

Food for Thought

How trophic cascades and photic zone nutrient content interact to generate basin-scale differences in the microbial food web

T. Frede Thingstad  ^{1*}

¹Department of Biological Sciences, University of Bergen, Bergen, Norway

*Corresponding author: tel: +47-90712022; e-mail: frede.thingstad@uib.no.

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In linear food chains, resource and predator control produce positive and negative correlations, respectively, between biomass at adjacent trophic levels. These simple relationships become more complex in food webs that contain alternative food chains of unequal lengths. We have used a “minimum” model for the microbial part of the pelagic food web that has three such food chains connecting free mineral nutrients to copepods: via diatoms, autotrophic flagellates, and heterotrophic bacteria. Trophic cascades from copepods strongly modulates the balance between the three pathways and, therefore, the functionality of the microbial food web in services such as food production for higher trophic levels, DOM degradation, and ocean carbon sequestration. The result is a theoretical framework able to explain, not only apparent conflicts in Arctic mesocosm experiments, but also biogeochemical features of the Mediterranean. Here, the fundamental difference between Arctic and Mediterranean microbial food webs is the way they are predator driven by seasonal migration of large copepods in the Arctic, but resource driven due to the anti-estuarine circulation in the Mediterranean. In this framework, global change effects on microbial ecosystem functions are more like to come indirectly through changes in these drivers than through direct temperature effects on the microbes.

Keywords: Arctic Ocean, bottom-up, Mediterranean Sea, microbial food web, Nansen Legacy, top down, trophic cascades

Introduction

The abstract to this article can be seen as a state-of-the-art summary of research in marine microbial ecology rooted in a single event >40 years ago: the 1977 blowout from the Bravo platform, releasing something like 15 000 tonnes of crude oil (Gunkel *et al.*, 1985) into the North Sea. One important aspect of oil pollution is that it is an addition of a largely degradable carbon source to the ocean’s photic zone. In the stratified season, this is an environment where mineral nutrients, typically nitrogen, phosphorous, or iron (Moore *et al.*, 2013), are believed to limit phytoplankton growth. Efficient growth of oil-degrading bacteria can then only occur in competition with phytoplankton, leading to a kind of Hutchinsons Paradox (Hutchinson, 1961) in disguise: “How can bacteria and phytoplankton coexist if limited by the same mineral nutrient.”

The solution suggested was a strong predator control on the biomass of the best competitor (bacteria), leaving limiting resources for the inferior competitor (phytoplankton) with less predator control on their biomass (Thingstad and Pengerud, 1985). Using 100-ml laboratory chemostats, we could demonstrate experimentally how this worked (Pengerud *et al.*, 1987) and how degradation of even a readily available carbon source like glucose could be severely restricted due to the combined controls of both bacterial biomass (through predation) and bacterial growth rate (through mineral nutrient competition with phytoplankton).

The principle was later generalized (Figure 1) using the “Killing-the-Winner” (KtW) structure (Thingstad and Lignell, 1997). Despite its simplicity, this KtW structure contains “a little bit of everything” (see, e.g. Våge *et al.*, 2018). It combines

bottom-up and top-down controls to relate resources to diversity and diversity to life strategies; it relates trade-offs between traits to resource partitioning and allows food chains to split into food webs. Fundamental biological questions like “What makes SAR 11 the world’s most abundant organism?” can therefore be discussed in a KtW framework (Thingstad *et al.*, 2014). Today, more than four decades after the Bravo blowout, I believe that the principles of the KtW structure are fundamental also for understanding some of the basin-scale differences in the ocean ecosystem. The rest of this article is an attempt to explain why and how.

In terms of orders of magnitude in organism size, the pelagic “virus-to-whales” food chain is split approximately in two at the level of copepods: an upper, macroscopic, “copepods-to-whales” (ca. 10^{-3} – 10^1 m) food web with multicellular organisms and a lower, microbial, “virus-to-copepods” (ca. 10^{-8} – 10^{-3} m) food web containing viruses, prokaryotes, and protists. Over sufficiently long time and space scales, the biomass distribution along the whole food chain may hypothetically approach steady state and the entire food chain will be resource driven. At shorter time and space scales, however, the ability for self-movement in organisms in the macroscopic part creates a potential for variations in abundance that depend on factors other than food availability in their immediate environment. For the microbial part, this means that grazing loss to metazoan predators can vary due to factors outside the microbial system, potentially creating cascading effects that apparently can propagate all the way through the microbial web to affect composition and dynamics in the virus community five orders of magnitude “below” (Sandaa *et al.*, 2017). Regional differences in the abundance and behaviour of metazoan predators may therefore cause differences in structure and function of the microbial food web. This structure and function will, however, also depend on the amount of limiting nutrients available, typically nitrogen, phosphorus, iron, organic material (for heterotrophic prokaryotes), and

