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Investigation of population dynamics, ecological traits and molecular phylogeny of bacterivorous chrysomonads

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Tobias Pietsch

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Berichterstatter:	Prof. Dr. Hartmut Arndt
	PD Dr. Kenneth Dumack
Vorsitzende der Prüfung:	Prof. Dr. Ute Höcker
Beisitzerin:	Dr. Anja Scherwaß
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Abstract

The recognised high biodiversity of planktonic microbes in the absence of a comparable high variability of limiting conditions has fascinated scientist and is known as the “paradox of plankton”. The high number of species which coexist in aquatic ecosystems at the same time contradicts the principal of competitive exclusion and requires further investigations to understand the mechanisms allowing the coexistence of multiple species on a limited number of resources. In the last decades empirical and theoretical studies provided some explanations to solve this issue as for instance environmental variability, spatial patchiness, competition or selective predation. Most of these studies focused on environmental and biotic interactions of species and did not consider potential intrinsic mechanisms originating from a single population itself.

The aim of this study was to investigate growth related differences within a single species population and their potential influence on complex nonlinear population dynamics favouring the coexistence of relatively similar species. Bacterivorous chrysomonads were chosen as a model group because they are essential and dominant bacterivorous in aquatic food webs. Phylogenetic studies revealed an unexpected high biodiversity of morphologically mostly indistinguishable species which classifies this group as an interesting model group to study mechanisms allowing their coexistence. Ten isolated strains were phylogenetically described and different growth-related traits were compared. Three of the isolated bacterivorous chrysomonads have a mixotrophic nutrition while the others are heterotrophs. For the comparison of traits, the mixotrophic species *Chlorochromonas danica* (SAG strain) was also included.

The phylogenetic analysis revealed that only three of the ten investigated strains could be assigned to known species of which one (*Ochromonas vasocystis*) needed to be redescribed (*Poteriospumella vasocystis* comb. nov.). One strain could only be identified on the genus level. The remaining six strains could not be assigned to known species and were morphologically and phylogenetically described as new species (*Pseudapoikia anjascherwassiae* gen. nov., *Vivaspumella atacamiensis* gen. nov. sp. nov., *Chlorospumella boenigkii* gen. nov. sp. nov., *Atacamaspumella andiensis* gen. nov. sp. nov., *Poteriospumella maldiviensis* sp. nov.). The trait comparison of those strains, including *C. danica*, showed that cell size and size range of ingested bacteria overlap for all investigated strains of chrysomonads while growth rate and dynamics differed to a notable extent. This was not only due to different nutritional strategies (mixotrophy, heterotrophy) but also due to species-specific differences which could not be explained by the other investigated traits.

Bacteria-free and well controlled single-species chemostat systems with two mixotrophic species were established to investigate intrinsic nonlinear dynamics and a continuous-time model was developed to study intracellular processes and their potential cause for nonlinear dynamics in those single-species systems. For the investigation of clonal trait differences as putative source for nonlinear population

dynamics, an individual based model was developed and the coexistence of different traits was studied under natural temperature fluctuation.

The time series analysis of single-species chemostat experiments resulted in nonlinear population dynamics under well controlled and stable experimental conditions with indications of chaos-like dynamics. The continuous-time model was able to explain those nonlinear dynamics in single-species systems by considering the cell cycle as a complex intracellular process. For the first time it was shown that individuality and intrinsic aperiodic dynamics have to be considered for explaining the coexistence of species and genotypes. Moreover, the individual based model allowed the coexistence of clonal traits which differed in their temperature related resource uptake because they responded differently under natural temperature fluctuation causing nonlinear dynamics of the whole population. The results of the study point to the great significance to consider not only differences among species to explain their coexistence but also to consider differences within a population of a single species on the clonal and individual level to estimate effects on population dynamics.

Contents

General introduction

Biodiversity, ecosystem functioning and stability

The recognised high biodiversity of planktonic species in freshwater has challenged scientists and the principal of competitive exclusion. Hutchinson (1961) described this issue as the “paradox of plankton”. First experiments which led to the development of the principal of competitive exclusion were carried out by Gause (1934) who showed that two *Paramecium* species reached comparable abundances when grown separately while in a mixed culture one species suppressed the other one. In the following decades researchers further developed this idea. In brief, the competitive exclusion means that two populations that occupy the same ecological niche and the same geographic territory are competitors and if one of those populations grows better than the other, the population with higher growth rate will displace the other one (Hardin, 1960). With this concept in mind, Hutchinson (1961) addressed the issue of the high diversity of phytoplankton in an environment of nutrient deficiency which should lead to competition and thus to a competitive exclusion. His main argument why the principle does not hold true under natural conditions was the implied equilibrium system which should never obtained under natural conditions due to environmental changes. Moreover, he mentioned effects of symbiosis, commensalism and predation as beneficial for the coexistence of species. A review of mechanisms to explain the paradox of plankton is given by Roy and Chattopadhyay (2007). Those mechanisms can be divided into two main parts, firstly the system is out of equilibrium, and secondly additional limiting factors which prevent the competitive exclusion of species (Fig. 1).

Environmental properties change continuously due to external factors and influence the mixing of epilimnion in lakes avoiding an equilibrium. This can favour temporal and spatial patchiness and thus coexistence of species (Christensen et al., 2022; Richerson et al., 1970). Model approaches which assume a continuous variation in environmental properties demonstrated the possible coexistence of species under non-equilibrium conditions (Letten et al., 2018; Levins, 1979; Powell and Richerson, 1985). Although most studies of environmental fluctuation have focussed on resource variability, temperature fluctuation as promoting factor was also shown empirically to be important for species coexistence (Jiang and Morin, 2007). Moreover, the addition of a single nutrient in pulses prevents an equilibrium and allows the coexistence of several species (Ebenhöh, 1988). Such pulsing effects can be caused by excretion of zooplankton (Dini et al., 1987; Lehman, 1980; Pérez-Martínez and Gulati, 1999). The importance of nonlinear dynamics caused by the competing system itself has been shown with simple competition models. With a single resource, coexistence of two or more species is possible when limit cycles are present (Armstrong and McGehee, 1980). Moreover, Huisman and Weissing (1999) demonstrated that competition of species for at least three resources can cause oscillation and chaotic dynamics allowing multiple species to coexists.

Other important limiting factors which prevent a species from outcompete other species are different physiological and life-cycle patterns as well as predator-prey interaction. Huisman et al. (2001) investigated physiological and life-cycle parameters which were either chosen randomly or reflecting a plausible trade-off between those and found that randomly chosen parameters supported only a low biodiversity while plausible trade-offs supported the coexistence of more than 100 species in some cases. Predator-prey interaction can contribute to the coexistent of prey species by either preferring the most abundant competitor (Murdoch and Oaten, 1975; Roughgarden and Feldman, 1975) or the most competitive one (Armstrong, 1979).

The mechanisms mentioned above show that biodiversity is the result of complex interactions between species and changes of abiotic and biotic factors. They determine the population dynamic by either influencing the growth rate (e.g. limitation of physiological processes) or changing the population size as a consequence of trophic interactions (e.g. predation). Simple population dynamics can be mathematically described by their general pattern. The damped oscillation describes an oscillating

