

Pelagic microbial food web organization

Extending the theory for structure and diversity generating
mechanisms based on life strategy trade-offs

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Scientific environment

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Abstract

This dissertation explores food web interactions controlling structure and biodiversity in the pelagic microbial community. Through a theoretical approach, mathematical models of simplified microbial food webs are used to investigate when particular microbial life strategies are successful in the pelagic ocean, to what extent the success is dependent on life-strategy trade-offs, and how different life strategies influence the biogeochemical functioning of the marine ecosystem. Trade-offs between competition, defense, predation and different foraging modes are found to strongly influence the structure and functioning of the microbial community.

A steady-state 3-population model with a predator, a competition specialist and a defense specialist partially defended against the predator is analyzed with respect to defense strategy and trade-off between competition and defense (**Paper I**). The food web structure is found to intricately depend on the functional shape of this trade-off, the investment of the defense specialist into defense and the system's nutrient content. High defense results in high biomass of the defense strategist, whereas low defense increases production, and strategies corresponding to maximum biomass or production are generally different from evolutionary stable strategies. Through its diamond-shaped food-web structure, this study links the 'Killing-the-Winner' concept known in microbial ecology to the classical macroecological principle of 'Keystone Predation'.

Using a dynamic model with high resolution in foraging mode and cell size, food web structures are investigated as emergent features of basic ecological interactions such as size-selective predation, allometric uptake kinetics and trade-offs between different nutritional modes (**Paper II**). Mixotrophy (a combination between osmotrophic and phagotrophic foraging) is found to be a successful strategy under different environmental conditions, even at high costs relative to specialized foraging (pure osmotrophy and pure phagotrophy). Furthermore, the emergent food web structure is found to be highly sensitive to size-dependent model parameters.

Coexistence and diversity within the prokaryote community are analyzed at steady state in a virus-host community model (**Paper III**). A trade-off between competitive and defensive abilities in hosts is found to potentially explain inverse rank abundance curves of host groups and their associated viruses in the pelagic ocean. Cost of resistance (COR) and viral control of fast growing competition specialists is proposed as an explanation for the dominance of slow growing bacteria in the oligotrophic ocean, rather than dormancy due to a lack of resources. **Paper IV** extends the ongoing discussion of why the abundant bacterial clade SAR11 may be so successful in the pelagic ocean. When interpreting host

groups in the virus-host community model of Paper III as strains of different species, the model provides an alternative and counterintuitive explanation for high viral abundances in connection with host populations that may be dominated by defense specialists.

Paper V takes this discussion one step further and resolves host groups at the level of species and strains of species. In an idealized host-virus arms race model, control of prokaryote abundance and diversity is analyzed under the influence of lytic viruses in a chemostat environment. A COR for host strains as well as potential reductions of viral abilities to infect ancient strains is incorporated. Competitive traits of the strains are found to determine the number of strains each species can establish, whereas defensive traits of the strains determine the number of individuals in each strain. High numerical abundance at the species level, such as obtained by SAR11, thus seems dependent on a successful combination of competitive and defensive skills on the strain level.

The dissertation and papers therein extend our conceptual understanding of how ecological trade-offs are fundamental in structuring the pelagic microbial community across different levels, and encourage experimental studies to quantify and gain a mechanistic understanding of these trade-offs. The presence of a generic mechanism allowing coexistence of competition and defense specialists at different trophic levels motivates the formulation of a fractal hypothesis of the pelagic food web, where trade-offs acting repeatedly at different trophic levels may give rise to a self-similar organization of the pelagic microbial food web.

List of publications

Paper I

Våge S., Storesund E. J., Giske J. and Thingstad T. F. Optimal defense strategies in an idealized microbial food web under trade-off between competition and defense. Manuscript submitted to PLoSOne.

Paper II

Våge S., Castellani M., Giske J. and Thingstad T. F. (2013) Successful strategies in size structured mixotrophic food webs. *Aquatic Ecology* 47:329-347.

Paper III

Våge S., Storesund E. J. and Thingstad T. F. (2013) Adding a cost of resistance description extends the ability of virus-host model to explain observed patterns in structure and function of pelagic microbial communities. *Environmental Microbiology* 15:1842-1852.

Paper IV

Våge S., Storesund E. J. and Thingstad T. F. (2013) SAR11 viruses and defensive host strains. *Nature* 499:E3-E4.

Paper V

Thingstad T. F., Våge S., Storesund E. J., Sandaa R.-A., Giske J. Control of species diversity by strainspecific viruses. Manuscript submitted to PNAS.

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1 Introduction

Science is pursued on the premise of underlying mechanisms and principles that govern our world, which we strive to understand. Working on theory of marine microbial ecology during the last three years in an environment where both experimental work and theory has been developed since early on in the field has been instructive. The work presented in this thesis is motivated by the idea of fundamental and relatively simple ecological principles underlying much of the complexity of microbial network organization and dynamics in the pelagic ecosystem.

The significance of the prokaryote microbial community for pelagic ecosystem functioning in addition to eukaryotic marine microbes was realized already some 40 years ago, when improved counting methods allowed better estimates of bacterial abundances in the ocean (Hobbie et al, 1972; Pomeroy, 1974; Azam et al, 1983). Subsequent realization of prokaryote diversity by accumulation of datasets through the genomics revolution of molecular biology in the past 20 years (Fuhrman et al, 1994; Höfle and Brettar, 1995) further increased our awareness of the important and versatile roles that pelagic microbes play in the global ecosystem. Yet, the development of a conceptual understanding of underlying mechanisms and principles that control and shape this important part of the pelagic ecosystem has not advanced in the same pace as new methodologies. A rapid advancement of molecular methods required to grasp the largely invisible prokaryote diversity may be responsible for that, as it has promoted a focus on quantifying abundance and diversity of microbes in natural environments (Green-Tringe et al, 2005; Edwards and Rohwer, 2005). Although mapping microbial diversity is important for understanding the system, it does not explain how the diversity is maintained and controlled.

Besides the methodological development that led to a focus on metagenomics and mapping of microbial diversity, another challenge to develop the theoretical framework of aquatic microbial ecology further may be the nature of this system itself. It is intrinsically challenging to understand complex systems conceptually. My motivation to engage in the work presented here is a conviction that the world around us, including fundamental properties such as the existence of matter and advanced system properties such as biological complexity, can be understood from underlying laws and principles. Based on different modeling studies of the microbial food web, the presented work extends our conceptual understanding of top-down and bottom-up regulating mechanisms and the fundamental role of ecological trade-offs for structure and diversity in the pelagic microbial food web. A major part of the thesis is dedicated to structure and diversity in prokaryote-phage systems (**Papers III - IV**), although the eukaryotic part of the microbial food web is

also treated specifically in **Paper II**, and **Paper I** deals with unspecified predator-prey or parasite-host interactions. The work discusses how trade-offs between competition and defense acting repeatedly on different trophic levels may give rise to a complex, fractal-like organization across different levels of the pelagic food web.

2 Background

2.1 Abundance and types of pelagic microbes

Prokaryotes are by far the most abundant and genetically diverse types of organisms constituting the major part of biomass on Earth (Madigan and Martinko, 2006). Their long evolutionary history, starting more than 3.5 billion years ago, may explain the overwhelming diversity compared to eukaryotes (Woese, 1987). Understanding the interplay of mechanisms controlling diversity in microbial communities at different temporal and spatial scales remains a fundamental challenge of microbial ecology and evolution, and is central to this dissertation.

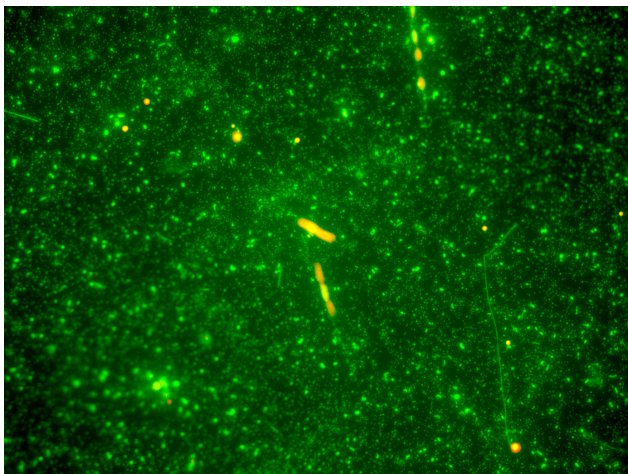


Figure 1: Epifluorescence microscopy showing SYBR-green stained bacteria (large dots) and several-fold more abundant viruses (small dots) in Norwegian coastal water. Photo Gunnar Bratbak.