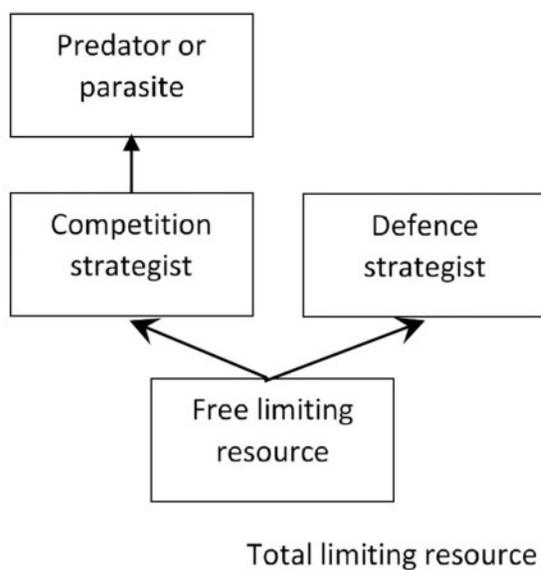


Figure 1. Idealized “Killing-the-Winner” structure where a “defence strategist” can coexist stably with a “competition strategist” on a single shared limiting resource. This is because biomass of the “competition strategist” (Winner) is limited by predator-control which leaves some of the “Total limiting resources” for the “defence strategist” with inferior competitive abilities.

silicate (for diatoms). How such top-down and bottom-up controls interact is not intuitively obvious.

The Arctic pelagic ecosystem is an interesting case in this context. Arctic copepods have adapted to cold water and a short productive season by seasonal vertical migration and diapause in deep waters (Falk-Petersen *et al.*, 2009). As this behaviour generates seasonal variation in the grazing pressure on microbes in the photic zone layer, one of the main conditions for trophic cascades is present.

In the Mediterranean, net evaporation sets up a negative thermo-haline circulation that creates an oligotrophication gradient along the African coast (Millot and Taupier-Letage, 2005). The Arctic and Mediterranean oceans therefore appear to have fundamentally different drivers for the surface layer microbial food web, making them interesting case studies for studying the properties of top-down- and bottom-up-driven microbial food webs.

To illustrate the basic concepts behind top-down and bottom-up drivers, we can use the extreme simplification of a nutrients–autotrophic flagellates–ciliates (NFC) food chain (i.e. analogous to classical nutrients–phytoplankton–zooplankton models) in Figure 2A. Using simple Lotka–Volterra equations (see Supplementary Material for mathematical assumptions), we can solve for the steady state (N^* , F^* , C^*) as function of two external drivers: total nutrient content $N_T = N + F + C$ (Figure 2A) and loss rate δ_C of the ciliate community C to their copepod predators (Figure 2B). Variations in N_T are subsequently discussed as “resource” or “bottom-up” driving. Similarly, variations in the loss rate δ_C is discussed as “predator” or “top-down” driving. Figure 2B and C illustrate how the resource and predator driver create different steady-state correlations between microbial predators (C^*) and their prey (F^*) in this simple linear food chain. The general bottom-up effect is that more resources give more producers which again give more predators. Variations in N_T therefore tend to produce positive prey–predator correlations in bottom-up driven systems. In top-down-driven systems, an increase in the stock of a top predator will reduce the abundance of its prey, which again will release grazing pressure for the next, lower level in the food chain (Frank *et al.*, 2007). This produces negative correlations between predators and their–prey, and therefore lead to alternating negative and positive effects down a linear food chain, usually referred to as a “trophic cascade” (Carpenter *et al.*, 1985).

In limnology, trophic cascades have not only been of theoretical interest but have also served as a central conceptual tool in the restoration of eutrophied shallow lakes. The shallow lake case may also serve as an important reminder of the need to understand the ecological context within which such controls work. Since bottom vegetation provides refuges where the dominating meso-zooplankton (cladocerans) can hide from their predators, disappearance of this vegetation due to light limitation in the eutrophied state prevents easy restoration of the original food chain through nutrient reduction (Scheffer *et al.*, 1993).

Based to a large extent on the high occurrence of defence structures in pelagic organisms, Verity and Smetacek (1996) argued many years ago that top-down forces were likely to be more important in marine food webs than usually recognized and that the dominating bottom-up perspective of marine ecologists had led to a biased view on how marine ecosystems work. In a more recent review, also Hessen and Kaartvedt (2014) concluded that there is an urgent need for more focus on the existence of trophic cascades in the marine environment.

