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Questioning the role of phenology shifts and trophic mismatching in a planktonic food web

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ABSTRACT

In a warming climate, differential shifts in the seasonal timing of predators and prey have been suggested to lead to trophic "mismatches" that decouple primary, secondary and tertiary production. We tested this hypothesis using a 25-year time-series of weekly sampling at the Plymouth L4 site, comparing 57 plankton taxa spanning 4 trophic levels. During warm years, there was a weak tendency for earlier timings of spring taxa and later timings of autumn taxa. While this is in line with many previous findings, numerous exceptions existed and only a few taxa (e.g. *Gyrodinium* spp., *Pseudocalanus elongatus*, and *Acartia clausi*) showed consistent, strong evidence for temperature-related timing shifts, revealed by all 4 of the timing indices that we used. Also, the calculated offsets in timing (i.e. "mismatches") between predator and prey were no greater in extreme warm or cold years than during more average years. Further, the magnitude of these offsets had no effect on the "success" of the predator, in terms of their annual mean abundance or egg production rates. Instead numerous other factors override, including: inter-annual variability in food quantity, high food baseline levels, turnover rates and prolonged seasonal availability, allowing extended periods of production. Furthermore many taxa, notably meroplankton, increased well before the spring bloom. While theoretically a chronic mismatch, this likely reflects trade-offs for example in predation avoidance. Various gelatinous taxa (*Phaeocystis*, *Noctiluca*, ctenophores, appendicularians, medusae) may have reduced these predation constraints, with variable, explosive population outbursts likely responding to improved conditions. The match–mismatch hypothesis may apply for highly seasonal, pulsed systems or specialist feeders, but we suggest that the concept is being over-extended to other marine systems where multiple factors compensate.

1. Introduction

Change in phenology (the seasonal timing of annually-repeated events) is a fundamental response to climatic warming, alongside range shifts and reductions in body size (Beaugrand et al., 2002; Parmesan and Yohe, 2003; Forster et al., 2012). As time series lengthen, the topic has received increasing research interest in terrestrial, limnic and marine environments (e.g. Both et al., 2009; Thackeray et al., 2013; Mackas et al., 2012). Despite numerous exceptions, some generalisations can be made. For example, in a warming climate spring processes tend to occur earlier and autumn processes shift later (Parmesan and Yohe, 2003; Richardson, 2008). Another broad generality is that the spring timing of primary production events on land and sea tends to change less (perhaps related to day-length and light; Wiltshire et al., 2008; Ji et al., 2010) than the timing of the primary consumers, which may relate more to temperature (Both et al., 2009; Aberle et al., 2012).

These differential shifts in phenology have long interested ecologists, because they have the potential to uncouple the food web. Cushing (1990) refined the "match–mismatch" hypothesis for marine fish, whose spawning within a relatively narrow time window was suggested to lead to their larvae either matching or missing the subsequent peak of their zooplankton food. Since then, the concept that differential phenology shifts lead to mismatches has expanded rapidly throughout the terrestrial, limnic and marine literature (Visser and Both, 2005; Ji et al., 2010; Miller-Rushing et al., 2012; Thackeray, 2012; Mackas et al., 2012).

While there is no doubt that a changing climate induces differences in the timing of predators and prey, the ecological ramifications of this are far from clear. The resultant mismatches have been suggested to lead to de-synchronisation of trophic levels, with implications for food web productivity (reviewed by Richardson, 2008). In contrast Thackeray (2012) emphasised that, in planktonic systems at least, this decoupling was based more on speculation

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than on fact. For example (Thackeray, 2012) could find only about a dozen plankton studies that have measured the relative shifts in phenology across multiple trophic levels. Of these, he found only one (Winder and Schindler, 2004) that actually quantified whether the degree of mismatch had any adverse effect on the grazer populations. Terrestrial workers have richer time-series and more advanced understanding, and are building on the match–mismatch hypothesis. Thus life-cycles are examined in the context of multiple trade-offs; for example mistiming with optimum food may not be so selectively disadvantageous if this means a lower predation risk (e.g. Both et al., 2009; Lof et al., 2012). Within aquatic systems these refinements are also being introduced to understand the role of phenology shifts in structuring the food web (Varpe, 2012; Thackeray et al., 2013; Durant et al., 2013).

The L4 site in the Western English Channel has been sampled on a weekly basis since 1988. It has warmed in this time, as part of the rapid, larger-scale warming of the NE Atlantic area in the last 50 years (Smyth et al., 2010; Holt et al., 2012). Its strong seasonality, plus a 25-year history of intensive sampling of multiple trophic levels, also make it a good site for examining phenology shifts and the resultant timing offsets. We decomposed the match–mismatch hypotheses into 3 sequential hypotheses for testing. First, that warmer years lead to earlier spring- and later autumn timings; second that the taxa show differential timing shifts such that extreme years lead to larger mismatches between trophic levels; and third that years with large mismatches are associated with measureable penalties for species in terms of decreased abundance or secondary production. We analysed these effects at both species and functional group levels, using four indices of seasonal timing. A well-studied copepod, *Calanus helgolandicus*, was selected as a "case study" of how offsets in timing with food affects various indices of performance.

2. Methods

2.1. Sampling overview

The Plymouth L4 monitoring site is 13 km SSW of Plymouth in a mean water depth of 54 m (Harris, 2010; Smyth et al., 2010). It is classified as a transitionally mixed site (Southward et al., 2005) that stratifies in summer. Its dynamic hydrography is influenced both by inputs of more oceanic water during periods of strong SW winds as well of riverine flood water influence from the rivers Tamar and Plym outflowing at Plymouth (Rees et al., 2009).

Sampling at L4 is ongoing and has been on a weekly basis, weather permitting, since March 1988 (http://www.westernchannelobservatory.org.uk/). This sample set encompasses 1085 sampling events up to December 2012, the last time-point considered in this analysis. Initially only zooplankton and surface temperature were measured, but this was augmented later with CTD profiling and nutrients, chlorophyll *a* (Chl *a*), phyto- and microzooplankton species abundance and biomass, plus *Calanus helgolandicus* egg production rates; key measurements that are included in our study (Table 1). The time-span thus includes 25 years of zooplankton and temperature data and typically about 20 years for the other data.

2.2. L4 sampling methods

For full details of sample analysis methods we refer the reader to http://www.westernchannelobservatory.org.uk/ and the other papers in this Special Issue and the previous one devoted to the L4 site (Harris, 2010). Key papers describing the sampling methods and main seasonal- and longer-term trends are Smyth et al. (2010) for physics, nutrients and Chl *a*, Widdicombe et al. (2010) for phyto- and microzooplankton and Eloire et al. (2010) and Highfield et al. (2010) for holo- and meroplankton.

In brief, surface water temperatures were derived in the early L4 years from a thermometer in a stainless steel bucket of surface water and later by this method alongside CTD-based surface measurements (Table 1). Surface measurements of the major nutrient species were taken weekly at L4 since 2000. After 2004 analysis was on live (rather than frozen) samples to overcome possible sampling and storage artefacts. All nutrient concentrations were determined using recognised analytical techniques (Woodward and Rees, 2002).

For Chl *a*, 1 or 2 L of seawater was filtered onto a Whatman® GF/F filter which was stored in liquid nitrogen until analysis. For the analysis stage, pigments were extracted from the thawed GF/F filter into 2 mL methanol (Llewellyn et al., 2005) and sonicated for 35 s. These extracts were then centrifuged to remove filter and cell debris (5 min at 4000 rpm) and analysed using reversed-phase HPLC (Barlow et al., 1997). Pigments, including Chl *a*, were identified using retention time and spectrally matched using photo-diode array spectroscopy (Jeffrey and Wright, 1997). Pigment concentrations were determined by response factors, generated at the time of instrument calibration, using a suite of pigment standards. For fluorometrically-determined Chl *a*, 0.1 L of

Table 1
Data coverage and method summary for the variables presented here. Major gaps in coverage are marked as footnotes.

Variable (units)	Method used	Span of coverage	No. of years of data (no. of timepoints)
Surface temperature (°C)	Thermometer in bucket (1988–2012) Surface CTD (2000–2012)	March 1988–December 2012	25 (1070)
Surface nutrients (μMol L^{-1})	CTD profile	January 2000 –December 2012	13 (490)
Surface Chl *a* (mg m^{-3})	Fluorescence (1988–2012) and HPLC (2000–2012) analysis	February 1992–December 2012	21 (931)
Phyto- and microzooplankton biomass (mg C m^{-3})	Taxonomic analysis by microscopy of 10 m CTD depth samples	October 1992–December 2012	19[a] (827)
Mesozooplankton biomass (mg C m^{-3})	CHN analysis of 200 μm WP2 net samples from 50 m to 0 m	January 1993–July 1998	5[b] (135)
Mesozooplankton abundance (No. m^{-3})	Paired WP2 nets from 50 m to 0 m	March 2012–December 2012	25 (1085)
Calanus helgolandicus egg production rate (eggs $female^{-1}$ d^{-1})	25 females incubated for 1 day at ambient L4 temperature	February 1992–December 2012	20[c] (794)

[a] Includes a gap from October 1993–June 1995 and absent data for aloricate forms during 2005.
[b] Complete annual coverage in two years only: 1993 and 1997.
[c] Includes a gap from September 2006–September 2007.

seawater was filtered through GF/Fs in triplicate and the JGOFS (JGOFS, 1994) protocols adhered to.

Detailed phyto- and microzooplankton taxonomic microscope counts were from water samples collected from 10 m depth. These samples were formalin-preserved for coccolithophore enumeration and preserved in 2% acid Lugols iodine solution for all other taxa >2 μm. These were analysed using the Utermöhl (1958) technique, usually settling 100 ml of the formalin samples and 50 ml of the lugols (see Widdicombe et al., 2010). Cell volumes were calculated from approximations to simple geometric shapes, from which carbon contents were calculated based on equations of Menden-Deuer and Lessard (2000).

