Comment. What drives plankton seasonality in a stratifying shelf sea? Some competing and complementary theories

Comment on Kenitz et al. (2017) Limnol Oceanogr 62:1184-1197

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Abstract.

The Plymouth L4 time plankton series in the Western English Channel is a textbook example of a shallow, stratifying shelf sea system. Over its 30 years of weekly sampling, this site has provided a diverse and contrasting suite of numerical and conceptual models of plankton bloom formation, phenology and seasonal succession. The most recent of these papers, by Kenitz et al. (2017) has initiated this comment, partly because we feel that it has presented a slightly misleading picture of the plankton composition at this site, and of a robust, recurring seasonal succession. We address this by illustrating the extent of inter-annual variability in phenology that occurs at the site, and which needs to be captured better within models. However our main aim is to foster a much better integration of the variety of top-down and bottom-up processes that have all been suggested to be key in driving seasonal succession. Some of these, particularly the multiple grazing and growth controls contributing to the so-called “loophole hypothesis” may be complementary, but others, such as the role of copepod feeding traits in driving species succession (Kenitz et al. 2017) offer testable competing hypotheses. The basic assumptions and outputs of all these models need to be validated more critically, both against time series data and process studies that include the finding of unselective feeding. We suggest that the variability in plankton phenology (and not just mean timing and amplitude) could be used to diagnose the performance of alternative models of plankton succession.

Introduction

Within marine environments, productive, stratifying shelf seas are disproportionately important in nutrient cycling and providing services to humans such as fishing, aggregate extraction or waste disposal (Simpson and Sharples 2012). In temperate seas the amplitude of seasonal variability in temperature is maximised, and the effects of this seasonality have been studied intensely for decades. A recent study of plankton seasonality in one such system was published last year in Limnology and Oceanography by Kenitz et al. (2017).

These authors examine the plankton time series from station L4, an inshore site near Plymouth in the Western English Channel.

While we do comment specifically on this paper, with a focus on L4, our primary aim is to stress the need for an evaluation and integration of the suite of mechanisms proposed to explain seasonality and plankton succession based on time series. We think that this exercise is now timely, since various studies have arrived at sometimes very different conclusions over what is driving L4 seasonality (**Table 1**). With this comment we want to initiate this process by: 1) providing an overview of functional group biomass and seasonality observed at L4; 2) bringing the various explanations of L4 seasonality (including Kenitz et al. 2017) under one umbrella, comparing and contrasting their suggested mechanisms; and 3) suggesting fruitful ways in which sometimes competing hypotheses can be evaluated, tested critically and, where appropriate, amalgamated to provide a better framework for understanding plankton succession.

Plankton biomass and seasonality at L4.

The L4 site is a shallow (~54 m water depth) site 13 km SSW of Plymouth, a textbook stratifying shelf sea system that has been sampled at weekly resolution since 1988 (Southward et al. 2005; Harris 2010). This provides a rich, taxon-resolved time series of plankton coupled to profiling of physics and nutrients; a valuable resource for modellers and empiricists alike (Southward et al. 2005; Harris 2010; Smyth et al. 2015; www.westernchannelobservatory.org.uk/). L4 stratifies typically between May and September with a thermocline at ~10-20 m. Surface temperatures typically range from ~8-9^{o}C in winter to ~16-17^{o}C in summer, when surface layer macronutrients are depleted to limiting levels (Smyth et al. 2010; 2015). Average surface chlorophyll *a* (chl *a*) values range typically from ~0.5 mg chl *a* m^{-3} in winter to ~2-3 mg chl *a* m^{-3} during blooms that can occur throughout the spring to autumn period (Widdicombe et al. 2010; Atkinson et al. 2015).

