REVIEW AND SYNTHESIS

Simple models combining competition, defence and resource availability have broad implications in pelagic microbial food webs

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Abstract

In food webs, interactions between competition and defence control the partitioning of limiting resources. As a result, simple models of these interactions contain links between biogeochemistry, diversity, food web structure and ecosystem function. Working at hierarchical levels, these mechanisms also produce self-similarity and therefore suggest how complexity can be generated from repeated application of simple underlying principles. Reviewing theoretical and experimental literature relevant to the marine photic zone, we argue that there is a wide spectrum of phenomena, including single cell activity of prokaryotes, microbial biodiversity at different levels of resolution, ecosystem functioning, regional biogeochemical features and evolution at different timescales; that all can be understood as variations over a common principle, summarised in what has been termed the 'Killing-the-Winner' (KtW) motif. Considering food webs as assemblages of such motifs may thus allow for a more integrated approach to aquatic microbial ecology.

Keywords

Bottom-up control, competition, Keystone predator, Killing the Winner, microbial diversity, microbial food webs, predation, resource partitioning, top-down control.

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INTRODUCTION

With the introduction of new methodologies to microbial ecology starting more than 35 years ago, the classical idea of a linear nutrients – phytoplankton – zooplankton pelagic food chain was rapidly replaced by one of a more complex microbial food web (Fenchel 1987). Resolution in description of this food web then expanded drastically as molecular techniques became powerful enough to reveal high richness in the protist (Diez *et al.* 2001; López-García *et al.* 2001; Moon-van der Staay *et al.* 2001; de Vargas *et al.* 2015), prokaryote (Britschgi & Giovannoni 1991; Fuhrman *et al.* 1993; Hagström *et al.* 2002; Rappé & Giovannoni 2003; Ferrera *et al.* 2015) and viral (Chen *et al.* 1996; Breitbart *et al.* 2007; Suttle 2007) communities. As a result, focus has shifted from the classic emphasis on system simplicity, to a widespread fascination with the apparent complexity of the pelagic microbial food web.

Despite the huge experimental and observational efforts put into this field by now, the theoretical basis for our understanding of how these systems work remains relatively weak. We lack, for example, a generally accepted theory explaining how all this diversity is generated and maintained. Also, for the flux of energy and material through the system, we have well-established concepts like the 'microbial' and 'viral' loops, describing re-introduction of dissolved organic carbon into the particulate food chain (Azam *et al.* 1983) and shunting of

particulate matter back into the dissolved pool by viral lysis (Bratbak *et al.* 1992; Fuhrman 1999; Riemann & Middelboe 2002), respectively. The experimentally verified and generally accepted theory describing the control of viral abundance, virus-to-host ratios and partitioning of prokaryote production between these two alternative pathways is, however, largely lacking.

Other enigmatic observations include a consistently reverse J-shaped (e.g. Sano 1997) activity distribution of heterotrophic prokaryotes (Malmström *et al.* 2004; Galand *et al.* 2009; Campbell *et al.* 2011; Nikrad *et al.* 2012; Samo *et al.* 2014), implying that most individual cells have low activity, despite environmental conditions that allow a few individuals to grow rapidly. Also, high genetic micro-diversity in prokaryote populations led to the concepts of core- and pan-genomes (Mira *et al.* 2010; Grote *et al.* 2012; Santinelli *et al.* 2012), but, the theoretical framework to understand how such micro-diversity is driven and its consequences, is weak.

It is generally expected that competition and defence are central structuring factors in microbial communities, as reflected in the debate of what makes the SAR11 clade the probably most abundant organism on earth (Morris *et al.* 2002). Until 2013, lacking reports on SAR11 viruses was an argument for SAR11 as a defence specialist with evolved immunity against viral lysis. However, documentation of abundant SAR11 viruses (Zhao *et al.* 2013), turned the argument around to favour the hypothesis that SAR11's success

(in terms of abundance) is due to its competitive abilities. Top-down control is, however, a control of abundance (Thingstad & Lignell 1997), and the argument therefore seems to harbour a possible inconsistency: How can a SAR11 population whose abundance is strongly virus-controlled become abundant due to its competitive abilities?

The SAR11 question is an important special case of the more general question of what mechanisms determine community composition, species richness and evenness. Intra and interspecies competition, defence against predators and viruses with different prey or host selectivity and resource availability are clearly central in this, but we lack the theoretical framework to understand exactly how.

Two decades ago, Verity & Smetacek (1996) called for an improved theoretical understanding of the mechanisms structuring pelagic food webs; suggesting that progress in the field was hampered by a too narrow focus on bottom-up mechanisms. Although awareness of the role of top-down factors has clearly improved since (e.g. Hessen & Kaartvedt 2014; Pancic & Kiørboe 2018), we believe that the full consequences of considering competition, defence and resources in combination, are still not fully acknowledged. We here review how the use of very simple models combining these can provide insight into a broad spectrum of phenomena in the microbial part of pelagic food webs.

IDEALISED MODELS CONNECTING COMPETITION, DEFENCE AND LIMITING RESOURCES

The basic principle we discuss is negative density control, preventing a superior competitor from sequestering all of a limiting resource, allowing coexistence with an inferior competitor if the latter is subject to less density control.

An early hint for this appears in Hutchinson's (1961) influential article on the Paradox of the Plankton: 'It can be shown theoretically, as Dr MacArthur and I have developed in conversation, that if one of two competing species is limited by a predator, while the other is either not so limited or is fed on by a different predator, coexistence of the two prey species may in some cases be possible. This should permit some diversification of both prey and predator in a homogeneous habit'. A more explicit reference to the interaction between trophic controls and resource availability was formulated by Paine (1966): 'It is suggested that local animal species diversity is related to the number of predators in the system and their efficiency in preventing single species from monopolising some important, limiting, requisite'. Mathematical analysis of these relationships appeared later (Roughgarden & Feldman 1975; Thingstad & Pengerud 1985) and the principle is now mostly referred to as 'keystone predator' (Leibold 1996) or 'Killing-the-Winner' (Thingstad & Lignell 1997), primarily used in macro-faunal and microbial ecology, respectively.