Mesozooplankton were collected each week with two replicate (successive) 0–50 m vertical hauls with a WP2 net (0.57 m diameter, 200 μm mesh). Each of these were analysed in two aliquots, the first being a stempel pipette – derived small subsample for enumeration of the more numerous taxa and the second larger fraction, often one-half to one-eighth, analysed for the larger or rarer taxa. The weekly *Calanus helgolandicus* egg production experiments were based on females collected with a slow, short duration oblique net haul through the surface layer, as described in Maud et al. (2015). Briefly, this involved 24 h incubations of 5 batches of 5 freshly caught adult females in filtered seawater. These were maintained for 24 h at ambient L4 surface temperature in 500 μm mesh-bottomed 2 L chambers to reduce egg cannibalism. After the incubation, eggs were screened off and counted under a microscope to quantify mean egg production rate as the number eggs produced per female per day.

2.3. Data sources

Even nowadays relatively few time series span >20 years, are weekly in frequency and provide data spanning multiple trophic levels (Mackas et al., 2012). This combination is required to address our study hypotheses, but we needed to make some trade-off decisions between vertical data coverage and duration of measurements. For example modern L4 monitoring includes profile–based data on the hydrography and phytoplankton pigments. However in the valuable early years that contained some of the greatest climatic extremes of interest, key supporting data were just collected from the surface. We have therefore used these more basic measurements to ensure that the measurement time-span is as long as possible (Table 1).

We analysed the data at two broad levels of taxonomic resolution. At the broader level we examined the timing and the seasonal- and inter-annual variability of 11 major functional groups or bulk indices (Table 2). At the finer level we selected species (or where not possible then genera or broader taxa) that were identified consistently and for as long as possible. While ~400 micro- and mesozooplankton taxa are recorded at L4, most are rare and we further restricted the taxonomic list to those that are sufficiently abundant to provide a repeated signal of their seasonality. The 46 selected taxa, analysed alongside the 11 functional groups, are shown in Table 3.

For ciliates and heterotrophic dinoflagellates which comprise numerous relatively rare species, we pooled these at the genus and size level (e.g. "*Gyrodinium* spp." or "*Strombidium* small") and then calculated timings based on their summed biomass at each sampling timepoint. While this misses possibly critical species-level information, it is pragmatic in dealing with species rarity and identification consistency.

2.4. Calculation of temperature anomalies

We first calculated surface water temperature anomalies for each sampling time-point. These were calculated as the recorded value minus the 10-day running mean value for the given Julian Day of sampling, based on the means for the entire 25-year time series. These anomalies were then averaged into two-month blocks for each year. Provisional analyses of these showed a degree of temporal autocorrelation, as would be expected (e.g. if it is a very cold winter, the high specific heat capacity of water means that temperatures will also likely remain cool into spring).

Preliminary analyses (not reported here) showed that summer water temperature anomalies tended to relate best to expected phenology shifts (i.e. spring species becoming earlier in warmer years) better than either winter or spring temperatures. This was also found in a previous phenology analysis of the 1988–2007 L4 data by Mackas et al. (2012). Thus the anomaly over April–August inclusive, spanning the main duration of seasonal warming,

Table 2
Composition, sampling method and measurement units of the 11 plankton functional groups analysed. Note that some component taxa, such as members of the fish larvae and medusae, belong to multiple functional groups but their primary classifications for this analysis are as below.

Functional group	Depth, data source	Units	Composition
Chlorophyll *a*	0 m (CTD)	mg chl *a* m^{-3}	–
Nanoflagellates	10 m (CTD)	mg C m^{-3}	See Widdicombe et al. (2010)
Coccolithophores	10 m (CTD)	mg C m^{-3}	See Widdicombe et al. (2010)
Phaeocystis spp.	10 m (CTD)	mg C m^{-3}	See Widdicombe et al. (2010) Includes single cells
Diatoms	10 m (CTD)	mg C m^{-3}	See Widdicombe et al. (2010)
Ciliates	10 m (CTD)	mg C m^{-3}	*Strombidium* spp. *Mesodinium rubrum* and *Akenasia stellaris* are major biomass contributors
Autotrophic dinoflagellates	10 m (CTD)	mg C m^{-3}	Autotrophic forms defined here as those with chloroplast See Widdicombe et al. (2010)
Heterotrophic dinoflagellates	10 m (CTD)	mg C m^{-3}	*Gyrodinium spirale*, *Noctiluca scintillans*, *Polykrikos schwarzii*, *Protoperidinium depressum*, *P. ovatum* are major biomass contributors due to large size
Meroplankton	0–50 m (WP2 net)	No. m^{-3} Biomass data (mg C m^{-3}) in period 1993–1998	Larvae of cirripedes, echinoderms, molluscs and decapods are most common
Holoplankton	0–50 m (WP2 net)	No. m^{-3} Biomass data (mg C m^{-3}) in period 1993–1998	Copepods, cladocerans and appendicularians are most common
Carnivorous zooplankton	0–50 m (WP2 net)	No. m^{-3} Biomass data (mg C m^{-3}) in period 1993–1998	Chaetognaths, medusae, siphonophores, ctenophores, *Tomopteris* spp., fish eggs and larvae, amphipods, euphausiids and the copepods *Euchaeta* spp. *Candacia armata* and *Ditrichocorycaeus anglicus*

Table 3
Individual taxa and whole functional groups (FG, underlined) analysed here. Abbreviations are; N: small flagellates (>2 μm); C: ciliates; HD: heterotrophic dinoflagellates;); M; meroplankton; H: holoplankton; P: carnivorous zooplankton. Their mean Julian Day (JD) of appearance and change in days per 1 °C temperature are averages of all 4 timing indices as plotted in Fig. 6a. The direction of changes (minus means earlier when warmer) from the individual indices are coded with one symbol for R^2 < 10%, two symbols for R^2 10–30% and three symbols for R^2 > 30%. Where all 4 relationships were in the same direction and/or one R^2 was >30% the mean shift value is in bold large font. Species are ordered into functional groups. Inter-annual variability is calculated as the year of maximum average abundance divided by the year's value when mean abundance is minimum. To make this inter-annual comparison fair across all taxa here, only 19 years with data for all taxa throughout the year were included (Table 1). ND: insufficient data for calculation. Final column describes the extent of their seasonal variability (calculated as the calendar month value when mean abundance is maximum divided by that of the minimum).

Taxon or functional group	Mean JD	Phenological change per 1 °C increase in temperature					Inter-annual variability	Seasonal variability
		Threshold	25%	50%	c.o.g	Mean (days)		
Nanoflagellate biomass (FG)	140	+	+	+	+	**12**	3.9	3.1
Colourless flagellates[a] (N)	153	–	––	++	+	–18	ND	ND
Bodonids[a] (N)	231	–	–	–	–	–13	ND	ND
Phaeocystis spp. biomass (FG)	108	–––	–––	–––	––	**–15**	2632	5200
Diatom biomass (FG)	145	+	–	–	–	–8	12	30
Autotrophic dinoflagellate biomass (FG)	199	+++	–	–	+	**4**	21	386
Coccolithophore biomass (FG)	180	+	+	++	++	**24**	10	43
Ciliate biomass (FG)	127	––	+	+	+	3	8.1	30
Mesodinium rubrum (C)	122	–	–	++	+	1	7.2	52
Strombidium spp. small (C)	150	+	–	–	–	–4	7.9	9.6
Strombidium spp. medium size (C)	147	–	–	–	–	**–13**	16	7.7
Strombidium spp. large (c)	148	–	–	–	+	–8	32	21
All other ciliates[b] (C)	167	–––	–––	–––	–––	**–72**	ND	ND
Heterotrophic dinoflagellate biomass (FG)	166	–	–	–	–	**–7**	7.7	49
Gyrodinium spp. (HD)	164	–	–––	––	––	**–39**	28	23
Katodinium spp. (HD)	167	–	–	–	–	**–8**	15	38
Noctiluca scintillans (HD)	241	+++	++	++	++	**44**	239	115,250
Protoperidinium spp. (HD)	149	+	+	–	+	5	12	22
Small Peridinian species[a] (HD)	171	–––	–	––	–––	**–32**	ND	ND
All other colourless dinoflagellates[c] (HD)	160	–	++	+	+	16	7.7	17
Meroplankton abundance (FG)	107	+	++	–	+	3	7.0	46
Anemone larvae (M)	68	–	ND	ND	+	–4	1035	8866
Polychaete larvae (M)	118	–	++	+	+	12	6.4	11
Gastropod larvae (M)	186	–	+	+	+	2	39	48
Bivalve larvae (M)	213	ND	ND	ND	++	28	29	11
Echinoderm larvae (M)	195	ND	–	–	–	**–10**	14	1860
Cirripede nauplii (M)	92	+	+	+	+	**4**	14	2699
Cirripede ciprid (M)	112	+	+	+	++	**11**	133	6333
Decapod larvae (M)	111	+	+	+	–	3	3.8	23
Holoplankton abundance (FG)	139	+	+	+	+	**7**	2.4	4.8
Appendicularians (H)	134	+	+	+	+	5	15	272,381
Evadne spp. (H)	143	++	+	–	–	5	14	1945
Podon spp. (H)	143	+	–	–	–	–7	8.1	36
Gammarid amphipods (H)	212	–	–	–	–	–4	11	51
Copepod nauplii (H)	143	–	+	+	+	5	14	17
Acartia clausi (H)	163	–	–	–	–	**–16**	19	48
Calanus helgolandicus (H)	139	––	–	+	+	–4	4.2	19
Centropages typicus (H)	178	+	+	+	+	**17**	12	28
Euterpina acutifrons (H)	214	ND	+	+	+	13	21	10
Metridia lucens (H)	147	ND	ND	ND	–	–21	6563	38
Microsetella spp. (H)	236	ND	ND	ND	+	28	633	16
Oithona spp. (H)	114	+	–	–	–	–4	8.6	6.0
Oncaea spp. (H)	268	–	–	–	+	1	4.1	18
Paracalanus parvus (H)	170	–	+	–	+	0	2.8	9.4
Pseudocalanus elongatus (H)	105	–	–––	––	––	**–14**	4.6	6.8
Subeucalanus spp. (H)	255	+	+	+	–	5	44	508
Temora longicornis (H)	157	+	–	+	–	1	1.6	111
Carnivorous zooplankton abundance (FG)	199	+	+	+	+	10	6.1	12
Medusae (P)	178	+	+	+	+	**6**	47	118
Siphonophores (P)	206	–	+	–	–	–6	13	85
Ctenophores[d](P)	139	–––	–––	–––	–––	**–66**	32	1925
Chaetognaths (P)	190	–	+	+	+	2	11	18
Candacia armata (P)	179	ND	ND	ND	+	18	ND	ND
Ditrichocorycaeus anglicus (P)	233	–	+	+	+	2	4.4	14
Fish eggs (P)	101	+	+	–	+	3	45	128
Fish larvae (P)	95	+	––	–	+	–7	14	94