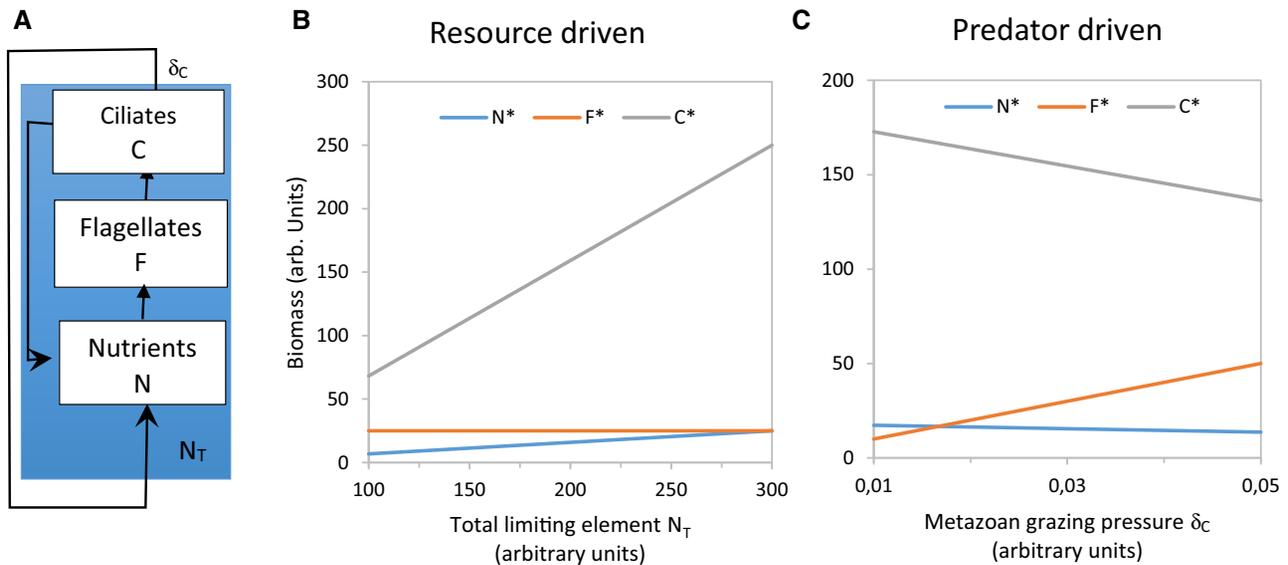


Figure 2. (A) Linear NFC food chain used to illustrate the steady-state effect of (B) resource control (variations in total nutrient content N_T with ciliate predation loss rate δ_c kept constant) and (C) predator control (variations in δ_c with N_T kept constant) (see [Supplementary Material](#) for details).

In a meta-analysis based on correlations in known predator–prey pairs from the macroscopic part of the food chain, [Frank et al. \(2007\)](#) classified North Atlantic shelf systems as top-down or bottom-up controlled. Intriguingly, systems with top-down control turned out to be located in cold-water regions, while bottom-up control seemed to be a characteristic of more temperate waters.

I here argue for a somewhat similar difference in the external drivers for the photic zone microbial food web, i.e. with copepod predators being the central driver in cold Arctic waters, as opposed to a dominating resource-driven microbial food web in the warm Mediterranean Sea. The arguments are based on published observations for the west-to-east oligotrophication gradient in the Mediterranean Sea ([Santinelli et al., 2012](#)) and our use of trophic cascades to explain seemingly conflicting results in Arctic mesocosms ([Larsen et al., 2015](#)),

The marine microbial food web

By adding a two-step “classic” nutrients–diatoms–copepods food chain to the three-step NFC–copepods food chain in [Figure 2A](#), we get what [Wollrab et al. \(2012\)](#) have termed a “pentagon” food web structure ([Figure 3A](#)). Among the interesting aspects of this pentagon are its predictions for copepod–chlorophyll correlations. Since there is a direct link between copepods and diatoms, but an intermediate ciliate link between copepods and flagellates, this pentagon predicts cascades that produce negative and positive copepod–chl-a correlations, respectively, depending on whether the system is diatom or flagellate dominated. Experimental support of this theoretical prediction has been found using mesocosm experiments manipulated at the copepod level ([Vadstein et al., 2004](#)). Important for our subsequent discussion, the simple pentagon structure of [Figure 3A](#) thus seems to have sufficient elements to capture essential aspects of how the flagellate–diatom balance is controlled.

Adding also a “microbial loop” where dissolved organic material is fed into the food web through heterotrophic bacteria and

their heterotrophic flagellate predators ([Figure 3B](#)), we get the “minimum” model for the microbial food web suggested originally for the Mediterranean by [Thingstad and Rassoulzadegan \(1999\)](#); later given a mathematical formulation and used for successful simulation of transient dynamics in mesocosm perturbation experiments ([Thingstad et al., 2007](#)). The long copepods–ciliates–heterotrophic flagellates–bacteria trophic cascade introduced by this addition has also been verified experimentally ([Zöllner et al., 2009](#)).

With this, the minimum model contains three alternative food chains of different lengths connecting mineral nutrients to copepods: through diatoms (two steps), autotrophic flagellates (three steps), and heterotrophic bacteria (four steps). This three-food-chain structure can also be described as two coupled pentagons with ciliates and copepods occupying the upper right corner of a left and a right pentagon ([Larsen et al., 2015](#)). The important difference between the two pentagons is the rapid numerical response of ciliates, allowing the left pentagon to reach internal steady state over much shorter time scales than the right pentagon where variations in copepod stock may be decoupled from variations in the microbial part.

Using simplifying assumptions similar to those used for the linear NFC model, the steady states of this minimum model can be solved analytically. As before, the steady states of the minimum model depend on its two external drivers, such as total limiting nutrient N_T (resources) and copepod stock Z (predators), but also modified by the presence/absence of silicate and whether the supply of labile dissolved organic carbon (DOC) is smaller or larger than the bacterial carbon demand ([Thingstad et al., 2007](#)).

