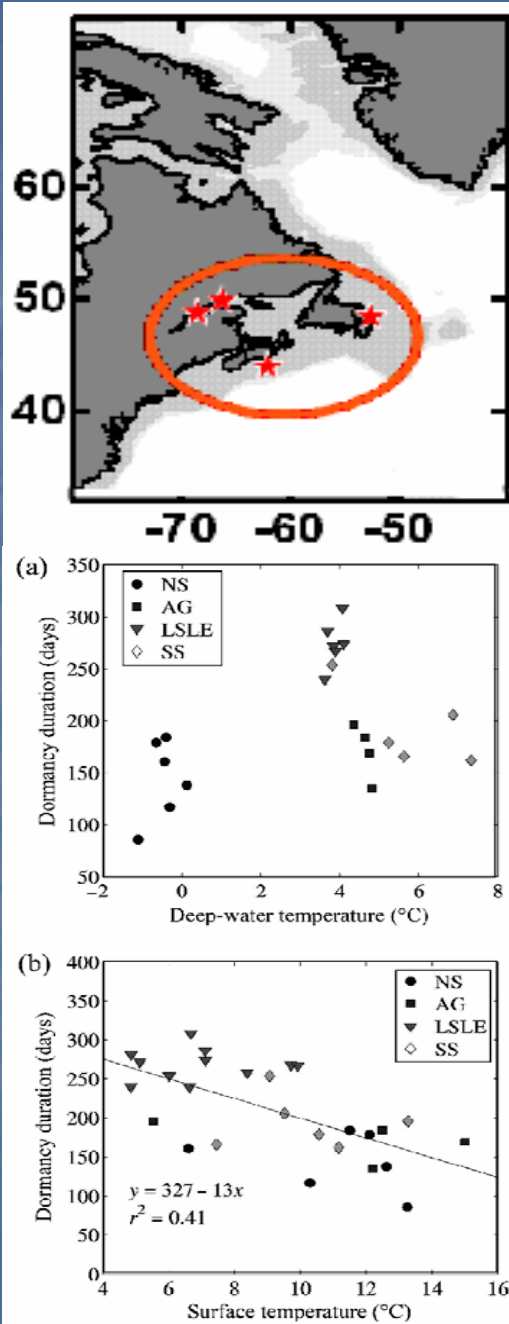


The North Sea has warmed $\sim 1^\circ\text{C}$ during the past 50 years, driving earlier seasonal timing of both *Calanus* species. However, the warming has also helped *helgolandicus* replace *finmarchicus* as the dominant *Calanus*.

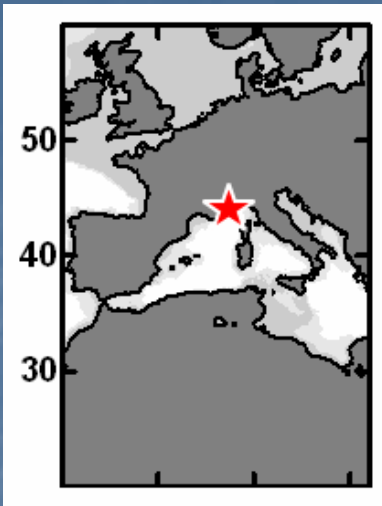
(see Beaugrand et al. 2003 and Helaouet & Beaugrand 2007 for more detail)

Complication #2. Seasonal dormancy is an important timing control, but regulation of entry & exit is complex

- In NW Atlantic, duration of *C. finmarchicus* dormancy is linked to upper ocean T°C in their growing season BUT
- No single environmental (T°, photoperiod, chl a, ...) gives consistent prediction of start or end date.
- 'Internal' control (lipid reserve, biological clock) also important



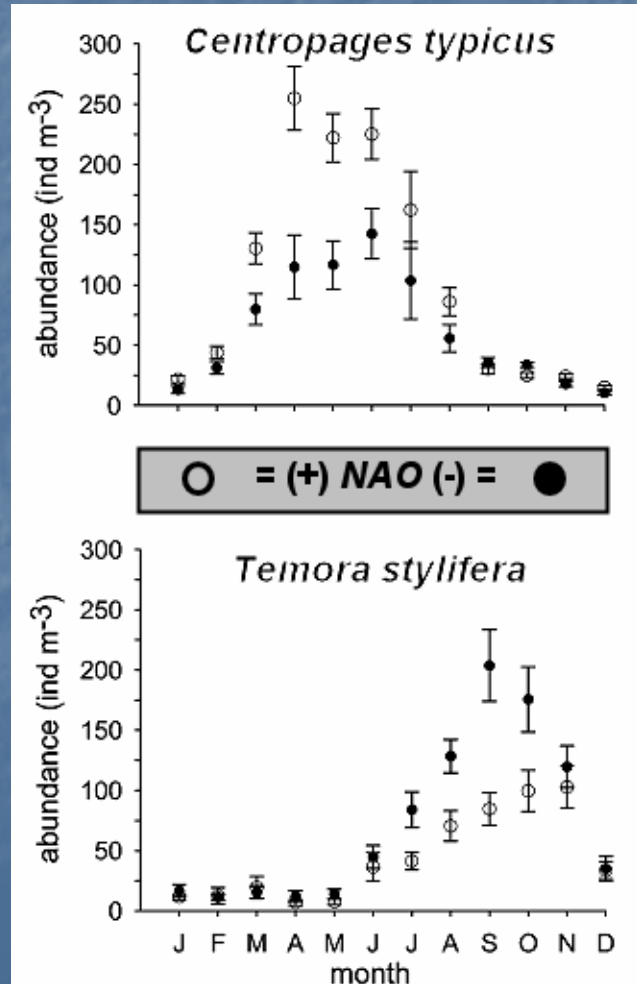
(C. Johnson et al. 2008)



Complication #3. Strong seasonal predation or competition may select against shared T°C dependence in the Balearic Sea (Ville-Franche)

When NAO swung from negative phase (moist, cool) to positive phase (dry, warm) in the late 1980s:

- *Centropages typicus* became earlier and more abundant but
- *Temora stylifera* became later and less abundant, while
- Salps (competitors) and jellyfish (predators) increased, especially nearshore (Molinero et al. 2005)



Suggestions for future research:

- Apply genomic/proteomic methods to study of dormancy onset/termination
- Timing 'misinformation' and climate change
- Role of differential survival in controlling within year phenology
- How fast can timing adaptations evolve?

Again, if you have a zooplankton time series you are willing to include in this comparison, please contact us.