[a] Data obtained consistently by one analyst (Derek Harbour) until end of 2004 so only this period used.
[b] Represents pooled biomass of all ciliates other than the genera *Strombidium* and *Mesodinium*.
[c] Data represent pooled biomass of all heterotrophic dinoflagellates except the genera *Gyrodinium*, *Katodinium*, *Protoperidinium* and *Noctiluca*.
[d] Only last 5 years of data available for this analysis due to rarity before so the relationship is still questionable.

was chosen as an index of annual water temperature for the analyses presented here.

2.5. Calculation of phenology indices

Since studies have used different indices of timing and their choice has been suggested to be important to the outcome of the study (Ji et al., 2010; Thackeray et al., 2013) we used and compared 4 different timing indices, rather than pre-selecting a single "best" index. These were first; "Threshold", the timing of the initial increase of abundance above a defined value (analogous to the "median plus 5%" criterion often used for phytoplankton timing); second, the time that abundance reaches the 25th cumulative percentile of the annual abundance; third, the timing of the 50th cumulative percentile; and fourth, the centre of gravity of the population. The four indices tend to mark respectively later parts of the seasonal cycle, with threshold and 25% cumulative sensitive to initiation events at the start of the growth season and the 50% and centre of gravity occurring later and integrating across the whole growth season.

Detailed methods for calculating cumulative percentiles and centre of gravity are presented in Mackas et al. (2012). Our only departure from these was for a few of the taxa that occurred mainly in autumn/early winter (e.g. *Oncaea* spp.), which had the declining phase of their seasonal cycle often continuing into the early months of the following year. In these cases, the Julian Day (JD) assignations of the January–February declining phase abundances were adjusted (to 365 + JD), and removed from the subsequent years calculation, to keep single seasonal cycles together for calculations of timing. Because we also wanted to look at the initiation phase of increases we also used a threshold value. This was defined as the JD (January 1st = 1) on which abundance increased and was maintained above a threshold value, typically set as half of the long-term mean value. This was the only index of the 4 used that allowed subjective decisions on the level at which to set the threshold and what constituted a maintenance of the population above that level. Despite this disadvantage, the use of thresholds allowed us to observe and allow for patterns such as spring and autumn peaks of varying relative sizes, which can cause problems with more objective classifications of timings.

The objective was not to test which index was the "best", but rather to use a suite of timings to ensure that simply the choice of index was not influencing our conclusions. For each taxon/functional group and for each timing index, we plotted timing against April–August temperature anomalies for each of the years and derived the slope value and its significance level. These were then averaged across each of the 4 timing indices for presentation in Table 3 and Fig. 6.

2.6. Calculation of trophic level mismatch

For each of the taxa/functional groups, we quantified, for each timing index, and for each year, the JD of its timing minus that of its food. These provided indices of "mismatch", and the mean of the separate determinations using each phenology index were then obtained to give a single, average mismatch value for each species for each year.

We conducted preliminary analyses comparing timings of grazers with various food "yardsticks" (for example *Acartia clausi* timing was compared with those of combinations of biomass of the various phyto- and microzooplankton functional groups). However these required often subjective decisions of what each species actually eats, and in any case, trial analyses returned similar results to those provided by the simple bulk analysis of Chl *a*. Thus to reduce the problem of presenting too many comparisons we eventually simplified to using Chl *a* as the common food yardstick for the various grazer taxa. This provides a good proxy for a range of small autotrophic and heterotrophic foods (see Fig. 1b and c) and has the key advantage of providing more years of coverage than the more refined phyto- and microzooplankton biomass estimates (Table 1). In the same way, total mesozooplankton abundance (excluding carnivores) provided the food yardstick from which to compare the timings of carnivorous zooplankton.

2.7. Quantifying the penalty for mismatch

Calculated mismatches were often large and/or had negative values, signifying that grazers sometimes increased before their food, potentially reducing their ability to feed optimally. To assess whether these had any detrimental effect on the mismatched grazers we selected indices of their annual "performance". For the whole species set we defined their mean annual abundance in the same year as a simple index of performance. For the case study species *C. helgolandicus* (see Section 2.8) we were also able to use their mean annual egg production rate as an additional performance index. These indices were regressed as response variables against the same season's degree of mismatch (again, calculated as a the mean mismatch based on each timing index).

2.8. Calanus helgolandicus case study

Calanus helgolandicus provides a good case example of how a single species overlaps and interacts with its food. It is abundant at L4, large enough for more of its copepodite stages to be caught, and its egg production rate is measured weekly. As an index of performance, the mean monthly egg production rates for the period March–August were calculated over the 20 years of measurements. These months were selected because they coincide with peak egg production rates (Maud et al., 2015), with the seasonal increases of *C. helgolandicus* and Chl *a* (Table 3), and because they negate the effects of a few data gaps earlier and later in the year (Table 1). By relating the annual timing offsets (*C. helgolandicus* abundance versus Chl *a*) to the mean egg production rate, we tested the hypothesis that years with large mismatches were detrimental to egg production.

To determine how well the calculated mismatches related to the overlap with food, we used an annually integrated "food benefit index" (*FBI*). This was calculated by summing over the successive sampling time points of the year, t_n as:

$$FBI = \Sigma(t_n - t_{n-1}) \cdot F_n \cdot a_n \quad (1)$$

where F_n is the Chl *a* value measured at the time-point and a_n is the respective *C. helgolandicus* abundance, normalised as a fraction of its mean value for the year. This is similar to the calculation of "area of overlap" with food (i.e. overall success) used by Durant et al. (2005) although here grazer abundance was first normalised across years to reduce the effect of their inter-annual variability. To determine the role mismatch plays (compared to variation in food amount) in the *FBI* we regressed the *FBI* indices against the mean mismatch of *C. helgolandicus* and Chl *a*.

3. Results

We first describe the general "average" pattern of the seasonal cycle for the major functional groups, and then their inter-annual variability in abundance. These provide the context for understanding variability in timing.

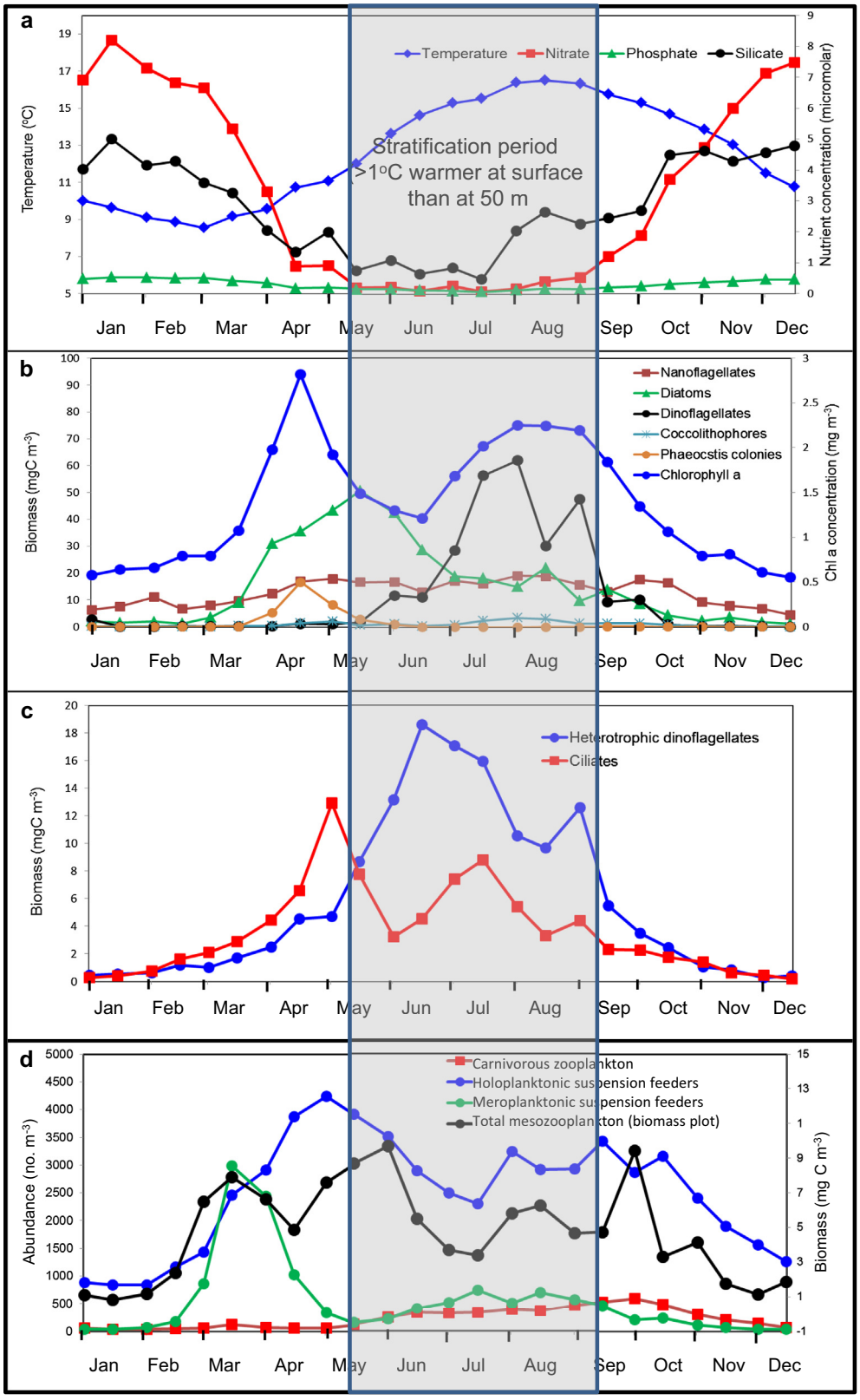

Fig. 1. Seasonal succession of (a) environmental variables, (b) phytoplankton biomass (left axis) and Chl *a* (right axis), (c) microzooplankton biomass, (d) metazoans (abundance of carnivores, holo- and meroplankton on left axis, total mesozooplankton biomass on right axis). Data are averaged within 2 week blocks to present these climatologies. The biomass units are the same to enable direct comparison, but note that the depth integration of samples differed (Table 1). Also for mesozooplankton biomass, only 135 samples between 1993 and 1998 were available, compared to 19 comparable years of typically weekly data for the other values.

