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# Impact of zooplankton food selectivity on plankton dynamics and nutrient cycling

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Within models, zooplankton grazing is typically defined as being dependent on total prey concentration, with feeding selectivity expressed only as a function of prey size. This behavior ignores taxonomic preferences shown by the predators and the capacity of some zooplankton to actively select or reject individual prey items from mixtures. We carried out two model experiments comparing impacts of zooplankton displaying passive and active selection, which resulted in contrasting dynamics for the pelagic system. Passive selection by the grazer resulted in a top down control on the prey with a fast turn-over of nutrients. Active selection, on the other hand led to a bottom-up control, with slower nutrient turnover constraining primary production by changing the system toward export of particulate matter. Our results suggest that selective feeding behavior is an important trait, and should be considered alongside size and taxonomy when studying the role of zooplankton impact in the ecosystem.

**KEYWORDS:** feeding behavior; prey selection; plankton dynamics; zooplankton; stoichiometry

## INTRODUCTION

Predator–prey interactions between zooplankton and phytoplankton play a critical role in determining the relative contribution of primary production to higher trophic levels or loss through export. However, within ecosystem models, the equations that describe them are highly sensitive to the choice of parameter and equation (Buitenhuis *et al.*, 2006; Anderson *et al.*, 2010), and models often relate feeding rates to prey biomass in a predictable and

rigid way (Sailley *et al.*, 2013). This rigidity of the predator–prey interactions is due to being defined by a sometimes arbitrary choice of a single Holling type equation without consideration of some of the more complex behaviors and processes driving these interactions (Gentleman *et al.*, 2003; Anderson *et al.*, 2010; Morozov, 2010; Mitra *et al.*, 2014). Model parameterizations of prey selection are often based on prey size through the use of weighted prey preferences (Sarmiento *et al.*, 1993;

Broekhuizen *et al.*, 1995; Baretta-Becker *et al.*, 1997; Gentleman *et al.*, 2003) and/or different grazing parameter values for each prey (Anderson *et al.*, 2010; Flynn, 2010). Consequently, key aspects of zooplankton behavior and physiology are ignored, such as the response of selectivity according to prey stoichiometry, or the variation of assimilation (absorption) efficiency with prey concentration and quality (Mitra and Flynn, 2005; Thor and Wendt, 2010; Montagnes and Fenton, 2012).

All zooplankton display some level of prey selectivity (Mitra *et al.*, 2014). For example microzooplankton (Martel, 2006), copepods (Poulet and Ouellet, 1982) and krill (Hamner *et al.*, 1983) are capable of selecting prey based on chemical clues. On the other hand, prey selectivity in feeders such as tunicates is dependent on size and numeric density of prey. Kiørboe (Kiørboe, 2011) defined feeding behavior along four broad lines: (i) passive ambush feeders (chance encounter with prey and capture based on hydrodynamics); (ii) active ambush feeder (chance encounter with prey but active capture); (iii) feeding current feeders (create a feeding current to lead the prey to the capture structure) and (iv) cruise feeders (actively looking for prey while swimming). These feeding categories are blurred, have exceptions and several species can exhibit multiple feeding modes (e.g. the copepod *Acartia tonsa* can demonstrate active ambush feeding and cruise feeding depending on food availability). Therefore, for this work we have further generalized the feeding modes into two broader categories which we term S1 (passive selection) and S2 (active selection). The former (S1) is the more mechanical mode often used in feeding models, where ingestion rate depends only on the prey size and abundance, formulated by a Holling functional response (Anderson *et al.*, 2010; Sailley *et al.*, 2013). Grazers displaying “active selection” (S2) are defined here as having these attributes (like S1), but also having an ability to switch from one prey to another based on the quality of the prey item (food quality). While food quality in reality reflects a suite of factors additional to size (such as morphology, motility, elemental stoichiometry, composition of essential molecules, micronutrients or toxins), it is defined here by prey elemental stoichiometry of C:N and C:P. We choose this approach as changes in phytoplankton nutrient status, typically associated with nutrient exhaustion (Cembella, 2003), can stimulate changes in zooplankton predation behavior (Cowles *et al.*, 1988; Flynn and Davidson, 1993; Jones and Flynn, 2005; Mitra and Flynn, 2005; Tiselius *et al.*, 2013).

Mitra and Flynn (Mitra and Flynn, 2006) developed a physiologically based prey selectivity function where grazing on a food item will decrease or stop with a decrease in its quality. Thus, when confronted with prey of poor quality, such as a *Phaeocystis* colony high in mucus

content, the grazer would reject this prey type (null grazing). Here, we introduced this dynamic prey selectivity function, termed “Stoichiometric Modulation of Predation” (SMP; Mitra, 2006; Mitra and Flynn, 2006) in a simplified version of the European Regional Seas Ecosystem Model (ERSEM; Blackford *et al.*, 2004; Baretta *et al.*, 1995) with the aim of exploring how prey selectivity by the grazer affects phytoplankton dynamics (i.e. bloom timing and extent), nutrient cycles and export in a realistic ecosystem framework.

## METHOD

### Stoichiometric modulation of predation

ERSEM (Blackford *et al.*, 2004) is a biogeochemical state of the art marine ecosystem model that describes the carbon and nutrient cycle within the lower trophic levels of the marine ecosystem. Crucially for this work, ERSEM accounts for variable stoichiometry within phytoplankton functional types and, therefore, it is particularly suitable to explore the feedbacks between prey quality (given as carbon-to-nutrient ratio) and zooplankton prey selection behavior.