High abundances of pelagic bacteria have only been recognized upon development of molecular staining techniques in the 1970s (Zimmermann and Meyer-Reil, 1975), which allow bacterial counts independently of culturing methods (Figure 1). Together with more



Figure 2: Metazooplankton (rotifer, appendicularian and copepod, top) microzooplankton (ciliates and heterotrophic dinoflagellates, middle) and microalgae (coccolithophore and diatoms, bottom) in Norwegian coastal water. Photos Jean-Marie Bouquet, Rakhesh Madhusoodhanan and Mikal Heldal.

automated cell counting methods (e.g. flow cytometry, Legendre and Yentsch, 1989), they reveal bacterial abundances on the order of 10^6 cells per mL in the euphotic zone (Fenchel, 2008). Viral abundances (counted by ultra-centrifugation, Bergh et al, 1989) typically exceed bacterial abundances by one order of magnitude. Oceanwide, there are estimated 10^{31} viruses (compared to estimated 10^{21} stars in the universe), making viruses the most numerous organismal entities on Earth (Whitman et al, 1998; Wilhelm and Suttle, 1999; Suttle, 2007). If one was to stretch the DNA of all viruses in the ocean, their DNA would stretch beyond the 60 nearest galaxies (Suttle, 2007)! Clearly, this huge reservoir of genes and metabolic pathways shapes the global ecosystem in a fundamental way.

Whereas bacteria and viruses are fundamental parts of the pelagic microbial community, the microbial food web also includes unicellular eukaryotes such as autotrophic microalgae, mixotrophic flagellates and heterotrophic protozoa (Figure 2, bottom and middle). Metazooplankton (Figure 2, top) grazing on different size-classes within the microbial community link the microbial food web to higher trophic levels (e.g. marine vertebrates). Box 1 summarizes groups of important prokaryotic and eukaryotic microbes in the pelagic food web. Among the microalgae, the most prominent clades are dinoflagellates, coccolithophores and diatoms (Falkowski et al, 2004), whereas heterotrophic nanoflagellates and ciliates typically dominate the protozoan community (Karayanni et al, 2005). Mixotrophic microorganisms that combine osmotrophic (nutrient uptake through

dissolved matter) and phagotrophic foraging (uptake of nutrients and energy through particulate matter) behavior are widespread and found in almost all clades of microbial eukaryotes, with the exception of diatoms, which are strictly osmotrophic (Flynn et al, 2013).

Box 1 Major groups of pelagic microbes and links to higher trophic levels

- Femtoplankton ($< 0.2 \mu\text{m}$)
 - Viruses
- Picoplankton ($\approx 0.2 - 2 \mu\text{m}$)
 - Heterotrophic bacteria
 - Autotrophic cyanobacteria
 - Archaea
- Nanoplankton ($\approx 2 - 20 \mu\text{m}$)
 - Heterotrophic nanoflagellates
 - Mixotrophic nanoflagellates
 - Autotrophic nanoflagellates
- Microplankton ($\approx 20 - 200 \mu\text{m}$)
 - Heterotrophic protozoa (e.g. dinoflagellates and ciliates)
 - Mixotrophic protozoa (e.g. dinoflagellates and ciliates)
 - Autotrophic phytoplankton (e.g. dinoflagellates and diatoms)
- Metazooplankton ($> 200 \mu\text{m}$) linking microbes to higher trophic levels
 - Rotifers
 - Copepods
 - Appendicularia

Abundances of the relatively large eukaryotic microbes (Box 1) are several orders of magnitude less than those of prokaryotes. Primary grazers of bacteria, i.e. heterotrophic nanoflagellates, may be found on the order of 10^3 cells per mL in the euphotic zone (Fenchel, 2008), while larger protozoa such as ciliates may occur at abundances of roughly 10 cells per mL (Leakey et al, 1992). Abundances of microalgae strongly vary depending on growth conditions, but may be found around 10^3 to 10^4 cells per mL (Holligan et al, 1993).

2.2 Microbial food web interactions

Ecological investigation of pelagic bacteria range back to the first half of the 20th century (Bigelow, 1931; ZoBell, 1946), but their significance for element cycling in the ocean has only been pinpointed in the 1970s and 80s upon the improved understanding of bacterial biomass and microbial activity (Hobbie et al, 1972; Pomeroy, 1974; Azam et al, 1983). Based on bacterial metabolization of dissolved organic matter (DOM) that is released by their grazers (Legendre and Rassoulzadegan, 1995) or produced through viral lysis, byproducts of animals or excretion through phytoplankton (Cole et al, 1982; Jumars et al, 1989; Baines and Pace, 1991), the microbial loop concept was formulated (Azam et al, 1983). Whereas heterotrophic bacteria to a large extent depend on phytoplankton for organic carbon as an energy source, the two groups are direct competitors in terms of mineral nutrients including nitrogen, phosphorous and iron (Thingstad et al, 1999). The microbial food web hence forms pathways for elemental cycling outside of the classical food chain that goes from nutrients to phytoplankton to zooplankton and carnivores (Fenchel, 1988) (Figure 3). Lytic viruses significantly influence biogeochemical cycling of organic matter in marine ecosystems (Fuhrman, 1999; Wilhelm and Suttle, 1999; Weinbauer, 2004). Bacterial production is partitioned in roughly equal parts to grazing and viral lysis (Fuhrman and Noble, 1995), influencing whether bacterial biomass is transferred to higher trophic levels or directly remineralized within the microbial loop (Suttle, 2007). Viral infections may also abruptly terminate phytoplankton blooms, influencing vertical export of organic matter on the short term (Bratbak et al, 1993). Besides their significance for marine food webs, pelagic microorganisms play several other important roles for global ecosystem functioning (Box 2).

Which of the pathways through the microbial food web dominate in a given aquatic system depends to a large extent on environmental conditions (Legendre and Rassoulzadegan, 1995; Thingstad and Cuevas, 2010). Larger phytoplankton such as diatoms and dinoflagellates typically dominate primary production and biomass in eutrophic upwelling

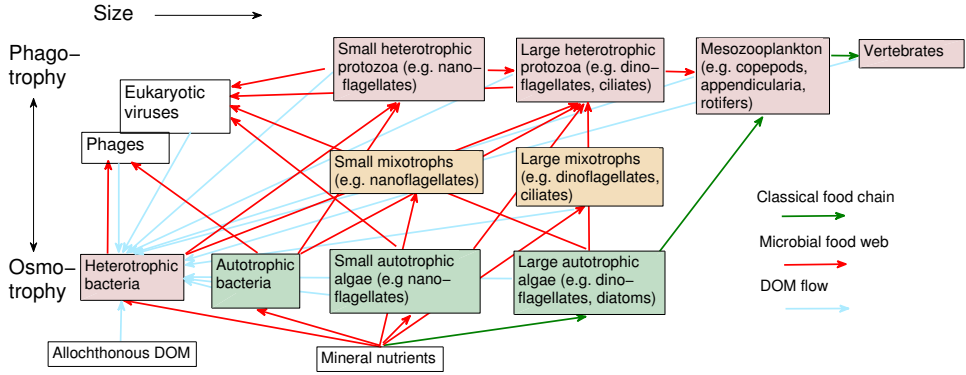


Figure 3: Simplified microbial food web organized by size and trophic mode with link to higher trophic levels. Green boxes indicate photoautotrophs, red boxes heterotrophs, and orange boxes mixotrophs. Important trophic interactions (including foraging and viral infection) are shown by red (microbial food web) and green arrows (classical food chain), whereas bacterial metabolism of organic material (DOM) originating from within the pelagic food web and allochthonous sources is indicated by light blue arrows. Mineral nutrient requirements of osmotrophs are simplified to one shared limiting resource for clarity.

systems and in nutrient replete and seasonally stratified waters where blooms are initiated. In such environments, they lay the basis for productivity of herbivores and higher trophic levels (Cushing, 1971; Legendre and Rassoulzadegan, 1995). Smaller members of the microbial food web, including hetero- and autotrophic picoplankton as well as nanoflagellates, are more dominant in oligotrophic regions, where bacterial biomass often exceeds that of phytoplankton (Legendre and Rassoulzadegan, 1995; Baretta-Bekker et al, 1998; Raven, 1998; Hartmann et al, 2012). The success of picoplankton in oligotrophic environments can be explained by higher growth rates of small cells when nutrient uptake is diffusion limited. Diffusive flux of nutrients to a spherical cell with radius r is given by $J = 4\pi Dr(S_{inf} - S_r)$, where D is the diffusion constant of the particular nutrient molecule of interest, and S_{inf} and S_r are ambient nutrient concentrations in the seawater and nutrient concentrations at the surface of the cell, respectively (Jumars et al, 1993). Assuming diffusion limitation, such that all nutrient molecules arriving at the surface of the cell are absorbed (i.e. $S_r = 0$), diffusive flux to the cell is proportional to the cell radius, i.e. $J = 4\pi DrS_{inf}$. Growth rate is expressed as the diffusive flux of the limiting nutrient to the cell, divided by the cell quota of the limiting nutrient. Assuming cell quota to be proportional to the cell volume (i.e. $\propto r^3$), we thus get a growth rate proportional to r^{-2} (Tambi et al, 2009). Hence in oligotrophic environments, following normal allometric scaling rules, being big is generally very costly in terms of reduced growth rates.