3.1. Average seasonality

The L4 site experiences considerable summer warming (typically from ~9 °C in March to ~17 °C in August) that is typical of temperate latitudes (Fig. 1a). Summer warming is associated with seasonal stratification roughly between June and September, with concomitantly low nutrient concentrations; nitrate is limiting and below the limit of detection for this period.

Phytoplankton biomass comprises a background population of flagellates which increase steadily into summer (Fig. 1b). Superimposed on that is firstly a diatom bloom often starting in April and a highly variable *Phaeocystis* spp. bloom, present only in some years. With the onset of summer stratification and nutrient limitation, Chl *a* levels dip often around June as the diatom bloom is later replaced by a peak of autotrophic dinoflagellates. Coccolithophores increase in the autumn of some years but overall their contribution to biomass is minor.

There is a rich microzooplankton protist assemblage at L4, dominated by the ciliate and colourless dinoflagellate (defined here as heterotrophic) functional groups (Fig. 1c). Ciliates typically peak at around the same time as the spring diatom bloom, whereas the stronger peak of dinoflagellates appears later. The high C biomass of microzooplankton compared to the mesozooplankton suggests their importance in this inshore shelf system. The seasonal cycle of micro-metazoa (small species and stages that pass through the 200 μm WP2 net) is not depicted in Fig. 1, although these also appear to be an important component of the L4 plankton (Elaine Fileman, PML unpublished data).

For the metazoans retained on the 200 μm net, the first spring peak is of meroplankton, which often increase over a month before the spring bloom (see also Smyth et al., 2014). The non-carnivorous holoplankton also start increasing before the spring bloom and often sustain multiple peaks right through until October (Fig. 1d). In contrast the carnivorous zooplankton typically peak during autumn.

3.2. Inter-annual and seasonal variability in abundance

Simple linear regression of the April–August temperature anomalies (Fig. 2a) suggests that the temperature has warmed ($y = 0.0276x - 0.3574$, $R^2 = 0.17$, $p = 0.038$, $n = 25$). This accords with the longer timescale warming trend in the Western English Channel, of 0.5 °C over the second half of last century (Smyth et al., 2010; Holt et al., 2012). Great year-to year variability in L4 conditions was observed, particularly before 2000 when several years of elevated temperatures were interspersed with cold seasons (Fig. 2a). Since 2010 there has been a rather less fluctuation in temperature.

The amplitude of seasonal- and inter-annual variability in the abundance of taxa provides a context for understanding timing variability (Fig. 2, Table 3). Among the phytoplankton (Fig. 2b) the individual functional groups show great inter-annual variability in biomass. While the very high average diatom biomass in 2011–2012 is eye catching, much greater inter-annual variability is in fact shown by coccolithophores, *Phaeocystis* spp. and autotrophic dinoflagellates. Further, the years with most intense/long lasting diatom blooms coincided with low autotrophic dinoflagellates (likely due to different environmental requirements). This partial replacement of one functional group with another resulted in lower amplitude fluctuations in surface Chl *a* (Fig. 2b).

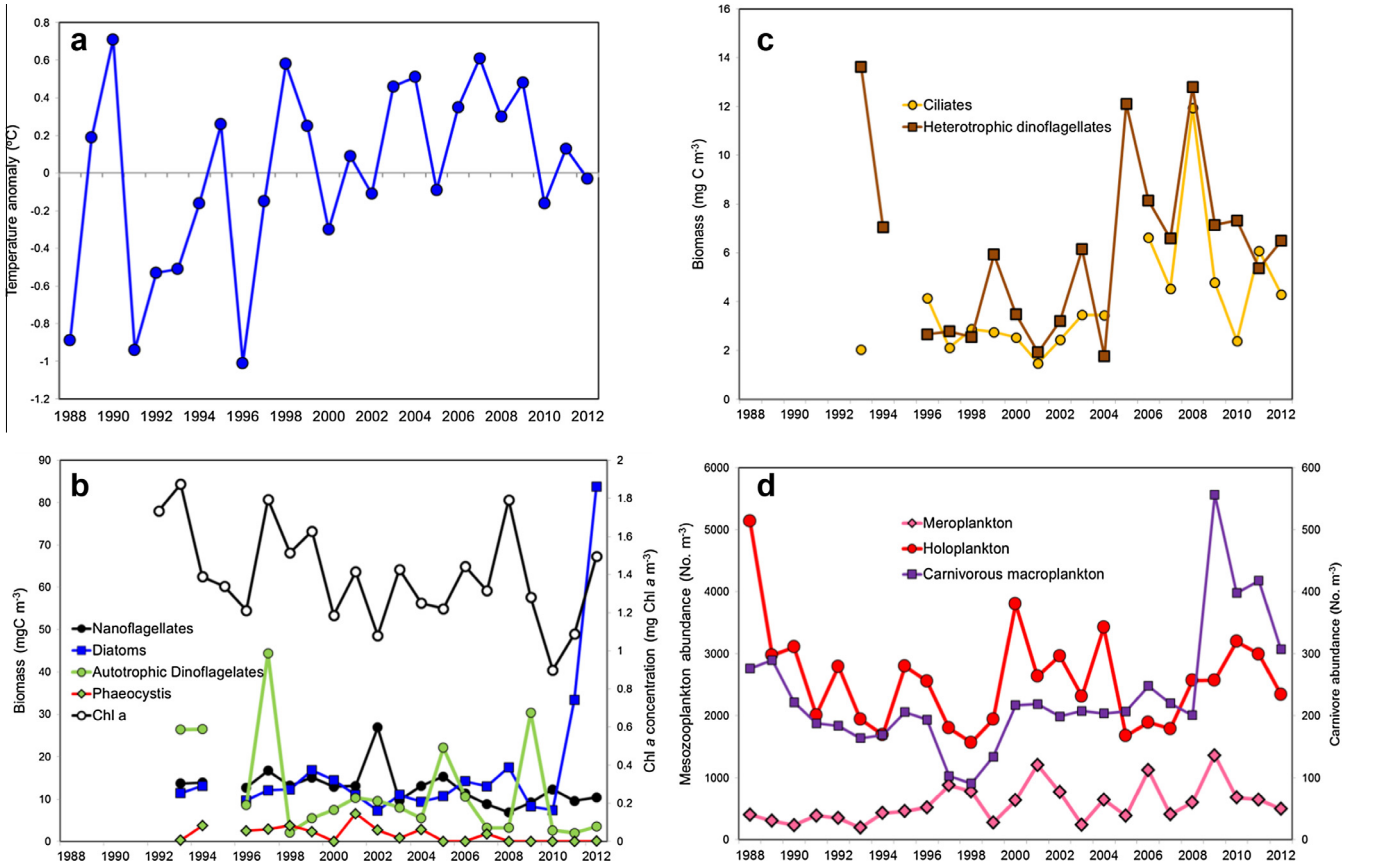

Fig. 2. Inter-annual variability of (a) April–August temperature anomaly; (b) biomass of autotrophic functional groups (left axis) and Chl *a* concentration (right axis); (c) ciliates and heterotrophic dinoflagellates; (d) metazoans (holo- and meroplankton on left axis and carnivorous zooplankton on right axis).

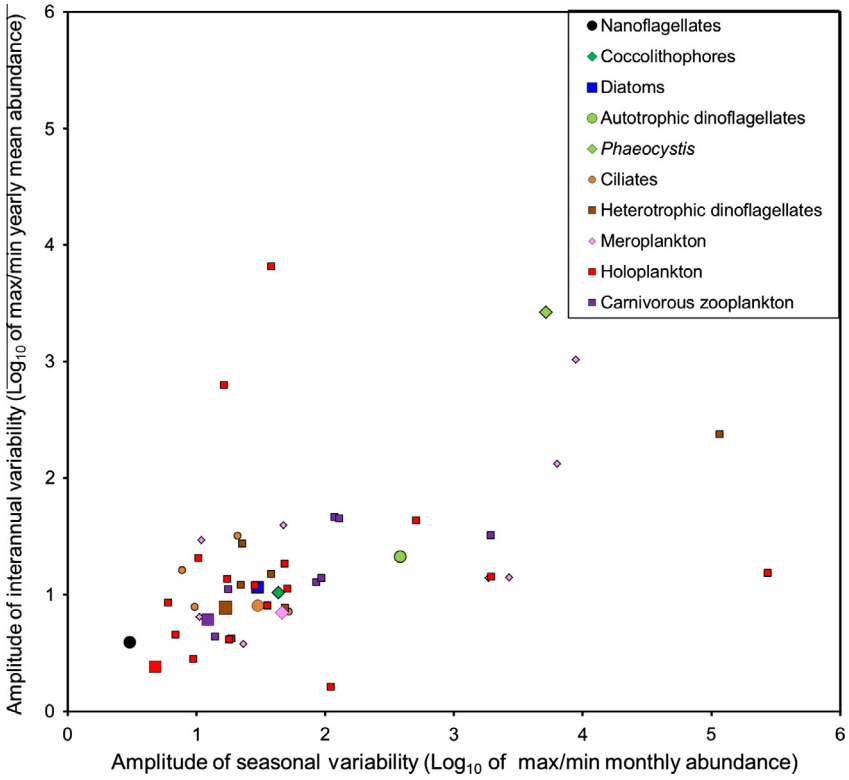

Fig. 3. Inter-annual versus seasonal variability of the 56 taxa/functional groups. These are the logged values in the final two columns of Table 3 (see its caption for calculation methods). Throughout this plot and all the subsequent plots, symbol shape and colour have been standardised. Small symbols represent the component taxa in each functional group, large symbols represent the values for the whole functional group; i.e. total biomass (for phyto- and microzooplankton) or total abundance (metazoans). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