In aquatic microbial ecology, these ideas have been used to address the theoretical problem of how coexistence of size-classes of phytoplankton is controlled by combining size-selective predators and photic zone nutrient content (Thingstad & Sakshaug 1990; Armstrong 1994). The principle also provided a theoretical solution to the question how phytoplankton and bacteria can coexist when both are mineral nutrient-limited, and how this affects the ability of bacteria to consume organic compounds (Thingstad & Pengerud 1985). Although general in nature, the term 'Killing-the-Winner' (KtW) has primarily become associated with virus ecology and the hypothesis that viruses prevent sensitive, but competitive, hosts (the 'winner') from monopolising the limiting resource. This allows coexistence with resistant hosts, even when such defence is associated with a cost of resistance (COR) in the form of reduced competitiveness. Note that the 'winner' is the organism that would become dominant in the absence of the virus due to its superior competitive abilities, not the organism dominating when viruses are present.

The subsequent discussion uses the KtW motif for convenience, although it basically pertains to the family of ecological concepts including 'keystone predators' (Leibold 1996), 'loopholes' (phytoplankton blooms caused by lack of negative density control from predators (Irigoien *et al.* 2005), 'pentagon food web structures' (Wollrab *et al.* 2012; Wollrab & Diehl 2015) and 'Killing-the-Winner' (Thingstad & Lignell 1997), all describing consequences of negative density control.

BASIC KTW MOTIF WITH THREE POPULATIONS

Figure 1a shows the basic KtW structure with three populations: competition strategists (C), defence strategists (D) and predators (P). Abundance of C and P are determined by the properties of the predator-prey interaction and the predator and not, importantly, by C's competitive abilities. As long as the loss rates of P and D remain constant, an increase in total resources (R_T) therefore increases only the population size of D (see Supporting Information (SI) for symbols and mathematical formulation).

Therefore, in the steady state of this idealised structure:

-the competition strategist (C) is predator (P)-controlled,
-the defence strategist (D) is resource-controlled;

The KtW motif affects both the richness and evenness aspects of diversity; With top-down control allowing coexistence of C and D, and resources controlling the balance between C and D, the motif reduces richness at low total resources (because D disappear) and reduces evenness at high resources (because D dominate). Diversity indexes combining richness and evenness, such as the Shannon index, are therefore expected to give unimodal resource–diversity relationships, with highest diversity at intermediate resource levels. This is a general pattern found in microbial and macro-organism ecosystems (Smith 2007).

Also, with fixed loss rates from D and P, the ratio $P/(C+D)$ will decrease with increasing total resources (R_T) (because only D will increase). The KtW motif thus gives more room for defence strategies in eutrophic systems, suggesting a possible general mechanism behind the somewhat counter-intuitive observation of decreasing predator-to-prey ratios with increasing eutrophication in a wide range of systems (Hatton *et al.* 2015). Perhaps a special case of the same general mechanism is a decrease in virus-to-host ratios as host abundance increases (Knowles *et al.* 2016; Wigington *et al.* 2016; Parikka *et al.* 2017).

There is substantial experimental evidence supporting the theoretical predictions of the KtW motif, encompassing
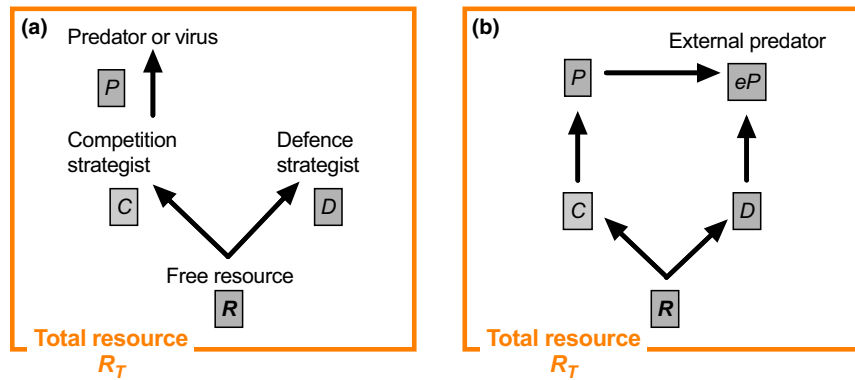
Figure 1 (a) Idealised «Killing-the-Winner» motif. (b) Pentagon food web structure when extending idealised KtW motif with external predator (eP).

virus-host communities as well as interactions between other organism groups in the microbial food web. Pure culture (gnotobiotic) chemostat experiments with sensitive and immune strains of *E.coli* in combination with virus (Bohannan & Lenski 2000) demonstrated the predicted increase in abundance of the resistant strain with increasing reservoir nutrient concentration. Also using gnotobiotic cultures, the predicted (Thingstad & Pengerud 1985) coexistence of competitively inferior phytoplankton with phosphorous-limited bacteria exposed to flagellate grazing, has been shown in chemostat cultures (Pengerud *et al.* 1987). Selection of inedible bacteria in mixed prokaryote communities exposed to grazing by flagellates (Matz & Jürgens 2003) is also consistent with the KtW mechanism. In controlled laboratory experiments with mixed phytoplankton communities, Steiner (2003) combined predation with various mineral nutrient levels, confirming the predicted interactive effect with grazing-resistant forms dominating at high nutrients level under grazing. Using a mesocosm approach and metazoan predators, (McCauley & Briand 1979) also confirmed the selection of grazing-resistant phytoplankton types when exposed to grazing. All these demonstrate the same principles across different experimental and ecological systems. Both the theoretical and the experimental basis for the basic KtW motif are thus well established.

Note that trade-offs are not explicitly included in the mathematical formulation in the SI. Clearly, an organism that can combine superiority in both competition and defence will take over all of R_T. Ultimately, it is thus the physical, chemical and biological constraints that generate trade-offs that determine the response of the KtW motif to the external drivers (R_T, δ_D and δ_P).

EXTENDED KTW MOTIF WITH EXTERNAL PREDATOR

The internal structure of the KtW motif depends, not only on the total amount of limiting resource (R_T), but also on the specific loss rates of the defence strategist (δ_D) and the predator (δ_P) (see SI for mathematical expressions). Replacing these loss rates with a top predator feeding on D and P therefore generates a top-down control of the structure in the KtW motif (Fig. 1b). Such a common top predator merges the pathways from C and D, and the result is a 'pentagon food

web structure' as analysed theoretically for stability and bottom-up and top-down effects by Wollrab & Diehl (2015). Important for the subsequent discussions is the specific example where omnivorous ciliates prey on both auto- and heterotrophic flagellates (see SI). For bacteria, a reduction in flagellates reduces both predation pressure and mineral nutrient competition and thus has positive effects on both bacterial abundance and activity (as long as the bacteria are mineral nutrient-limited). As the number of trophic links from ciliates to autotrophic flagellates and bacteria are odd (one) and even (two), respectively, the cascading effects from ciliates on the two mineral nutrient competitors, bacteria and autotrophic flagellates, are opposite. The outcome of phytoplankton-bacteria competition for mineral nutrients is thus not simply a function of their relative competitive abilities, but is strongly modulated by the structure of the predator (heterotrophic flagellates – ciliates) food chain. A more general analysis of the effect of top-predators, the length of alternative pathways, and whether they are reconnected by the top predator is given by Wollrab *et al.* (2012).