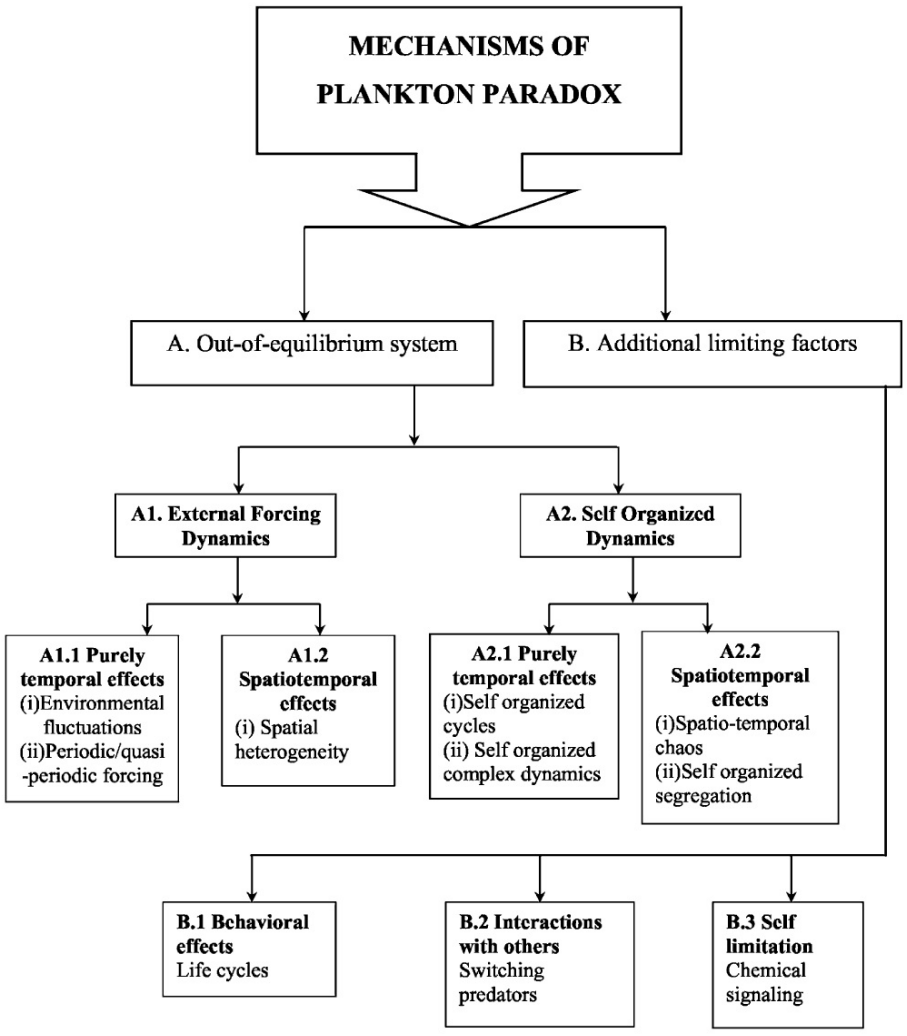

Figure 1. Conceptual scheme of mechanisms to explain the plankton paradox (taken from Roy and Chattopadhyay, 2007).

dynamic towards the system equilibrium with continuously reduced amplitude while limit cycles oscillate periodically within an upper and lower limit around the equilibrium. A more complex and unpredictable dynamic is the so called chaotic dynamic, a deterministic aperiodic dynamic with a sensitive dependency on the initial condition (Hastings et al., 1993). Such chaotic dynamics can already appear in simple population models (May, 1974) and were repeatedly found in theoretical studies mentioned above and several other theoretical studies (e.g. Costantino et al., 1997; Hastings and Powell, 1991). Experimental evidence for chaotic dynamics as predicted from models is rare, but Becks and co-workers (2005; 2008) demonstrated the appearance of chaos in laboratory experiments of a predator-prey system. The importance of those nonlinear dynamics was rarely considered in former studies compared to other mechanisms facilitating the coexistence of species and was addressed mainly in analytical models.

The causes for high biodiversity are not only of scientific interest. During the course of climate change and anthropogenic influence, the importance of biodiversity is nowadays widely discussed. Ecosystem stability and services rely on a diverse and complex community. Mason et al. (2005) presented a concept of how species richness and species evenness can be linked to functional richness and functional evenness and discussed both for ecosystem productivity. A high functional richness may indicate that the available resources are effectively used by the community while a low functional richness will reduce productivity of the community (Petchey et al., 2004). Biodiversity can stabilise ecosystems because species can respond differently to environmental fluctuation and can differ in the speed at which they respond to disturbance (Loreau and de Mazancourt, 2013). In the first case species can differ in their preference of abiotic or biotic factors causing asynchronous population dynamics which in turn stabilise ecosystem properties. The second case describes differences in growth rates and thus a different speed to respond to perturbation. Although mechanisms allowing a high biodiversity are intensively studied so far, a debate remains open and gives rise for further research. Recently, Kléparski et al. (2022) showed that the ecological niche of 117 marine plankton species of three different taxonomic groups is sufficiently distinct to allow their coexistence and moreover that marine pelagic environments are more diverse in space and time than assumed by Hutchinson (1961). The potential importance of nonlinear processes which are not directly determined by environmental changes may affect the population dynamic of a single species. Such influences on the coexistence of species were mainly overlooked in this debate. Cellular processes, however, are complex biochemical processes and should influence a population dynamic independently from environmental changes as nonlinear intrinsic process. The eucaryotic cell cycle is a biochemical process regulated by a complex network (Morgan, 2007; Tyson et al., 2002). Such biochemical processes depend on changes in concentrations of biomolecules and thus on dynamic changes of those (Morgan, 2007) and their oscillations are never exactly repeated (Tyson et al., 2002). Consequently, chaotic behaviour is likely appearing within cellular processes and might cause unpredictable dynamics with significant consequence for growth related parameters as intrinsic and not environmental driven mechanism. However, this has been seldom considered (Massie et al., 2010). Protists are excellent

model organisms to investigate the underlying mechanisms for biodiversity. Because Chrysophyceae are a common and often the dominating group in aquatic food webs, this group of protists is a reasonable group to provide new knowledge of mechanisms allowing the coexistence of many species. Further reasons for the choice of chrysomonads were their high growth rates and the possibility to grow under well controlled axenic (without bacteria) conditions.

Chrysophyceae

The Chrysophyceae belong together with several other clades like Placidida, Bicosoecida, Xanthophyceae and Diatomeae to the eukaryote clade of Stramenopiles (Adl et al., 2019). In fresh water ecosystems chrysophytes are common and often dominate the protist community (Bock et al., 2022; Matz et al., 2002). Only a few species are known from marine environments. However, a culture-independent analysis of chrysophytes diversity revealed the existence of several yet unknown marine clades (del Campo and Massana, 2011). Autotrophic Chrysophyceae can dominate the phytoplankton fraction of an aquatic environment by the formation of blooms (Kammerlander et al., 2015; Nicholls, 1995; Rott, 1988; Tolotti et al., 2003) while heterotrophs and mixotrophs are important bacterivorous flagellates (Boenigk et al., 2005; Boenigk and Arndt, 2000). Because of their importance in aquatic ecosystems and their diverse nutritional strategies chrysophytes were intensively studied in the last decades. Physiological studies focused on comparative investigations of autotrophic, heterotrophic and mixotrophic growth and their competitive advantages under experimental conditions (e.g. Pålsson and Daniel, 2004; Rothhaupt, 1996a, 1996b; Rottberger et al., 2013; Sanders et al., 1990). Other studies investigated and compared the ingestion mechanism and size of food particles (Boenigk and Arndt, 2000; Pfandl et al., 2004).

The morphological appearance of chrysophytes is diverse and often allows the identification of genera and species (Fig. 2). The Synurales and Paraphysomonadida are characterised by their siliceous scales, an important identification feature for genera and species. The colony forming genus *Synura* and the solitary genus *Mallomonas* represent prominent genera of the chloroplast bearing Synurales (Andersen, 1987). In contrast, *Paraphysomonas* which is the name giving genus for the Paraphysomonadida, is a heterotrophic genus feeding on bacteria (Scoble and Cavalier-Smith, 2014). The Ochromonadales is the most diverse group among Chrysophyceae and comprises heterotrophic and mixotrophic genera as well as solitary and colonial forming genera. Typical examples are the heterotrophic genus *Spumella* and the mixotrophic *Ochromonas*, both genera are solitary while the mixotrophic genus *Dinobryon* possesses a lorica and forms branching colonies (Andersen et al., 2017; Grossmann et al., 2016; Jeong et al., 2021; Piątek et al., 2020). The genus *Poterioochromonas* is a mixotrophic solitary and typically loricated genus (Andersen et al., 2017). Other mixotrophic and colony forming genera are *Uroglena* and *Uroglenopsis* (Pusztai and Škaloud, 2019).