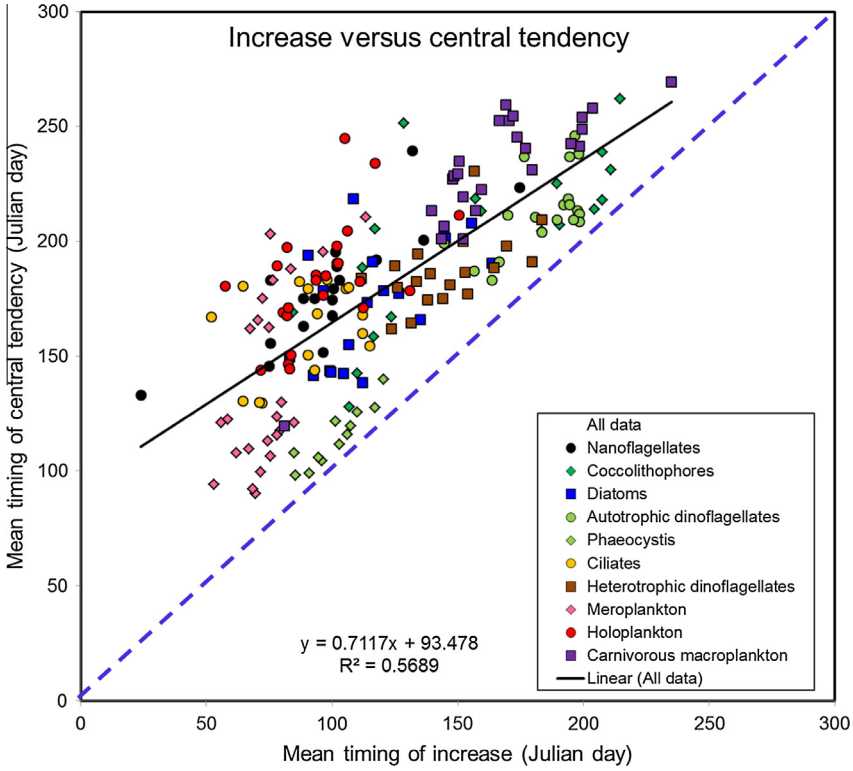

Fig. 4. Comparison of the appearance of the main functional groups in each year based on the average of the two central tendency indices (*y*-axis: JD derived from mean timing of the centre of gravity and 50% cumulative) and the average of the two indices of the timing of initial increase (*x*-axis: JD derived from mean timing of threshold and 25% cumulative). The black regression line ($p < 0.01$) pertains to all data pooled. The dotted blue line represents the line of equality as a reference. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The 11 main functional groups as well as the 46 selected taxa are plotted in "variability space" in Fig. 3. These data, with associated species identities, are shown in Table 3. Most (70%) of the taxa cluster into the bottom left hand corner of the plot, varying up to ~50-fold in mean abundance between years and increasing up to ~50-fold from their minimum to maximum average seasonal abundance. This includes all the important functional groups except autotrophic dinoflagellates and *Phaeocystis*, so despite variability of some of their component species, at the functional group level the variation is much smaller. However 18 of the taxa/functional groups had variability far exceeding these bounds. These comprise a diversity of taxa but common to many is their gelatinous or semi-gelatinous body plans (e.g. appendicularians, medusae, *Phaeocystis* spp., *Noctiluca scintillans*, ctenophores, siphonophores). This high variability group also contain cladocerans, meroplanktonic larvae of cirripedes and echinoderms plus fish larvae. A few more oceanic species (e.g. *Metridia lucens*) were also highly variable in mean abundance from year to year, possibly reflecting variable degrees of oceanic water influence at the site.

3.3. Comparison of timing indices

Fig. 4 compares the timing of the early season indices of initial increase (i.e. mean JD of threshold and 25th cumulative percentile) with the two later/whole season indices of the functional groups in each year. While a positive relationship is expected, Fig. 4 emphasises that it is loose, with initial timing explaining little more than half of the variability in central tendency. For spring species in particular, the central tendency indices bear little relationship to the timings of the initiation of the growing season. This reflects the extended growing season, often with several peaks, of many of the taxa. While a few of the functional groups in Fig. 4, for example *Phaeocystis* spp. have tighter relationships due to their much sharper seasonal pulses, the weak overall relationship between the timing indices for many taxa (Fig. 4) and the fact that they deliver sometimes conflicting results (Table 3) underscores the need to use multiple indices for plankton (Thackeray et al., 2013).

3.4. Phenological shifts among the trophic levels

Fig. 5 illustrates the large degree of variability in timing of the main functional groups. Each varied often by well over 1 month in its timing between respective years, and regression analyses showed that this timing variation of each group was independent of that of the other groups. The only exceptions were firstly diatoms, whose inter-annual variation in timing was (unsurprisingly) related to that of Chl *a* (R^2 = 36%, p = 0.007, n = 19 years). Secondly the holoplankton and meroplankton (Fig. 5) were weakly related in their timing variability (R^2 = 24% p = 0.014, n = 24 years). The early phase indices (threshold and 25% cumulative) were particularly sensitive to periodic late winter blooms preceding the growth season (e.g. in 2005, 2006) and this also levered the average values presented in Fig. 5, which are based on all the indices.

For each taxon/functional group we regressed each of the 4 timing indices for each year against firstly the respective April–August temperature anomaly and secondly against year of sampling. This produced a large number of regressions, so our approach was to present the regression slopes for all of the taxa irrespective of their value, sign or significance. This approach was analogous to that used by Edwards and Richardson (2004; their Fig. 1) and was chosen to provide an overview of trends across the whole species assemblage, rather than to apply significance-level adjustments to allow for multiple testing (Mackas et al., 2012). However in Table 3 which presents these values, we have signified in bold

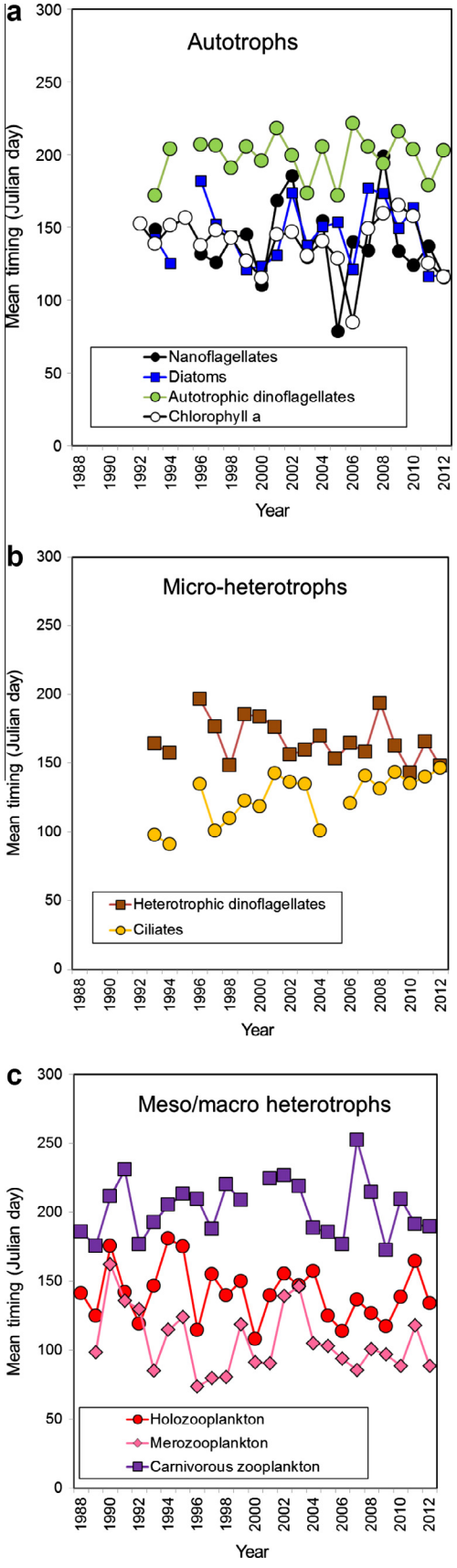

Fig. 5. Comparison of the mean timing (all 4 phenology indices averaged) for the major functional groups over time: (a) autotrophs, (b) ciliates and heterotrophic dinoflagellates and (c) metazoans.

the 18 taxa whose timing shifts we have more confidence in, based on all four indices showing the same trend and/or R^2 values exceeding 30%.

Fig. 6 shows the degree of phenological shift across all taxa/functional groups, averaged across all 4 timing indices. Most individual taxa (and all functional groups except coccolithophores) changed in their timing by less than 20 days per 1 °C change in annual water temperature. Further, the dominant phytoplankton functional groups (diatoms and autotrophic dinoflagellates), as well as Chl *a* changed by less than 6 d per 1 °C.