Microbial organism size and eutrophication are correlated with small- and large-celled phytoplankton species dominating in oligotrophic and eutrophic marine systems, respectively ([Irigoien et al., 2004](#)). The minimum model reflects this, as there is a transition from left to right from dominantly predator control of the small, competitively efficient bacteria on the left side to

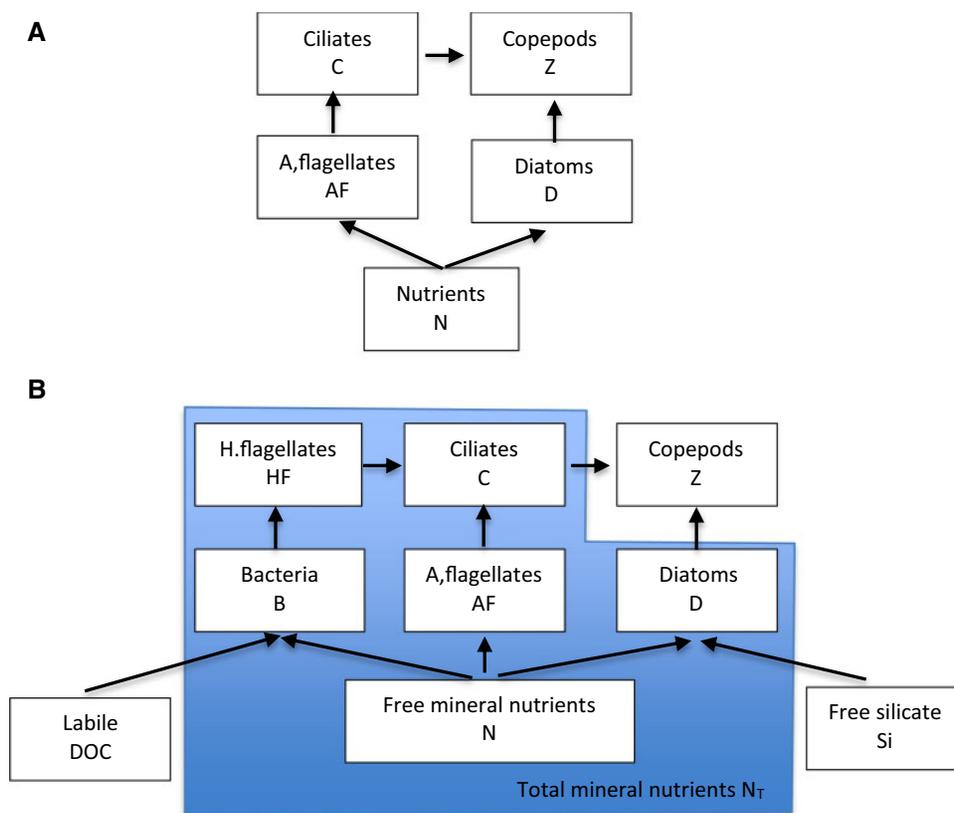


Figure 3. (A) “Pentagon structure” with two pathways from mineral nutrients to copepods. Because of the difference in length, the cascading effect of copepods on autotrophic flagellates and diatoms is opposite. (B) “Minimum model” for the microbial food web with three alternative pathways connecting mineral nutrients to copepods. These also form two coupled pentagons with ciliates and copepods occupying the upper right corner of the left and right pentagons, respectively.

dominantly resource control of the large, chain-forming diatoms on the right side. Reductions in N_T therefore tend to reduce biomass on the right “classical” side of the model (Figure 3B), increasing the relative dominance of small-celled “competition strategists” on the left side. These mechanisms also provide a simple solution to Ryther’s seemingly counter-intuitive observation that nutrient-rich and oligotrophic systems tend to have short and long food chains, respectively (Ryther, 1969).

Using a qualitative and intuitive approach to the cascading effects, the negative correlation in predator–prey pairs along each linear food chain produces negative correlation between copepods and diatoms, as well as between copepods and bacteria (odd-numbered steps along linear food chains) but positive correlation between copepods and flagellates (even numbered food chains to both auto- and heterotrophic flagellates). This generates two reciprocal states of the food web: a flagellate-dominated food web for high copepod levels (High-Z) and one that is either diatom-dominated or bacteria-dominated for low copepod levels (Low-Z). Whether the Low-Z state of the minimum model becomes dominated by bacteria or by diatoms depends on the availability of easily degradable organic carbon and silicate. Note that Figure 4 illustrates states where the cascades have established. Transients such as where a large diatom spring bloom is grazed down by a large copepod stock are not represented here. Analysis of such transient states requires the

dynamic mathematical version of the model (Thingstad *et al.*, 2007). The classification scheme in Figure 4 has allowed a unifying interpretation of population dynamics in mesocosm experiments that otherwise appeared to give conflicting results (Table 1).

For some of these experiments, additional mechanisms had to be added to the minimum model to explain special effects. An illustrative example is the effect of small-celled diatoms. Adding the ability of ciliates to graze on small diatoms (the dotted line in the lower right food web of Figure 4), the model outcome shift: Instead of the Low-Z outcome with diatom dominance and mineral nutrient-limited bacteria for large, chain-forming, Si-replete diatoms (as observed in the MEDEA experiment), it shifts to bacterial dominance and carbon limitation for small, ciliate-grazed diatoms (as observed in the PAME I experiment). Another model modification affecting the trophic cascades is the formation of grazing resistant bacteria in situations replete in labile organic carbon (MicroPolar experiment, Table 1). This terminated the cascades at the heterotrophic flagellates–bacteria connection (Tsagaraki *et al.*, 2018). There are also experiments where the minimum model does not seem to explain copepod–diatom predator–prey dynamics well (MINOS experiment; Pree *et al.*, 2017; Table 1) possibly due to complex meso-zooplankton communities and/or diatom toxicity (Hardardottir *et al.*, 2019).