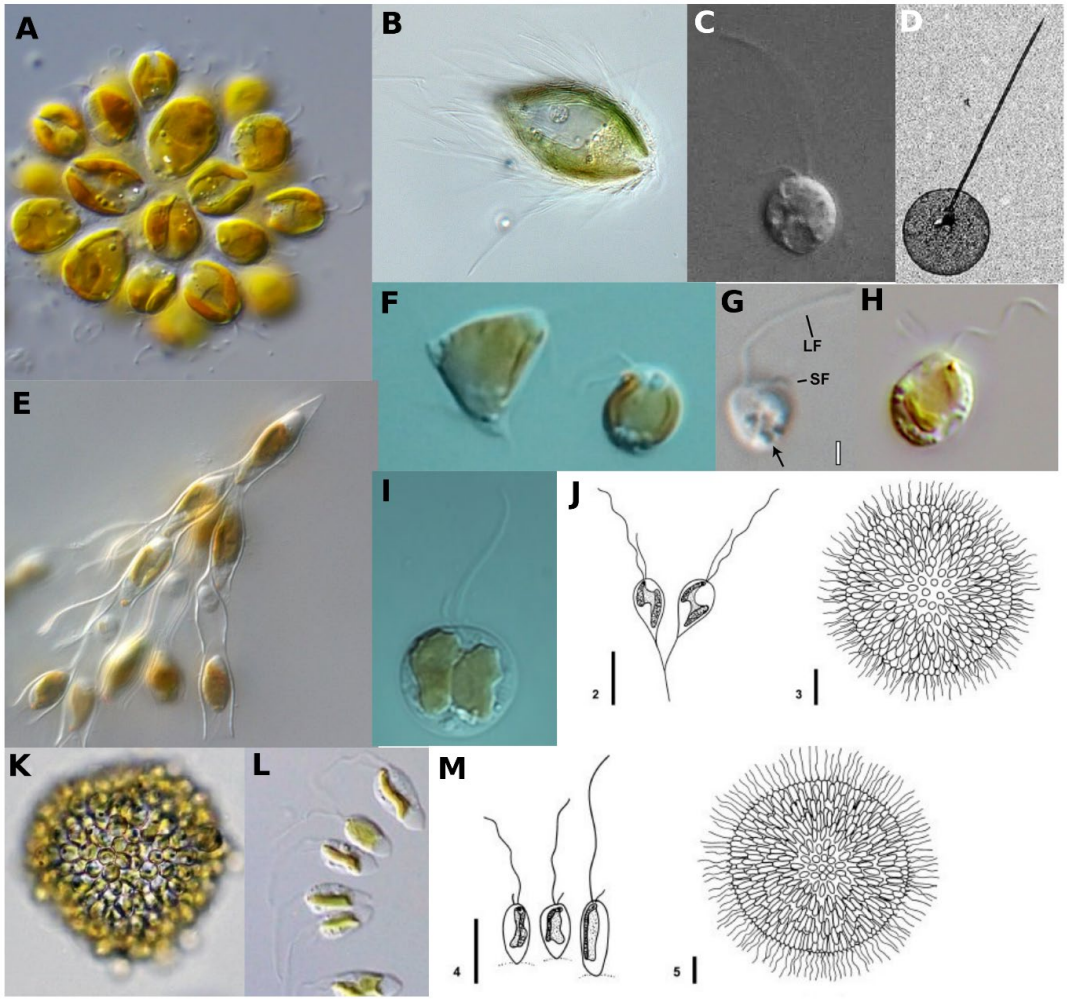

Figure 2. Examples of different chrysophyte species. A. Colony of *Synura petersenii* (SAG 24.86). B. *Mallomonas caudata* (CCAP929/8), scaled. C. Vegetative cell and D. Scales of *Paraphysomonas longispina*. E. Colony of *Dinobryon* sp. (CCAP917/5). F. *Ochromonas triangulata*, unscaled. G. *Spumella communis,* unscaled. H. *Poteriospumella vasocystis,* unscaled. I. *Poterioochromonas* sp., unscaled J. Morphology of *Uroglena* K-L. *Uroglenopsis turfosa*. M. Morphology of *Urostipulosphaera*. Source of Image: A. Strain site of Catalogue of Collection of Algae (SAG). B. and E. Strain site of Catalogue of Culture Collection of algae & protozoa (CCAP). C-D. Scoble & Cavalier-Smith (2014) F. and I. Andersen et al. (2017) G. Jeong et al. (2021). H. Pietsch et al. (2022). J. and M. Pusztai & Škaloud (2019). K. and L. Pusztai & Škaloud (2022).

Despite the comprehensive morphological diversity among genera of chrysophytes molecular studies of the last decades revealed an even higher and unexpected biodiversity. Two main reasons for the underestimation of diversity may be named: Firstly, the morphological description of species is only possible if those are isolated and kept in culture for detailed studies. It is well known, that only a small portion of the protist community can be cultivated from an environmental sample because several species are relatively rare and fragile (Jeuck et al., 2017). Environmental sequencing surveys demonstrated that uncultured and thus unknown species of Chrysophyceae

exist because sequence data are often distant from known species (Bock et al., 2022; del Campo and Massana, 2011; Finlay and Clarke, 1999; Izaguirre et al., 2021). Secondly, molecular studies demonstrated that the morphospecies concept based on morphological distinct criteria is not always sufficient because several genera and species lack those distinct criteria (Andersen et al., 2017, 1999; Findenig et al., 2010; Grossmann et al., 2016; Pusztai and Škaloud, 2019). Species which correspond to the morphology of the genera *Ochromonas* and *Spumella* are two examples of those misleading morphology. More than 125 species of the genus *Ochromonas* have been described (Andersen et al., 2017). The identification of *Ochromonas* species is often difficult by means of light microscopy and morphological criteria. Important identification features are the intracellular organisation like the presence or absence of a stigma, the number of chloroplasts and contractile vacuoles (Starmach, 1985). This shows how similar genetically distant chrysophytes can be in the sense of morphology and thus it is not surprising that those genera are nowadays often recognised as polyphyletic. The same applies for other chrysophytes which were commonly termed as *Spumella* sp. because of their indistinguishable morphology. However, recently several new genera and species of "*Spumella*"-like chrysophytes were described (Findenig et al., 2010; Grossmann et al., 2016). All these species lack a reliable morphological feature to distinguish those from *Spumella* and each other. Thus, it is doubtful that chrysophytes which were identified by means of light microscopy as *Spumella* sp. are necessarily species of this genus.

Aims

The motivation for this thesis was to investigate population dynamics and ecological traits, their contribution to biodiversity and thus their importance for ecosystem functioning and stability. Protists are excellent model organisms to study population dynamics because their generation time is short and cultivation as well as experiments are affordable and easily to implement compared to other organisms. Since Chrysophyceae represent a diverse and important clade among protists for freshwater ecosystems. This was the reason to focus on species and strains of this taxonomic group. Within this group heterotrophic and mixotrophic bacterivores species were chosen because recent molecular studies demonstrated that the phylogenetic diversity of those species is higher than expected from their morphological appearance. Moreover, bacterivores chrysomonads are important and dominant members of most aquatic food webs which points to the importance to study their biodiversity, functional traits and population dynamics to enhance our knowledge of the complexity of aquatic food webs.

For the investigation of this subject elven isolates of bacterivores chrysomonads were compared representing both, heterotrophs as well as mixotrophs, (Chapter 1 and 2). Beside one species (SAG 933-7, *Chlorochromonas danica*; obtained from the Culture Collection of Algae at Goettingen University) all isolates were either already available from our Heterotrophic Flagellate Collection Cologne (HFCC) from previous samplings or were isolated during this study to enhance the available set of strains. Bacteria-free

chemostat experiments were conducted and a continuous-time model was developed to examine intrinsic driven population dynamics (Chapter 3).

The following hypothesis were addressed on the basis of the available strains:

1. Isolates of bacterivores chrysomonads are morphologically almost indistinguishable, but represent a high phylogenetic diversity.
2. Different species and strains differ in ecological traits and population dynamics.
3. Instrinsic nonlinear dynamics appear in single-species systems and contribute to population dynamics.