Plankton from the site are identified under a microscope to species, genus or broader groupings. The protists are enumerated from Lugol's- and formaldehyde-preserved water samples taken at 10 m depth (~280 taxa) and mesozooplankton are from paired 0-50 m

WP2 net hauls (~180 taxa). Based mainly on measurements on individual taxa sampled from L4 and literature conversion factors (e.g. Menden-Deuer and Lessard 2000 for protists) we have estimated biomass of major functional groups (**Fig. 1**). While diatoms comprise the non-motile component, overall the protistan assemblage is dominated strongly by motile cells, chiefly autotrophic dinoflagellates and nanoflagellates, with colourless (presumed mainly heterotrophic) dinoflagellates and ciliates also contributing strongly in some years. Biomass of the metazoan component at L4 is dominated roughly equally by copepods that can employ feeding currents such as *Calanus helgolandicus and Pseudocalanus elongatus* (Green et al.1993; Eloire et al. 2010; Maud et al. 2015) and by non-copepod taxa including a diverse meroplankton assemblage (Highfield et al. 2010; Lindeque et al. 2013). By comparison strict ambush feeders such as *Oithona similis* comprise a small portion of the estimated mesozooplankton biomass **(Fig. 1).** It is important to note here that many of the early life stages of small copepods (including *Oithona similis*) are not retained by the meshes of the 200 µm nets and therefore are strictly defined as microzooplankton rather than mesozooplankton.

The phenology at L4 is intriguing as the increases in both copepod and meroplankton often precede those of their prey (**Fig. 2**; see also Smyth et al. 2014; Atkinson et al. 2015). Based on overall average values across all years, diatoms and *Phaeocystis* bloom in spring, with nanoflagellates and dinoflagellates dominating in summer or autumn (Widdicombe et al. 2010). Coccolithophores are important in some years, blooming in summer or autumn. However, **Fig. 2** emphasises the great year-to-year variability around this average picture. For instance, in some years the motile taxa peak first and in other years diatoms bloom in autumn. Indeed, interannual timings of each of these groups typically vary from year to year by about two months and independently of each other (Atkinson et al. 2015).

A suite of explanations for plankton seasonality at L4

What are the processes causing the seasonal timing and succession that we observe at L4? **Table 1** presents the Kenitz et al. (2017) study in the context of a series of other seasonality process studies from the same site. The first four processes in **Table 1** could loosely be described as variations within the so-called “loophole hypothesis” (Irigoien et al. 2005; Kiørboe 2008). This provides an appealing framework, whereby physical perturbations (for example causing improvement in the light environment) allow specific taxa that are better defended against attack to escape from grazing control and thus bloom. Importantly, this model invokes microzooplankton rather than mesozooplankton as the main grazers, given their frequent dominance in this role (Calbet and Landry 2004). This would seem a fair assumption at L4 given the measured high grazing impact of microzooplankton (Fileman et al. 2002), minor impact from mesozooplankton (Bautista and Harris 1992; Bautista et al. 1992), and the substantial biomass of motile protists that can participate in heterotrophy (**Fig. 1**).

Irigoien et al. (2005) only speculate on what causes the hiatus in tight grazing pressure and on the subsequent feedbacks that allow blooms to develop. Later publications invoked the inversion of the net heat flux (Smyth et al. 2014) and the variations in phytoplankton nutritional status (Polimene et al. 2015) as alternative (but not necessarily incompatible) explanations for when and why some taxa can escape grazing control during the spring bloom. Beside traits of predation deterrence, other works also suggested that different photophysiological properties (light acclimation and adaptation), affinity for nutrients and growth rates within the phytoplankton community contribute to bloom dynamics and species succession at L4 (Polimene et al., 2014; Edwards et al 2013).

A different angle on seasonal succession is provided by empirical studies of phenological timing in relation to water temperature. Differential sensitivities to temperature could explain observed patterns which are not consistent with the classic prey-predator dynamics. For example, copepods often increase at L4 even earlier than their prey (**Fig. 2).** Differential phenological temperature sensitivities between taxa has attracted much interest, because it could lead to changes in the relative match or mismatch between trophic levels in a warming climate (Edwards and Richardson 2004; Aberle et al. 2012; Thackeray et al. 2013). The taxonomic richness and weekly resolution of L4 is good for determining phenology (Mackas et al. 2012), and indeed some major heterotrophs showed strong temperature sensitivity in their timings (earlier when warmer), for example the heterotrophic dinoflagellate *Gyrodinium spp*, and the copepod genera *Pseudocalanus* and *Acartia* (Atkinson et al. 2015). By contrast diatom timing remained overall unrelated to temperature as found elsewhere (Wiltshire et al. 2008), being possibly cued also by light (Ji et al. 2010). However, Atkinson et al. (2015) found much individual variability around the textbook generality under warming of “spring species increasing earlier and autumn species later”. This trend was perhaps obscured by other factors dictating seasonal timings.