The implementation of SMP was done using Equations (3–5, 8, 9 and 10) from Mitra and Flynn (Mitra and Flynn, 2006). To do this, we adapted these equations accounting for the multi-nutrient dynamic explicitly resolved in ERSEM, and incorporated them in the ERSEM code. The general idea of SMP is simplified in the following equations, derived from Equations (8) and (15) from Mitra and Flynn (Mitra and Flynn, 2006):

$$G = G_{\max} \times \frac{C_{rp} \times P}{(C_{rp} \times P) + K_I} \quad (1)$$

$$C_{rp} = C_{rp}^{\max} \times (1 + K_q^{H_q}) \times \frac{NC_p^{H_q}}{NC_p^{H_q} + K_q^{H_q}} \quad (2)$$

With  $G$  the ingestion rate,  $P$  the phytoplankton biomass,  $G_{\max}$  the maximum ingestion rate achievable,  $K_I$  the ingestion half-saturation equivalent and  $C_r$  the capture rate dependent on the prey nutrient content ( $NC_P$ ).  $K_q$  and  $H_q$  are parameters defining the shape of the response to  $NC_P$ , with  $H_q = 4$  and  $0 < K_q < 1$  (Mitra and Flynn, 2006). The key feature we are implementing in ERSEM is the switch trigger (st, Equation (3); Equations (13) and (14) in Mitra and Flynn (Mitra and Flynn, 2006).

$$st = \frac{C_{rp1} \times P1}{G_{\max} \times td} \quad (3)$$

The switch trigger (st) enables active switching from prey P1 to prey P2 depending on the prey nutrient content

( $NC_p$ ). In fact, the switch trigger works by disabling grazing on a less preferred prey while the preferred prey is of adequate quality (i.e. active selection of a food item). The nutrient content below which the prey is judged as inadequate is determined by the threshold demand ( $td$ ).  $st$  is used in calculating the capture rate ( $Cr$ ) of P2 in the following equation:

$$Cr_{P2} = Cr_{P2}^{\min} + (st < 1) \times (Cr_{P2}^{\max} - Cr_{P2}^{\min}) \times \left[ 1 - \frac{1 + K_{st}^{H_{st}} + st^{H_{st}}}{st^{H_{st}} + K_{st}^{H_{st}}} \right] \quad (4)$$

where the capture rate of P2 ( $Cr_{P2}$ ) depends on the quality of P1.  $Cr_{P2}^{\min}$  and  $Cr_{P2}^{\max}$  are assigned minimal and maximal value that bound  $Cr_{P2}$  variation in response to  $st$ . The parameters  $K_{st}$  and  $H_{st}$  are similar to  $K_q$  and  $H_q$  both in value and role in the equation (see Mitra (2006) for sensitivity analysis).

For full details on the adaptation of the equations and the difference between the standard ERSEM setup and one with implementation of stoichiometric modulation of predation and variable assimilation efficiency, we refer the reader to Polimene *et al.* (Polimene *et al.*, in press).

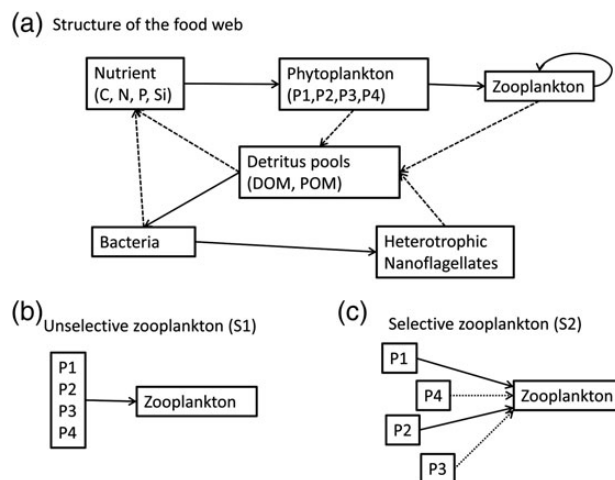
### Model setup: unselective and selective feeder

We used a food web structure with four size-based phytoplankton functional types (P1, diatoms  $>20 \mu\text{m}$ ; P2, nanophytoplankton  $2-20 \mu\text{m}$ ; P3, picophytoplankton  $<2 \mu\text{m}$  and P4, macrophytoplankton  $>20 \mu\text{m}$ ), heterotrophic

nanoflagellates (HNF,  $2-20 \mu\text{m}$ ), a generic zooplankton (zooplankton for short, defined as any heterotrophic organism,  $\mathcal{Z} > 20 \mu\text{m}$ ) and bacteria are explicitly modeled (Fig. 1a).

To facilitate the analysis of the potential effect of zooplankton selectivity without any trophic cascade due to a top predator, or competition from another grazer, the predator-prey interactions are deliberately kept simple. We built the model with one generic zooplankton (representing a mixture of microzooplankton and mesozooplankton) grazing on four phytoplankton types, with a density-dependent mortality as a top closure. The bacterial loop (bacteria and HNF) is kept separate from the phytoplanktonic food web (Fig. 1a), to avoid interference in predator-prey interactions linked to the prey selection process.

The four phytoplankton types are divided between two large (P1 and P4, low growth rate and nutrient affinity) and two small (P2 and P3, high growth rate and nutrient affinity). For each size class, one of the phytoplankton prey is considered to be more strongly selected for or against depending on its quality (good or bad, respectively). The large phytoplankton that is preferentially selected is P1, the silicifier, which is more likely to be nutrient limited since it stays above the thermocline, and is generally the preferred phytoplankton prey for metazoans (in the absence of protozoans). P2 and P3 have the same parameter values and, thus, it does not matter which one is subjected to strong selection in relation to potential nutrient limitation and preferences. In term of predation, P2 is ascribed as the preferred small phytoplankton and is therefore susceptible to strong selection.