In the subsequent discussion, we argue that the mechanisms in the KtW motif have been (and are) central forces in the evolution of structure and function at two levels of resolution in the microbial food web: (1) the host–virus interactions and their generation of diversity *within* communities such as, for example, the heterotrophic prokaryotes and the autotrophic flagellates, and (2) the network of trophic interactions *between* such communities, constituting the microbial food web with its main functional types of pro- and eukaryotic microbes. There is no generally accepted theory for control of viral abundance, as opposed to predators that are eaten by higher order predators. While the two levels of resolution are similar since they both build on the KtW motif, an important difference is that the KtW motifs only expand into pentagon structures at the 'between-community' level (level 2). We discuss how this difference relates to the partitioning of bacterial production between the viral and the microbial loop.

EVOLUTIONARY ARMS RACES AND MICROBIAL 'WITHIN-COMMUNITY' DIVERSITY

Competition, defence and resources are central, not only to the structure and function of existing food webs, but also to

how they evolve. As argued below, the KtW motif contains a potential for antagonistic evolutionary arms races, thereby linking organism and system perspectives of ecology to speed and direction of evolution. Using a hypothetical virus–host example, arguments for an idealised arms race based on Fig. 1a can be developed as follows (Fig. 2a) (adapted from Thingstad *et al.* (2014)): The KtW motif of Fig. 1a corresponds to a situation with one virus (V_0), one sensitive (H_0) and one immune (H_1) host strain population. At high

concentrations of total resources (R_T), the immune strain H_1 dominates this system. H_1 thus represents a large unused potential resource for a mutant virus (V_1) that acquires ability to overcome H_1's defence system. The system then changes to a state with two virus-controlled competitors (H_0 and H_1) and most of the total limiting resources in the free form (R). This high free resource (R) then represents a potential resource for a new immune host mutant (H_2), allowing it to increase in abundance even if the price (COR) is a considerable reduction
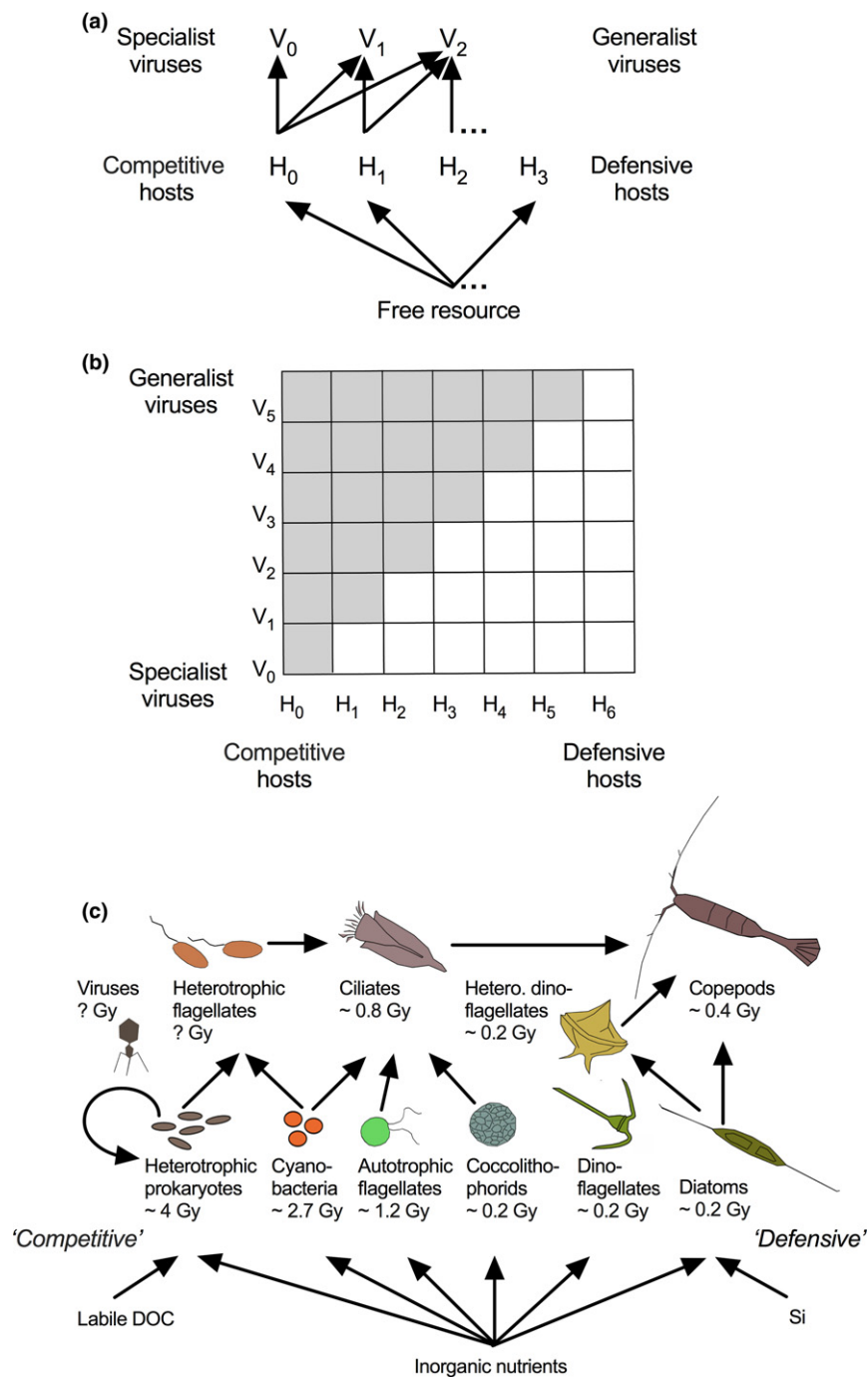

Figure 2 (a) Idealised arms-race model based on the KtW motif. (b) Nested (triangular) interaction matrix resulting from such an arms race. (c) Simplified present-day food web as the result of an arms race occurring over geological time scales.

in competitive ability. The immune strain H_2 is then a potential resource for a new virus mutant (V_2), which suppresses its abundance, freeing more R, and so on. In the simple representation of Fig. 2a, the state is shown for three sensitive (H_0, H_1, H_2) and one immune (H_3) host strain. For each step in this antagonistic arms race, more and more of the total resource is tied up in the growing host-virus network. As a result, the remaining resources alternating between the free form (R) and the immune strain diminish as the arms race progresses. The evolutionary speed of the arms race is therefore likely to slow down, not because of reduced mutation rates, but because of reduced remaining free resources and thus reduced probability that mutants can successfully exploit them. Such arms races are thus expected to have an asymptotic approach to a mature state as the remaining resources vanish. Similar situations have been analysed by Härter *et al.* (2014) who introduced the analogy of a 'narrowing staircase' to describe this type of community maturation. Developments observed in laboratory experiments (Perry *et al.* 2015) resemble early stages of this arms-race model.