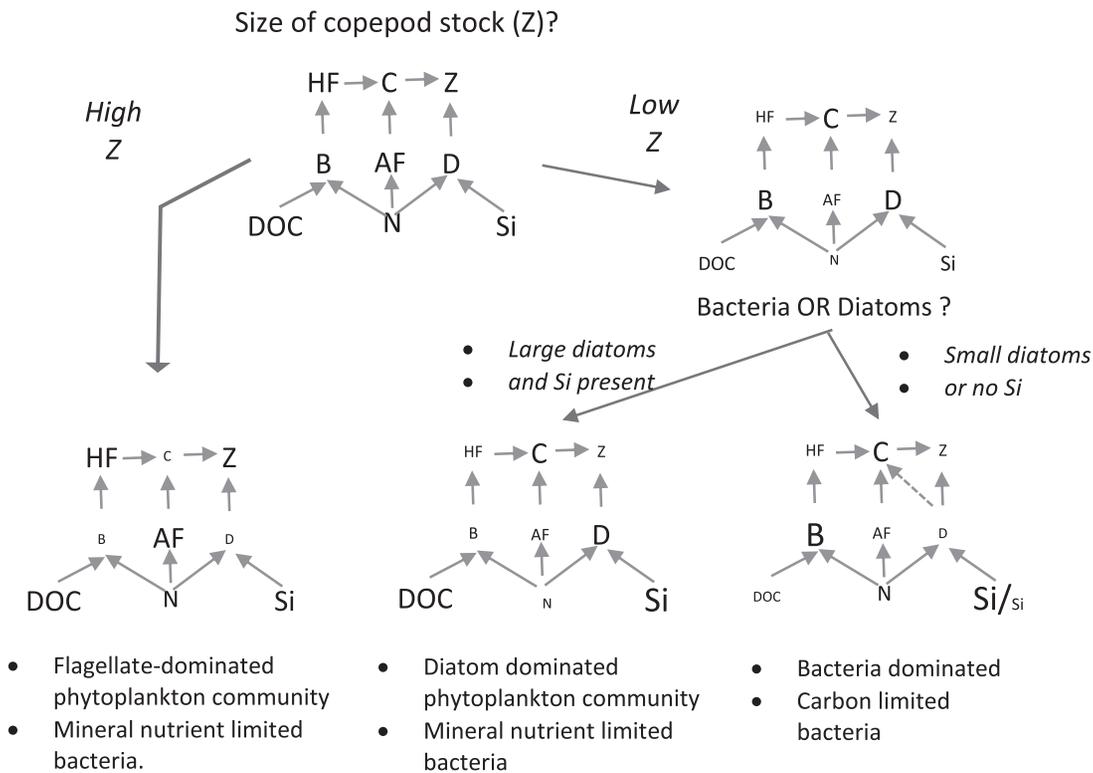


Figure 4. Trophic cascades from copepods (Z) determining the balance among the bacteria, autotrophic flagellates and diatoms. In the High-Z situation to the left, the food web becomes flagellate dominated and differences in the availability of DOC and Si have little food web effects. The Low-Z situation to the right is more complicated since the diatom vs. bacteria outcome is influenced by the availability of silicate and labile DOC, favouring diatoms and bacteria, respectively. An additional complication has been identified in the size structure of the diatom community where ciliate grazing on sufficiently small diatoms (dotted arrow) was found to shift the dominance towards bacteria (see Table 1 for mesocosm experiments corresponding to the three different outcomes).

Table 1. Summary of mesocosm experiments interpreted using the minimum model in Figure 3B.

Experiment	Location	Dominating pathway	Bact. lim. ^a	Comments
High copepod initial situation (High-Z)				
PAME II (Larsen et al., 2015)	Kongsfjorden, Early Arctic summer	Autotrophic flagellates	M	No effect of glucose because of M-limited bacteria
MicroPolar (Tsagaraki et al., 2018)	Kongsfjorden, Early Arctic summer	Flagellate/bacteria	M	Copepod removal/addition Excess of organic carbon allowed for predation-resistant bacteria
Low copepod initial situation (Low-Z)				
PAME I (Thingstad et al., 2008; Larsen et al., 2015)	Kongsfjorden, Late Arctic summer	Bacteria/small diatoms	K	Small diatoms outcompeted when glucose added
MEDEA (Thingstad et al., 2007)	Isefjorden, Denmark	Bacteria/large diatoms (Si limited)	M	Bacterial limitation shifted from K to M when large Si-limited diatoms were stimulated by Si addition
MINOS (Pree et al., 2017)	Raunefjorden, Norway	Diatoms (large)	M	Diatom-copepod dynamics not well described by minimum model

^aM and K: bacterial growth limited by mineral nutrients and labile organic carbon, respectively.

Regional differences in the external drivers select ecosystem state

Arctic Ocean

In the terminology used here, top-down forcing of the microbial food web from copepods occurs when variations in copepod abundance are driven by factors other than their immediate microbial food supply. Vertical positioning in the water column is a well-studied life-strategy adaptation in copepods, believed to optimize

the difference between food supply and predatory loss (Fiksen and Carlotti, 1998). As both their food supply (phytoplankton) and the efficiency of their visual predators (fish larvae) are affected by light, diel and seasonal light variations are important ultimate drivers, but in shelf seas also modulated by the depth restrictions of a variable bottom topology (Aarflot et al., 2019).