**Fig. 1.** Model food web setup. (a) Overall structure of the food web with link between each compartment. Solid line: trophic interaction as uptake or grazing; dashed line: production through excretion and/or egestion. Note that export is not included for clarity of the figure. (b) Unselective zooplankton setup (S1) where grazing is based on biomass and there is no preferred prey. (c) Selective zooplankton setup (S2) with solid line indicating preferred prey and dotted line indicates secondary prey in case the quality of the first one declines.

Using our food web model described earlier (Fig. 1a), we conducted two experiments on the effects of selectivity. In both cases, the assimilation efficiency of ingested food decreases with lowering of the prey quality (i.e. food with high C:P and C:N will cause the assimilation efficiency of all elements to decrease by the same amount). In the first experiment (S1), the generic zooplankton is an unselective feeder. Thus, decreasing prey quality will cause the ingestion rate to decline, although prey abundance will still be the first-order factor directing the predator–prey interaction (Fig. 1b). The second experiment (S2) addressed selective feeding enabling the grazer to switch from or indeed reject a poor quality prey (switch trigger). When quality of the preferred prey declines, the grazing pressure is switched from the designated prey to another (Fig. 1c). As a result, selection is actively based on prey quality, although prey availability will still affect the ingestion rate significantly. Please note that some unselective grazers (S1, mostly filter feeders) increase their ingestion rate in case of decreasing prey quality, compensating quality by quantity. We ran the model with such a setting, and the differences in result between decrease and increase of the ingestion rates were not significant enough to use both settings and have three experiments. We therefore used a decrease in the ingestion rate in S1 for comparison with S2.

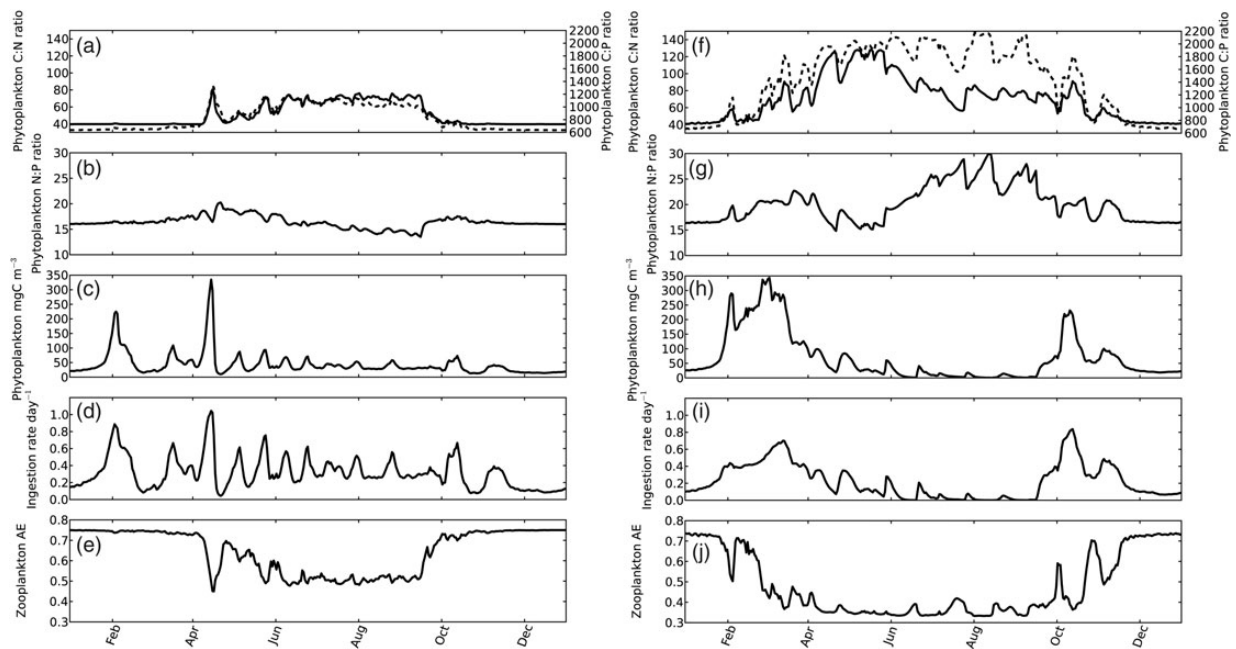
For both experiments, simulations were analyzed after a 10-year spin-up of the model to each equilibrium. For

our purposes, ERSEM was coupled with the general ocean turbulence model (GOTM, Burchard *et al.*, 2006) and implemented at station L4 (50°15.00' N 4°13.02' W) in the Western English Channel. L4 was chosen as the physical environment because GOTM-ERSEM has already been successfully implemented there, and it is the site of a long-term time series enabling us to compare model output with weekly resolution data collected over two decades. The GOTM-ERSEM setup used in this work is the one previously used to simulate phytoplankton dynamics at L4 station (Polimene *et al.*, 2014).