This arms race model generates a nested (triangular) interaction matrix (Fig. 2b), where competitive hosts are infected by virulent specialist viruses, whereas defensive hosts are infected by less-virulent generalist viruses. Interaction matrices derived from both laboratory and field studies tend to resemble this nested structure (Holmfeldt *et al.* 2007; Flores *et al.* 2011; Frickel *et al.* 2016), providing circumstantial evidence that the arms-race description above is relevant to processes in nature.

In this arms race model, viruses drive strain-diversification. Most data on prokaryote diversity are, however, on the 16S rDNA level, more representative of a 'species' level. It is thus not immediately evident how to compare diversity data with this model. Illustrating population size as the size of rectangular boxes (Fig. 3), lytic viruses give the top-down control that determines abundance (box-size) at strain level. Assuming a non-selective protozoan predator for bacterial prey gives the top-down control for the size of the large (community) box. With non-selective grazing, this model contains no explicit top-down control of box-size at the intermediate (species) level. Without this, there is no immediate way to tell how many strains can fit inside each species, nor how many species can fit inside the community.

Using a steady-state chemostat model containing a mixed-species community with mature arms races (Thingstad *et al.* 2014), abundance at species level emerges as the combined result of two mechanisms: 1) the number of competing strains a species can establish, and 2) the number of individuals within each of these strains. The number of strains depends in this model on competitive properties, while within-strain abundance of individuals depends on defensive properties. In order to become abundant, a species thus has to be both competitive and defensive. This means that species that have found a way to reduce the costs of defence without losing too much in competitive ability, will reach the highest abundances. Testing this model in explaining abundance of SAR11 would thus require the so far missing knowledge of its defence mechanisms and their associated trade-offs against competition.

Note that the arguments here are developed using steady-state relationships and mature arms races. Mechanisms driving transient responses in prokaryote diversity may be rather complex. A perturbation would on short-term favour growth of the fast growing, undefended strains of opportunist species with high maximum growth rates. The successional pattern towards climax communities would depend on the outcome of arms races that interact through competition for shared resources, and whose characteristic evolutionary timescales may be different.
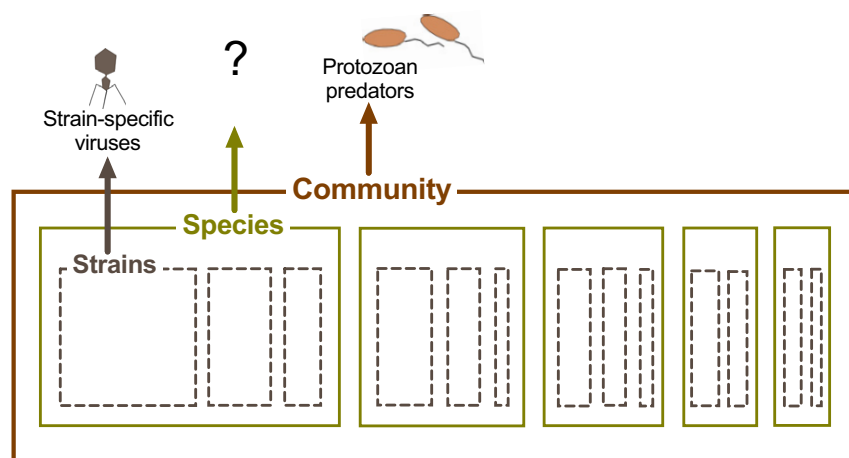

Figure 3 Hierarchical combination of KtW motifs illustrating the problem of top-down control of prokaryote 'species' diversity. In an idealised model with non-selective protozoan grazers controlling the size of the prokaryote community (brown) and strain-specific viruses controlling population sizes at strain level (grey), there is no explicit top-down control at the intermediate 'species' level (green). The suggested solution is that the competitive abilities of a species determine the number of strains it can establish. If there is a trade-off between competition and defence, a competitive species (#1) can establish many strains, but with few individuals per strain. A defensive species (#3) has more individuals per strain, but less strains. In the illustration, competitive and defensive species end up with comparable abundances. A species with low trade-off between competition and defence could, however, combine high within-strain abundance with many strains, and therefore become numerically dominant.

VIRAL ABUNDANCE AND HOST ACTIVITY 'WITHIN COMMUNITY'

There is no generally accepted theory for control of viral abundance and virus-to-host ratios. Some insight into the underlying mechanisms can, however, be obtained using the steady-state models discussed above. With the simplifying assumption that predation is non-selective among prokaryote hosts, host-selective viruses become the only mechanism that compensate for differences in host growth rates, allowing all hosts to have zero net growth rates (Thingstad 2000). With this, a system with no difference in host gross growth rates will have zero viral abundance, and thus no mechanism maintaining coexistence of multiple hosts on one shared limiting resource. Systems with large differences in host growth rates will on the other hand have many viruses, necessary to create sufficient loss to compensate for fast growth in undefended (or low COR) hosts. In the arms-race model, the sequence of increasingly defensive host strains H_0, H_1 …..H_n represents a sequence of increasing COR, and thus a sequence of decreasing growth rates. With hosts that are more defensive, more hosts will be needed to produce viruses at a rate compensating loss through viral decay and the increasingly defensive host strains will therefore also tend to be increasingly abundant (Thingstad *et al.* 2014). With a trade-off between competition and defence, the result is thus a reverse J-shaped growth-rate distribution with few high-active (competitive, low COR) and many low-active (defensive, high COR) individuals (Våge *et al.* 2013).