Chapter 1

<u>High molecular diversity in the functional group of small bacterivorous non-scaled chrysomand flagellates</u>

In this study the molecular diversity of non-scaled bacterivorous chrysomonads was investigated. From ten HFCC strains the SSU rRNA sequences were isolated and analysed. Most strains represent heterotrophic strains representing the "*Spumella*"-like morphology. Their morphology was studied with light microscopy. To evaluate potential fine structured differences stains were further investigated by electron microscopy. The main hypotheses and aim of this study were to elucidate the hidden diversity of morphologically undistinguished species, their taxonomic position within the clade of Chrysophyceae and the description of undescribed species to resolve the diversity. The main result of this study was that most strains could not be distinguished morphologically but they represented phylogenetically distinct species of which five were yet undescribed. The results reflect the high biodiversity of morphologically almost indistinguishable bacterivorous non-scaled chrysomonads.

Chapter 2

<u>Overlap and differences in ecological traits of bacterivorous flagellates: Comparison of mixotrophic and heterotrophic chrysomonads</u>

The aim of this study was to characterise ecological traits of the strains and described species from Chapter 1 including the SAG 933-7 strain to address the hypothesis that strains and species have different characteristics of those traits. This might allow the coexistence of morphological similar species. Cell length and cell volume of strains and species were measured and calculated to compare those among strains. The second investigated trait was the prey size. Size and cell volume of ingested bacteria were measured and calculated to examine whether species and strains differ in their prey size preference. The last trait was the population dynamic. Growth rates and growth dynamic were analysed and compared. A second hypothesis was that individual difference in growth rates among individual cells exist and might contribute

to complex population dynamics. Therefore, the growth rate of single cell lines under well controlled and homogenous (axenic) conditions were analysed for two mixotrophic strains. This hypothesis is also addressed in Chapter 3. The main result of this study was that the trait differences of cell size and size range of ingested bacteria overlapped for all investigated chrysomonads while growth rates and growth dynamics differed to a notable extent. It was shown that those differences were partly among species representing different nutritional strategies (heterotrophy and mixotrophy), but also species-specific.

Chapter 3

Intrinsic nonlinear dynamics drive single-species systems

The hypothesis that nonlinear growth dynamics in single-species systems of protists without trophic interaction and under well controlled conditions appear was addressed in this chapter. The cause of those dynamics might be nonlinear cellular processes and thus differences in growth among single individuals of a species population (compare Chapter 2). To study intrinsically driven dynamics in single-species populations bacteria-free chemostat experiments were conducted and their time series analysed. Beside experimental investigations a continuous-time model was developed to evaluate to which extent the cell cycle as complex cellular process might cause nonlinear dynamics. The main result of this study was to show for the first time that individuality and intrinsic aperiodic dynamics have to be considered for explaining the coexistence of species and genotypes.

Chapter 1: High molecular diversity in the functional group of small bacterivorous non-scaled chrysomonad flagellates

Pietsch, T., Nitsche, F., & Arndt, H. **2022**. High molecular diversity in the functional group of small bacterivorous non-scaled chrysomonad flagellates. *European Journal of Protistology*, 125915. https://doi.org/10.1016/j.ejop.2022.125915

Chapter 2: Overlap and differences in ecological traits of bacterivorous flagellates: Comparison of mixotrophic and heterotrophic chrysomonads

Pietsch, T. & Arndt, H., **2024**. Comparison of mixotrophic and heterotrophic chrysomonads of similar size regarding bacterivory and growth rate. *European Journal of Protistology*, 126109. https://doi.org/10.1016/j.ejop.2024.126109.

Chapter 3: Intrinsic nonlinear dynamics drive single-species systems

Werner, J., **Pietsch, T.**, Hilker, F. M., & Arndt, H. **2022**. Intrinsic nonlinear dynamics drive single-species systems. *Proceedings of the National Academy of Sciences*, *119*(44). https://doi.org/10.1073/pnas.2209601119

Conclusive summary and perspectives

The high biodiversity and the coexistence of species is crucial for ecosystem stability and services (Loreau and de Mazancourt, 2013). Therefore, it is important to understand underlying mechanisms to allow the coexistence of several species within ecosystems. Most research focussed on species-species interactions and influences of environmental conditions as mechanisms of species coexistence. Potential mechanisms originating for the population itself were mainly overlooked. Those intrinsic driven population mechanisms should influence the population dynamics to a notable extent. Consequently, nonlinear population dynamics driven by intrinsic mechanisms may change species-species interactions and may contribute to the coexistence of species (Huisman and Weissing, 1999).

Chrysophyceae are a diverse and important taxonomic group of protists in aquatic ecosystems and were therefore chosen for the study of phylogenetic diversity, ecological traits and population dynamics. The phylogenetic analysis on the bases of the SSU rRNA sequence (18S) revealed that most of the investigated strains represented yet undescribed species and genera (Chapter 1). Those were morphologically described by means of light and electron microscopy and their phylogenetic position within the clade of Chrysophyceae based on sequence differences. The morphological investigation revealed that heterotrophic strains could not be distinguished from each other neither by light nor electron microscopy while the phylogenetic analysis revealed significant sequence differences and different taxonomic relationships. The analysis illustrated not only that strains belong to different species and genera but also to different families and orders. Most strains could be affiliated to the Ochromonadales which is the most diverse group among Chrysophyceae. The phylogenetic position of the other two strains (HFCC 236 and 1230) remains unclear (*Incertae sedis*) but they represented two distinct clades allowing a species description. Within the clade *Incertae sedis*, *Pseudapoikia anjascherwassiae* gen. nov. sp. nov. (HFCC 236) and *Vivaspumella atacamiensis* gen. nov. sp. nov. (HFCC 1230) were newly described. Within the Ochromonadales, three more new species could be described *Atacamaspumella andiensis* gen. nov. sp. nov. (HFCC1250), *Chlorospumella boenigkii* gen. nov. sp. (HFCC 1534 and 1538) and *Poteriospuemlla maldiviensis* sp. nov. (HFCC 660). The mixotrophic HFCC 668 was morphologically identified as *Ochromonas vasocystis* but needed to be redescribed as *Poteriospumella vasocystis* comb. nov. because it does not phylogenetically belong to the genus *Ochromonas* (Andersen et al., 2017) and the low sequence difference compared to HFCC 1532 and 660 (below 1.5%) did not justify a description as separate genus. The description of heterotrophic and mixotrophic species within a genus is supported by the finding of plastidal remains, different stages of reduction in photosynthesis related pathways and plastid structure in heterotrophic *Spumella*-like chrysophytes (Graupner et al., 2018; Grossmann et al., 2016). The last two strains HFCC 75 and 210 could be morphologically and phylogenetically confirmed as

Poteroochromas sp. HFCC 75 was identified as *P. malhamensis* while HFCC 210 could not be associated to a distinct species due to uncertain assignments of morphologically described species and phylogenetic data (Andersen et al., 2017).

The phylogenetic analysis was an important prerequisite for the investigation of ecological traits (Chapter 2), because a reliable morphological discriminability was limited to mixotrophic strains. The different strains of Chrysophyceae represented a comprehensive set of different species and genera and allowed a reliable trait comparison across phylogenetic distinct taxa. The investigation of cell length and corresponding cell volume revealed significant differences only between mixotrophic and heterotrophic strains. Mixotrophs were significantly larger than heterotrophs. An exception was the mixotroph *P. vasocystis* (HFCC 668) which was as large as heterotrophs. However, considering the size range measured from all strains (~4-8.5 µm), their effective size difference was relatively low. As an important trait for bacterivorous flagellates the size range of ingested bacteria was analysed by direct observation using light microscopy. The range of the length and cell volume of bacteria taken up by the investigated strains was in the same range and the mean length and cell volume did not differ significantly. Moreover, it could be observed that most strains attempted to ingest large filamentous bacteria which were, however, finally released without digestion. The investigation led to the conclusion that all strains investigated herein feed on the same size range of bacteria and can be described as unselective bacterivores. However, strains may differ in the efficiency to graze on different bacteria caused by different size relationships between flagellate and prey as well as other phenotypic properties of bacteria (Jürgens and Matz, 2002; Matz et al., 2002). Such potential influences were not considered in the study and should be addressed in further studies. As a third trait important growth-related parameters were investigated in growth experiments with bacteria as diet. The exponential growth rate as well as the maximal observed growth rate and the long-term growth rate were calculated from growth curves. The comparison of the exponential and the maximal observed growth rate revealed for all strains that the maximal achieved growth rate was higher than exponential growth indicating that all strains grazed effectively on bacteria causing food limitation effects. For two species, *C. boenigkii* (HFCC 1534 and 1538) and *A. andiensis* (HFCC 1250), the food limitation caused decreasing abundance already after two days. The long-term growth rate was calculated after the exponential growth phase. Mixotrophic strains were able to keep a stable but decreased growth rate until the end of the experiment while the abundance of most heterotrophs decreased, causing a negative growth. However, two species of heterotrophs (*P. maldiviensis* HFCC 660 and *V. atacamiensis* HFCC 1230) were able to keep a stable abundance (growth rate ~0.0 d^{-1}). As a second growth related parameter the achieved maximal abundance during the experimental duration was determined. Mixotrophic strains grew over the whole experimental duration and reached therefore maximal abundance at the end of the experiment while heterotrophs achieved the maximal abundance typically within a few days. The range of achieved abundance for heterotrophs varied strongly among strains (from ~2.5 to ~17.0 individuals per ml).