Of the species that changed their timing by more than 20 days per 1 °C, the four that shifted earlier in warming years (negative values in Fig. 6a) appeared before June and the four that became later when warmer were autumn species. This fits with the general finding of phenological shifts (Richardson, 2008), but the high variability about this trend is reflected in a non-significant regression line that explains only 4% of the variability. The explanatory powers of this regression were not improved by basing it on the use of just one of the timing indices which may have been better than the others. Most variability was explained using just the centre of gravity index and least was explained by using the threshold, but all indices showed the same weak, albeit non-statistically significant, tendency.

Many phenology studies relate timing shifts not to temperature but rather to the year of sampling. By doing this (Fig. 6b) we found no long-term trend at all. Despite several of the functional groups advancing or appearing earlier by over 10 days per decade (e.g. ciliates getting later – Figs. 5b and 6b) there was no suggestion of a pattern across all species.

3.5. Degree of trophic level "mismatch" in relation to temperature

Fig. 7 quantifies the delays between the timing of the food and the grazers in relation to temperature anomalies. The key result is that extreme warm or cold years caused no more trophic level "mismatching" than near-average years. This is evident in both the trend and the degree of scatter of the data. At the whole functional group level (red dots in Fig. 7) ciliates and holoplankton increased at roughly the same time as the spring bloom, on average, while heterotrophic dinoflagellates appeared after it and meroplankton before. This fits with the "climatology" illustrated in Fig. 1. However Fig. 5 illustrates the unrelated, high degree of variability across trophic levels. This factor is responsible for the very high degree of scatter but no trend in degree of mismatch with temperature (Fig. 7).

The main exceptions were the minority of species that showed clear and consistent evidence for phenological shifts across all four of the timing indices (Table 3). We illustrate these with 3 small grazers, *Gyrodinium* spp., *Pseudocalanus elongatus* and *Acartia clausi* (Fig. 8) which appeared consistently earlier in warmer years. Because their food did not show this shift, then the grazer–food timing offsets related to temperature.

3.6. Penalties for mismatch

While Fig. 7 does not support our second hypothesis that anomalously warm or cold years lead to increased trophic level mismatching, the calculated offsets were nevertheless sometimes over 3 months. We therefore tested our third hypothesis that large offsets (however caused) lead to observable penalties. For each taxon/functional group in turn we regressed mean abundance achieved in each year against that year's mismatch. The sign of the relationship (negative means that years of large mismatch coincide with low grazer abundances) and its R^2 are plotted for each taxon in Fig. 9. The points are roughly evenly distributed above and below the zero line, and the degree of mismatch for most taxa explained <20% of their inter-variability in abundance. Therefore, factors other than timing with food seemed to be driving the inter-annual variations in abundance of zooplankton taxa. This is illustrated by a specific example of a species,

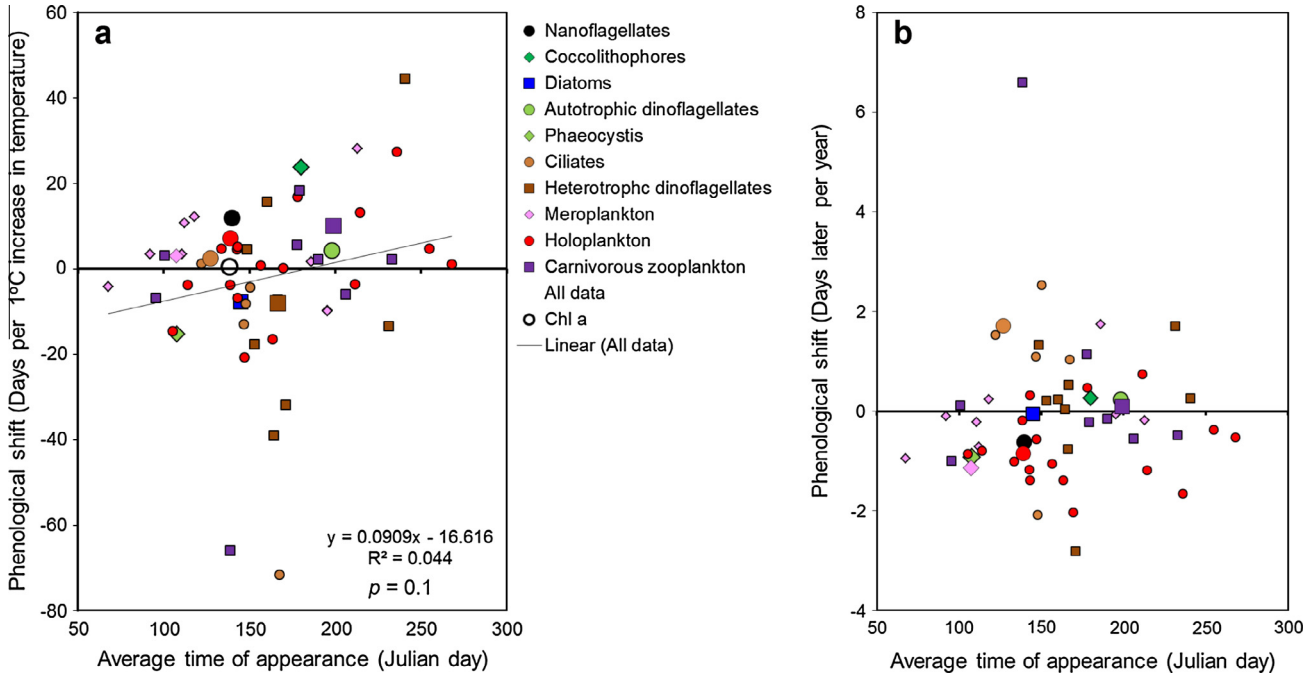

Fig. 6. Extent of phenological shift with temperature (*y*-values) of the 56 taxa/functional groups in relation to their mean timing of appearance in the plankton (*x*-values; see second column of Table 3). The *y*-values are plotted (a) as numbers of days change in timing per 1 °C change in temperature (i.e. values in Table 3 column 7, with positive signifying later appearance in warmer years) and (b) numbers of days change per year (again positive values signify later). Both *x* and *y* values are presented as means for each of the 4 timing indices. Symbol notations are as described in Fig. 3.

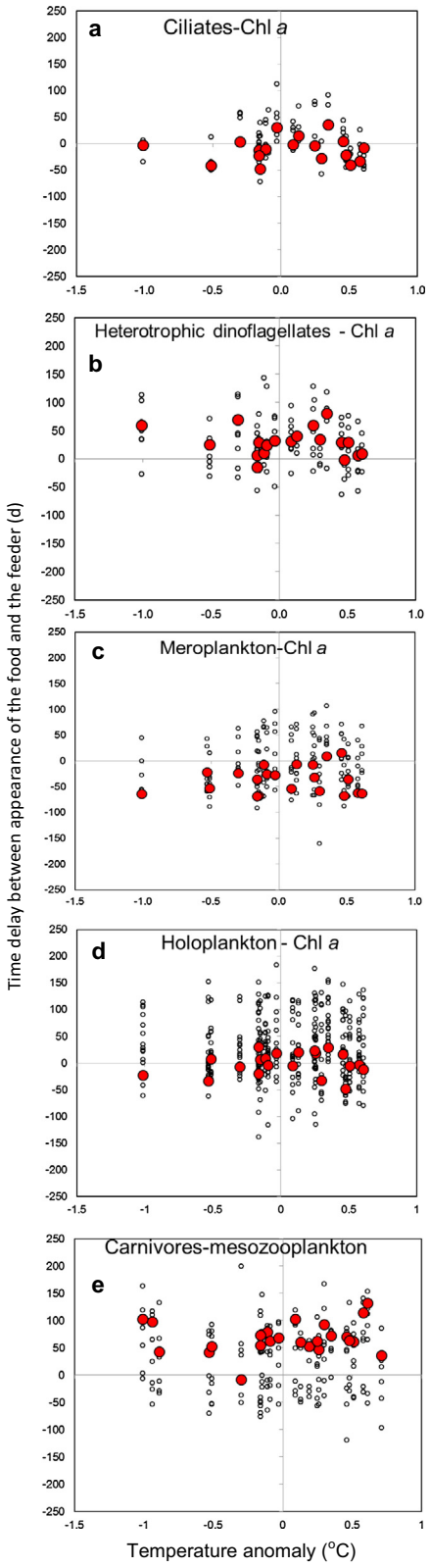

Fig. 7. Calculated delay between the timing of a food index (either Chl *a* or total zooplankton; see Section 2.6) and each of the taxa (open symbols) or whole functional groups (red symbols) in each of the years. These values are mean values for the delay, first calculated separately using each of the 4 timing indices and then averaged. Negative values on the *y*-axis signify that the feeder increased before its food. Timing offsets are plotted for (a) ciliates, (b) heterotrophic dinoflagellates, (c) meroplankton, (d) holoplankton and (e) carnivorous meso-macrozooplankton. These values are plotted against *x*-axis values of the respective April–August temperature anomaly (positive values being warm years). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Pseudocalanus elongatus, that shows a strong "earlier when warmer" shift such that in warm years it increases around a month before the main Chl *a* increase (Fig. 8). The analysis in Fig. 9 showed that this often large "mismatch" did not explain its variability in abundance ($R^2 = 0.002$).

3.7. *Calanus helgolandicus* as a case example of the effects of timing with food

Because only the first of our three hypotheses had any support, we examined the mechanisms by which timing effects could operate in more detail for *Calanus helgolandicus*. Using its spring–summer egg production as an index of performance, we found that this was unrelated to the degree of mismatch with food (Fig. 10a). Likewise the annual "Food Benefit Index" (*FBI*; see Section 2.8), which integrates food quantity as well as its timing, was statistically unrelated to the mismatch (Fig. 10b).

To understand why these expected relationships were not found, we have plotted *C. helgolandicus* abundance alongside Chl *a* (Fig. 10c). In 2009 the species increased 50 days before the bloom when Chl *a* concentrations were still only 0.5 mg m^{-3}. By contrast, in 2012 *C. helgolandicus* appeared very late and "missed" most of the bloom.