With characteristic time scales for microbial population changes in the order of days, the microbial food web is likely to

function as a long-pass filter, not effectively transmitting the signal from diel vertical migrations in meso-zooplankton to bacteria. Seasonal signals, however, such as the stop in copepod grazing pressure from mid-summer (Levinsen *et al.*, 2000) until spring, should give the microbial system ample time to respond.

In near-natural Arctic systems, experimental evidence for this seasonal effect comes primarily from the PAME I and PAME II experiments (Table 1). In these, the initial meso-zooplankton (dominated by *Calanus finmarchicus*) was $3\times$ higher in the PAME II compared with PAME I, presumably as a consequence of their timing in late and early Arctic summer, respectively. In these experiments, the top-down effects have been documented not only to the level of the size of the prokaryote community but also to the community composition of both prokaryotes and viruses (Sandaa *et al.*, 2017).

Winter diapause in deep waters is an adaptation of the large Arctic copepods to a short productive season in cold waters, allowing stage V to mature so that eggs from stage VI can be hatched in, or in front of, the food supply becoming available during the spring phytoplankton bloom (Falk-Petersen *et al.*, 2009). Already in mid-June, feeding seems to be terminated prior to overwintering (Levinsen *et al.*, 2000). Winter diapause has also been found in some, although not all, copepod species from the Southern Ocean investigated by Atkinson (1998). The hypothesis is therefore that top-down control of the microbial food webs is typical of high-latitude, cold-water systems; rooted, not in a microbial adaptation to such environments, but in the life-cycle adaptation of their metazoan predators.

Mediterranean Sea

A marine system particularly well suited for studying resource-driven microbial food webs is the Mediterranean west-to-east oligotrophication gradient. Net evaporation in the Mediterranean Sea sets up a negative thermo-haline (anti-estuarine) circulation (Millot and Taupier-Letage, 2005). Therefore, limiting elements released from particles sinking into the sub-surface counter-current (the Levantine Intermediate Water) are exported through the Gibraltar Strait. This loss of limiting nutrients (= reduction in our N_T driver) generates a west-to-east oligotrophication gradient along the African coast: from mesotrophic “Atlantic” conditions in the western Alboran Sea to ultra-oligotrophic conditions in the Levantine Basin in the eastern Mediterranean (Berman *et al.*, 1985). As expected, the phytoplankton community shifts from a considerable diatom component in the western Alboran Sea (Arin *et al.*, 2002) to a phytoplankton community dominated by small unicellular cyanobacteria in the Levantine Basin of the Eastern Mediterranean (Raveh *et al.*, 2015).

Somewhat counter-intuitively, the oligotrophication is also accompanied by an increase in DOC eastwards along this gradient. The value of ca. $40\ \mu\text{M-C}$ in the west is comparable to the ocean’s background level of recalcitrant DOC. This increases to $50\text{--}55\ \mu\text{M-C}$ in the east (Santinelli *et al.*, 2012). Apparently, consumption of DOC thus decreases faster than production as the system gets more oligotrophic. Importantly, the ca. $15\ \mu\text{M-C}$ of accumulated DOC appears to be labile or semi-labile as it disappears during the return transport westwards in the aphotic Levantine intermediate water (Santinelli *et al.*, 2012).

To get a better understanding of mechanisms that may generate this, one can use the left pentagon of the minimum model (Figure 3B). There is a strong correlation between the

oligotrophication and ciliate numbers as illustrated by the near-linear relationship between upper layer particulate-P and ciliate numbers along the gradient (Figure 5A and B). Using the same arguments of trophic cascades as before, the pentagon structure will give positive correlations, both between ciliate biomass (C) and the free limiting nutrient (N) and between ciliate biomass (C) and bacterial biomass (B). For mineral nutrient-limited bacteria, both biomass and growth rate will therefore be proportional (to a first linear approximation) to C and bacterial production (growth rate \times biomass) therefore scales as the second power of C . Assuming a fixed bacterial yield (bacterial biomass formed per unit DOC consumed), also bacterial carbon demand of mineral nutrient-limited bacteria (BCD_M) will then scale as the second power of C ($\text{BCD}_M \propto C^2$). If autochthonous production of DOC (Ψ) and ciliates scale are proportional to N_T , the relationship between Ψ and ciliates will be linear ($\Psi \propto C$). The curves for BCD_M and Ψ will then cross in one point (Figure 5C). This divides the system in an oligotrophic and a mesotrophic part. In the oligotrophic part, $\Psi > \text{BCD}_M$ (production $>$ consumption), bacteria are mineral nutrient limited and DOC will accumulate. In the mesotrophic part, bacteria are carbon-limited, $\text{BCD}_K = \Psi$, and only recalcitrant forms of DOC will accumulate.

This model not only seems to give a reasonably good fit to the data for ciliates and BCD reported by Santinelli *et al.* (2012) but also locates the crossing point from carbon to mineral nutrient-limited bacterial growth to somewhere in the Sardinian channel. In this dataset, the transition between carbon-limited and mineral nutrient limited bacteria occurs at a concentration of particulate-P of $\sim 16\ \text{nM-P}$, and a ciliate abundance slightly below $1\ \text{ciliate ml}^{-1}$ (Figure 5B). Importantly, this interpretation appears reasonably consistent with bioassays for bacterial growth limitation where stations with carbon limitation were found in the Alboran Sea and Sicily Strait, other stations having phosphorous-limited bacteria or giving inconclusive results (Van Wambeke *et al.*, 2002).

