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Response to comment ‘What drives plankton seasonality in a stratifying shelf sea? Some competing and complementary theories’.

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Seasonality

Seasonal cycles are imprinted on marine ecosystems from the poles to the tropics, but nowhere more so than in temperate shelf seas. While the proximate cause of these cycles can be traced back to physical conditions (e.g. temperature, light, stratification, nutrient supply), the abundance of the various taxa (e.g. phytoplankton, microzooplankton, mesozooplankton, forage fish, etc.) emerge from the complex interactions of the ecosystem itself where any given player is exposed to top-down and bottom-up pressures. In a comment to our recent manuscript (Kenitz *et al.* 2017), Atkinson *et al.* (2018) rightly point out that no single mechanism is likely to explain observed variations, and we support their call to carefully re-consider how seasonal plankton dynamics are described and modelled.

In the study of Kenitz *et al.* (2017), we present a dynamic model where zooplankton can adapt their feeding behavior to target different types of prey (motile or non-motile). To identify the extend to which the adaptive feeding can shape the temporal distribution of prey motility and predator feeding traits, we compare the model output to the plankton trait distributions observed at the L4 station. In their comment, Atkinson *et al.* (2018) brought to our attention the miscalculated biomass estimates for a couple of the considered trait groups (motile protists and feeding-current feeders) at the L4 station. Indeed, during the analysis of zooplankton abundance data, the juvenile correction factor was implemented incorrectly resulting in underestimated biomass in some zooplankton taxonomic groups. Here, we illustrate the corrected biomass and feeding traits distribution (Fig. 1, a-d), considering adult stages only, based on the size and carbon content assumptions listed in Table 1 of Kenitz *et al.* (2017). For protists, we report the distribution of the motility traits with inclusion of phytoflagellates (inc. *Phaeocystis* spp.) in the motile trait group (Fig. 1e). Despite the changes in the relative biomass of the considered trait groups resulting from these corrections, we confirm that the temporal distribution of the motility and feeding traits remain qualitatively similar to those illustrated in Figure 3 of Kenitz *et al.* (2017). Therefore, the conclusions related to the comparisons of the output of the idealized model with observations stand as discussed in our recent manuscript.

The mechanism of trophic trait cascade proposed by Kenitz *et al.* (2017) is only one of many mechanisms (listed in Table 1 of Atkinson *et al.* (2018)) that can shape seasonal succession in planktonic communities. In reality, variability in species distribution is controlled by multitude of interacting processes that swing in and out of prominence on temporal and spatial scales. In our response, we would like to echo the main message of Atkinson *et al.* (2018) comment: there is a tremendous need to combine the suggested mechanisms to investigate their cumulative effects on shaping plankton community structure. In this, the L4 station time series provides an invaluable resource that traces 30 years of highly resolved physical and biological observations. Only by incorporation of multiple mechanisms in ecosystem models, and testing them against detailed observations such as the L4 time series, will we be able to draw meaningful conclusions regarding the ecological significance of these processes.

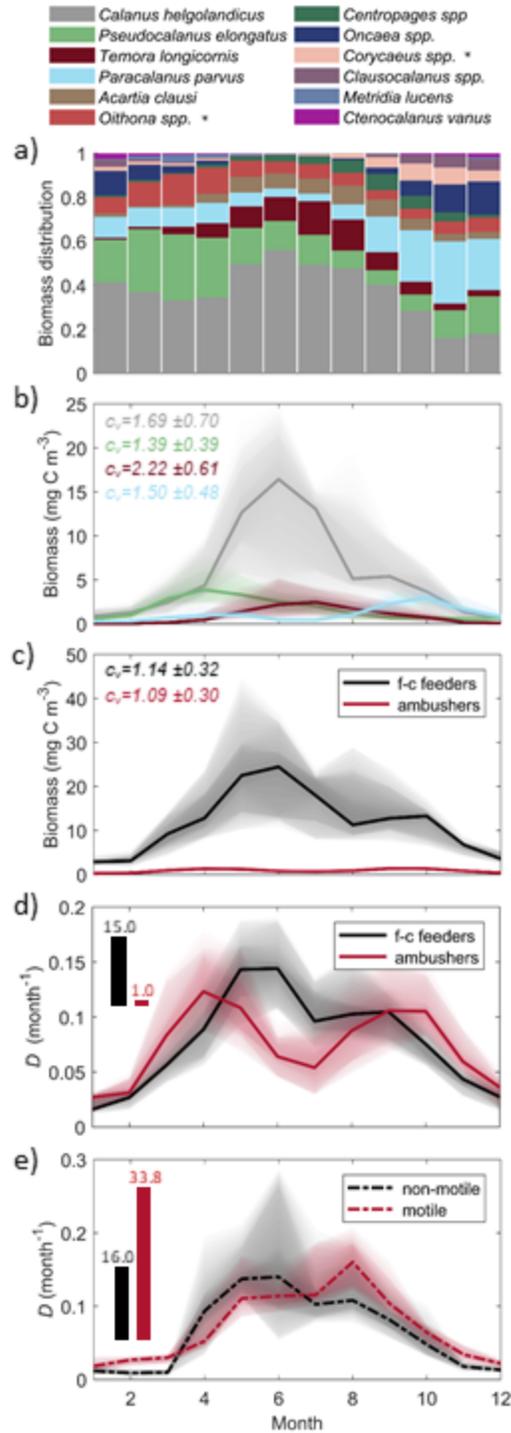


Figure 1. Plankton community at the L4 station, English Channel: a) seasonal contribution of different copepod species to total copepod biomass (adult stages only), b) seasonal variability of the four most dominant copepod species (first 4 species listed in the legend), c) biomass and d) seasonal biomass distribution (D) of all feeding-current feeders and ambush feeders (marked with * in the legend), e) D of their corresponding non-motile and motile prey, sampled at 10m depth. Shaded areas denote the inter-quartile range (IQR; median \pm 25%). The mean annual

variability is measured by variance index, $c_v = IQR/median$. Bars indicate the annual mean biomass (mg C m^{-3}) for corresponding groups, averaged over the years (calculated as in Fig. 1b of Atkinson *et al.* (2018)).

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