Life strategy trade-offs in pelagic microbial communities How trade-offs between competition, defense and forging modes may influence food web structure and ecosystem functioning

## Objectives

Using mathematical models of simplified microbial food webs and virus-host communities, we address the following questions:

- \* Are trade-offs between competition and defense fundamental in structuring pelagic microbial food webs?
- \* How may trade-offs between different microbial life strategies influence ecosystem functioning in the pelagic?
- \* When are particular life strategies in marine microbial communities successful, and what may their success depend on?

1. Optimal defense strategy To study the influence of trade-offs on food web structure and functioning, a simplified Killing-the-Winner (KtW) model with top-down control of predators was used (Fig. 1, top). A tradeoff ( $\tau$ ) between competitive (affinity) and defensive (inverse of predator's clearance rate) abilities of the defense strategists was introduced (Fig. 1, bottom), allowing partial defense.

#### 2. Defensive strains dominate virus-host systems

Discerning the success of bacterial groups in the pelagic is an open challenge that will help understand biogeochemical cycling and ecosystem functioning.

Inverse rank-abundance curves of hosts and their associated viruses have been hypothesized, where slow growing defense specialists and viruses infecting faster growing but rare competition specialists dominate the pelagic microbial community<sup>[1]</sup>. A virus-host system KtW<sup>[2]</sup> model with trade-off  $\tau$  between competition and defense<sup>[3]</sup> (cost of resistance, CoR, Fig. 4) reproduces such inverse rank-abundance curves (Fig. 5).



# 3. Successful strategies in mixotrophic food web

Using a model with high resolution in foraging mode (including a trade-off  $\tau$  between osmo- (V<sub>max</sub>DIP) and phagotrophic (V<sub>max</sub>prey) uptake abilities, Fig. 8) and cell size, we study the success of different life strategies in microbial communities.

Mixotrophs that combine osmo- and phagotrophy are widespread and significant for ecological and biogeochemical functioning of the pelagic<sup>[7]</sup>, yet little is known of the actual costs that mixotrophy implies<sup>[8]</sup>. In our model, mixotrophs of varying degrees coexist with pure osmo- and phagotrophs, even when the cost of mixotrophy is high (i.e. when  $\tau > 1$ ). This suggests that benefits of mixotrophy may outweigh potentially high costs. However, the success and diversity of mixotrophic strategies is highest in our model when  $\tau < 1$  (Fig. 9). Recalling the high abundance and variety of mixotrophs in nature, this indicates that costs of mixotrophy may in fact be smaller than previously assumed<sup>[9]</sup>.

The optimal amount of defense is highly restricted, in particular when gain in competition is similar to the loss in defense (i.e.  $\tau$  close to 1) and at low nutrient concentrations (Fig. 2). High defense is superior when biomass (Fig. 2A), rather then production (Fig. 2B), is to be maximized.

The steady state biomasses of predators, competition and defense strategists depend on the systems nutrient content and  $\tau$  (Fig. 3). Excess nutrients are consumed by the defense strategists (Fig. 3, middle), supporting a larger predator population (Fig. 3, bottom). Thus, the area in the defense - trade-off plane where competition specialists are outcompeted increases (Fig. 3, top).





 $\mu$  (h<sup>-1</sup>)  $\mu$  (h<sup>-1</sup>)  $\mu$  (h<sup>-1</sup>)

0.025 0.05

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0.025 0.05

Fig. 5: Inverse rank-abundance curves for host strains and their associated viruses<sup>[3]</sup> ( $\mu$  = host growth rate).

High CoR (i.e.  $\tau > 1$ ) and a high maximum growth rate ( $\mu_{max}$ ) increase bacterial biodiversity and total virus abundance (Fig. 6). Consequently, more bacterial production is shunted down into the viral loop. Strategy trade-off seems thus directly linked to ecosystem functioning.



Fig. 6: Trade-off effects biodiversity and ecosystem functioning<sup>[3]</sup>.

An interesting question is how strains of species are distributed along the growth rate axis. If CoR increases with high  $\mu_{max}$  and  $\mu_{max}$  differs between species, our model predicts a clustered scenario (Fig. 9A). If  $\mu_{max}$  and CoR are similar for all species, a dispersed scenario is expected (Fig. 9B), which could explain recent findings of abundant SAR11 viruses<sup>[4]</sup> and a hypothesized dominance of defensive SAR11 strains<sup>[1],[5]</sup>. Some evidence for interspersed SAR11 strains exists<sup>[6]</sup>.



Fig. 9: Emergent populations (Foraging mode = 0: pure osmo-, 1: pure phagotrophs) for different foraging trade-offs and optimal predator-to-prey size ratios (SR) <sup>[8]</sup>.

## Conclusions

Viruses (I<sup>-1</sup>)

0.025 0.05

- Trade-offs between life strategies strongly influence the food web structures in the presented models
- High trade-offs between competition and viral defense reproduce inverse rank-abundance curves of hosts and their associated viruses.
- High trade-offs between competition and viral defense lead to high viral abundances. This shunts more of the bacterial production into the viral loop. Hence, ecosystem functioning seems directly linked to strategy trade-offs.
- → An interspersed strain scenario (Fig. 7B) can explain high virus abundances in bacterial species dominated by defensive strains. This may apply to SAR11.
- → Strong defense is optimal to maximize biomass but not production. Slow growth and high abundance of SAR11 may thus hint at a dominance of defensive strains.
- → Size-dependent strategies and trade-offs strongly influence the emerging food web structure in our mixotrophy model. Hence,

Fig. 3: Biomass of competition, defense and predator populations at steady state for two different nutrient regimes.

### References

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Fig. 7: Clustered (A) vs interspersed (B) scenario for how strains of bacterial species may be distributed along the growth rate axis<sup>[5]</sup>.

size should be better resolved in future plankton models.

→ Mixotrophs are successful under a variety of conditions, in particular when trade-offs are small. Comparing with their high prevalence in nature, his suggests that mixotrophy may be less costly than previously assumed.

### Open questions

\* What are the actual costs of resistence for microbes, and how do they vary between groups and defense mechanisms?

\* Are strains of pelagic bacterial groups dispersed or clustered along the growth rate axis?

\* Is SAR11 dominated by competition or defense specialists?

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