Predation control is one such confounding factor that can shape the observed seasonality. Since the concentrations that we see reflect the dynamic balance between gain and loss processes, the seasonality of concentrations observed may follow trajectories (such as predators increasing before their prey) that are counterintuitive if viewed solely from a bottom-up perspective. Thus, for example the seasonal timing of increase of *Calanus helgolandicus* copepodites is poorly related to that of their egg production rate but more closely to the timing of stratification (Irigoien and Harris 2003; Maud et al. 2015). These authors speculate that summer stratification is required to prevent eggs settling to the seabed and subsequently being predated. For the ambush feeding copepod *Oithona similis* at L4, similar decoupling between the timings of maximum egg production rate (in late summer) and copepodite abundance (in spring) has been observed (Cornwell et al. 2018). Thus overall there is no congruence between timings of ambush or active-feeding copepods and their suggested motile and non-motile food sources (Djeghri et al. 2018).

The importance of zooplankton feeding behaviour in shaping seasonal succession is also a feature of the last two studies listed in **Table 1**. Sailley et al. (2015) emphasise the importance of unselective and selective zooplankton feeding (the latter triggered by prey C:N and C:P ratios) in determining the duration of the spring bloom and the amount of zooplankton biomass in summer. While the model proposed by Sailley et al (2015) describes a generic zooplankton (defined as any heterotroph larger than 20 μm), the authors propose a correspondence between modelled unselective grazers and copepods that can generate feeding currents and modelled selective grazers and ambush or cruise feeder copepods. The model of Sailley et al. (2015) does not consider phytoplankton type succession and does not imply any coupling between feeding behaviour and prey seasonality.

In contrast, the Kenitz et al. (2017) study is based on the controls exerted by ambushing and active feeding mesozooplanktonic copepods on the seasonality of their respective motile and non-motile food sources. Kenitz et al. (2017) conclude by proposing the existence of two-way coupling of functional traits, namely motility among the prey and feeding mode among the grazers. Based on their model and the time series, they suggest a regular and robust seasonal succession of non-motile cells in late spring/summer, followed by motile cells in summer-autumn. These in turn are linked to respective increases in active (i.e. feeding current and cruise-feeding) copepods best suited to capturing non-motile prey followed by ambush feeders that target motile cells. They state that "*Our model highlights the importance of mesozooplankton in shaping the seasonal succession of protists, and reveals how the seasonal trait succession can be explained as a trophic trait cascade*".

Thus, unlike most of the other studies listed in **Table 1**, the Kenitz et al. (2017) study explicitly invokes mesozooplankton as the main grazing agents shaping the seasonality of their prey by selective feeding in their trait-based model (ambushers eating motile prey only, more active feeders eating non-motile prey only). We believe that these conclusions may have been driven by some misunderstandings about the L4 dataset. More specifically, we think that Kenitz et al. (2017) have substantially underestimated biomass of protists at the 10 m sampling depth by not including several key prey groups at this site, namely phytoflagellates and *Phaeocystis* spp. We also estimate biomass of ambush feeding mesozooplanktonic copepods of 0.43 mg C m^{-3} that are only one-third of their values; in any case ambushing copepods likely have minor grazing impact at L4 compared to other taxa **(Fig. 1)**. We therefore suggest to subsequent authors not to use the L4 observational data presented in Table 1, Fig. 2 and Fig. 3 of Kenitz et al. 2017), but instead to obtain the original source data (www.westernchannelobservatory.org.uk/). Notwithstanding this caveat over data, the Kenitz et al paper provides a testable alternative mechanism to the loophole hypothesis.

So, what controls plankton seasonality in a stratifying shelf sea?

Over the years a variety of authors have approached the question of what controls seasonality in stratifying shelf seas. Based on the L4 time series, they have arrived at a suite of different mechanisms. Several of these are not mutually exclusive and could fruitfully be combined. As one example, variations around the general theme of the "loophole hypothesis" have been invoked to explain the development of phytoplankton blooms (Irigoien et al. 2005; Smyth et al. 2014; Polimene et al. 2015). For copepod seasonality, the mechanisms of temperature-related phenology and the match-mismatch hypothesis (Atkinson et al. 2015) could be combined with the concept of strong top-down control (Irigoien and Harris 2003; Maud et al. 2015; Durant et al. 2013).