## RESULTS

### Zooplankton interaction with phytoplankton

In both S1 (Fig. 2a–e) and S2 (Fig. 2f–j), phytoplankton quality is highest (C:P, C:N above Redfield value and N:P near Redfield value) during the winter months (Fig. 2a, b, f, g). Since the magnitude of the zooplankton assimilation efficiency (AE) depends on the C:N and the C:P ratio of phytoplankton (whichever is lowest at any given time), the highest possible AE is observed during the winter months (Fig. 2e, j). However, the low phytoplankton biomass (Fig. 2c, h) provides a “refuge” from grazing resulting in a low ingestion rate (Fig. 2d, i). Differences between S1 and S2 arise in the March to November period, after the spring bloom, once phytoplankton biomass increases and



**Fig. 2.** Model outputs for S1 (a–e) and S2 (f–j). From top to bottom: phytoplankton C:N ratio (left axis, full line) and C:P ratio (right axes, dotted line); phytoplankton N:P ratio; phytoplankton biomass ( $\text{mg C m}^{-3}$ ); zooplankton specific grazing rate ( $\text{day}^{-1}$ ) and zooplankton assimilation efficiency.

internal nutrient ratios move away from Redfield values (C rich phytoplankton, N or/and P limited).

In S1, short intense increases in biomass happen throughout the year (Fig. 2c), while in S2 there are two prolonged periods of increase in phytoplankton, in spring and autumn. Phytoplankton quality starts decreasing from February in both S1 and S2, but the decrease only affects AE noticeably after the April bloom in S1, and at the initiation of the spring bloom in February in S2. In S2, the phytoplankton is overall more nutrient-depleted than in S1 (Fig. 2a, f), both in terms of the length of the depletion and the higher C:P and C:N. In both S1 and S2, phosphorus is the most limiting nutrient.

Figure 3a and b (for S1 and S2, respectively) illustrates the daily changes in the grazing rate as a function of both biomass and quality (N:P ratio) of a single phytoplankton, P2 the dominant phytoplankton in the model outputs. For S1 (Fig. 3a), grazing clearly increases with biomass only and changes in quality have little to no impact on the grazing rate. For S2 (Fig. 3b), the increase in the grazing rate with biomass is complemented by the effect of quality: for example for a prey biomass of  $200 \text{ mg C m}^{-3}$ , the grazing rate may be  $0.2 \text{ day}^{-1}$  (N:P of 17) or  $0.6$  (N:P of 20).

In both S1 and S2, the AE respond to phytoplankton stoichiometry. For S1, the ingestion rate (Fig. 2d) will vary with phytoplankton biomass only. For S2, variations of ingestion rate (Fig. 2i) do not change in relation to changes in phytoplankton biomass, and show variation related to changes in prey stoichiometry. Zooplankton in S2 exert a strong grazing pressure on a mid-quality prey, and thus have an AE that varies between 0.7 and 0.4 (Fig. 2j) while ingestion increases (AE  $\sim 0.7$  for  $g \sim 0.4$ ; AE  $\sim 0.4$  for  $g \sim 0.8$ ). On the other hand, in S1, AE and grazing impact are unrelated (Fig. 2e). In S1, zooplankton maintain an AE above 0.45 (when 0.25 is the minimum allowed in the model) just by sheer amount of food ingested (compensating overall low quality with high ingestion rate).

### Impact on plankton dynamics

In S1, phytoplankton is characterized by a base biomass of  $\sim 20 \text{ mg C m}^{-3}$  with short and intense peaks that can reach from 100 to  $220 \text{ mg C m}^{-3}$ . With the highest biomass (above  $200 \text{ mg C m}^{-3}$ ) seen in the two intense but short (less than a week) peaks in February and end of April (Fig. 4b). By comparison, in S2, the initial bloom is stronger and longer (Fig. 4h) reaching a maximal value of  $\sim 350 \text{ mg C m}^{-3}$ . Furthermore, S2 phytoplankton biomass remains high (i.e.  $>$ above  $200 \text{ mg C m}^{-3}$ ) for a prolonged period (from February to April), while for S1 phytoplankton biomass exceeds  $200 \text{ mg C m}^{-3}$  for only few days in February. The summer biomass is lower in S2 ( $< 20 \text{ mg C m}^{-3}$ ) with respect to S1 (between 20 and

$50 \text{ mg C m}^{-3}$ ). The autumn bloom, like the spring bloom, is better defined in S2, where the model simulates phytoplankton biomass increasing from 50 to  $250 \text{ mg C m}^{-3}$  between September and October. In the same period of the year, the phytoplankton biomass simulated in S1 is below  $50 \text{ mg C m}^{-3}$ .