Several conclusions can be made from the trait study. All investigated species and strains are in a comparable size range from about 4 to 8 µm and feed on a comparable size range of bacteria. Considering only these two traits one would conclude that their ecological impact within an aquatic food web would be at least comparable if not equal. Taking the nutritional strategy (heterotrophy and mixotrophy) as a third trait into account one would assume that mixotrophs are more competitive under poor nutrient conditions than heterotrophs and vice versa under high nutrient levels (Rothhaupt, 1996). Growth related parameters such as growth rate and maximal abundance differed to a notable extent among species with different nutritional strategies (heterotrophy and mixotrophy) but also among species. The species *P. vasocystis* (HFCC 668) represents a remarkable exception. Although it is a mixotrophic species the cell size and growth rate are more comparable with heterotrophs (Fig. 3). Thus, it might be the most competitive species under most environmental conditions of all investigated strains because it combines both, the high growth rate of heterotrophs (compared to mixotrophs) and the ability to grow under poor nutrient conditions, although this was comparatively low. This is also supported by the phylogenetic relationship to the two heterotrophs *P. lacustris* and *P. maldiviensis* (Chapter 1). The mixotroph *C. danica* (SAG 933-7) was phylogenetically closely related to the heterotrophic species *Chlorospumella boenigkii* but less than *P. vasocystis* to the next heterotrophs. The lower growth rate (compared to heterotrophs) of *C. danica* was more comparable to the mixotrophic genus *Poterioochromonas*. Considering the phylogenetic distance to *C. boenigkii* (HFCC 1534 and 1538) it seems that the degree

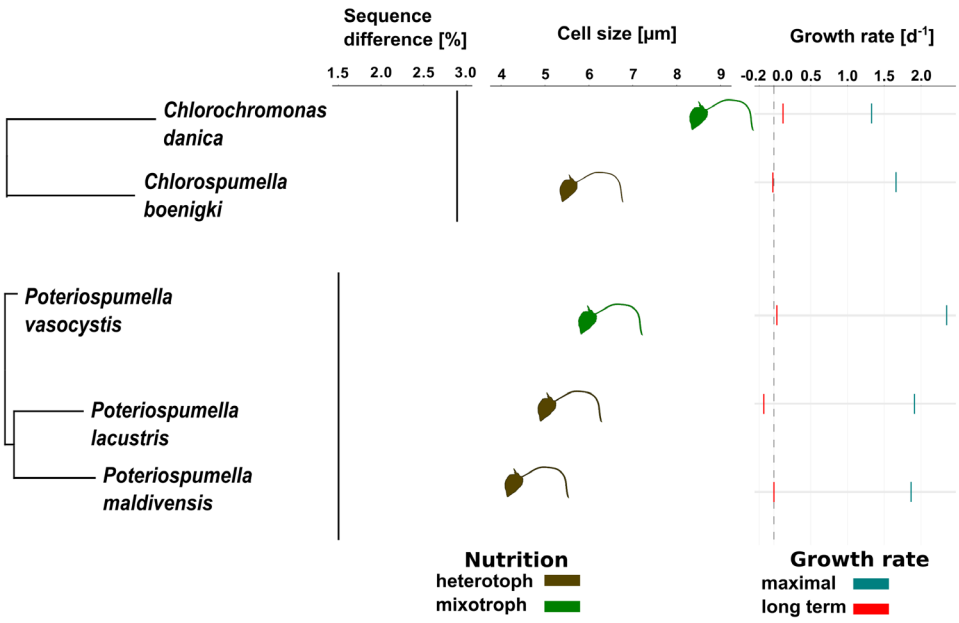

Figure 3. Trait comparison of phylogenetically closely related heterotrophic and mixotrophic chrysomonad species. Depicted are phylogenetic information (phylogenetic clades and sequence differences of SSU rRNA sequences), the mean cell size, maximal observed growth rate and long-term growth rate. Data from Chapter 1 and 2.

between mixotrophy and heterotrophy could be derived from the phylogenetic distance to heterotrophs. The polyphyletic origin of the same morphological appearance among chrysophytes reflected by the heterotrophic stains investigated herein is currently assumed as independent evolutionary process from mixotrophic ancestors (Graupner et al., 2018; Grossmann et al., 2016). Thus, the comparison of closely related mixotrophic and heterotrophic species should be addressed in future studies to provide more conclusive results for the phylogenetic relationship and the degree of mixotrophy. This is of importance because the ecological impact of mixotrophs obviously cannot be directly derived from the nutritional strategy as shown for *P. vasocystis*. In this study it was demonstrated that neither cell size, range of prey size nor the nutritional strategy were sufficient traits to derive the impact and potential coexistence of different chrysophyte species within an ecosystem. The growth dynamic, however, differed among species and such differences play a crucial role for coexistence (Huisman and Weissing, 2001). Although the investigated strains grazed on a comparable size range of bacteria they may differ in the preference of specific bacteria size and properties as mentioned above. Other feeding traits, which were not considered, could be responsible for differences in growth dynamics. The prey richness plays an important role for predator productivity. Both, prey as well as predator diversity, can be suggested as important factor for microbial ecosystem processes (Saleem et al., 2013). Small differences in traits can allow the coexistence of species and contribute to ecosystem functioning and productivity when an ecological niche is effectively used due to functional richness (Loreau and de Mazancourt, 2013; Petchey et al., 2004). The results show how morphologically similar species feeding on a comparable bacteria size range can differ in growth rates and growth dynamics. More research should be done with comparable protists groups, for example those which are affiliated with the diverse morphospecies complex *Neobodo designis* (von der Heyden and Cavalier-Smith, 2005), to extent the knowledge of small trait difference and their influence of the coexistence of morphologically similar species.

Such trait differences are not necessarily restricted to different species. They also exist among different clones of a species as shown for ciliates (Weisse and Rammer, 2006). The coexistence of different growth traits simulated by a temperature dependent nutrient uptake was part of a bachelor thesis (see Appendix A.4.). The conducted model is an individual based model which allows the definition and calculation of individuals separately. Previous models relaying on differential equations treat individuals uniformly and do not allow the analysis on the basis of individuals. Such clonal “subpopulation” may be influenced by environmental changes to a different degree which in turn influences the population differently depending on the actual state of clonal trait diversity within the population. This would mean that two populations are differently affected by the same environmental change because they differ in clonal trait frequency. This assumption is synonymous to a generalised view on phytoplankton as ecological functional unit (corresponding to the population) and different species which are part of it (corresponding to different traits). However, trait differences between different species should be generally larger than differences among individuals of the same species. Moreover, several other species-specific

differences need to be considered causing higher differences among different species than among clones of the same species. The model revealed that different clones were able to coexist under natural temperature fluctuation (from the River Rhine), causing nonlinear dynamics of clones as well as the whole population. Differences in traits correspond to differently realised ecological niches. An appropriate distinct ecological niche allows the coexistence of several species by reducing the competition (Kléparski et al., 2022). This mechanism should also allow the coexistence of different clonal traits of a single species as shown by the model results if the differences are distinct.