While 2009 and 2012 represent extremes of mismatching, the mean egg production rates (Fig. 10a) and the overlap with food (*FBI*; Fig. 10b) are not seriously compromised in these years. By contrast 2010 and 2011 have much better matches between grazer and bloom, but both egg production and *FBI* are no greater than those in the years of great mismatch. This is due either to multiple Chl *a* peaks not coinciding with the multiple *C. helgolandicus* peaks (2010) or the low overall food levels (2011). Even though *Calanus helgolandicus* shows no clear timing shift compared to *Acartia clausi* and *Pseudocalanus elongatus* (Table 3) Fig. 10 shows how even large grazer–food offsets are easily cancelled, thus having little influence on species performance.

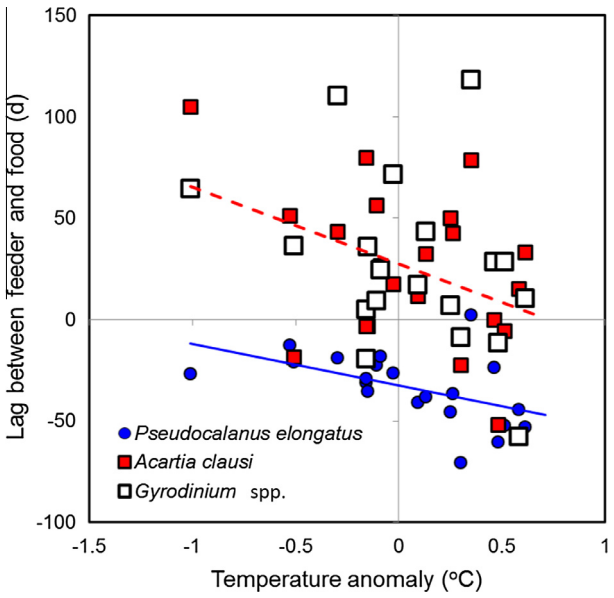

Fig. 8. Example of three important L4 taxa that showed consistent "earlier when warmer" tendency (Table 3). Their lead or lag with food timing (proxied by Chl *a* and calculated as in Fig. 7) is plotted against the temperature anomaly in each year. For *Pseudocalanus elongatus* (solid regression line): $y = 21x - 33$, $R^2 = 25\%$, $p = 0.02$, $n = 21$ years. For *Acartia clausi* (dotted regression line to signify non-significance at 5% level): $y = -38x + 27$, $R^2 = 17\%$, $p = 0.062$, $n = 21$ years. The regression line was not significant for *Gyrodinium* spp.

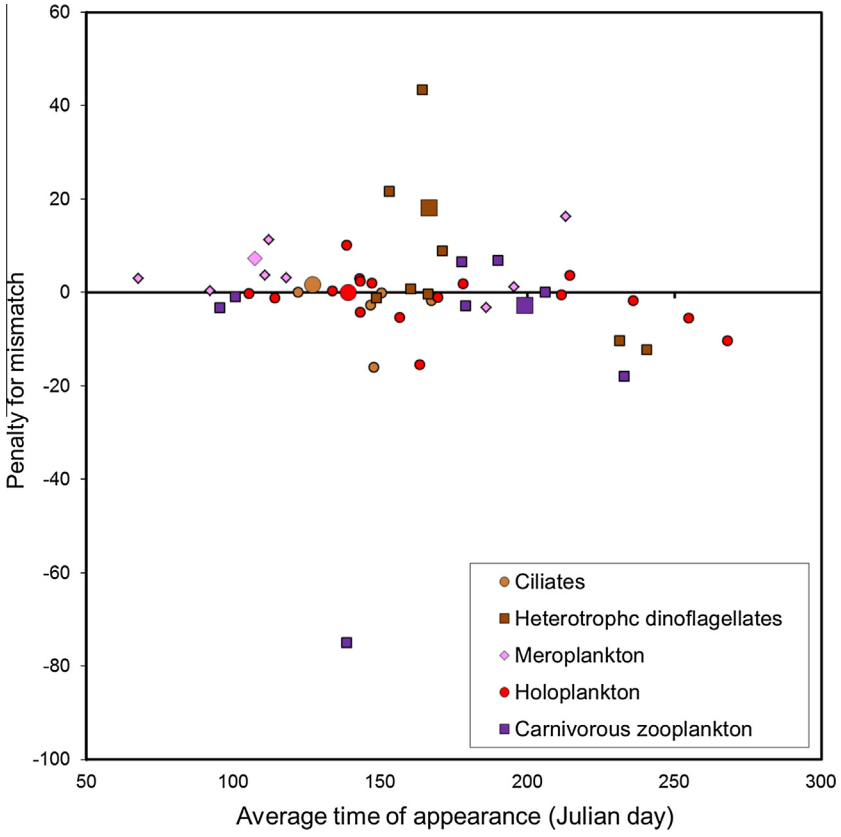

Fig. 9. Analysis of whether years of large mismatch between feeder and food timings relate to years of depressed grazer abundances in the same year. For each taxon a regression was first done between the mean abundance in each year and the amount of mismatch in that year. If years of greater mismatch were related to lower mean abundance (negative slope) the values are plotted below the line, with *y* values signifying the R^2 of the relationship.

4. Discussion

Within the 1988–2012 study period, the inter-annual range of water temperatures at L4 was nearly 2 °C. To put the magnitude of this variation in context, the rapidly warming North Sea rose in temperature by 1 °C over the last half century (Hinder et al., 2012). Since large fluctuations and "extreme weather" are predicted side effects of climate change (Coumou and Rahmstorf, 2012; Kendon et al., 2014), one would expect L4 to display trophic mismatches and their adverse effects. Our findings, however, force us to question whether these adverse effects apply at L4. Below we address each of our three hypotheses in turn to understand why the L4 plankton do not show the types of responses commonly speculated upon in the literature.

4.1. Hypothesis 1: warmer temperatures lead to earlier appearance of spring species and later appearance of autumn species

The earlier appearance of spring and a later lingering of autumn is a classic phenological response reported in the sea, lakes and on land. While we found some evidence for it (Fig. 6), there was a prevalence of exceptions, contra-indications between timing indices (Table 3) and negligible shifts in timing. Is this because the conditions or the sampling at L4 obscure the "real" signal, or because there really are many exceptions to the phenology shift generalisation?

The L4 site is certainly dynamic, subject to the criticism of any monitoring site that advective events confound interpretation of time series. This almost certainly contributes to some of the variability that we see. Another factor, particularly important for the meroplankton, is that zooplankton identifications were frequently not possible to species level (Lindeque et al., 2013, Table 3). Thus variability in timing at the broader taxonomic level could represent partial replacement of some species with others having differing timing. Notwithstanding these issues, previous comparisons of time series (e.g. Mackas et al., 2012) show that some species consistently shift much more than others. Even in a textbook example of phenological change in the North Sea (Edwards and Richardson, 2004) the advancing timing trend was shown not by the spring species but by the summer ones, and across the whole data set over 30% of taxa showed the reverse. So overall, given the dynamic nature of L4, the level of species identification and the fact that other studies find many exceptions, it is perhaps not surprising to find only weak support for the first study hypothesis.

The high inter-annual variability at L4 allows us to separate the effects of temperature, time and food on phenology shifts. A suite of factors point to temperature as a major factor, as suggested previously (see Mackas et al., 2012). First, timing shifts were totally unrelated to time (Fig. 6b). Second, food timing was not a driving variable as there were no relationships between timings of successive trophic levels (Fig. 5), and third, even though the temperature relationship (Fig. 6a) was weak its direction fits expectations. Several species seem to be particularly temperature sensitive in their timings (Mackas et al., 2012) and this L4 analysis also highlighted these. Good examples are *Pseudocalanus elongatus* and *Acartia clausi* which show strong "earlier when warmer" trends across multiple time series. Some protozoans also seem temperature sensitive (Fig. 6a) for example *Gyrodinium* spp. (Fig. 8). This also fits previous experimental studies (Aberle et al., 2012; Calbet et al., 2014). Likewise, terrestrial studies have found that the strongest timing shifts can occur among the lower trophic level consumers (Both et al., 2009).