However, all of the studies in **Table 1** are hampered by a fundamental uncertainty: we still do not know exactly how zooplankton feed in the open sea. Feeding traits of zooplankton have been categorised elegantly (Kiørboe 2011), and we know that copepods can select certain prey types from mixtures in bottles. Trait-based approaches have emphasised the link between feeding mode and diet, with the notion that feeding currents are more effective for catching non-motile cells and that ambush feeders target motile cells (Litchman et al. 2013; Kenitz et al. 2017). But what actually happens in the sea, with its plethora of sizes, types and qualities of available particles? Even among the copepods there is a diversity of opinions on their feeding selectivity in natural food assemblages; a variety of methodological approaches find much less specialised feeding than that which underpins the trait-based models (Huntley 1981; Hopkins 1987; Atkinson 1995; Fileman et al. 2010; Pond and Ward 2011; Isari et al. 2013, Djeghri et al. 2018). Likewise, for protists the variable role of mixotrophy blurs distinctions of traditionally-defined functional groups (Flynn et al. 2013), requiring improved functional definitions (Mitra et al. 2016). These issues are matched by the diversity of ways of dealing with top down control in **Table 1**. In some studies, for example, models are based or validated around selective feeding traits based on prey motility whereas in others prey stoichiometry is invoked as a modulator of predation.

In attempting to deal with the thorny issue of feeding (Mitra et al. 2014), the models in **Table 1** reflect an upsurge in "trait-based" approaches to modelling plankton (Litchman et al. 2013; Benedetti et al. 2016). This provides an appealing conceptual approach, because it is built from a mechanistic basis, getting to the heart of predator-prey interactions. In this sense we believe that Kenitz et al. (2017) provide an appealing and exciting approach to examine the traits and trade-offs involved with feeding mode and how they interact between predators and prey (Kiørboe 2011).

Notwithstanding the attractions of trait-based models, we suggest that it is time to critically re-evaluate the models for seasonality presented in **Table 1.** It may then become possible to synthesise the plausible and complementary components of each into a single conceptual framework. Equally important, models need to be validated more rigorously against observed seasonal patterns. Since models built very differently can all recreate a bloom of diatoms in spring, it is clear that average bloom timing is not enough to evaluate the reality of model assumptions. Other, more counterintuitive properties of the system need to be considered, for example the occurrences of mesozooplankton increasing before their prey, or the patterns of phenological succession of motile and non-motile protists that can vary greatly between years. Many of the time series around the NW European shelf are lengthening and have sampling resolution sufficient to resolve bloom development (O'Brien et al. 2017). The L4 time series has now reached its 30th anniversary, and this and other time series provide ideal testbeds for models of phenology, seasonal succession, bloom formation and decay. With these resources at hand, we hope that this comment will help towards integration of the multiple factors driving the seasonality of stratifying shelf seas.