This pattern allows for two predictions verifiable with existing data: (1) Measuring per-cell activity in natural aquatic samples should give a dominance of low-active cells, and (2) removing the viruses experimentally should lead to a shift in the population where previously rare (but active) hosts should become rapidly dominant. Both when measuring single cell activity as silver grain area around radioactively labelled cells (Nikrad *et al.* 2012), and when using the incorporation of fluorescent amino-acid analogues (Samo *et al.* 2014), the prokaryote community is highly dominated by low-active cells. If these low-active individuals starve, the theory above suggests this to be because they 'have locked the gates to keep the enemy out', rather than because 'there is no food out there' (Thingstad *et al.* 2014). Another experimentally confirmed prediction is a shift to dominance of previously rare host types when viral control is reduced (Bouvier & del Giorgio 2007; Cram *et al.* 2016).

This idealised virus-host arms race model resolves an apparent paradox in virus ecology, referred to as Weinbauer's Paradox (Weinbauer & Rassoulzadegan 2004): Why are natural systems characterised by a high virus-to-host ratio (typically around 10), as opposed to laboratory host-virus systems with low virus-to-host ratios. Considering the laboratory systems as early stages of such arms races, most of the free resource is bound in an abundant resistant strain and few viruses are needed to compensate for a small difference in host strain growth rates, both giving low virus-to-host ratios. Assuming natural systems to have more matured arms races, the situation is opposite, with little free resources left for the immune strain and many viruses needed to compensate for

large differences in growth rates between the many sensitive strains.

The exact distributions depend on the magnitude of COR, which should vary between defence mechanisms that all have different molecular signatures (e.g. CRISPR-Cas systems vs. genomic islands (Rodríguez-Valera *et al.* 2009; var der Oost *et al.* 2014)). With high COR favouring viruses over grazers and thus shifting steady state towards more bacterial production being shunted into the viral loop, this theory thus links observable genomic diversity from different defence mechanisms to biogeochemical functioning of the pelagic ecosystem.

EVOLUTIONARY ARMS RACES 'BETWEEN COMMUNITIES'

The host-virus arms races discussed above work within a community influenced by nutrient availability and predation by the hosts' trophic neighbours in the microbial food web. One perspective is to see also this microbial food web as the present state of an arms race, perhaps 4.1 Gy old (Bell *et al.* 2015). The major functional groups (hetero- and autotrophic prokaryotes, hetero-, auto-, and mixotrophic flagellates, ciliates, coccolithophores, dinoflagellates and diatoms) represent major inventions in war technology (Fig. 2c) with the 'new' phytoplankton groups that appeared ca. 0.2 Gy BP (Falkowski *et al.* 2004) possessing the most 'modern' defence strategies (Strom & Loukos 1998; Hamm *et al.* 2003; Butterfield 2011). Butterfield (2011) uses similar ideas to argue more generally that predatory control from animals was a central evolutionary mechanism in shaping the Phanerozoic world.

In summary, arms races may have structured food webs with its major functional groups over geological time, while the signature of arms races at the strain level within communities can be seen on much more accessible timescales. With the fast arms races at the strain level (order of weeks?) being responsible for shunting material into the viral loop, and the slow (order of 0.5 Gy) arms race at food web level containing the microbial loop as well as groups with different biogeochemical roles (e.g. bacteria, coccolithophorides and diatoms), this hierarchy of arms races creates an ecosystem where microbial diversity is closely linked to many of its biogeochemical functions.

'BETWEEN-COMMUNITY' FOOD WEB DYNAMICS AND BIOGEOCHEMICAL CYCLING

We previously described the pentagon structure using the example with ciliates as the top predator, preying on auto- and heterotrophic flagellates, and bacteria subject to predation and mineral nutrient competition from heterotrophic and autotrophic flagellates, respectively. A simple representation of the microbial loop, defined as the pathway where labile dissolved organic carbon (L-DOC) is re-introduced into the food web via bacterial uptake (Azam *et al.* 1983) can be fitted to this pentagon food web by adding L-DOC as a required bacterial substrate (Fig. 4a). This allows for two different states of the pentagon, depending on whether bacterial growth rate is limited by mineral nutrients (M-limited) or L-DOC (C-limited). The shift between the two states depends
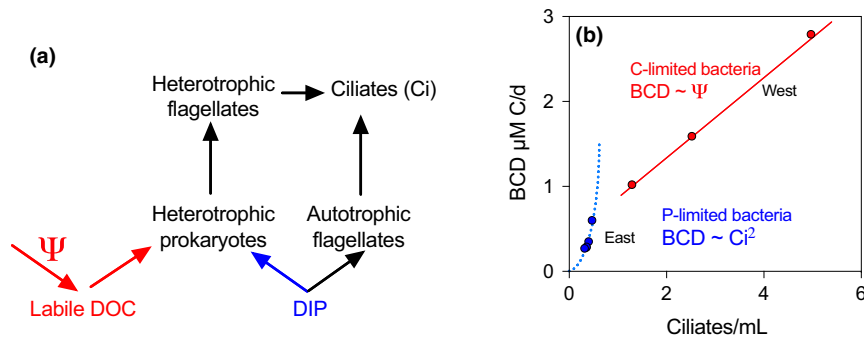
Figure 4 Relating bacterial limitation and DOC accumulation to food web structure. (a) As argued in the text, the pentagon structure leads to bacterial carbon demand being proportional to the square of ciliate abundance (BCD ~ Ci^2) and to the supply rate Ψ (BCD ~ Ψ) of labile DOC at low and high ciliate abundances, respectively (see SI). (b) Bacterial carbon demand plotted against ciliates, for a west-east transect in the Mediterranean. Stations with DOC accumulation indicated by blue, as opposed to red (non-accumulating) symbols (BCD data from Santinelli *et al.* (2012) and ciliate abundance from Dolan *et al.* (2002), data shown as weighted averaged of values above the pycnocline). In this interpretation, autochthonous production (Ψ) appears to increase towards the mesotrophic conditions at Gibraltar, while accumulation of DOC occurs in the oligotrophic eastern part, the transition occurring somewhere around the Sicily strait.

on the balance between carbon supply (Ψ) and consumption, i.e. the bacterial carbon demand (*BCD*). With demand less than supply, bacteria are M-limited and L-DOC accumulates at a rate given by the difference Ψ - *BCD*. Alternatively, when bacteria use all L-DOC supplied (*BCD* = Ψ), bacteria are C-limited, and there is no accumulation of L-DOC (Thingstad *et al.* 1997). In the pentagon, there is an even (two) number of trophic steps from ciliates to bacteria as well as from ciliates to the shared mineral nutrient. The cascading effect from ciliates (*Ci*) is thus positive on both. Assuming all food consumptions to be proportional to food concentration, both bacterial growth rate (μ) and bacterial abundance (*B*) are thus proportional to ciliate abundance (see SI). With the additional simplifying assumption that bacterial yield on L-DOC (Y_{BC}, bacteria formed per unit L-DOC consumed) is constant, consumption scales as the square of ciliate abundance (*BCD* = Y_{BC}^{-1}μ*B*~ *Ci*^{2}).