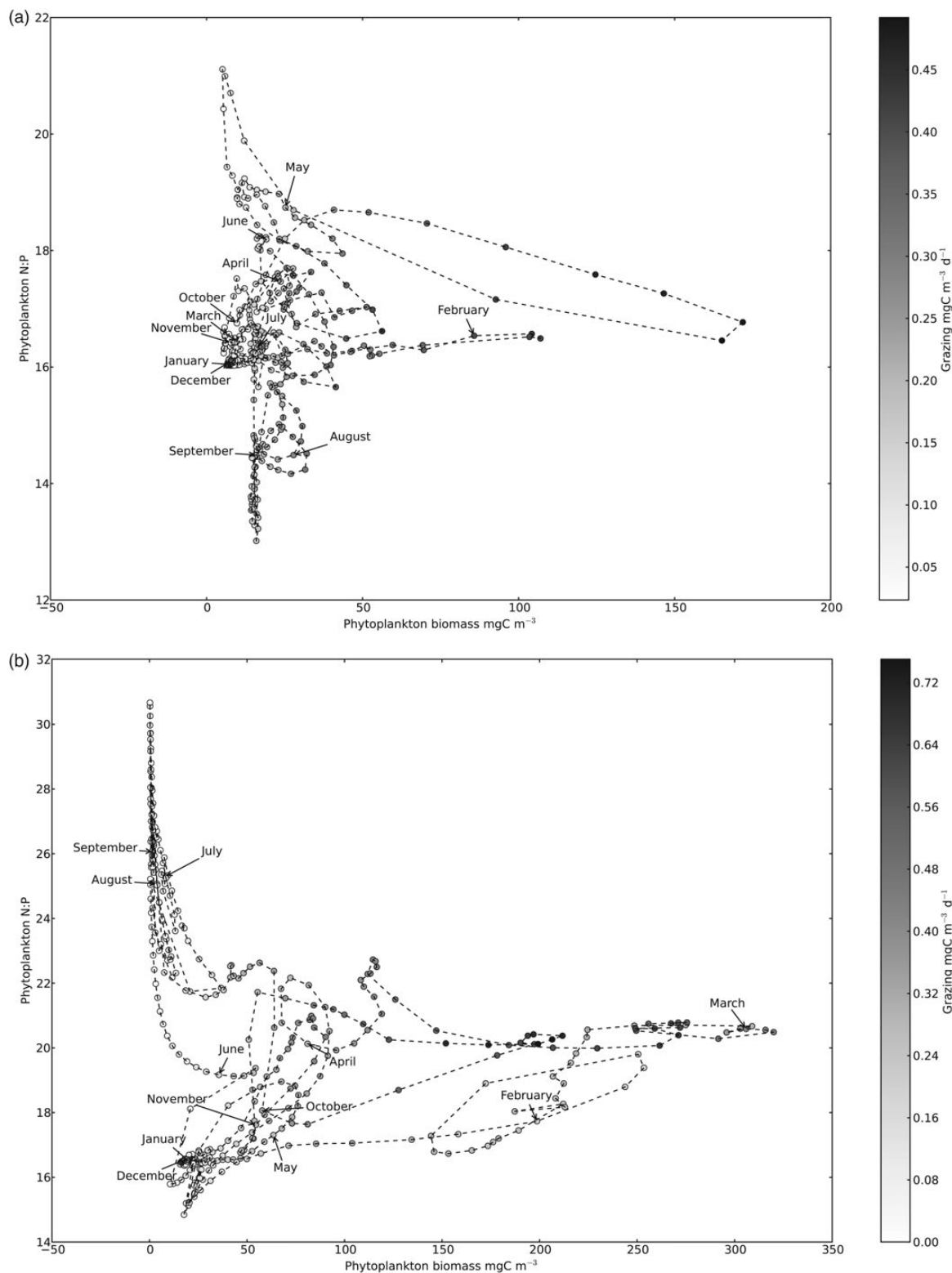
Zooplankton simulated in experiment S1 exhibits a sharp increase during the spring bloom, reaching biomass concentrations equivalent to those of the phytoplankton ( $\sim 250 \text{ mg C m}^{-3}$ , Fig. 4c). Through summer (May to September period) zooplankton biomass is still high (between 100 and  $170 \text{ mg C m}^{-3}$ ) and starts to decrease only in autumn, decreasing to  $70 \text{ mg C m}^{-3}$ . Zooplankton simulated in S2 generally has a lower biomass ( $\sim 1/10$ th that of S1, Fig. 3i); it increases concomitantly with the spring and autumn blooms (up to  $50 \text{ mg C m}^{-3}$ ) and it falls below  $10 \text{ mg C m}^{-3}$  in summer.

### Nutrient cycling

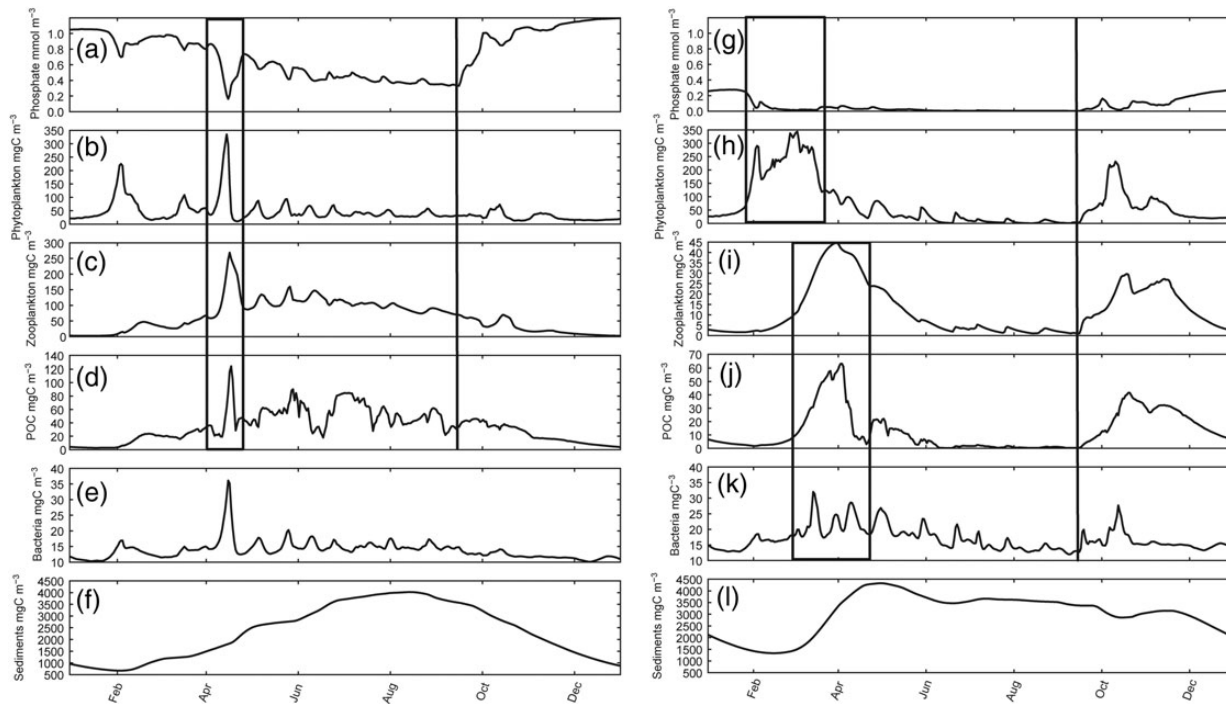
The differences between S1 and S2 in how zooplankton chooses its prey, and the resulting plankton dynamics, have consequences for nutrient cycling. This is reflected in the chemical composition of phytoplankton (Fig. 2a and f), with a higher N:P ratio in S2 than in S1 (maximal value of 20 and 18, respectively). Also phytoplankton is sometimes N limited in S1 (N:P  $< 16$ , June to September), while is it always P limited in S2 (N:P  $> 16$ ).