In these relationships, phytoplankton–bacteria competition for the limiting mineral nutrient is essential for the accumulation of degradable DOC. At higher latitudes where deteriorating light conditions are likely to release the nutrient competition long before deep-water formation, one would expect the labile DOC pool to be consumed before it is transported to the ocean’s interior. DOC accumulation due to mineral nutrient limitation of the heterotrophic bacteria and due to chemical recalcitrance of course not mutually exclusive mechanisms. In regions with differences in plankton species composition, differences in circulation pattern, or in other physical conditions, the balance between recalcitrance and mineral nutrient limitation may differ from what seems to be the case in the Mediterranean.

Relevance and perspectives

With almost all of oceanic primary production occurring in the microbial end of the pelagic food chain, the mechanisms controlling diatom-flagellate balance are relevant to the food supply for the entire food chain. With catches in the world’s large fisheries declining since the late 1980s (Pauly *et al.*, 2003), today’s marine fisheries cannot meet the needs of a human population expected to pass 10 billion by year 2057 (United Nations, 2019). As standard ecological theories assume ca. 10% transfer efficiency between adjacent trophic levels, a shift in harvest to lower trophic levels in the macroscopic part of the food chain gives a theoretical

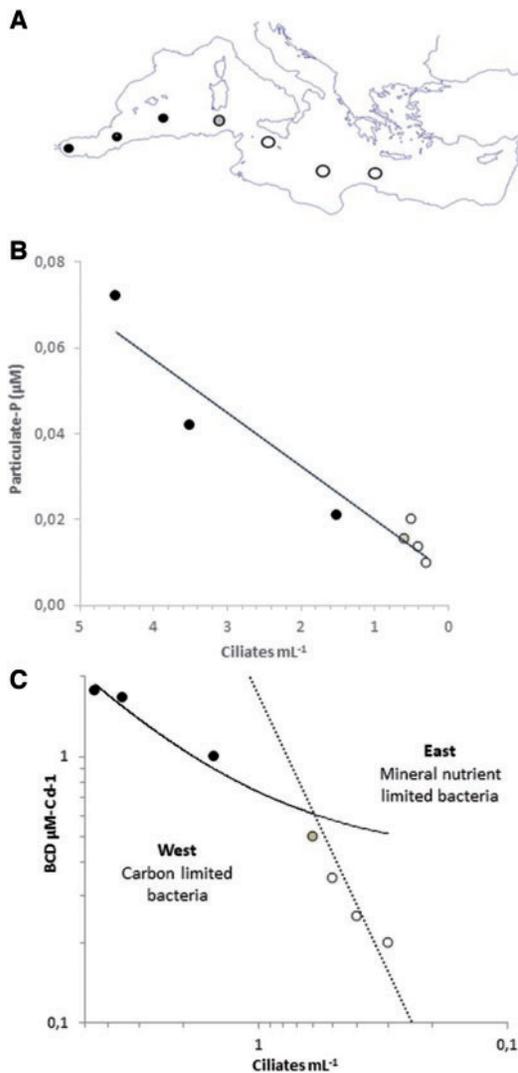


Figure 5. (A) Stations of the Prosope cruise in the Mediterranean discussed in the text. Stations west of, in, and east of the Sardinian channel marked with filled, grey, and white circles, respectively. (B) Illustration of the oligotrophication as the west-to-east decline in particulate-P (x -axis) and the linearly correlated decrease in ciliate abundance (regression line: $y = 73.99x - 0.43$, $R^2 = 0.922$). (C) Suggested relationship between ciliate abundance and bacterial carbon demand (log-log plot) based on the left pentagon of the minimum model [redrawn from Våge *et al.* (2018)]. In this model, bacterial carbon demand under mineral nutrient limitation scales as ciliates to the second power [fitted line (dotted): $BCD_M = 1.7C^2$, $R^2 = 0.916$], while autochthonous DOC production and therefore BCD under carbon limitation (solid line) is assumed to scale to the first power of C (fitted line $BCD_K = 0.32C + 0.42$, $R^2 = 0.955$). The feasible BCD is the minimum of these two. The two curves appear to cross somewhere around the Sardinian channel (grey circle), suggesting carbon-limited bacteria in the Alboran Sea to the west and mineral nutrient-limited bacteria to the east. Data from Santinelli *et al.* (2012) and Prosope cruise (http://www.obs-vlfr.fr/cd_rom_dmtt/pr_main.htm). Note the reversed x scales for comparison with the geographical west–east oligotrophication.

potential for substantial increase in sustainable catches. The ecological effects may, however, be complex (Pauly *et al.*, 1998). The alternatives of increasing harvest at the adjacent trophic levels of planktivorous fish (Irigoien *et al.*, 2014) or copepods (Grimaldo *et al.*, 2011) would be expected to have opposite effects on the copepod stock. In the framework discussed here, this would tend to drive the microbial food web in the directions of flagellate-dominated High-Z states, or diatom (alternatively bacteria)-dominated low-Z states (Figure 4). Such fisheries-induced changes in top-down forcing may therefore affect not only the quality and possibly the amount of primary production but also the length and therefore transfer efficiency through the food chain supporting the harvested level.