In Chapter 3 the hypothesis was addressed that intrinsic nonlinear dynamics appear in single-species systems and that those contribute to population dynamics. Consequently, nonlinear population dynamics which allow the coexistence of several species (Huisman and Weissing, 1999) are not implicitly driven by external factors if this hypothesis holds true. For the proof of the hypothesis single-species systems with either *P. malhamensis* (HFCC 75) or *C. danica* (SAG 933-7) as model organisms were established in well controlled experimental bacteria-free chemostat systems. The analysis of time series revealed aperiodic fluctuations for nearly all experimental systems. In two of the time series analyses a positive Lyapunov exponent indicated chaos-like dynamics while in another time series the exponent was close to zero, indicating stable limits. For the last experimental system, the Lyapunov exponent could not be robustly determined. Since the amount of data derived from such empirical systems and the distinguishing between noise and deterministic dynamics is limited, a mathematical model is more promising to provide enough data to analyse the dynamic behaviour. For the mathematical analysis, a simple continuous-time model was developed. This model considered the different phases (G1, S, G2 and M) of the cell cycle as cellular process and aimed in the investigation of qualitative systems dynamics. The analysis revealed that all types of dynamics (damped oscillation, stable limit cycles and chaotic dynamics) can appear by modification of a single parameter. Cellular processes are complex and the cell cycle represents the main process of cell division and thus the increase of abundances of single celled organisms like protists and bacteria. The nonlinear dynamics found in the empirical chemostat systems seems to be driven by cellular nonlinear processes caused by complex cell processes like the cell cycle. It highlights that not only direct interactions between individuals and their environment can cause nonlinear dynamics. Consequently, cell processes can cause nonlinear dynamics and should influence population dynamics and thus the coexistence of species (Huisman and Weissing, 1999). Additional indications for the appearance of nonlinear dynamics caused by differences in growth rates of individual cells could be found (Chapter 2). The growth of single cells could be observed under well controlled conditions after separation via cell sorting (FACS). The observed growth rates which were individually calculated for cell lines originated from a single separated cell ranged from ~1.0 to 1.5 per day and supports the hypothesis that cellular processes influence growth dynamics.

With the studies presented herein it was possible to explain aspects which should contribute to the high biodiversity and the important questions formulated by

Hutchinsons “paradox of plankton” (1961). Different growth dynamics of morphologically similar species (Chapter 2), clonal differences in growth related traits (Appendix A.4.) and intracellular processes (Chapter 3) influence the population dynamics and should allow the coexistence of relatively similar species. Most of those aspects were mainly overlooked in both, empirical as well as theoretical studies. The population growth rate is usually described as a function of environmental factors (e.g. temperature, resource concentration) and assumed to be identical among all individuals within a species. The results of the study point to the great significance to consider not only differences among species to explain their coexistence but also to consider differences within a population of a single species on the clonal and individual level to estimate effects on the population dynamic. According to the chaos theory even small differences in starting conditions can have a huge impact on the pattern of nonlinear dynamics and should therefore favour the coexistence of several species. Other and more obvious mechanisms like predator-prey interactions contribute in addition to the high biodiversity in aquatic ecosystems. Thus, the complexity of foodwebs is the result of diverse interactions among species and within a species population. It is difficult, if not impossible, to disentangle these mechanisms because they influence each other and stretch over several trophic levels. A consequence of this complexity is the difficulty to consider all those important parts at once in a study. This present study showed for the first time that individuality and intrinsic aperiodic dynamics have to be considered for explaining the coexistence of species and genotypes and gives new insights of mechanisms to explain the complexity of biodiversity.

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Subpublications and records of achievement

Publications mentioned in chapters

Chapter 1

Pietsch, T., Nitsche, F., & Arndt, H. **2022**. High molecular diversity in the functional group of small bacterivorous non-scaled chrysomonad flagellates. *European Journal of Protistology*, 125915. https://doi.org/10.1016/j.ejop.2022.125915

Sampling and strain isolation was carried out either by T.P., F.N. or H.A. Some students were involved in this process. T.P. was responsible for culture maintaining and laboratory work. He isolated genetic material and prepared strains for electron microscopy, did the light microscopic investigation and transmission electron microscopy. F.N. supervised the electron microscopic investigation and analysed the preparations with the scanning electron microscope. Data were analysed by T.P supervised by F.N. for phylogenetic analysis and H.A. in general. T.P. wrote the first draft of the manuscript. All authors were responsible for the review and revise of the manuscript.

Chapter 2

Pietsch, T. & Arndt, H. **manuscript.** Overlap and differences in ecological traits of bacterivorous flagellates: Comparison of mixotrophic and heterotrophic chrysomonads.

Publication:

Pietsch, T. & Arndt, H., **2024**. Comparison of mixotrophic and heterotrophic chrysomonads of similar size regarding bacterivory and growth rate. *European Journal of Protistology*, 126109. https://doi.org/10.1016/j.ejop.2024.126109.

All experiments and light microscopic investigations were carried out by T.P.; project was launched and supervised by H.A.; T.P. wrote the first draft of the manuscript. Both authors reviewed and revised the manuscript.

Chapter 3

Werner, J., **Pietsch, T.**, Hilker, F. M., & Arndt, H. **2022**. Intrinsic nonlinear dynamics drive single-species systems. *Proceedings of the National Academy of Sciences*, *119*(44). https://doi.org/10.1073/pnas.2209601119

T.P. developed the chemostat system and the continuous cultivation of species, J.W. contributed the automatic registration. T.P. and J.W. performed research. Both were responsible for the development, construction and maintenance of the chemostat systems. F.M.H. and H.A. designed and supervised the research.

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Appendix

A.1. High molecular diversity in the functional group of small bacterivorous non-scaled chrysomonad flagellates

A.2. Overlap and differences in ecological traits of bacterivorous flagellates: Comparison of mixotrophic and heterotrophic chrysomonads

A.3. Intrinsic nonlinear dynamics drive single-species systems

A.4. Investigation of trait based nonlinear dynamics with individual based models

A.1. High molecular diversity in the functional group of small bacterivorous non-scaled chrysomonad flagellates

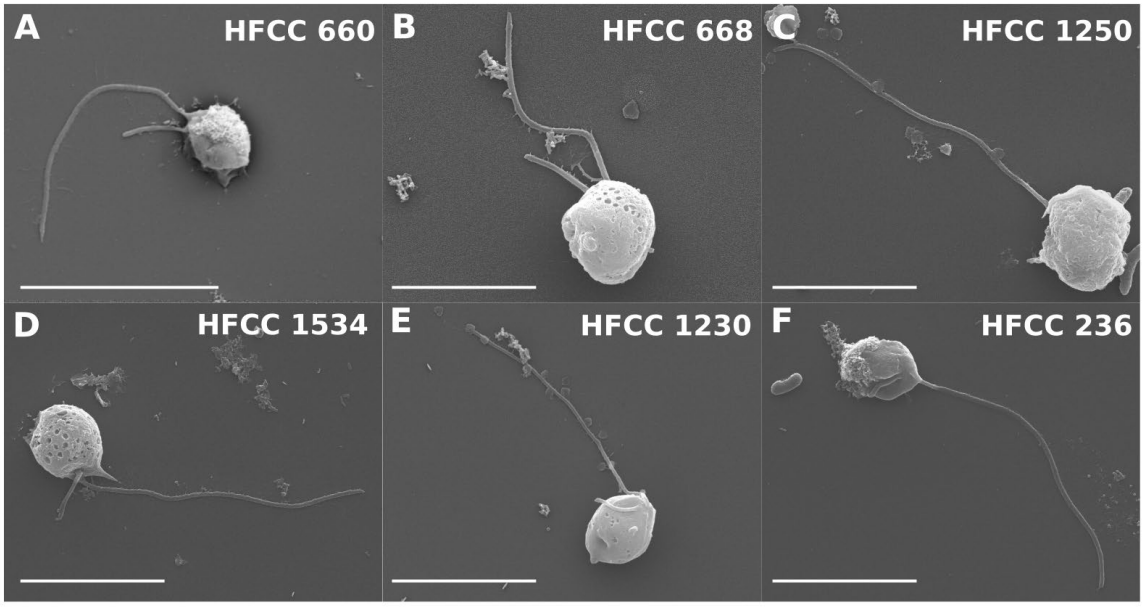

Figure A.1-1. Additional SEM images showing vegetative cells of new described species A. HFCC 660 = *Poteriospumella maldiviensis* sp. nov. B. HFCC 668 = *Poteriospumella vasocystis* comp. nov. C. HFCC 1250 = *Atacamaspumella andiensis* gen. nov. sp. nov. D. HFCC 1534 = *Chlorospumella boenigkii* gen nov. sp. nov. E. HFCC 1230 = *Vivaspumella atacamiensis* gen nov. sp. nov. F. HFCC 236 = *Pseudapoikia anjascherwassiae* gen. nov. sp. nov.