The dynamics of phosphorus (Fig. 4a and g) reflect nutrient availability and cycling in the water column; it is also the main limiting nutrient. In S1 (Fig. 4a), the second bloom in spring depletes the phosphorus stock to about  $0.2 \text{ mmol m}^{-3}$  from an initial level of  $1.2 \text{ mmol m}^{-3}$  in January. Afterward the phosphate stock is maintained at around  $0.4 \text{ mmol m}^{-3}$  until shortly before the fall bloom, where phosphorus levels recover ( $\sim 0.1 \text{ mmol m}^{-3}$ , vertical mixing). In S2 (Fig. 4g), the phosphate stock is depleted by the spring bloom (from 0.28 to  $0.01 \text{ mmol m}^{-3}$ ) and stays depleted until vertical mixing promotes a fall bloom. Although the levels of phosphate in the system are very different in each run (Fig. 4a and g, 0.2–1.2 vs. 0.01– $0.21 \text{ mmol m}^{-3}$  in S1 and S2, respectively), the interesting fact is that S1 sees a factor 6 difference in its phosphate level while it is an order of magnitude difference for S2. This begs the question: where are the nutrients?

This is answered by the amount of carbon (or other nutrient) that reaches the sediments (Fig. 4f and l), slightly higher in S2, as well as less POC in the surface (maximum 60 vs.  $120 \text{ mg C m}^{-3}$  for S2 and S1, respectively, Fig. 4d and j). Once POC reaches the sediment, it will slowly be degraded and remixed through the water-column in winter. The high almost constant biomass of zooplankton through summer in S1 contributes to a



**Fig. 3.** Model outputs for unselective zooplankton, S1 (a) and selective zooplankton, S2 (b). Variation in the P2 phytoplankton biomass ( $\text{mg C m}^{-3}$ , x-axis) and quality expressed as the N:P ratio (y-axis) on a daily basis for 1 year. Labels denote first day of the month. Shade of the dots illustrate the change in the zooplankton grazing rate on P2 ( $\text{mg C day}^{-1}$ ), see color bar for value range.



**Fig. 4.** Model outputs for S1 (a–f) and S2 (g–l). From top to bottom: phosphate concentration, phytoplankton biomass ( $\text{mg C m}^{-3}$ ), zooplankton biomass ( $\text{mg C m}^{-3}$ ), particulate organic carbon/detritus concentration ( $\text{mg C m}^{-3}$ ), bacteria biomass ( $\text{mg C m}^{-3}$ ) and organic carbon in the sediment ( $\text{mg C m}^{-3}$ ). The boxes mark the spring bloom, the lines mark the autumn bloom as well as deepening of the mixed layer depths and mixing of the water column.

continuous production of POC that slowly builds up the amount of carbon to reach the sediments (Fig. 4d and f). In S2, POC is produced at the time of the bloom (spring and fall; Fig. 4j and l) resulting in most of the carbon export to the sediment occurring by May (compared with mid-August in S1).