How production of L-DOC (Ψ) and ciliate abundance are related is not obvious, but the simplest possible assumption is they both increase with eutrophication, and therefore are positively linearly correlated. Since the squared relationship at some point will cross the linear, this model predicts a critical abundance of ciliates where the system shifts from M-limited to C-limited bacteria (Fig. 4b).

An interesting system suitable to explore the applicability of this simple model for understanding oceanic biogeochemistry is the Mediterranean with its West-East oligotrophication gradient from Gibraltar towards Crete (Santinelli *et al.* 2012). Ciliate abundance and bacterial carbon demand data from the Prosope cruise (Santinelli *et al.* 2012) fit this simple model surprisingly well (Fig. 4b). In this interpretation, there is a shift from C-limitation (linear *Ci* – *BCD* relationship) in the mesotrophic west, to M-limitation (squared *Ci* – *BCD* relationship) in the east, occurring somewhere around the Strait of Sicily. This location is consistent with bioassays indicating bacterial C-limitation at stations in the Alboran Sea and the Sicily strait, while stations further east had phosphorous-limited bacteria (Van Wambeke *et al.* 2002).

This interpretation is interesting in the broader context of the global C-cycle (Thingstad *et al.* 1997). In the photic zone of stratified water masses, DOC tends to accumulate in the productive season (Hansell 2002). There are two, not mutually exclusive, mechanisms that may explain this (Williams 1995): recalcitrance of the material and/or mineral nutrient limitation of the bacteria. Arguing that production of recalcitrant material is likely to be higher in more eutrophic systems, one would expect this mechanism to generate elevated DOC levels in the western, Alboran Sea, region of the Mediterranean. If the mechanism is M-limited bacteria, the line of arguments above would predict elevated DOC concentrations east of Sicily Strait. As DOC concentrations are elevated from the Sicily Strait and eastwards (Santinelli *et al.* 2012), the M-limitation hypothesis is consistent with the observed DOC data.

Representing the microbial food web with a simple pentagon as in Fig. 4a will not work in systems with large-celled phytoplankton that are inedible for ciliates. A 'minimum' food web model that included diatoms (Fig. 5a) and their mesozooplankton predators, was shown to successfully reproduce a mesocosm experiment from a Danish fjord, where experimental addition of silicate stopped bacterial consumption of glucose. In the model, this response is caused by a strong mineral nutrient competition from Si-replete diatoms (Thingstad *et al.* 2007). With mesozooplankton feeding also on ciliates, this minimum model can be seen as two pentagons coupled in parallel. With this coupling, the minimum model contains the long trophic cascade from copepods, via ciliates and heterotrophic flagellates, to bacteria, demonstrated experimentally by Zöllner *et al.* (2009). It also generates three alternative pathways from free mineral nutrients to mesozooplankton. Importantly, these three pathways have different lengths with, 3, 2 and 1 (thus odd, even and odd) steps, respectively, between the primary nutrient consumer (bacteria, autotrophic flagellates or diatoms), and the mesozooplankton top predator. The result is a model where cascading effects from mesozooplankton strongly modulate the balance between the three mineral nutrient competitors (Fig. 5b and c).
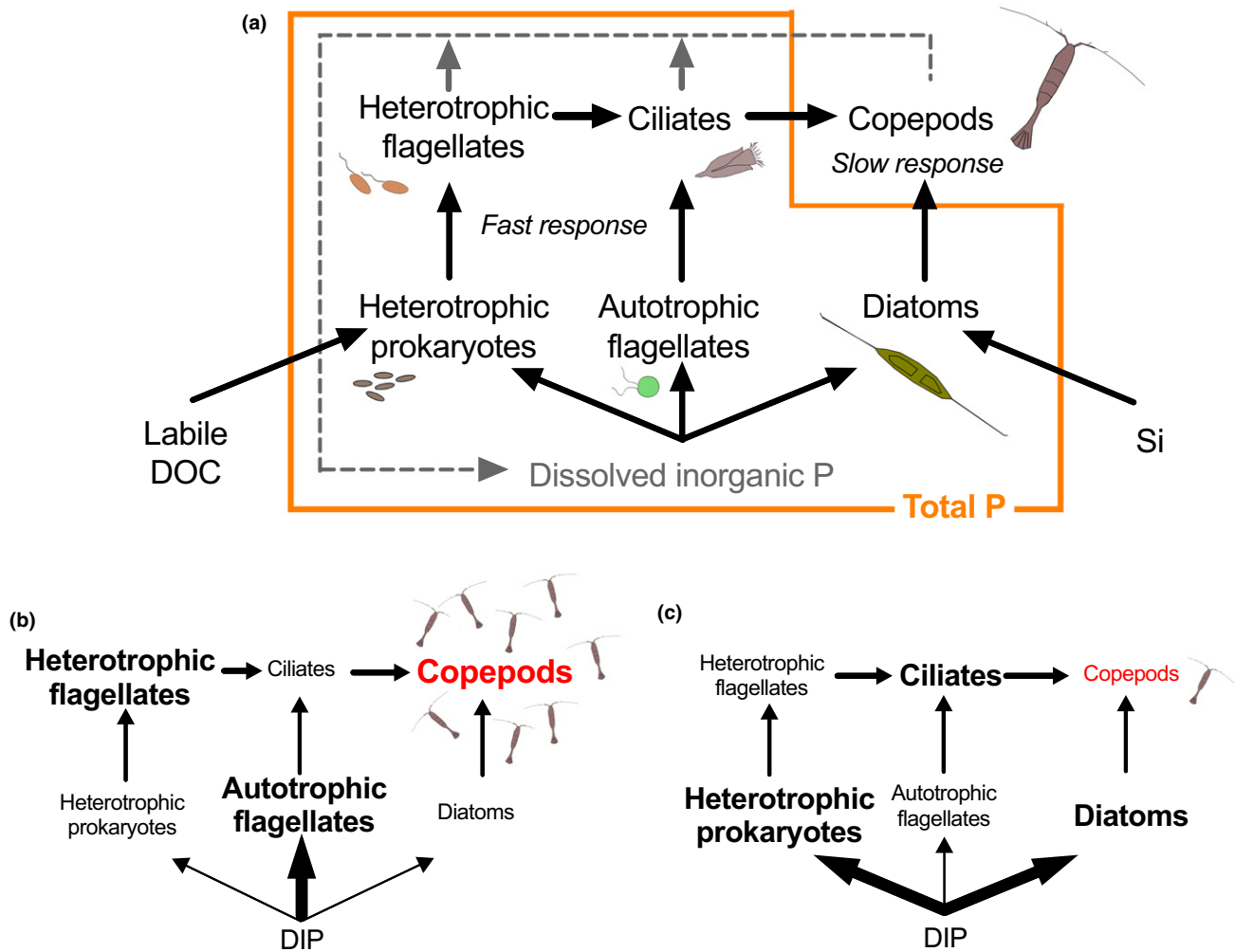
Figure 5 (a) Parallel combinations of KtW motifs in the 'minimum' food web model. For the discussion of trophic cascades, there are two important features with this model: 1) The simplicity in trophic links and 2) the difference in numerical response and in migration ability between the microorganisms (fast) and the copepods (slow). Trophic structure expected at (b) high- and (c) low-copepod levels. Note the difference in phytoplankton-bacteria competition in situation 'c' depending on presence/absence of diatoms.