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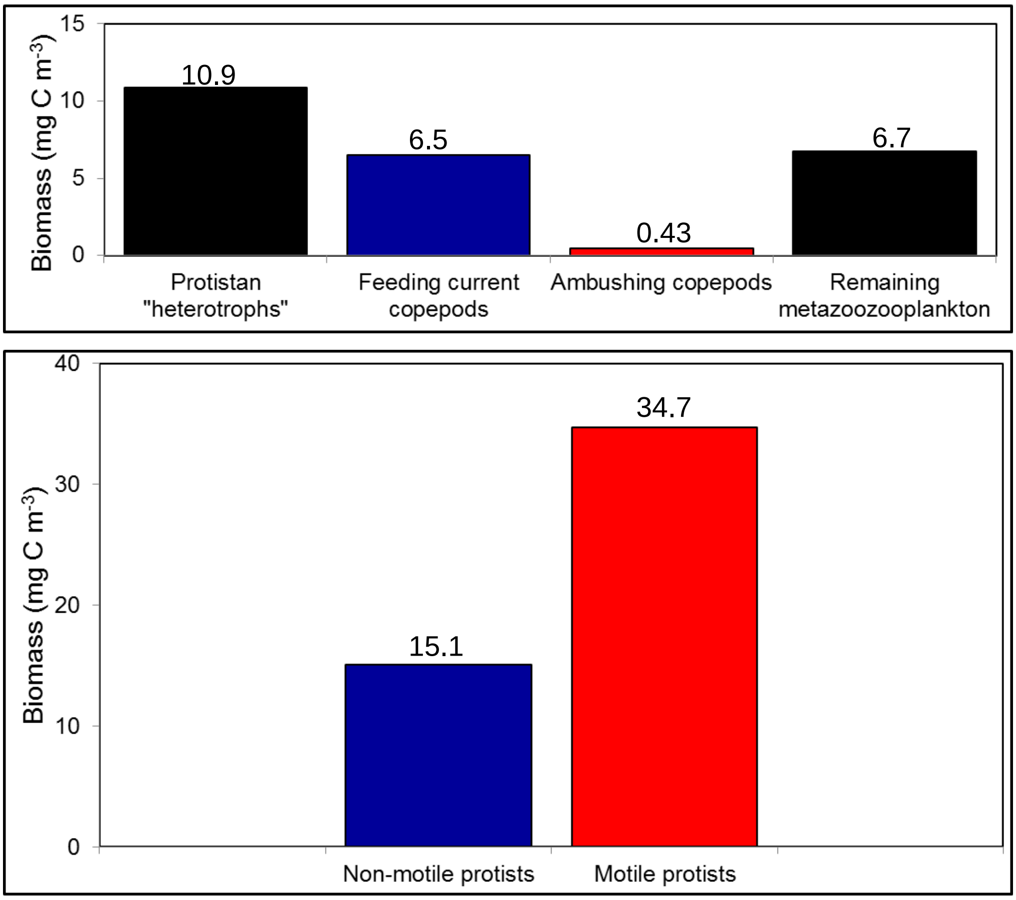

Fig. 1. Estimated carbon biomass (with values above the bars) in the nano-micro and mesozooplankton pools at L4, based on seasonal, L4-specific measurements of dimensions. **A** biomass of heterotrophic taxa, based on the mean of monthly values as calculated in Fig 2d and 2e of Kenitz et al. (2007). Protistan "heterotrophs" comprise colourless dinoflagellates and ciliates, thus designated to be semi-or wholly heterotrophic. "Feeding current copepods" and "ambushing copepods" comprise the 12 most abundant copepods modelled by Kenitz et al. (2007). Remaining zooplankton comprise mero-and holoplankton. Note that micrometazoa (i.e. metazoans passing through a 200 um net) are not included here. **B** Total biomass of non-motile protists (diatoms, coccolithophores and non-motile *Phaeocystis* forms) and motile protists (nanoflagellates, ciliates, plus all dinoflagellates). Note that some of the latter are included in panel **A**. Bars are colour coded and aligned to represent grazer and preferred prey combination based on Kenitz et al. (2017).