## DISCUSSION

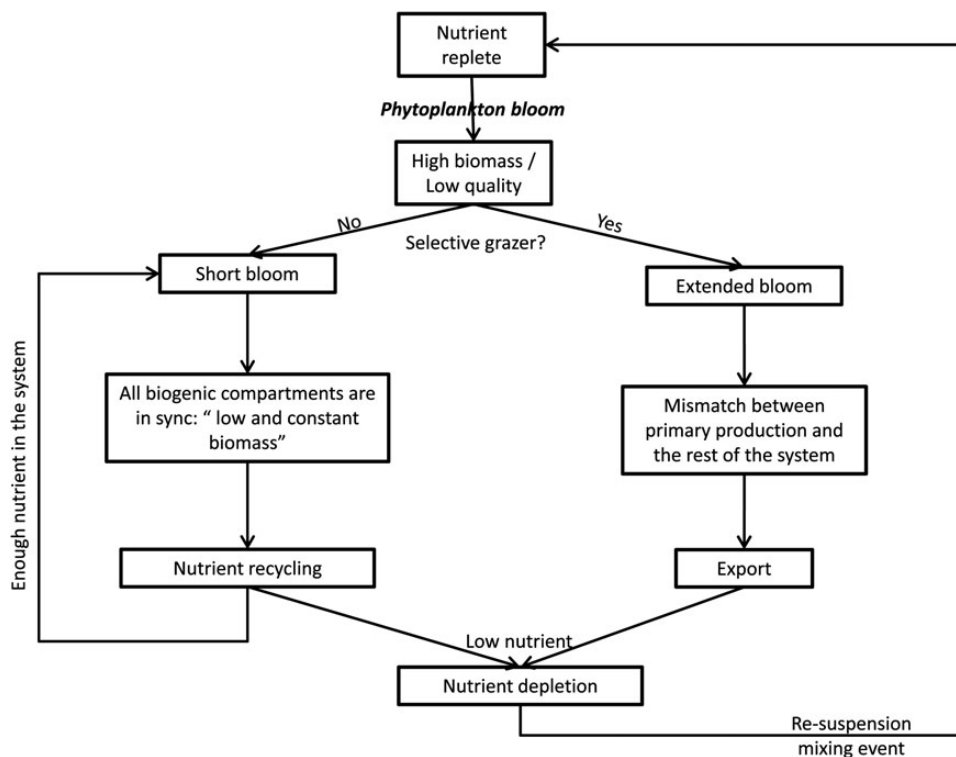
### Plankton dynamics

As we have seen, different feeding selection strategies result in different timing and intensity of primary production. Behind the idea of “prey quality” is the wider concept of ecological stoichiometry and the potential retention of one element over another by an organism (N or P mostly) inducing the depletion of the available nutrient stock for the retained element. The preferential retention of one nutrient and its impact on the surrounding ecosystem in the situation of two separate organisms with different nutrient requirement, and can be found in the same environment (Elser *et al.*, 1988, 2000; Loladze and Kuang, 2000). Here, the equations and parameters that describe the zooplankton metabolism are the same, except for the prey selection scheme. As such there is no incentive for the zooplankton from S1 or S2 to start

processing nutrients differently, except for the quality of their ingested food and how they select this food based on quality. Consequently, the difference in how prey is selected (within a model) has an impact on the nutrient cycle.

The explanation is linked to the zooplankton feeding behavior, which creates a different relationship between zooplankton and phytoplankton (Fig. 5). During a bloom, the phytoplankton will deplete the nutrient stock and slowly become nutrient limited, therefore reducing its own quality. If the grazer is unselective (Fig. 5, left hand side; S1), it responds to the increase in biomass, thus following and potentially controlling bloom development (Irgoien *et al.*, 2005). Unselective grazing results in all compartments being in synchrony (box marking the bloom, Fig. 4a–e), allowing for recycling of nutrients. The quick recycling allows for predator–prey-induced spikes or blooms of phytoplankton through the summer. However, a small portion of nutrients/organic matter is exported at all times (increase in carbon present in the sediment, Fig. 4f) and, at some point, the system will reach a state of nutrient limitation that can only be alleviated by external input or remixing of the water column (Fig. 4a–f, line marking the autumn bloom).

On the other hand, if the grazer is selective (Fig. 5, right hand side; S2), the decrease in phytoplankton quality



**Fig. 5.** Flowchart of the mechanism behind the plankton dynamics in S1 (left) and S2 (right).

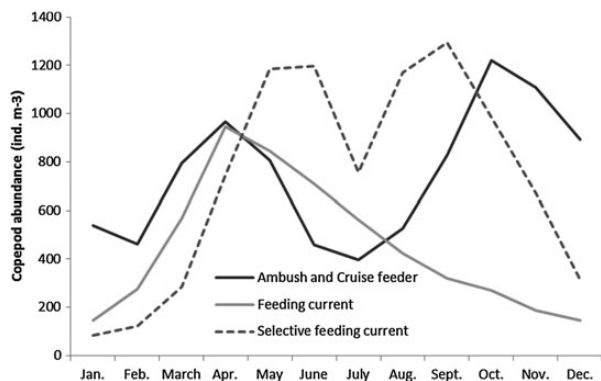
leads to a decrease in grazing pressure. As a result, the bloom will follow its course until the exhaustion of the nutrient stock results in the bloom decline. Zooplankton are less tightly linked (with respect to S1) to the biomass of their prey, peaking 1 month after the phytoplankton, creating a mismatch in the system (boxes marking the bloom, Fig. 4g–k). Particulate organic matter is copiously produced by grazing activity and this results in a strong export (through gravitational sinking) of carbon and nutrients shortly after the bloom (Fig. 4j and l). Summer stratification of the water column prevents the upward diffusion of the exported nutrients, making the surface layer nutrient depleted. This strongly limits phytoplankton growth during the summer. Phytoplankton picks up again in autumn when vertical mixing brings nutrients back to the surface (line marking the fall bloom, Fig. 4g–k).

### Parallels to the “real world”

To verify the tendencies observed in the model outputs, we used data for the most abundant copepods from the time series at L4 (Eloire *et al.*, 2010) and did a monthly average of the 20 years of data (number of individuals per m<sup>3</sup>, 1988–2012). The data are not divided by species or size but by the feeding behavior associated with them in the related literature. We had data for three species using

a feeding current: *Pseudocalanus elongatus* (Iversen and Poulsen, 2007), *Ctenocalanus vanus* (Mazzocchi *et al.*, 2003) and *Calanus helgolandicus* (Iversen and Poulsen, 2007); three species that use feeding current and display selectivity: *Paracalanus parvus* (Tiselius *et al.*, 2013), *Temora longicornis* (Moison *et al.*, 2013) and *Acartia clausi* (Donaghay and Small, 1979); and three ambush or cruise feeders (capture prey items individually): *Oncaea* spp. (Wickstead, 1962), *Oithona* spp. (Iversen and Poulsen, 2007) and *Clausocalanus* spp. (Isari and Saiz, 2011). Copepods described as current feeders are considered equivalent to unselective feeders (S1); ambush or cruise feeders are considered equivalent to selective feeders (S2); and the selective current feeder are considered to be between S1 and S2. Note that since model outputs are in carbon biomass units and data are in abundance units (number of individuals per unit volume), a rigorous quantitative comparison is not possible. The L4 data show that ambush and cruise feeders (selective) are more likely to be present in spring and autumn (Fig. 6) like the selective zooplankton in S2, while the copepods with feeding current (unselective) are present through the summer like the non-selective zooplankton in S1. Feeding current copepods with selectivity tend to have the same distribution of numbers as feeding current species. The overall dynamics for zooplankton shows that copepods that make use of a feeding