Box 2 Significance of pelagic microorganisms for the Earth system

Photosynthesis Photosynthetic cyanobacteria rendered Earth's atmosphere suitable for aerobic metabolism upon which complex life is based (Dismukes et al, 2001). Currently, marine phytoplankton contribute roughly 50% to the global primary production (Field et al, 1998).

Carbon cycle and climate Microorganisms are the major biological drivers of energy and matter cycles in the sea (Pomeroy, 1974; Fenchel, 2008). Export of organic material from plankton blooms and bacterial transformation of labile to refractory organic matter (Longhurst and Harrison, 1989; Ogawa et al, 2001; Volk and Hoffert, 2013) contribute to the climate relevant ocean carbon pump. Phytoplankton can also influence weather directly through excretion of aerosols (Charlson et al, 1987).

Industry By forming the basis of marine food webs, microorganisms directly influence marine harvest. Microalgae also have direct applications in the human food and biochemical industry (Spolare et al, 2006). Among the high diversity of metabolic pathways expressed in prokaryotes, metabolization of petroleum is important for bioremediation following industrial oil spills (Swannell et al, 1996).

2.3 Food web complexities at different scales

The pelagic food web is characterized by many different levels of organization and complexity. On the large scale, the biogeography of microorganisms is determined by chemical and physical environments (Follows et al, 2007), which sets the basis for secondary production and pelagic fish distributions. On local food web scales, different plankton functional types such as calcifiers (coccolithoporids) and silicifiers (diatoms) coexist, each filling different biogeochemical niches (LeQuéré et al, 2005). Within a particular functional group (such as heterotrophic bacteria, phytoplankton or zooplankton), size selective grazing may promote diversity and coexistence of different species (Gonzalez et al, 1990; Hahn and Höfle, 1999; Ward et al, 2013). On the species level, different clonal strains may coexist due to strain-specific viral control (Thingstad and Lignell, 1997; Fuhrman, 1999; Thingstad, 2000; Rodriguez-Valera et al, 2009). The structured complexity imposes a challenge for pelagic ecological modeling. Most simple models include nutrients, phytoplankton and zooplankton (so called NPZ models), reducing complexity to one functional

group per trophic level (Steele and Henderson, 1992). Such models have been widely used in oceanography and are still a valuable research tool (Franks, 2002). However, plankton dynamics in these models have only very limited resolution, and effects of important ecological processes such as temperature dependent bacterial remineralization (Rivkin and Legendre, 2001) and grazing rates (Buitenhuis et al, 2006) are neglected (LeQuéré, 2006; Mitra et al, 2007). Due to different chemical requirements and effects on ocean biogeochemistry, theoreticians have started to distinguish different plankton functional types in their models (Anderson, 2005). To resolve ecosystem dynamics adequately, LeQuéré et al (2005) suggest a minimum of 10 functional types with specific biogeochemical roles and distinct physiological and environmental requirements. They include hetero- and autotrophic picoplankton, phytoplankton groups including nitrogen-fixers, calcifiers, DMS-producers and silicifiers, mixotrophs, protozoa, mesozooplankton and macro-zooplankton. However, sparse data and fitting of parameters without a clear understanding of underlying ecological mechanisms (Fasham et al, 1990) require caution when interpreting output from these models (Anderson, 2005; Visser and Fiksen, 2013). A further step towards even more realistic resolution of biogeography and primary production is to seed global circulation models with many different functional types of phytoplankton, each with random combinations of physiological traits, where the environment selects favorable combinations of traits (Follows et al, 2007; Follows and Dutkiewicz, 2011; Ward et al, 2012). Also, adaptive models where functional foraging responses emerge based on the criterion of optimal fitness at the individual level avoid the problem of ecologically unjustified response functions (Visser et al, 2012; Visser and Fiksen, 2013). Highest resolution is typically obtainable in individual-based models (Judson, 1994), where physiological traits are resolved at the level of individuals. Due to computational costs, however, individual-based models have so far not been combined with global circulation models.

'Rhomboidal modeling' is a common approach in ocean ecosystem modeling to handle complexity at different scales (de Young et al, 2004). In this approach, complexity at a particular trophic level of interest is finely resolved in its characteristic temporal and spatial dimensions, while other trophic levels are represented with reduced detail (Figure 4). The method thereby reduces complexity to a manageable size. Relative to microbes, life histories of organisms in higher trophic levels are complex and may require such a selective approach (de Young et al, 2004). However, it may be fruitful to consider unifying mechanisms acting at all trophic levels, which could potentially open for ecosystem modeling where characteristic temporal and spatial resolution at all trophic levels could be combined. Previous studies (Bohannan and Lenski, 2000; Thingstad, 2000; Matz and Jürgens, 2003; Steiner, 2003; Haraldsson et al, 2012) and work presented in this thesis in-

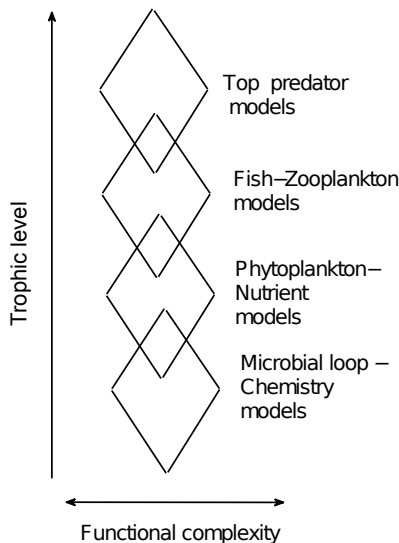


Figure 4: Illustration of 'rhomboidal' approach to ecosystem modeling. The width of the rhomboid illustrates functional complexity at different trophic levels in the model, and overlaps of rhomboids illustrate coupling of the model between different trophic levels. Modified from de Young et al (2004).

dicate that there may be a generic mechanism controlling biodiversity through top-down control of strong competitors in similar manners on different levels of the microbial food web. If this mechanism also applies to higher trophic levels, improved resolution of the characteristic complexities at all scales may become feasible in ecosystem models. This idea is explored at the end of the thesis (Section 5.3), where a fractal hypothesis of the pelagic food web is put forward.

3 Methods

3.1 Models used in this study

The modeling work presented in this thesis consists of a 3-population model with two competing prey and a predator (**Paper I**), a mixotrophic food web model (**Paper II**) and virus-host community models (**Papers III, IV and V**).

The 3-population model (**Paper I**) is based on idealized predator-prey interactions, where the competitively superior prey population (i.e. the competition specialist), which competes for the same resource as the defensively superior prey population (i.e. the defense strategist), is top-down controlled by a predator (referred to as 'Killing-the-Winner' (KtW) mechanism). In contrast to the traditional form of the KtW model (Thingstad and

Lignell, 1997; Thingstad, 2000), the competitively inferior defense strategist is partially predated upon by the predator, resulting in a diamond-shaped food web structure (Figure 5). A trade-off between defense and competition is incorporated such that increased defense reduces competitive abilities of the defense strategist. The analysis is conducted at steady state and explores the topology of steady state solutions with respect to trade-off, strategy choice and the systems nutrient content. Invadability of the defense strategy corresponding to maximum biomass or production is tested by calculating the evolutionary stable strategy based on partial derivative analyses of the net growth rate with respect to defense strategy. The KtW structure with incorporated trade-off between competition and defense used in this model is a minimum candidate for the underlying pattern generating mechanisms of a potentially fractal-shaped pelagic food web.