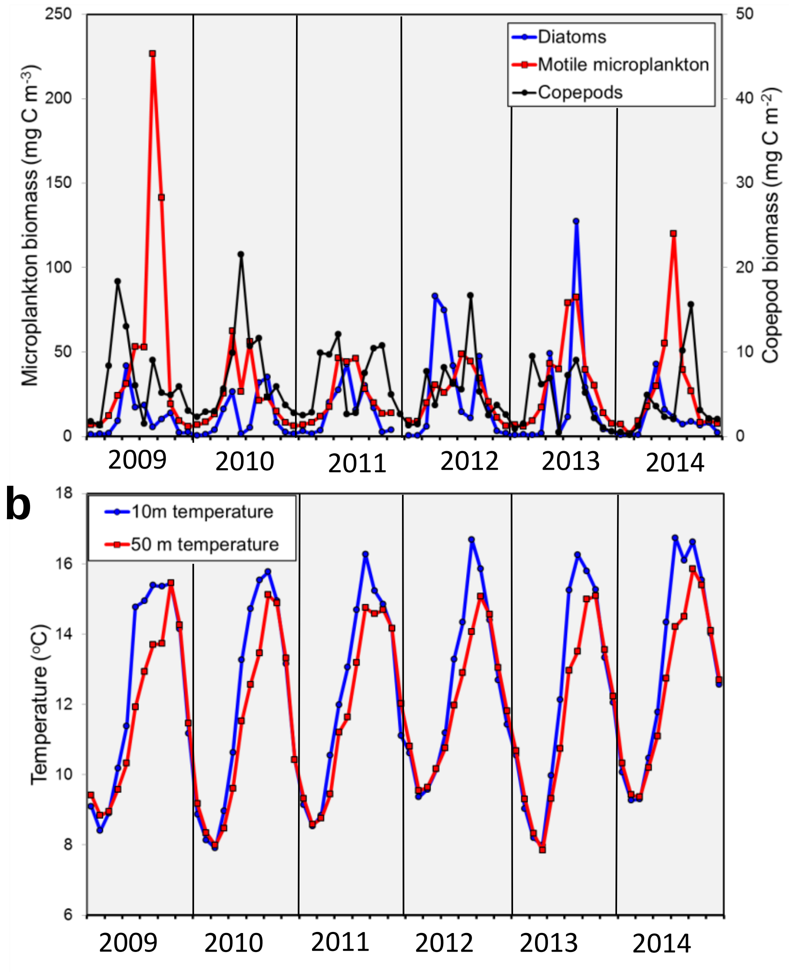

Fig. 2. Illustration of the degree of variation in seasonality observed at the L4 site. Monthly mean values of the weekly measurements are presented, for a 6 year period spanning 2009-2014 **a.** biomass of motile protists (see Fig 1B), diatoms and all copepod species, illustrating the great year-to-year variability observed in relative timings, duration and concentrations of functional group biomass. **b** temperature at 10m and 50m, illustrating the seasonal development and erosion of the thermocline

Table 1. The diversity of conceptual models of factors shaping protist and mesozooplankton seasonality, based on L4 time series data. The L4-specific publications listed here are not necessarily the first descriptions of these mechanisms. Also an array of other bloom drivers (e.g. dilution hypothesis) have been proposed for other systems but have not yet been applied to L4.

Process	**Application to L4**	**Suggested mechanisms**
Loophole hypothesis	From empirical data analysis (Irigoien et al. 2003)	Physical/chemical perturbations disrupt tight grazing control by microzooplankton, allowing certain taxa that are better defended (e.g. in terms of larger size, colonies, spines or toxins) to form blooms. Subsequent bloom development and decline are shaped by algal unpalatability (e.g. stoichiometric ratios), mesozooplankton controls on microzooplankton and ultimately by nutrients.
Change in sign of Net Heat Flux	From empirical data analysis (Smyth et al. 2014)	The physical perturbation (see above) is via the switch from negative to positive net flux of heat into the ocean, promoting initial stabilisation of the upper water column. Timing of spring bloom thus follows the timing of the change in heat flux. Autumn bloom timings are likewise cued to the transition to negative heat flux.
Phytoplankton Photophysiology	Models with data validation Edwards et al. (2013) Polimene et al. (2014)	Seasonal succession of phytoplankton taxa is strongly related to the phytoplankton functional traits, namely nitrate affinity, maximum growth rate and/or light-harvesting physiology.
Stoichiometric modulation of predation	Model with data validation Polimene et al. (2015)	Similar to “loophole hypothesis” above but it is the increasingly poor nutritional status of phytoplankton (high C:N and C:P) under increasing spring light that renders them unpalatable to microzooplankton and able to bloom.
Variable temperature-dependence of plankton phenology	From empirical data analysis Mackas et al. (2012) Atkinson et al. (2015)	In warm seasons there is a weak tendency for spring grazers to increase earlier in the year and autumn grazers to appear later, with timing of diatom blooms unrelated to temperature. However, at species and functional group level, grazer and food phenologies vary greatly between years and bear little relationship to each other.
Mortality- controlled copepod phenology	From empirical data analysis Irigoien & Harris (2002) Maud et al. (2015) Cornwell et al. (in review)	Phenology of major copepods bears little relationship to that of their food or even their egg production, being instead most likely dictated by variation in mortality.
Seasonal dynamics driven by zooplankton feeding trait	Model and data Sailley et al. (2015)	Zooplankton feeding behaviour according to prey quality can have a dominant role in structuring the plankton. Selection according to favourable prey stoichiometry could lead to reduced bottom-up control compared to that from more unselective feeding behaviour.
Trophic trait coupling	Model with data validation Kenitz et al. (2017)	Like Sailley et al. (2015) this invokes the importance of feeding trait in the phytoplankton succession. However, this study focusses on the seasonal succession of feeding current- and ambush feeding copepods as a driver of a repeating and robust seasonal succession of non-motile and motile preys.