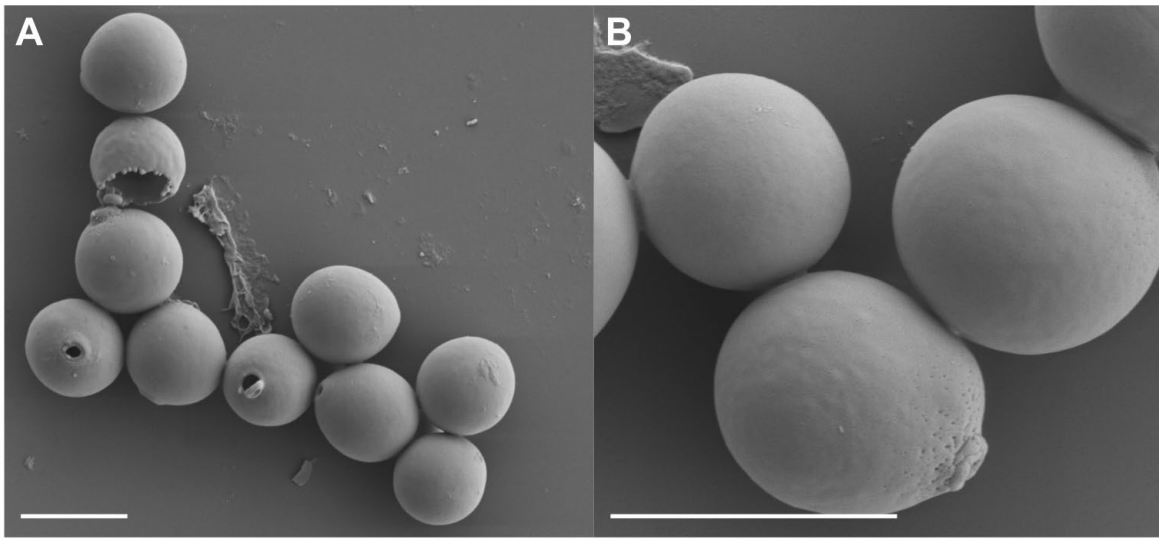

Figure A.1-2. Additional SEM images of stomatocysts from HFCC 668 = *Poteriospumella vasocystsis* comp. nov. Scale = 10 µm.

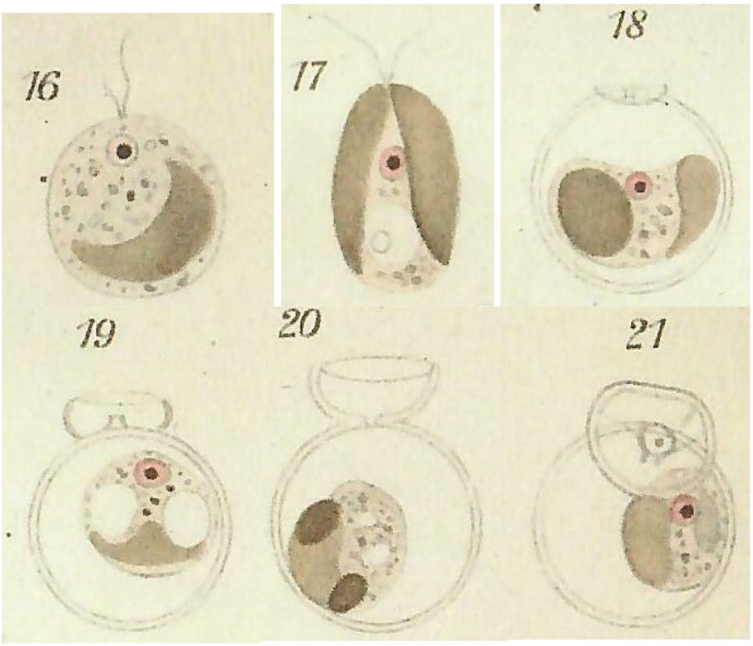

Figure A.1-3. Original drawings of *Ochromonas vasocystis* (described herein as *Poteriospumella vasocystis* comp. nov.). Vegetative cells (16-17) and different developmental stages of stomatocysts (18-21). Taken from Doflein (1923; Plate 17).

A.2. Overlap and differences in ecological traits of bacterivorous flagellates: Comparison of mixotrophic and heterotrophic chrysomonads

See supplementary data of the related publication:

Pietsch, T. & Arndt, H., **2024**. Comparison of mixotrophic and heterotrophic chrysomonads of similar size regarding bacterivory and growth rate. *European Journal of Protistology*, 126109. https://doi.org/10.1016/j.ejop.2024.126109.

A.3. Intrinsic nonlinear dynamics drive single-species systems.

See supplementary data of the related publication:

Werner, J., **Pietsch, T.**, Hilker, F. M., & Arndt, H. **2022**. Intrinsic nonlinear dynamics drive single-species systems. *Proceedings of the National Academy of Sciences*, *119*(44). https://doi.org/10.1073/pnas.2209601119

A.4. Investigation of trait based nonlinear dynamics with individual based models

Most theoretical models in ecology use differential equations to describe population dynamics as change over time. A consequence of this approach is the view at the entire population assuming that all individuals are identical units. However, differences in traits and the individual fate of a single individual can contribute to the population dynamics. Such individual differences can be modelled by individual based models where the entire population is the sum of individuals recognised as single unit.

An individual based approach was chosen to investigate the population dynamics of a single species whose population is structured by different traits. Considering the cell cycle and the required amount of biomass as important cellular processes for the growth rate, clones of a species may differ in such temperature dependent traits. In the individual based model, the resource uptake rate was formulated as function of temperature (Jöhnk et al., 2008) and traits with different optimal temperatures were formulated. The given model is a chemostat system with a given flow rate simulating the death of individuals and the turn over rate of nutrients. Cell division and thus growth depends on the required biomass and time to pass the cell cycle.

A simulation of five different traits at a flow rate of 0.5 d^{-1} and a natural temperature fluctuation (data from the River Rhine, Fig. A.4-1) revealed nonlinear dynamics for both, the whole population as well as for clonal subpopulation with different traits (Fig. A.4-2 and A.4-3). Coexistence of all traits was possible for the first days of the simulation and three traits coexisted until the whole population was extinct. The cause for the extinction of all traits was the strong decrease in temperature which was not appropriate considered for the trait definition. The frequency of traits changed over time depending on the temperature and all of the three coexisting traits dominated the population at a given time.

The model is a conceptual model with rather fictive but realistic parameters. However, it shows that different traits in a population can coexist and influence the population dynamic. Moreover, it shows that rapid environmental changes may influence the population differentially depending on the current trait frequency.

This model was developed by J. Edanackaparampil (formerly Platzen) as part of her bachelor thesis under supervision of T. Pietsch and H. Arndt.