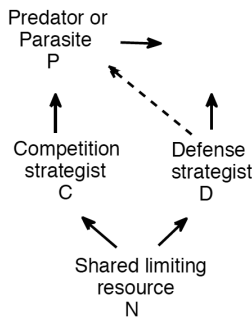


Figure 5: KtW structure with partial defense as analyzed in **Paper I**.

The mixotrophic food web model (**Paper II**) is developed to investigate how the trait-space of microbial organism size and foraging mode is populated within the microbial community, and what the success of particular combinations of cell size and foraging mode depends on. The model has a high resolution in both cell size (32 size classes) and foraging mode (11 modes). Foraging modes range from pure osmotrophy (applicable to heterotrophic bacteria and strictly autotrophic algae) to pure phagotrophy (applicable to strictly heterotrophic predators). Cell sizes range from small bacteria ($0.5 \mu\text{m}$ estimated spherical diameter (ESD)) to large eutrophic protists (several hundred μm ESD), and cell masses double between each size class. Differential equations for each combination of foraging mode and cell size describe the mass budgets for the particular microbial type. Interactions between the microbial types take place through competition for the same shared mineral nutrient pool, as well as through predation on each other. Nutrient affinity and clearance rate are diffusion limited at low resource concentration and solely

determined by physical constraints. In contrast, depending on the foraging mode, biological constraints are assumed to influence maximum uptake rates. A trade-off is thus incorporated to alter maximum uptake rates of mixotrophs relative to specialists (pure osmotrophs or pure phagotrophs). Simulations are run for 10 years to evaluate which microbial types are successful under various conditions.

The virus-host community model with a trade-off between nutrient competition and viral defense (**Papers III and IV**) consists of a bacterial community whose total biomass is controlled by protozoan grazing. Bacterial groups within the community have different growth rates depending on their competitive abilities. Coexistence is maintained through stronger top-down control of the faster growing host groups by host group specific lytic viruses. The model is analyzed at steady state and explores rank-abundance curves of host groups and their associated viruses. In **Paper IV**, host groups are considered as strains of bacterial species, and the model is applied to provide an alternative explanation for why SAR11 may be so successful, despite the recently discovered high abundance of SAR11 viruses (Zhao et al, 2013).

The virus-host model presented in **Paper III and IV** does not explicitly distinguish between bacterial species and strains, but instead resolves bacterial diversity to an unspecified level of 'host-groups'. In **Paper V**, strains and species are resolved in a simple chemostat arms race model, where evolutionary steps are discussed as a sequence of steady states following mutations. Coupled to new resistance mutations are growth rate reductions, and a memory factor is included to describe the ability of newly evolved viruses to infect previously evolved strains. Relevant for the understanding of success of particular bacterial clades in the ocean, control of species level diversity based strain-specific defense and competition mechanisms is analyzed. Hierarchical infection matrices combining resolution at the species and strain level are introduced in this model, indicating possibilities for a fractal-like representation of the microbial food web.

3.2 Strategy trade-offs as a common basis for the models

Trade-offs occur when one quality is gained on the cost of another quality, such that optimal performance of both qualities at all times is impossible. Trade-offs between different life strategies typically arise through limitations in space, energy or resources and are fundamental to obtain and maintain biodiversity (Stearns, 1989). Inclusion of trade-off representations between different life strategies in marine ecosystem models is timely and increasingly common (e.g. Bowers and Hodgkinson, 2001; Visser et al, 2009; Ward et al, 2011). All of the models in this dissertation have incorporated trade-off functions that regulate either competitive and defensive skills (**Papers I, III, IV and**

V) or different foraging mode abilities (**Paper II**). Except for **Paper V**, the trade-off functions are represented by a strategy index S and a trade-off parameter τ , which determines the shape of the trade-off functions. This shape is generally purely established empirically but has a strong influence on model outcomes (Boots, 2011). In the models presented here, different shapes are tested by varying the trade-off parameter τ . Generally, competitive abilities (f_C) and defensive abilities (f_D), are expressed as

$$f_C = (1 - S)^\tau$$

and

$$f_D = S^\tau,$$

respectively, where S is an index ranging from 0 to 1 describing investment into defense and τ is a dimensionless positive number. For $\tau < 1$, the trade-off function has increasing costs with increasing defense (Boots, 2011), such that an initial increase in S leads to a modest reduction in competitive abilities compared to the gain in defensive abilities, whereas loss of competitive abilities outweighs gains in defensive abilities for S approaching 1 (Figure 6, black curves). For $\tau > 1$, the trade-off function has decreasing costs, such that an initial increase in S leads to a drastic reduction in competitive abilities compared to the gain in defensive abilities, whereas increase in defensive abilities exceeds reduction in competitive abilities for S approaching 1 (Figure 6, blue curves). The trade-off between osmotrophic and phagotrophic foraging (**Paper II**) is represented with analogous functions for maximum uptake rates of dissolved and particulate matter, where $S = 0$ corresponds to pure osmotrophy and $S = 1$ to pure phagotrophy.

Mixotrophy trade-offs are purely established experimentally and remain debated (Stoecker, 1998; Rothhaupt, 1996; Litchman et al, 2007; McKie-Kriesberg et al, 2011), although it is conceivable that space conflict for uptake sites of two different nutritional machineries may induce a mixotrophy trade-off (Flynn and Mitra, 2009; Ward et al, 2011). Trade-offs between competition and defense are commonly assumed in theoretical ecology (Grover, 1995; Boots and Haraguchi, 1999; Bowers and Hodgkinson, 2001; Roff and Fairbairn, 2006; Follows and Dutkiewicz, 2011) and have been reported both for plants and animals as well as prokaryotes and even viruses (Winter et al, 2010, and references therein). In our simplified models, COR against viruses or predators is expressed in terms of reduced maximum growth rates, a trade-off observed experimentally (Bohannan and Lenski, 2000; Lennon et al, 2007; Middelboe et al, 2009), although other trade-offs such as reduced abilities to metabolize particular substrates (Middelboe et al, 2009) are also conceivable.

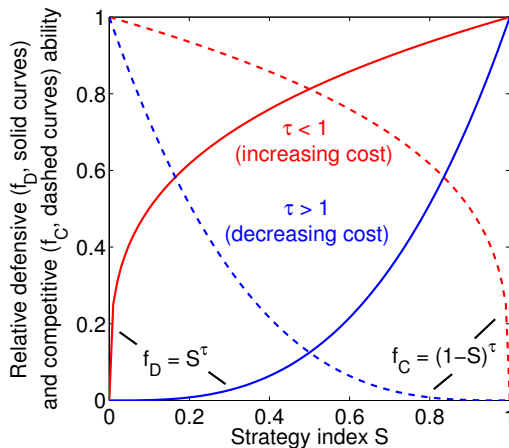


Figure 6: Trade-off functions used in the models. By varying the trade-off parameter τ , increasing or decreasing costs are modeled as a function of the strategy index S . The figure illustrates the example of a trade-off between competitive ability (f_C) and defensive ability (f_D) for $\tau = 0.3$ (red curves) and 3 (blue curves), where S represents the investment into defense ($S = 0$ pure competition, $S = 1$ pure defense). The trade-off between osmotrophic and phagotrophic foraging (**Paper II**) is represented with analogous functions for maximum uptake rates of dissolved vs particulate matter, where $S = 0$ represents pure osmotrophy and $S = 1$ pure phagotrophy.

The mechanistic understanding of trade-offs between competitive and defensive abilities in microbes is still relatively poorly developed. Genomic studies revealed that viral resistance mutations in prokaryotes often occur in highly variable 'genomic island' regions, which encode proteins for porin systems in the cell membrane (Avrani et al, 2011). Resistance mutations seem thus directly influential on nutrient uptake abilities of the host. This is in agreement with the observed trade-offs between nutrient uptake rates and defensive abilities in virus-host systems (Bohannan and Lenski, 2000; Lennon et al, 2007; Middelboe et al, 2009). Different resistance rendering machineries have most likely different COR, such that trade-offs most likely vary between species or strains with different defense mechanisms. For example, the relatively recently discovered internal immunity machinery called CRISPR (Barrangou et al, 2007) is likely to have different costs of resistance than the genomic island mutations associated with porin transport. Immunity through CRISPR is acquired by incorporation of viral DNA into an internal defense library (Barrangou et al, 2007). Whereas maintenance of the CRISPR machinery may be more costly than the porin system, acquisition of immunity against new viruses may be less costly. Systematic comparative studies of trade-offs between different microorganisms and coupling of those to particular defense mechanisms are, however, still missing.

4 Results

Coexistence and food web structures in our models are intricately influenced by relationships between resource availability, strategies at the cellular level and trade-offs between different strategies.