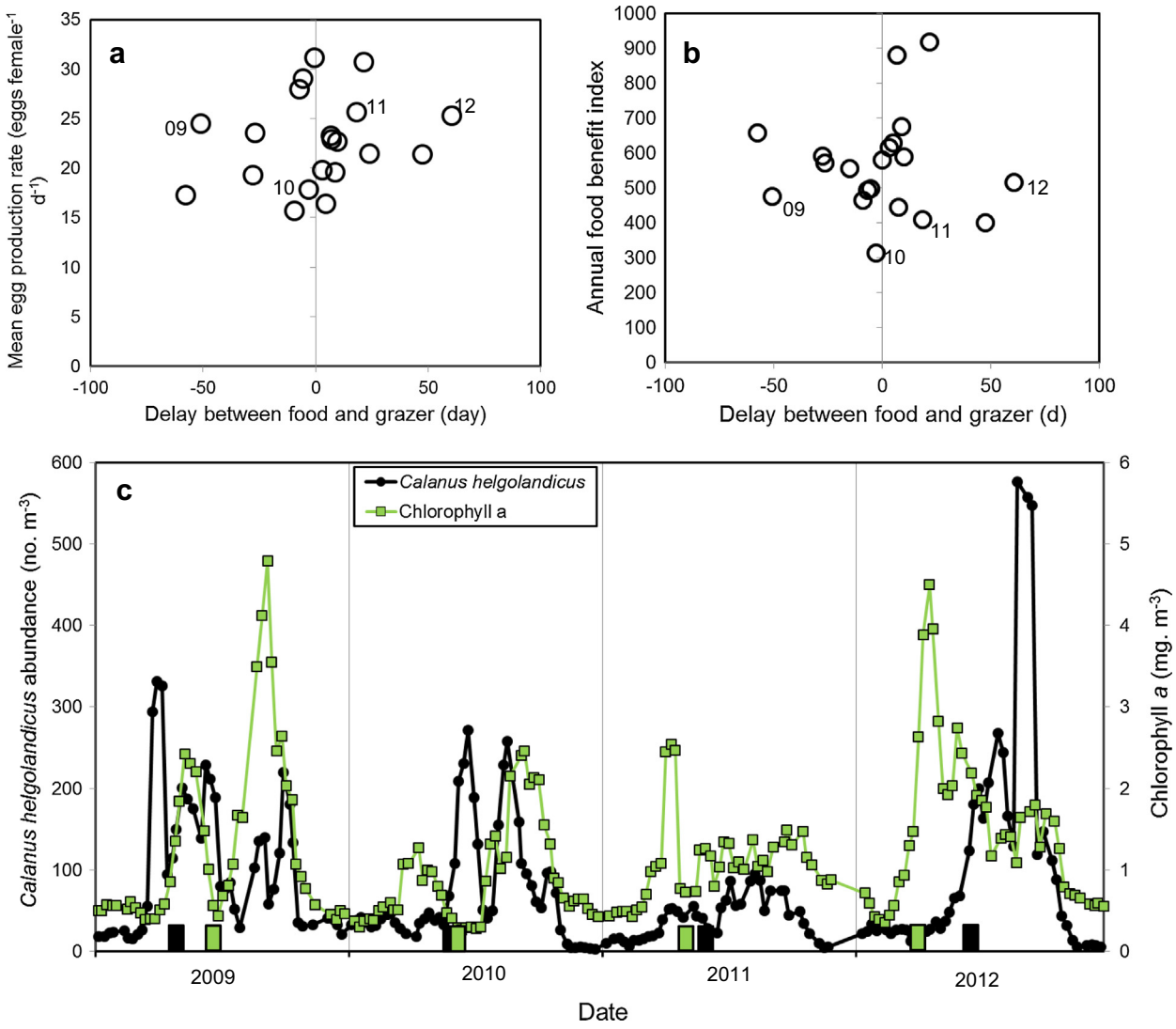

Fig. 10. *Calanus helgolandicus* as a case example of the implications of grazer–food overlaps or mismatches: (a) Mean monthly egg production rates (March–August) against time delay between food and grazer. The latter are calculated as in Fig. 7, using each of the 4 timing indices separately to calculate a mismatch, then averaging the results. Negative values signify that food (Chl *a*) increases before the increase of *C. helgolandicus*; (b) Annual Food Benefit Index (see Section 2.8) against time delay between food and grazer; (c) four recent years of L4 sampling illustrating extremes of calculated match and mismatch based on the four timing indices. These years are labelled on panels (a) and (b). A 3-point running mean has been fitted to these data to ease visualisation of the main peaks. Green and black bars on time axis mark the timings of Chl *a* and *C. helgolandicus* respectively, based on the mean of all 4 timing indices. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Hypothesis 2: the species show differential timing shifts such that extreme temperature anomalies lead to large mismatches between trophic levels

We could find no evidence that the time offset between grazer and their potential food was any different in very warm or cold years than during more normal years. This reflects the timings of each trophic level being both highly variable between years and unrelated to those of other trophic levels. Therefore subtracting one variable timing from another to derive an offset tended to compound the variability. While three particularly temperature sensitive taxa (*Gyrodinium* spp., *Acartia clausi* and *Pseudocalanus elongatus* showed offsets that related to temperature (Fig. 8) they were exceptions to this rule.

This discussion all points to high variability and poor predictability of when a species will increase in any given year, with grazer timing bearing little relation to that of food. This situation can be explained in several ways. For example, there could be selective advantages of pulsed, early spawnings of meroplankton to reduce predation impact from the other metazoans that appear later (Fig. 1d). Such trade-offs have been suggested as on explanation for sometimes counter-intuitive trophic level mismatches in both terrestrial- (e.g. Both et al., 2009; Lof et al., 2012) and aquatic systems (Varpe, 2012).

Top-down effects might help explain variable timing offsets between predators and prey in other ways. Fig. 3 provides some support for the role of mortality in controlling maximum abundances, since most of the taxa are constrained within boundaries of a 50-fold variation in seasonal and inter-annual variation in abundance. As an example, predation appears to exert a major control on *Calanus helgolandicus* abundance at L4 (Hirst et al., 2007; Bonnet et al., 2010; Maud et al., 2015), and this species varies surprisingly little in mean annual abundance throughout the time series (Table 3). The exceptions may prove the rule here; among the holoplankton only a handful of species (mainly gelatinous, meroplankton or asexually reproducing) appear to have escaped predation control. These have explosive population increases in some years (Fig. 3). Match–mismatch has been considered previously

mainly from a bottom-up perspective (see Durant et al., 2013) but predation may shape the abundance trajectory of the grazer for large parts of the year, thus influencing the cumulative percentiles and centre of gravity indices commonly used.

4.3. Hypothesis 3: years with large mismatches are associated with measurable penalties in terms of secondary production or abundance

We could not find evidence to support hypothesis 3. Across the whole planktonic assemblage, both at the species and functional group level, abundances were no different in years of large or small mismatch. Even sensitive species such as *Pseudocalanus elongatus*, which in the warmest years increased over one-month before their food, were not demonstrably affected by this. While it can be argued that mean abundance is only a crude index of annual "success", we benefitted from 20 years of weekly egg production rates of *Calanus helgolandicus* to examine how mismatching affected a production index (Fig. 10a). The lack of relationship found (and indeed the fact that eggs outputs were high even during the extremes of mismatching) casts further doubt on whether the match–mismatch hypothesis applies in this sort of system.

We have refined these simple, time-based calculations of the food mismatching into a "food benefit index" (Fig. 10b). Worryingly, even this slightly improved index of annual food availability bore no statistical relationship to the standard, purely time-based quantifications of mismatch. This is because the benefit of food depends heavily on its amount and not just its timing (Durant et al., 2005; Thackeray, 2012). Fig. 10b and c shows a year of good timing but low food (2011) being outweighed in benefit by very poor timing but large amount (2012). The multiple peaks and long growth seasons of temperate systems such as L4 also hamper the most commonly used timing indices such as cumulative percentiles and centre of gravity. These indicate what may seem like an overall good grazer–food timing match for 2010 (Fig. 10b) when in fact these contain multiple subsidiary peaks that are poorly aligned (Fig. 10c).

Fig. 10c also illustrates another feature that pervades the L4 time series: the grazers often increase rapidly well before any increase in food (Smyth et al., 2014). This is also illustrated by the big mismatches for many species in Fig. 7, and while it can be explained for meroplankton in terms of pulsed spawnings of many larvae into the plankton, it requires a different reason for holoplankton. The rapid increases of abundance to high values, even when Chl *a* is at winter values (e.g. for *Calanus helgolandicus* in 2009 and 2010: see Fig. 10c) are hard to explain in terms of artefacts of advection/frontal movement events, since these increases last several consecutive weeks while food remains low. Feeding flexibility may explain this; L4 studies have shown that *C. helgolandicus* ingests a diversity of high quality food items throughout the season (Irigoien et al., 2000; Fileman et al., 2010), and that all of these support reproduction (Pond et al., 1996). Thus in productive temperate environments such as L4, a single food source may not limit population increases.

4.4. Concluding remarks

On one hand it could be argued that L4 is not a good study site to examine phenological effects because of its dynamic nature and great inter-annual variability. On the other hand it is exactly this variability that is suggested to "confuse" the normal timing cues (Koeller et al., 2009), thus helping to de-synchronise trophic levels. Given that climatic fluctuations will likely increase in amplitude in a warming climate (Coumou and Rahmstorf, 2012), then this variability at L4 would make it a natural laboratory to test whether the system is sensitive or resilient to timing shifts.

Decadal scale changes in the plankton are the subject of other papers in this special issue (Maud et al., 2015), as well as earlier studies (Widdicombe et al., 2010; Eloire et al., 2010). While some shifts in abundance have been suggested (Reygondeau et al., 2015) we stress also a degree of resilience, in keeping with the findings of Mazzocchi et al. (2012) in another inshore time series. For example *Calanus helgolandicus*, a "sentinel" of climatic warming, has only ranged about fourfold in annual mean abundance and twofold in annual mean egg production rate over the whole time series (Atkinson et al., 2014; Maud et al., 2015, Table 3, Fig. 10). This is remarkable constancy given the ~2 °C range of water temperatures and the enormous variability in both timing and amounts of its food sources. Preserving healthy ecosystems underscores policy directives such as the Marine Strategy Framework Directive (MSFD). By quantifying the mechanisms of resilience (for example to grazer-food offsets) we are in a better position to define what is meant by a "healthy ecosystem".

While the importance of phenology shifts and trophic mismatching is being increasingly speculated upon, direct data to support their role in structuring planktonic food webs, particularly marine ones, is lacking. In marine environments, the strongest support seems to come from systems that have: (a) vertebrate predators with narrow breeding windows; (b) specialists on one type of prey; and (c) these prey having narrow production pulses. Good marine examples are planktivorous marine seabirds, especially in higher latitude systems (Bertram et al., 2001; Sydeman and Bograd, 2009; Burthe et al., 2012).

In productive, lower latitude or planktonic systems, however, the above criteria are often not met. Grazers tend to be generalists, reproduction periods longer and opportunistic, food is abundant or at least available over extended periods, and predation controls are often tight. All of these factors (and probably more) seem to operate at L4, and these likely compensate or counteract the great natural variation in relative timing of feeders and food. We certainly do not suggest that phenology changes are unimportant, but rather that the link from phenology shifts to trophic mismatch to adverse ecosystem effects has been made rather too unquestioningly in some plankton studies. Clearly we need to study phenology integrally with the plethora of other factors that together shape the resilience of the ecosystem (Mazzocchi et al., 2012). Taxonomically-rich, high-resolution time series are lengthening and increasing around the world (Mackas and Beaugrand, 2010; Mackas et al., 2012). Further analysis of these, including comparative studies and experimentation, will help to reveal the role of phenology shifts.

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