**Fig. 6.** Climatology of L4 time series copepod abundance (ind. m<sup>-3</sup>) separated by feeding behavior. Feeding current feeder (*Pseudocalanus elongatus*, *Ctenocalanus vanus*, *Calanus helgolandicus*), feeding current feeder with selectivity (*Panacalanus parvus*, *Temora longicornis*, *Acartia clausi*) and ambush or cruise feeder (*Oncaea* spp., *Oithona* spp., *Clausocalanus* spp.).

current dominate in summer (unselective zooplankton), while spring and fall blooms are dominated by ambush or cruise feeders (selective zooplankton).

The difference in the plankton dynamics also hints at a more complex life cycle or strategies for the zooplankton displaying selective rather than unselective feeding behavior. By this, we mean that zooplankton that are able to target high quantity of mid-quality food (spring and fall bloom, S2), correspond to organisms which evolved strategies allowing them to obtain the needed resource/reserve at specific times of the year, for example before the spawning season or before the over-wintering period. On the other hand, a feeding current zooplankton, which responds more to the quantity of the prey (i.e. S1), might have a tendency to have a uniform requirement of resources through the year (e.g. spawning all through the year). From this, we can expect to find unselective feeding behavior prevailing more in a system where food supply is low but constant, while selective feeding behavior will prevail in pulsed system where food is only periodically available. This concept may apply to different marine ecosystems (e.g. oligotrophic system vs. upwelling, polar vs. tropical open ocean vs. coastal area).

### Caveats

First, the values for quality-related parameters in Equations (1)–(4) have been fixed at the start rather than tuned to data. Detailed validation of the model parameters to experimental and/or field data is needed. However, due to lack of a comprehensive dataset, to enable the validation of ERSEM, this was not possible at this time. Therefore, this study has used values from OD-food web models which have been parameterized against experimentally derived datasets (e.g. Mitra and Flynn, 2006).

Second, the variable assimilation efficiency is incorporated within ERSEM with the assumption that nutrients will not be absorbed independently from each other (Atkinson *et al.*, 2012; Thor and Wendt, 2010). That is, the nutrient with the lowest Redfield ratio (C:N or C:P) will determine the assimilation efficiency for all the nutrients. While our choice of indicators for food quality can be questioned, in this study, we have chosen C:N:P because marine and freshwater experimental studies focus on C:N and C:P, respectively, to define food quality. Arguably we should be looking at various other indicators such as fatty acid content. Likewise, one could criticize that we have not considered situations where, under nutrient limitation (e.g. high C:N:P = severe stress), some phytoplankton produce toxins (Granéli and Flynn, 2006). Our choice in food quality indicators was based on data availability and, unfortunately, there is a severe lack of data which would enable model optimization and validation. However, based on our present understanding of the importance of ecological stoichiometry in nature, using a variable stoichiometry within food web model is a step in the right direction even though it is only the first one.

Finally, we would like to discuss the actual importance of feeding behavior and its impact in the “real world.” It is unlikely, for the simplified situation explored in the model, to happen; zooplankton with different feeding behaviors will co-exist or be present in short succession (Fig. 6). As such, their impact on the system will be dampened compared with the clear signal (recycling vs. export of nutrients) from the model experiments. Also, the ability of various zooplankton predators to prey on organisms at different trophic levels to adjust their nutrient intake (e.g. switching from preying on phytoplankton to preying on protozoans), could have major overall impacts on nutrient recycling while decreasing transfer efficiency of primary production to higher trophic levels.

### Perspectives

To date, representation of zooplankton in biogeochemical models is typically very simplistic (Mitra *et al.*, 2014 and references therein). In these models, the zooplankton groups are essentially treated as a closure term to ensure proper levels of primary production and community composition (Sailley *et al.*, 2013). Laboratory, field and modeling studies on the fate of primary production, and the linkage of primary production to higher trophic levels via zooplankton, highlights the importance of zooplankton in partitioning primary production to different fates (Stock and Dunne, 2010; Mitra *et al.*, 2014; Stock *et al.*, 2014). It is therefore important to incorporate processes beyond size and biomass to define the role of zooplankton within biogeochemical models. The work presented here explores

the role of zooplankton feeding behavior on biogeochemical cycling and thence trophic dynamics. This is the first time where selection and non-selection of prey by zooplankton depending on their stoichiometry has been incorporated within a biogeochemical model. While such an incorporation is rather simplistic, it is a first step and one which opens a new dimension for representation of zooplankton in ecosystem models.

Although the two extremes of food selection we explored are likely to be dampened in ecosystems, zooplankton feeding behavior still has the potential to play an important role. We often focus on an organism's taxonomy or size when looking at species succession or changes in community composition. Rarely do we look at the structuring effect arising from organisms of similar trophic level and size but with different feeding behavior. The implications of zooplankton feeding behavior are beyond simple plankton dynamics and composition; it also impacts the cycling and export of nutrients. This particular trait needs to be considered carefully when examining ecosystem response to external forcing of any kind. With appropriate ground truthing, the modeling community is now in a position to start implementing such behavior into biogeochemical models.

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