The simple 3-population KtW model (**Paper I**) with a trade-off between competition and defense gives rise to complicated steady state solutions. Coexistence of both prey populations is only possible when defense is increasingly costly ($\tau < 1$), a situation observed in experiments of arms-race coevolution (Buckling et al, 2006). For trade-off parameters close to but smaller than 1, the competition specialist outcompetes the defense strategist regardless of defense investment, whereas the defense strategists outcompetes the competition specialist when defense investment (S) and trade-off parameter (τ) are small or intermediate. The S - τ region where the defense strategist generally outcompetes the competition strategist increases with increasing nutrient load, which is in line with competition being a stronger selective force in oligotrophic systems and predation strongly controlling community structure in eutrophic systems (Thingstad and Lignell, 1997; Thingstad, 2000). Increasing nutrient load also increases the defense strategy associated with maximum biomass or production of the defense strategist, whereas the defense strategy corresponding to maximum biomass is generally higher than the strategy corresponding to maximum production. The strategies corresponding to maximum biomass or production are prone to invasion by mutants, although in the absence of the competition specialist, the evolutionary stable strategy resembles the strategy corresponding to maximum biomass. A balanced investment into defense and competition is evolutionary stable under coexistence of both prey populations.

The dynamic foraging mode and cell size structured mixotrophy model (**Paper II**) gives emergent food web structures that are strongly influenced by cell size-dependent parameters such as the ratio of predator cell size to prey cell size at which predation is most efficient (referred to as optimal predator-to-prey size ratio), the width of prey size range within which predation is successful, the systems nutrient content, and the mixotrophy trade-off. Success of different mixotrophic strategies is most prominent at low trade-off parameter ($\tau < 1$), when the combined maximum uptake rates of mixotrophs for dissolved and particulate matter exceed either of the maximum uptake rates of the specialists. Considering the high prevalence of mixotrophy in different taxa and marine environments (Hartmann et al, 2012), this may indicate that costs of mixotrophy are lower than often assumed (Ward et al, 2011). However, mixotrophs also frequently coexist with specialists for $\tau > 1$, where combined maximum uptake rates of mixotrophs for dissolved

and particulate matter do not add up to either of the maximum uptake rates of the specialists. Mixotrophs are particularly successful when optimal predator to prey size ratios are small, confirming that eating the most direct competitors (i.e. cells of equal or similar size) is an effective way to succeed as a mixotroph (Thingstad et al, 1996). The model is built on the basis of nutrient limitation, without considering light as a limiting factor. Mixotrophy as a strategy to increase energy intake under light limitation is therefore not included.

Trade-offs between maximum growth rates and viral defense also strongly influence community structure in the virus-host community model (**Paper III**). High COR reproduces inverse rank abundance curves of host groups and their associated viruses previously suggested in the literature (Suttle, 2007). The model predicts dominance of slow-growing prokaryotes as a necessary consequence of costly defense, rather than by dormancy due to unfavorable environmental conditions (Jones and Lennon, 2010). High COR (in terms of reduced growth rate) favors competitive host groups that support high abundances of viruses, but are themselves kept at low abundance due to viral lysis. Consequently, at high COR, a higher diversity of bacterial types (in terms of different growth rates) can coexist, and more of the bacterial production is shunted in to the viral loop. Hence, COR expressed at the individual level seems to directly influence biogeochemical cycling in the pelagic food web, exemplifying emergence of ecosystem level properties on the basis of individual-based traits and trade-offs (Mariani and Visser, 2010). Considering that different host groups may represent strains of particular bacterial species or clades, the recent finding of highly abundant SAR11 viruses (Zhao et al, 2013) does not contradict a dominance of defensive SAR11 strains as suggested by Suttle (2007) (**Paper IV**). In fact, the model predicts high virus abundances associated with a broad spectrum of host growth rates as observed for SAR11 (Malmstrøm et al, 2004).

Paper V confirms that numerical dominance at the species level depends on a successful combination of competition and defense at the strain level. The number of established strains of a species in an idealized chemostat environment is found to depend on the strains' competitive abilities, whereas defensive abilities of the strains determine the abundance of individuals within the strains. Species with defense mechanisms that have a low COR are predicted to be numerically dominant, as both the number of strains and abundance of individuals with each strain of the species can be high. Species level diversity emerges from summing up abundances over the virus-controlled strains that each species can establish.

5 Discussion

5.1 Scope and utility of used models

All of our models deal with the question how microbial food webs may be organized, and how coexistence may be promoted when neglecting spatial or temporal heterogeneity of the environment. The systems analyzed in this work are highly simplified, conceptual models of the microbial food web. As pointedly stated in Thingstad and Lignell (1997), "with a poor ability to intuitively grasp the behaviour of complex dynamic systems, the human mind may need the aid of simplified models to try to extract essential features from a complex and sometimes bewildering reality". This contrasts other developments of microbial ecological modeling, where as much known physiological complexity as possible is included (e.g. Mitra and Flynn, 2010). Clearly, it is a challenge to simplify models as much as possible while still representing reality in a meaningful way (Flynn, 2005), and the degree to which models should be idealized and simplified depends on the model application.

The models used in this thesis are not coupled to large-scale physical or biogeochemical circulation models, and hence do not allow predictions of regional or global ecosystem dynamics. Instead, they focus on underlying ecological mechanisms describing trophic interactions that are expected to act in all environments. Different food web structures and ecosystem dynamics are expected to arrive from varying environmental influences on the underlying interactions, as shown in the modeling studies presented here. Whereas this thesis predominantly treats general trade-offs between competition and defense applicable to any trophic level, trade-offs between different functional traits including competition for one vs. another nutrient (Tilman, 1982), competition for nutrients vs. light (Huisman and Weissing, 1994; Klausmeier and Litchman, 2001) and competition vs. maximum growth rates (Grover, 1991; Litchman and Klausmeier, 2001) have been identified for phytoplankton, which are clearly important for structuring plankton communities as well (Litchman et al, 2007). However, these trade-offs are constraint to certain functional groups and seem not to fulfill generality sought in this thesis ranging across different trophic levels within the pelagic food web. Although not considered in this work, it is noted that ecological network interactions exist where trade-offs appear to be absent (e.g. commensalism, mutualism, Ings et al, 2009).

While understanding equilibria in conceptual steady state models as presented in **Papers I, III, IV** and **V** arguably is necessary before a complete understanding of more complex system dynamics and eventually natural systems is possible (Thingstad et al, 1996; Ward et al, 2013), dynamic models including the one presented in **Paper II** give

insights into system dynamics that steady state analyses cannot achieve. Furthermore, understanding effects of individual heterogeneity on emergent system properties requires individual-based methods (DeAngelis and Gross, 1992; Grimm and Railsback, 2005), which are not explored in this thesis. However, a comparison between the differential-equation based model in **Paper II** was made with an individual-based model of the same system by Castellani et al (2012), revealing that differential equation-based population models with sufficient resolution in functional types can reproduce individual-based model dynamics.

The underlying theory for the models used in this thesis are generalities acquired through experimental work and observations in the past 40 years of pelagic microbial ecology. Biogeochemical regulations in the KtW model, e.g. nutrient rich environments favoring defense strategists (generally large cells) and competition strategists (generally small cells) dominating in oligotrophic conditions, are in agreement with field observations. In oligotrophic systems such as subpolar and subtropical gyres, small members of the microbial community including bacteria and nanoflagellates dominate (Raven, 1998; Casey et al, 2007). In nutrient rich systems such as upwelling regions and coastal areas after seasonal mixing, blooms of larger phytoplankton typically take place (Alvain et al, 2008). Besides improved nutrient storing capacities that can become favorable in adverse environmental conditions (Verdy et al, 2009), an advantage of being large can be related to smaller predation pressure due to less abundant predators specialized on large prey (Thingstad et al, 2005). This is reflected in the evolutionary history of the planktonic food web, where larger prey evolved to escape predation pressure, with the consequence of opening new niches for larger predators to evolve (Thingstad et al, 2010). However, it is noteworthy that most life has remained small and anatomically simple, proven by the global numerical dominance of prokaryotic cells and the vast majority of protists within the eukarya. Gould (1996) explains this with the 'left wall' for minimal organismal complexity, which turned out to be most successful in the course of evolution.