The three food chains of the minimum model also have different biogeochemical functionalities: carbon export by sinking particles such as Si-ballasted diatoms and faecal pellets is primarily associated with the right, “classical” food chain, while accumulation of degradable forms of DOC depends on mineral nutrient limitation of bacteria-restricting activity in the microbial loop on left side. The suggestion of a strong predator control of the balance between the three pathways is therefore also a suggestion of a strong predator modulation of biogeochemical functions in the photic zone ecosystem.

While the minimum model contains some biological detail in its description of microbial cycling of the limiting mineral nutrient, the coupling to the production of organic carbon is intentionally kept simple. A deeper analysis of resource-driven systems would require a better mechanistic description for the relationship between N_T and autochthonous production rate of labile DOC (Ψ). There are at least two important issues involved. The attractively simple assumption of a fixed stoichiometric coupling between primary production and phytoplankton uptake of the limiting nutrient was found to strongly underestimate carbon fixation as measured in mesocosms dominated by nutrient-limited diatoms. In these experiments, a model with diatom primary production proportional to diatom biomass gave a much better fit (Thingstad *et al.*, 2007). The consequence is a decoupling of carbon fixation from Redfield stoichiometry in diatom-dominated environments (Thingstad *et al.*, 2008). Another important issue is the transfer of this organic carbon through the microbial food web, including its release to forms available to bacteria (the labile DOC pool in the minimum model) through processes such as viral lysis, phytoplankton excretion, and sloppy feeding. Some of these mechanisms would be expected to depend primarily on biomass of a single group (e.g. phytoplankton excretion), others primarily on organisms meeting each other (e.g. sloppy feeding). Rates that involve collision frequencies are proportional to the product of two biomasses (e.g. predator and prey). If, in a resource-driven system, both of the two biomasses increase with nutrient content (N_T), such rates will thus scale as the square of N_T . Our Mediterranean example (Figure 5) demonstrates how a combination of linear and squared relationships may be crucial in creating shifts in resource-driven systems.

Considering the rather simplistic descriptions of a complex biology used in the minimum model, its ability to quantitatively explain the connection between top-down and bottom-up forcing in mesocosm and field data admittedly came to some extent as a positive surprise. The cascading effects in the minimum model

depend on its three well-defined linear food chains. Adding complexity in the form of more trophic crosslinking such as ciliates feeding directly on bacteria would tend to weaken the cascades. Intriguingly, the model's explanatory power therefore seems to some extent to be because of, rather than despite, its simplicity.

For a deeper analysis of the coupling between the microbial and macroscopic parts of the food chain, a more detailed description of the meso-zooplankton community seems, however, to be required. Biogeographical distribution of copepod traits such as ambush feeding may be important (Prowse *et al.*, 2019). There are also important additional phylogenetic groups of mesozooplankton (e.g. rotatoria, appendicularia, and cladocera) with feeding behaviour and biogeographical distributions differing from that of copepods.

A main insight from the mesocosm work is how the trophic cascades strongly modulates the system responses to bottom-up perturbations (Larsen *et al.*, 2015). Regional characteristics of lower food web functioning are therefore likely driven by regional-specific combinations of these two drivers. The two systems discussed here have the advantages of a well-understood physics behind the Mediterranean oligotrophication gradient and a well-documented copepod prevalence of diapause towards the poles (Record *et al.*, 2018), making the two systems ideal as “microbial laboratories” for comparing differences and interactions between the two types of drivers.

With the ocean accumulating most of the heat from global warming (Lyman and Johnson, 2014), temperature sensitivity of structure and function in the microbial food web is important. In the microbial ecology literature, much of the discussion has centred on possible differences in the temperature response of different functional groups, including the possibilities that heterotrophic bacteria (Pomeroy and Deibel, 1986) or micro-zooplankton (Rose and Caron, 2007) are more affected by temperature than phytoplankton. Such differences between functional groups would make the balance between the three pathways (and therefore the microbial food web's functionality) sensitive to temperature. Using the minimum model to analyse mesocosm dynamics at different temperatures, the need for temperature correction of the parameters has been surprisingly low (Larsen *et al.*, 2015). This may be because temperature adaptations at the physiological and/or phylogenetic level buffer the effect at food web level. It may, however, also be rooted in the physical nature of constraints experienced by food-limited organisms. The enzymatic processes constraining organism growth at or near maximum growth rates would be expected to have “biological” Q_{10} values ~ 2.5 – 3 . Under food limitation, however, physical processes such as diffusion and filtration dominate. Temperature dependence then comes from water viscosity, which has a Q_{10} of ~ 1.3 (Jumars *et al.*, 1993). Steady-state food webs with food-limited microbes may therefore be less temperature sensitive than predicted by laboratory experiments based on food-replete growth (Thingstad and Aksnes, 2018).

The suggestion here is therefore that climate-driven changes in water column stability (Yamaguchi and Suga, 2019; Lewandowska *et al.*, 2014) and/or in life-cycle adaptations in the metazoan top predators (Edwards and Richardson, 2004) may be more important for microbial ecosystem structure and function than the direct effects of increasing temperature on microbial activity.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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There is an extensive set of experimental mesocosm work behind the theoretical framework synthesized here. All co-authors on the original articles reporting these experiments have a role not only in the data collection but also in the intellectual process of developing this framework. The Mediterranean data for Figure 5 are based on the Prosope cruise (<https://doi.org/10.17600/99040060>) and collected by J. Dolan (ciliates), F. van Wambeke (bacterial production) and P. Raimbault (particulate-P).

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