The theoretical cascading effects in the minimum model (Fig. 5b and c) add considerable nuances to the basic concept of a cascade in linear food chains. Importantly, the right pentagon predicts opposite cascading effects from copepods on chlorophyll in systems dominated by diatoms (negative correlation) and flagellates (positive correlation), as confirmed experimentally in mesocosms (Vadstein *et al*. 2004). In the left pentagon, high ciliate abundance will suppress hetero- and auto trophic flagellates as before, with the consequences for bacterial abundance and activity discussed above. Biogeochemical functions such as degradation of dissolved organic material and vertical export of carbon and limiting nutrients thus depend on the balance between the three alternative food chains, and therefore on how top-down control from mesozooplankton interacts with the bottom-up controls from mineral nutrients, labile DOC and silicate.

Despite all the biological detail still ignored in this description, we found this minimum model able to reproduce the contrasting results of two Arctic mesocosm experiments

(Larsen *et al*. 2015). With the two experiments done in early and late Arctic summer, their timing corresponded to periods before and after copepod diapause, and therefore to high- and low-copepod abundance in the surface layer, respectively. The model reproduced an observed glucose-insensitive flagellate bloom in the high-copepod situation (as expected from Fig. 5a). In the low-copepod (Fig. 5c) situation, glucose addition led to a dynamic, glucose-sensitive, bacterial response and disappearance of the diatoms (Larsen *et al*. 2015), a result seemingly in contrast with the Danish experiment. This difference in diatom-bacteria balance was attributed to the difference in diatom community composition: large filamentous diatoms in Denmark fitting the minimum model of Fig. 5a, while, in the low-copepod Arctic situation, the dominance of a small single-celled *Thallasiosira sp.* presumably made diatoms vulnerable to ciliate predation. Dominance of each of the three pathways has thus been observed in mesocosms, and top-down control has been inferred as a crucial mechanism behind these outcomes.

The 'minimum' philosophy behind this model was rooted in a curiosity for how much detail one can remove, while retaining enough elements to explain major response features in mesocosms. Interestingly, the strong cascading effects needed to explain the observations are a consequence of this intended simplicity. To illustrate this, one can, for example, short-circuit the right pentagon with a link where copepods eat autotrophic flagellates. The cascading effect of such a one-step link would be opposite to that of the existing two-step copepods-ciliates-flagellates link, and the effects of the two cascades will tend to cancel out. The success of this model in explaining seemingly contrasting results as a consequence of such cascades, is therefore arguably more *because* than *despite* of its simplicity.

Cascading effects come from imbalances between abundance of a predator and its prey. This may be an essential point for understanding microbial dynamics in the Arctic, where copepod stock is largely a result of advection processes and seasonal vertical migration (Edvardsen *et al.* 2003; Falk-Petersen *et al.* 2009), and therefore uncoupled from their immediate microbial food resources. Differences in temperature sensitivity between phytoplankton and heterotrophic bacteria (Pomeroy & Deibel 1986), or between phytoplankton and micro-zooplankton (Rose & Caron 2007), have both been speculated to generate differences in microbial food web structure and function between warm and cold waters. The argument above instead focuses on trophic decoupling between a system of fast-reproducing microbes and their slow-reproducing metazoan predators. In this interpretation, metazoan life-strategy adaptation to low temperatures emerges as a more important element in the discussions of how the microbial food web will respond to a warming Arctic. Using correlation analysis of abundance data for predator-prey pairs to classify North Atlantic systems as bottom-up or top-down controlled, (Frank *et al.* 2007) found the two modes to be associated with temperate and cold-water masses, respectively. Field data, mesocosm experiments and models thus seem to converge on the indication that top-down control may be associated with cold-water systems.

It is encouraging that properties of the Arctic and Mediterranean ecosystem seem possible to interpret within a framework that uses the same minimum food web structure. Importantly, however, this interpretation also contains a fundamental difference in the control of ciliate abundance: a bottom-up, resource-driven control that is ultimately driven by the negative thermo-haline circulation in the Mediterranean, as opposed to a top-down, predator control of ciliates caused by seasonally migrating copepods in the Arctic.

C-export based on DOC accumulation can be substantial (Carlson *et al.* 1994), but the mineral nutrient limitation mechanism suggested above suggests a difference between systems located at different latitudes. Light conditions in the Mediterranean may be sufficient to maintain phytoplankton-bacteria competition up to the point where the water column becomes unstable (Dolan *et al.* 1995). Winter deep water formation may therefore carry degradable DOC to the deep Mediterranean where it is rapidly degraded (Santinelli *et al.* 2010). At higher latitudes such as the North Atlantic, light limitation would be expected to remove phytoplankton

competition for mineral nutrients, and thus bacterial consumption of accumulated labile DOC well before deep water formation, consistent with the mid-late summer culmination of upper layer DOC concentration found here (Børsheim & Myklestad 1997).

INTERACTIONS BETWEEN VIRUS–HOST AND PREDATOR–PREY LEVELS OF DESCRIPTION

One can see the viral loop and the microbial loop as two processes competing for bacterial production. The significance for ecosystem functioning is that the microbial loop transfers material up the particulate food chain, while the viral loop shunts material back towards detritus and dissolved material. The pentagon in Fig. 4a can be used to illustrate this by representing lytic viruses as a specific bacterial loss rate (δ_B). As shown in the SI, the steady-state effect is a shift in biomass from heterotrophic to autotrophic flagellates. This simple model does, however, not provide any clue to the mechanisms regulating the magnitude of δ_B.