The interplay between direct measurements in nature from which models and theories are constructed and construction of hypotheses and theories that are tested experimentally has proven to be highly successful to advance scientific knowledge (Kell and Oliver, 2003). Evolutionary arms race theory predicts the evolution of resistant bacterial strains and new infectious viruses at an ever decreasing rate in a chemostat setting due to increasing costs of resistance for the host (Buckling et al, 2006). An understanding of prolonged sequences between new resistance mutations thus allows planning of chemostat experiments with intervals suitable to resolve evolutionary events. Also, understanding the link of host growth rates and virus abundances (Thingstad, 2000), one could use host-

specific virus abundances as proxies for COR of the evolved defense mechanisms in the hosts (**Paper V**). Importantly, models can give alternative and at times counterintuitive explanations for observed features, which may be difficult to derive from common knowledge. In fact, counterintuitive explanations have repeatedly been essential to advance our fundamental understanding of the world, exemplified by the Copernican model of the solar-centric planetary system and the uncertainty principle of quantum mechanics. In aquatic microbial ecology, the dominance of slow growing prokaryotes in the ocean has typically been explained by resource sparsity and consecutive dormancy to preserve energy (Stevenson, 1978; Jones and Lennon, 2010). Alternatively, the KtW model with incorporated COR suggests that dominance of little active cells may be explained by high COR (**Papers III and V**). Furthermore, it explains a counterintuitive coupling of high virus abundance to a clade previously suggested (Suttle, 2007) to be dominated by defense strategists (**Paper IV**).

5.2 Complex systems

The pelagic microbial food web is highly complex, with a high level of diversity at different trophic levels. The increasing knowledge of physiological, ecological and phylogenetic detail in microbiology often inclines biologists to abandon simplifying approaches. This is somewhat different from a physicist's mindset who is trained to reduce problems to significant components. Admittedly, due to the intrinsic complexity of life, it seems more straight forward to find universal regularities and laws in physics than in biology. Nevertheless, fractal geometry and chaos theory (Box 3) teaches us that simple rules can lead to complex emergent structures and system dynamics. The idea that biological systems, despite their overwhelming complexity and diversity, may in part be derived and based on fundamental, universal and relatively simple ecological principles is worth to consider. However, finding such principles from which a general theory can be established is a major challenge in biology, and their existence remains debated (Judson, 1994; Scheiner and Willig, 2008). Ecosystem properties such as heterogeneous distributions of species in space and time, interactions of organisms with abiotic and biotic environments, contingency of organism distributions and their interactions, heterogeneous environments in space and time, limitation of resources, mortality of all organisms, and the evolutionary basis of ecological properties of species have been suggested as a basis for a general theory of ecology (Scheiner and Willig, 2008). Still, extracting fundamental ecological principles explaining these properties and constructing a general theory that unifies distinct ecological theories such as island biogeography theory (MacArthur and Wilson, 1967), niche theory (Chase and Leibold, 2003) and metabolic theory of ecology (Brown et al, 2004)

remains a challenge for the future.

Research on complex systems, including the economic market and social networks, has boosted in recent years through an increasing availability of large data sets and computer power to analyze the data (Brunk, 2002; Barrat et al, 2011). What does the pelagic microbial food web have in common with other such complex systems? A general criterion for complexity is that the large-scale behavior of the system has a rich internal structure that results from interactions among members of the system (Sornette, 2006; Barrat et al, 2011). This concept is known under emergence, where the structure of the system is not predefined according to a blue print, but instead results from self-organizing mechanisms that act on and between the constituents of the system. Similarly, properties of the pelagic ecosystem and food web structures ultimately emerge from interactions of individual organisms undergoing natural selection (Follows et al, 2007). With respect to individual organisms, complexity of (multi)cellular structures may be limited by phyletic heritage and architectural constraints (Gould and Lewontin, 1979). In this sense, the trade-off between viral susceptibility and nutrient uptake associated with the porin system (genomic island regions, Avrani et al, 2011) or potential mixotrophy trade-offs (Ward et al, 2011) can be understood as a consequence of 'Bauplan' (Gould and Lewontin, 1979) restrictions on the cell surface.

Complex systems are hard to predict due to their chaotic behavior, and long term dynamics are highly sensitive to initial conditions (Grebogi et al, 1987). Typically, heterogeneities in complex systems are repeated on different scales (Barrat et al, 2011), a characteristic typical for fractals (Box 3). Many natural systems have fractal like organization, both spatially and temporally. Examples of natural fractals include geological features such as coast lines and mountain landscapes (Mandelbrot, 1967, 1982), meteorological phenomena such as cloud and rain patches (Lovejoy, 1985; Cahalan and Joseph, 1989; Tuck and Hovde, 1999), and biological vascular systems such as the circulatory blood system, lungs and plant structures (West et al, 1999). In contrast to mathematical fractals, however, natural fractals have limited scale invariance, which seldom exceeds a few orders of magnitude (Biham et al, 1998). Also, while the pattern generating formulas for geometrical fractals are readily known, finding and understanding the rules that lead to natural fractals are not straight-forward. Nevertheless, since chaos theory shows that simple equations describing nonlinear deterministic systems can have apparently unpredictable and irregular behavior (Grebogi et al, 1987), meteorologists and ecologists wonder whether simple explanations can be found to account for chaotic and irregular behaviour in weather or ecosystem dynamics (Theiler, 1990; Zimmer, 1999; Halley et al, 2004). Mathematical models of simple predator-prey interactions predict chaos when

Box 3 Fractals, fractal dimensions and chaos theory

Fractals are mathematical structures that are constructed by simple rules, which, when applied iteratively, result in scale invariant self-similarity (Mandelbrot and Blumen, 1989). In other words, the same structural complexity and detail is found at any scale in a fractal. A famous example of a geometric fractal is the Sierpinsky triangle, where the central triangle is removed at each level (Figure 7). Random fractals lack a geometrical description, but are still self-similar at all scales based on their statistical properties, and natural fractals have a limited scale invariance. Fractals are generally characterized by their fractal dimension, which is a generalization of the classical Euklidian dimension. Fractal dimensions can be calculated analytically for geometric fractals as

$$D = \frac{\log(N)}{\log(1/\epsilon)},$$

where N is the number of downscaled copies at a particular scale and ϵ is the scaling factor of the downscaled copies (Mandelbrot et al, 1985). Due to their self-similarity at all scales, mathematical fractals do not fall into the classical Euklidian dimensions of either a line (1 dimension), a plane (2 dimensions) or a volume (3 dimensions). Instead, they fill in a space somewhere between these Euklidian dimensions. Hence, fractal dimensions are non-integer numbers and can intuitively be understood as the roughness of a fractal (Theiler, 1990). The closer a fractal dimension is to an integer, the smoother is the boarder of the fractal. As an example, the Sierpinsky triangle has a fractal dimension of roughly 1.6 due to the infinitely many holes that reduce the apparent 2-dimensional fractal surface to something less than a plane. For non-geometric fractals (e.g. natural fractals), fractal dimensions can be estimated numerically in different ways (e.g. Mandelbrot et al, 1985). An intuitive approximation is to plot the measured quantity of the fractal (e.g. length of the boundary) against the scale with which the measurement was conducted (e.g. the ruler length) on a log-log plot. The slope of the curve is then an estimate of the fractal dimension (Theiler, 1990). By these means, the coast of Norway has an estimated fractal dimension of roughly 1.52 (Feder, 1988). Fractals are closely linked to chaos theory. Chaotic systems are described by non-linear differential equations exhibiting sensitivity to initial conditions (Lorenz, 1993). They have periodic orbits of all periods, and all periodic orbits are unstable. In contrast to convergence to stable fixed points or limit cycles, trajectories of chaotic systems typically converge to a region in the phase space that has a fractal structure (called strange attractor, Auerbach et al, 1987).

growth rates are high (May, 1974, 1976), and experimental support for chaotic behavior in ecology has recently been found for a simple microbial food web and a natural plankton community (Becks et al, 2005; Beninca et al, 2008).

Focusing on microbial food web organization and community structure, it is proposed in the following that fractal theory may be directly relevant for a new system understanding of the pelagic food web. It is discussed why the pelagic food web may have a fractal-like organization, and what the underlying structure generating principle may be. Once underlying mechanism creating chaos and fractal-like organization in a natural system may be identified, longer term predictions of the systems may become more realistic. Also, ecosystem modeling with adequate resolution at all scales may become feasible.

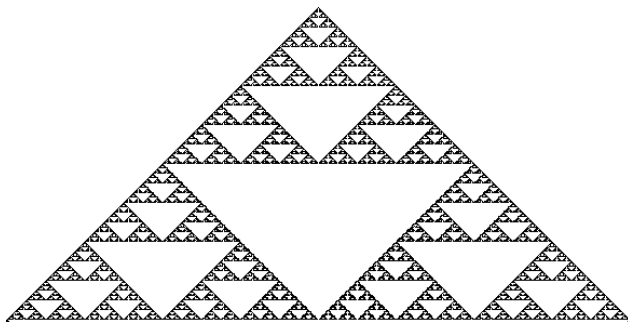


Figure 7: Sierpinski triangle generated by the chaos game as described in Barton (1990).

5.3 Fractal hypothesis of the pelagic microbial food web

The work presented in this thesis is guided by the idea that complicated food web structures in the pelagic ecosystem may be shaped by relatively simple ecological principles. Traditionally, according to the 'rhomboidal' approach (de Young et al, 2004), marine ecological models have a selected focus on particular trophic levels. Accurate descriptions of temporal and spatial scales and known physiological or behavioral detail are thereby restricted to a particular level of interest, while other trophic levels are typically included with much reduced detail (e.g. Megrey et al, 2007). Examples include models of microbial food webs, where higher trophic levels are simply represented as a pathway for organic carbon and mineral nutrients reentering the microbial loop (Thingstad et al, 2007), or

models of fish stocks and marine mammals, where lower trophic levels remain unresolved (Bogstad et al, 1997). Such approaches have the problem of underrepresenting important levels when it is aspired to obtain a truly ecosystem-based understanding. Efforts are made to combine detailed models in 'end-to-end' ecosystem models with detail at all levels (Travers et al, 2007; Fulton, 2010). However, merging models with detailed description at all trophic levels is not only computationally costly, but may also be little rewarding in terms of increased conceptual understanding. A risk is that such models become equally detailed as reality itself. While potentially useful for predictions of ecosystem responses to climate change, they may help little to understand underlying control mechanisms.

As a contrast to traditional ecological modeling with selective representation of detail, or merging of ever increasing detail on all trophic levels, the fractal hypothesis of the marine pelagic food web is presented as a means to potentially gain ecosystem understanding. According to this hypothesis, different trophic levels are controlled in similar manners within their respective characteristic temporal and spatial scales. An understanding of fundamental structuring mechanisms at one level gives thus a basic understanding of organization at other levels. If this concept is valid and can be formalized, less compromises between representation of complexity at different levels may be required, and a more fundamental understanding of system organization as a whole could be achieved. This would facilitate 'end-to-end' ecosystem modeling by efficiently resolving adequate complexity at different levels.

What evidence supports the hypothesis that the pelagic food web may be organized in a fractal-like manner? One characteristic property of the pelagic food web is its biomass-size spectrum, where roughly equal biomass is present in logarithmically spaced size classes (Sheldon et al, 1972). Plotting the logarithm of the normalized biomass in a size class against the logarithm of the cell size in the size class results in a straight line. This power law of the biomass-size spectrum is found in a variety of different marine environments including estuaries, coastal seas and oligotrophic gyres (Quinones et al, 2003; Irigoien et al, 2004; Tao et al, 2008). Although such power laws do not necessarily imply an underlying fractal structure, they are characteristic for fractals (Brown et al, 2002). Earlier attempts to explain the power law in the biomass-size spectra include the hypothesis that the roughly 10 percent efficiency of energy transfer between trophic levels, together with a reduction of metabolic rates by roughly 10 percent from one trophic level to the next, lead to the equal biomass per logarithmic size classes (Sheldon et al, 1972). However, this argument is based on a linear food chain, which does not apply to the pelagic food web and the microbial loop in particular, which is a highly interconnected network. Also, this hypothesis lacks the power to explain how many different types of equally sized organisms

can coexist.

The KtW principle (Thingstad, 2000; Winter et al, 2010) central to the models presented in this thesis is an alternative mechanism explaining coexistence and pelagic food web structure. By top-down control of winning competitors through predation or parasitism, excessive resources become available for the inferior competitors, given that the systems nutrient content is large enough (Figure 8). In macro ecology, the same principle is known as 'Keystone Predation' (KP) (Paine, 1966; Grover, 1995; Leibhold, 1996), although KP is used in more loose terms (Mills et al, 1993) than KtW, which is rooted in steady state analyses (Thingstad, 2000). The experimental verification of the KtW principle on different trophic levels of the pelagic microbial food web (Pengerud et al, 1987; Bohannan and Lenski, 2000; Matz and Jürgens, 2003; Steiner, 2003) and the late application of the same principle to analyze jellyfish and zooplanktivorous fish competition in the Baltic Sea (Haraldsson et al, 2012) suggests that this mechanism may indeed be a fundamental control mechanism at different trophic levels (Figure 9), leading to a fractal-like food web organization.

How may a visualization of a fractal-like organization of the pelagic food web look like? From virus-host infection studies, it appears that infection networks within host groups typically follow a nested infection pattern (Flores et al, 2011; Jover et al, 2013). Nested infection means that generalist viruses infect nearly all hosts, while specialist viruses only infect those hosts that are susceptible to most viruses, leading to an upper triangular infection matrix (Figure 10). Nested infection can arrive through expanded host range coevolution, where hosts evolve to become resistant against existing viruses, while viruses evolve to infect the ever increasing number of newly evolved hosts (Lenski and Levin, 1985; Buckling and Rainey, 2002). The result is that the most evolved viruses are generalists, able to infect most hosts, while the most evolved hosts are defense specialists and only susceptible to the most evolved viruses. The costs of being a generalist virus is assumed to be reduced virulence in terms of lower adsorption coefficients, while defensive hosts pay with lower competitive abilities (Flores et al, 2011).

Here it is hypothesized that nested infection (and analogously nested predation) occurs at different levels within the microbial food web, resulting in a self-similar structure with subsets of upper triangular infection and predation matrices. Each inward level of the fractal-like representation of the food web corresponds to a higher resolution of functional types (**Paper V**). The idea is illustrated in Figure 11, where infection and predation matrices are shown at three different levels of resolution. The yellow level in Figure 11 has smallest resolution in functional types. Focusing on the microbial part of the pelagic food web and assigning this level to microzooplankton grazers and their prey,

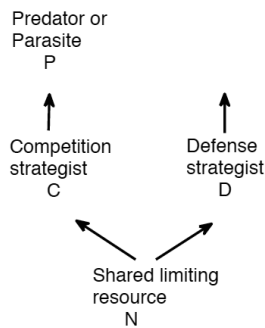


Figure 8: Basic trophic structure of the KtW principle. The biomass of the competition strategist is top-down controlled by a predator or parasite, whereas the biomass of the defense strategist is proportional to the excess of the shared resource. The defense strategist is an inferior competitor and has thus slower growth rates than the competition strategist.

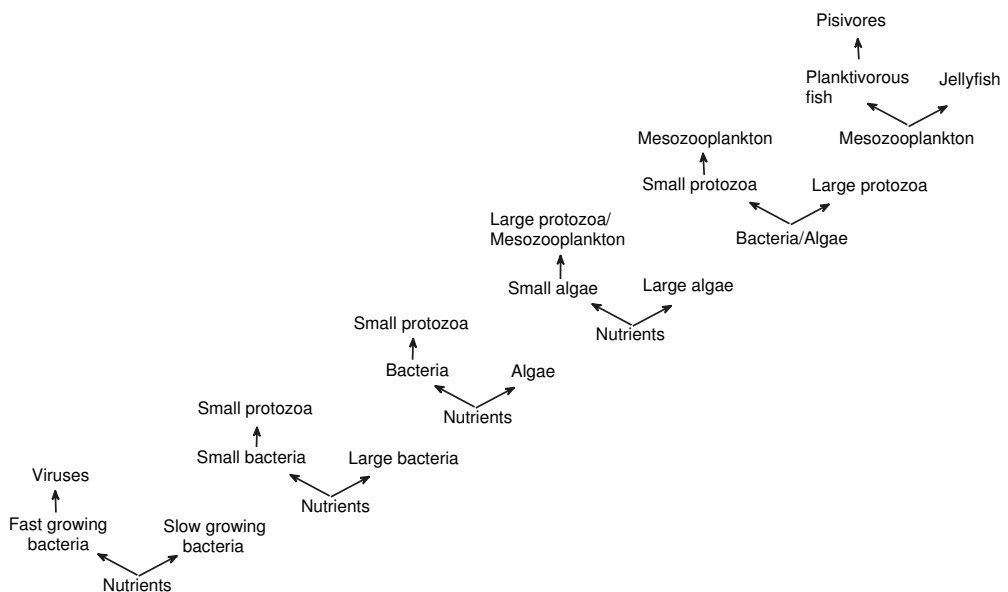


Figure 9: KtW mechanisms based on a trade-off between competition and defense at different trophic levels within the pelagic food web. Experimental evidence exists for bacteria-phage communities (lower left, Bohannan and Lenski, 2000), protozoa-bacteria food webs (lower middle, Matz and Jürgens, 2003), protozoa-bacteria-algae food webs (middle, Pengerud et al, 1987) and phytoplankton-metazoan food webs (upper middle, Steiner, 2003). Recently, the KtW concept has also been applied to analyze competition between fish and jellyfish (upper right, Haraldsson et al, 2012).