As discussed above, viruses are believed to be central in generation of diversity at species and strain level. The mechanisms determining how the virus-host and the predator-prey levels interact is thus also an interesting special case for the study of how biodiversity and ecosystem functioning are linked.

Our analysis of the virus-host level identified diversity in host growth rates, and thus the cost associated with viral defence, as an essential part of the mechanisms shunting material into the viral loop. At the predator-prey level, total bacteria community production was associated with the pentagon structures of the minimum model, placing ciliate abundance in a central controlling position. The mechanisms that control magnitude and fate of bacterial production in these models thus have a root in the fundamental difference between the two levels of description, where the KtW motifs expand into pentagon structures and their trophic cascades at the food web level, but not at the host–virus level.

The host-virus arms race model has two mechanisms that generate differences in host growth rates, one between strains and one between species. The between-strains mechanism is the COR associated with each new strain evolving resistance to established viruses. Intuitively, expensive defence (large CORs) will generate large between-strain differences in growth rate, shifting the competition in favour of the viral loop (Våge *et al.* 2016). Large interspecies differences in maximum growth rates will, however, also generate large within-community differences in individual growth rates and thus high virus abundances. An interesting, and in principle testable, prediction from these models, is that the width of the reverse J-shaped growth-rate spectra, representing the range in host growth rates, should be positively correlated with viral abundance and the shunting of material into the viral loop.

The previous diversity-ecosystem functioning discussion takes an 'inside-out' perspective to the interactions between community composition and food web functioning: high-resolution molecular details of competition and resistance at species and strain level determine properties at the outer level of food web functioning. There is, however, also an 'outside-in'

direction in these interactions, where availability of limiting substrates and predation pressure generated at the food web level constrain the growth conditions for members inside the community. An experimental illustration of this is how the two Arctic mesocosm experiments with food web structures as represented in Fig. 4b and c (Larsen *et al.* 2015) responded, under comparable experimental perturbations, differently at the level of bacterial and viral community composition (Sandaa *et al.* 2017). In analogy with the Mediterranean case, this was interpreted using the simple pentagon of Fig. 4a, where low and high ciliate situations favoured mineral nutrient and organic carbon limitation of bacterial growth, respectively (Fig. 4b). Consistent with this, the lack of community responses to experimental glucose additions in the high-copepod (low ciliate) Arctic situation (Fig. 5b) was explained as the lack of effects from adding glucose to a system already replete in labile organic substrates. This as opposed to the low-copepod (high ciliate) situation favouring C-limited conditions and strong observed community responses to the glucose treatments (Sandaa *et al.* 2017).

Properties of the minimum food web model depend on the parameters that define competitive and defensive properties for each community. A change in internal community composition large enough to alter these properties at the community level obviously creates an effect in the 'inside-out' direction from community composition to food web structure and function. Exposing bacterial communities to protozoan predators, Matz & Jürgens (2003) found an increase in bacteria with inedible morphologies. This effect was enhanced under phosphorous relative to carbon limitation. One may speculate that the significance of this substrate effect is not in the phosphate limitation *per se*, but in the accompanying replete glucose conditions. Excess glucose may provide the energy and building material needed for alternative defence strategies, and possibly also for improved competitive abilities (Thingstad *et al.* 2005). Such community composition-driven adaptability of the parameters could make the food web more resilient to perturbations as it would tend to dampen the strong cascading effects exhibited by the minimum model with its fixed community parameters.

Both competition and predation are (intentionally) extremely simplified in the minimum model. Regulatory mechanisms from the KtW motif are, however, present also in much more sophisticated state-of-the-art ocean models. The Darwin model (Follows *et al.* 2007) has high resolution of trait diversity in the phytoplankton community. Its ability to successfully describe the global distribution patterns with large-celled diatoms and pico-phytoplankton dominating in upwelling and stratified oceanic regions, respectively is, however, likely to originate in the assumption of a simple two-predator structure regulating the partitioning of limiting nutrients between small/competitive and large/defensive phytoplankton, a KtW mechanism similar to what has been discussed here. The Darwin model′s ability to resolve this coarse picture into finer details such as ecotypes of the unicellular cyanobacteria (Follows & Dutkiewicz 2011) thus seems to be an illustration of the interplay between the gross structuring effects of size-selective predation, and details in competitive abilities that structure composition within these size-defined phytoplankton communities. Refining such models by including also the multitude of existing phytoplankton defence strategies and their trade-offs (Pancic & Kiørboe 2018), presumably would increase within-size group diversity further.

FINAL REMARKS

While the basic interactions between negative density control and resource partitioning are simple (as represented in the KtW motif), their ecosystem consequences are not. The suggested repetition of such principles at hierarchical levels of food webs, communities, species and strains, gives associations to fractal systems where a simple, scale-independent mechanism can give self-similar system properties (e.g. Hutchinson 1981). This idea can be pursued a little further by noting that a hierarchical stacking of nested interaction matrices (Fig. 2b) gives compound matrices resembling the Sierpinsky gasket (Våge & Thingstad 2015), a classical example of a fractal structure. Exploring the consequences of such repeated mechanisms seems appealing considering the massive effort needed to understand microbial complexity.

One could suspect that the KtW motif, even if working nicely in simple idealised laboratory systems designed specifically to demonstrate its validity, may not work in the complicated settings of natural ecosystems. It is easy to envisage how a multitude of physical and chemical factors, interacting with a similar multitude of biological features, can blur the simple interactions of the KtW motif to such an extent that its explanatory power disappears. The examples discussed above, covering a range from laboratory experiments, via mesocosm experiments and field observations to oceanic regions with very different characteristics, suggest as an optimistic conclusion that such blurring is at least not the common rule.

Our restriction of this discussion to the viruses-to-copepods part of the pelagic food chain does not imply that the principles of Fig. 1 are restricted to microbial communities (see e.g. Haraldsson *et al.* 2012). Nor is it restricted to aquatic environments, as illustrated by the central role of the concept of keystone predators in the literature of the Serengeti ecosystem (e.g. Periquet *et al.* 2015). The short generation times of microorganisms, the relative homogeneity of aquatic environments, and a dominance of a single limiting element in the photic zone may, however, all contribute to make the underlying mechanisms more transparent in the microbial part of aquatic systems.

AUTHOR CONTRIBUTION

All authors contributed to the accumulated experimental work and the discussions generating the ideas presented. SV and TFT wrote the article with comments and contributions from the other co-authors. This article does not contain original data.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.