	Least susceptible hosts, most evolved			Most susceptible hosts, least evolved	
Generalist virus, most evolved					
Specialist virus, least evolved					

Figure 10: Nested infection matrix as explained by expanded host range coevolution (Flores et al, 2011). Colored matrix entries represent positive infections.

		Large Prey			Intermediate Prey			Small Prey				
		Spec. 1	Spec. 2	Spec. 3	Spec. 1	Spec. 2	Spec. 3	Spec. 1	Spec. 2	Spec. 3		
Specialist Predator	Spec. V3	Strain 1										
	Spec. V2	Strain 2										
	Spec. V1	Strain 3										
	Interm. Predator	Spec. V3	Strain 1									
		Spec. V2	Strain 2									
		Spec. V1	Strain 3									
		Generalist Predator	Spec. V3	Strain 1								
			Spec. V2	Strain 2								
			Spec. V1	Strain 3								
	Strain V3		Strain 1									
	Strain V2		Strain 2									
	Strain V1		Strain 3									

Figure 11: Idealized nested predation and infection fractal to illustrate the idea behind the fractal hypothesis of the pelagic food web. Nested infection and predation is suggested to occur at different trophic levels and resolutions of functional types. Each inward level of the fractal represents a higher resolution of functional types.

relatively large microbial predators such as heterotrophic dinoflagellates and ciliates may be classified as generalists, grazing on prey within a range of cell sizes including pico-, nano- and microplankton (although for particular dinoflagellate species, restrictions in terms of preferred cell size apply, Buskey, 1997), whereas the smaller heterotrophic nanoflagellates are more restricted to picoplankton prey and may be categorized as specialist predators. Large potential prey such as diatoms and dinoflagellates are the most evolved forms and are typically protected against the most abundant microbial predators such as heterotrophic nanoflagellates and ciliates due to their big size (Thingstad et al, 2010). They generally give up on their competitive abilities relative to smaller prey (e.g Tambi et al, 2009). Small prey with a longer evolutionary history including bacteria and nanoflagellates, on the other hand, are under more severe grazing pressure by highly abundant microbial predators such as heterotrophic nanoflagellates and larger protozoa (Thingstad et al, 2005). Similarly, within the functional types described on the yellow level, expanded host range coevolution is proposed to have led to nested infection and predation structures on the green level. Different prey species presumably evolved to emphasize defense during arms-race dynamics, while predator or parasite species may have coevolved to become generalists with broader host ranges. Within the species level (blue level in Figure 11), viruses are most important for structuring the host community due to their high host-specificity compared to predators. Strain-specific viruses with a narrow host range classify as specialist parasites, while other viruses with broader, species-specific host-ranges are generalist viruses (Flores et al, 2011; Jover et al, 2013). (The notion of prokaryotic species and strains can be problematic (Doolittle and Zhaxybayeva, 2009). Here the two terms are simply referred to as distinctive levels of phylogenetic relatedness where strains subdivide species.) Beyond the purely microbial food web, looking at mesozooplankton and their prey, copepods may be considered specialist predators compared to filter feeding appendicularia (chordata), which are less selective (Deibel, 1986) and thus classify as generalist predators.

Natural food webs are clearly not as regular as illustrated in Figure 11. More realistic are structures where the number of taxa varies between and within different trophic levels, as outlined in Figure 12. Depending on the number of distinguished functional types, species and strains, the fractal dimension varies. Regardless of the exact shape of the upper triangular infection and predation matrices, however, there is a noticeable resemblance of these with the well-known Sierpinski triangle (Figure 7). The fractal dimension of the regular fractal in Figure 11 is roughly 1.63 (calculated as $D = \log(6)/\log(3)$, where 6 is the number of downscaled copies and the scaling factor is $1/3$), whereas the Sierpinski triangle has a fractal dimension of roughly 1.58 (calculated as $D = \log(3)/\log(2)$).

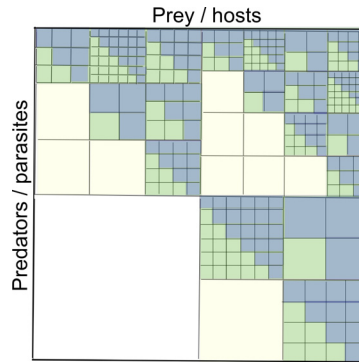


Figure 12: Illustrative example of a nested predation and infection fractal with varying numbers of functional types at different levels of resolution.

In summary, as an alternative to 'rhomboidal' ecosystem modeling (de Young et al, 2004), consideration of structuring mechanisms such as the KtW principle repeated at different trophic levels is proposed to be a useful approach to ecosystem understanding. Whereas different players within the pelagic food web fulfill the role of competition and defense strategists and top-down controlling parasites or predators at different trophic levels and phylogenetic resolutions, the basic principle of coexistence due to a trade-off between competition and defense remains the same. The pelagic food web is hypothesized to resemble an upper triangular fractal due to nested infection and predation at multiple trophic levels. Nested infection appears to prevail in many virus-host systems (Flores et al, 2011; Jover et al, 2013) and the potential benefit of a fractal understanding of the pelagic food web is large both for ecosystem modeling, allowing relevant resolution of detail at many levels, and for the building of a general ecological theory. Hence, the fractal hypothesis is arguably worth to pursue. It is conceivable that fractal-like organization of the pelagic food web is most realistic for the microbial community, where sufficiently high rates of evolution and a comparatively homogenous environment allow expanded host-range evolution to be more widely expressed. Higher trophic levels including vertebrates are to a larger extent influenced by biogeography (Hubbell, 2001) and randomness in their speciation and extinction patterns (Gould et al, 1977). The consequence may be a larger evolutionary disequilibrium in macro ecological food webs, which may imply less complete fractality. Clearly, extensive infection and predation studies over a range of different trophic levels, including quantitative analysis to identify COR (Jover et al, 2013), are required to establish and test this hypothesis further and to potentially get a more robust estimate of a fractal dimension of the pelagic food web.

6 Conclusions and future perspectives

The work presented in this thesis addresses the challenge of handling and understanding complexity in the pelagic microbial food web. Competition, defense, predation and parasitism are assumed to be fundamental specializations in life strategies, and trade-offs between these strategies were shown to be important for food web structure with respect to coexistence, biodiversity, abundance and biogeochemical functioning of the pelagic microbial food web. The models deliberately represent simplified and abstract versions of real microbial food webs, with the aim to identify system regularities and patterns that are driven by fundamental ecological mechanisms acting across all food web levels. Based on previous studies and work presented in this thesis, a fractal-like organization of the food web is hypothesized. The fundamental structure-generating mechanism leading to the fractal-like organization of the food web is proposed to be the KtW mechanism based on a trade-off between competition and defense, allowing repeated nested infection and predation networks at different trophic levels and resolutions of functional types. Although experimental evidence for the KtW mechanisms regulating competitive interactions at different trophic levels exist, and nested infection networks seem common in virus-host communities, more extensive, systematic and quantitative studies across the entire food web are required to thoroughly challenge the fractal hypothesis of the marine pelagic food web.

Mechanistically understanding and quantifying trade-offs between microbial life strategies remain important challenges in marine ecology. Besides experiments necessary to quantify trade-offs in different predator-prey and parasite-host systems, future analyzes of trade-offs and their role in food web structuring would benefit from an individual-based model of a virus-host community, where host species seeded with different defense mechanisms could be simulated. Strains and strain-specific viruses could evolve through mutations, and emergent species diversity and strain abundance in the system could be studied as a consequence of variable trade-offs between different defense mechanisms. An ultimate goal may be to build an individual-based evolutionary model of the pelagic food web with bottom-up and top-down control mechanisms that are regulated by different trade-offs between emergent life strategies. If an increasing complexity and different trophic levels would emerge based on nested infection and predation dynamics, quantitative network properties potentially confirming fractal-like architecture of the food web could be derived.

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