References

Jöhnk, K. D., Huisman, J., Sharples, J., Sommeijer, B., Visser, P. M., & Stroom, J. M. (2008). Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biology*, *14*(3), 495–512. https://doi.org/10.1111/j.1365-2486.2007.01510.x

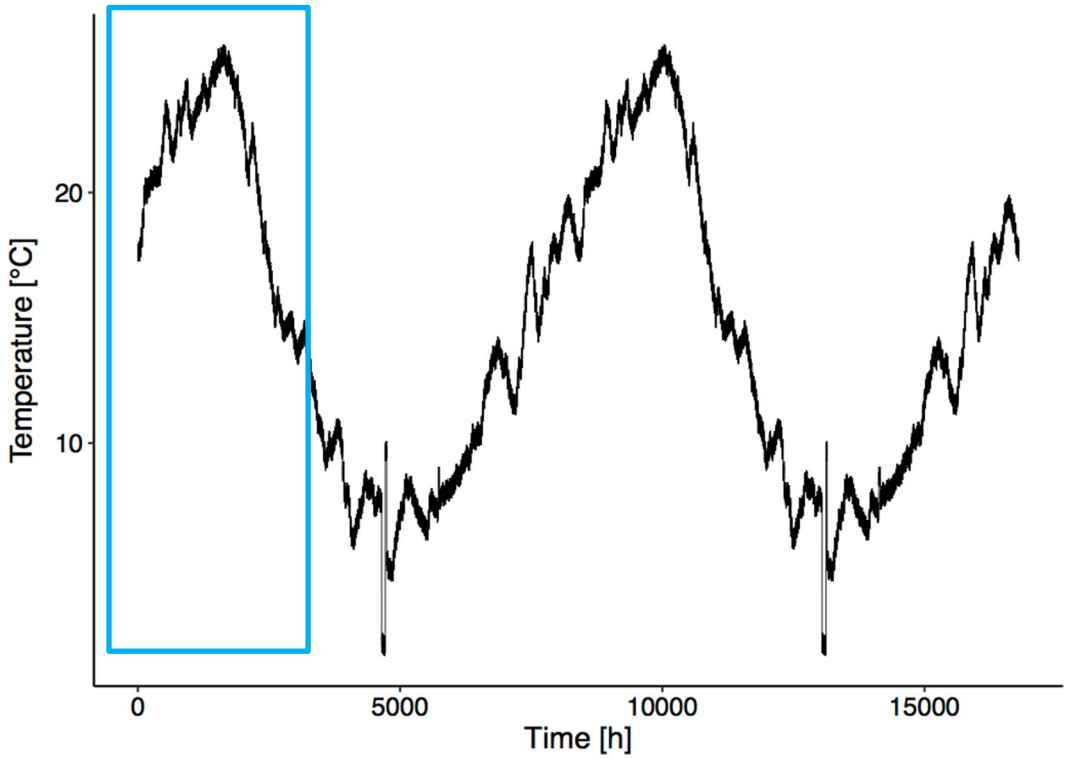

Figure A.4-1. Time series of water temperature of the River Rhine at the measuring site Bad-Honnef for the year 2016 (Source: Landesamt für Natur Umwelt und Verbraucherschutz. NRW; LANUV). Blue rectangular represents the section used for model simulation.

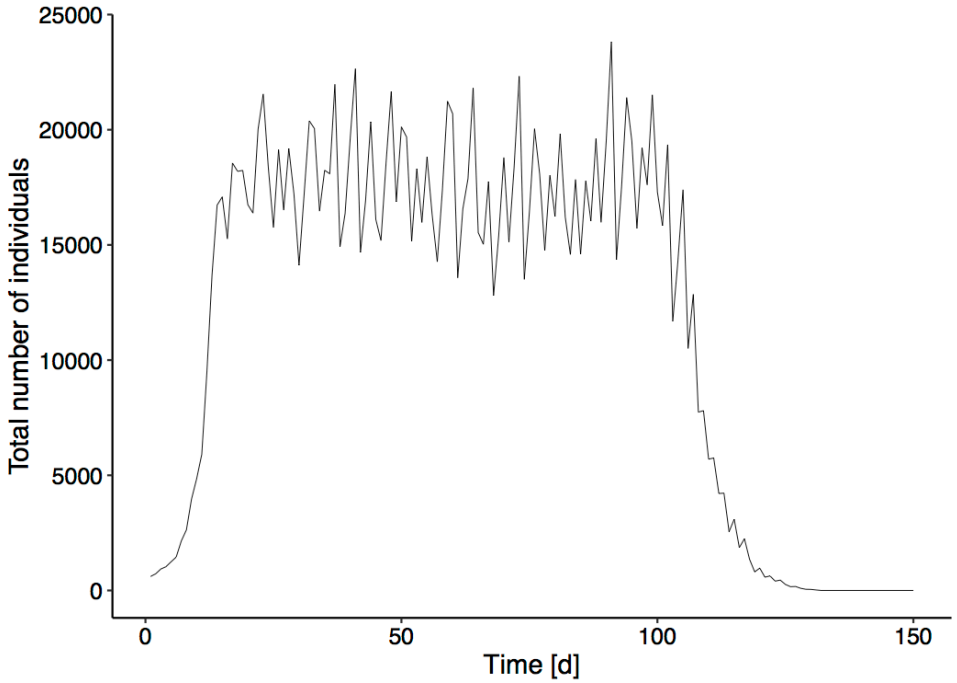

Figure A.4-2. Result of model simulation, depicted is the entire population dynamic over time. The time series of the temperature from the River Rhine (Fig. A.4-1) was set as temperature parameter. Temperature decline caused the extinction of the population after 130 days at a flow rate of 0.5 d^{-1} (compare section Fig. A.4-1).

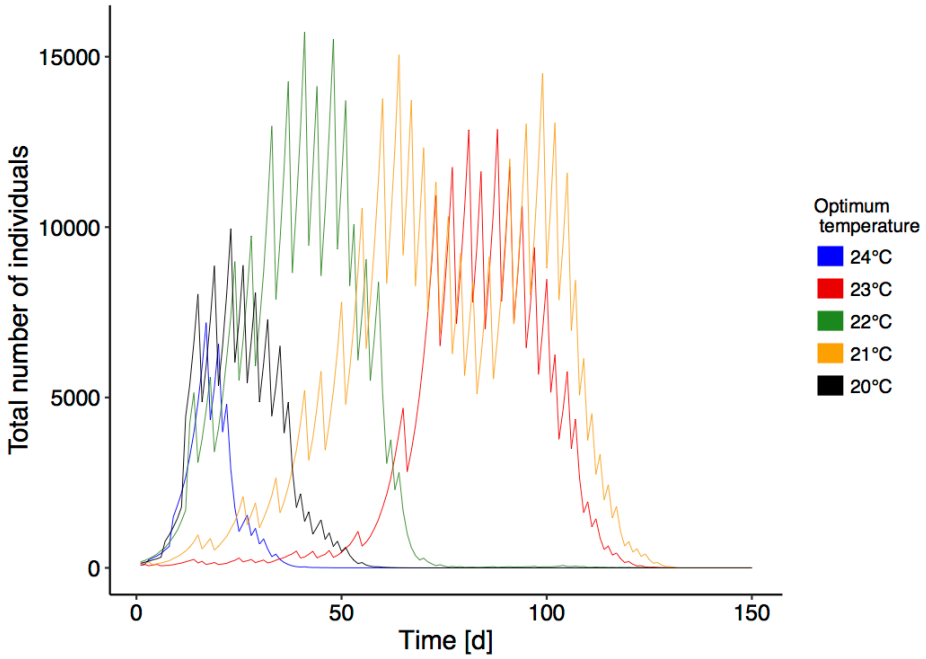

Figure A.4-3. Results of model simulation, depicted are abundances of different temperature traits, corresponding to Fig. A.4-2. Coexistence of three traits (temp.$_{opt}$ 21, 22 and 23°C) was possible until extinction of all traits but abundance was low for temp.$_{opt}$ 22°C (below 100 individuals).

R Code of the individual based model

Parameter settings

```
temperaturdaten=read.csv("TemperaturDaten.csv",sep=";",dec=",")

temperature = temperaturdaten$wert

D = 0.5/24              # Turnover rate per hour calculated from daily turnover rate
cMed = 1500             # Ressource concentration in mg

reqBM = 0.0225          # Required biomass for cell division
reqAge = 7.5            # Required cell age for cell division (cell cycle)
c = 0.2 # Conversion efficiency of carbon into biomass (conversion factor)

day=length(temperaturdaten$wert)/24         # Days of simulation
t=day*24        # Timesteps in hours

N0 = 1000       # Startabundance (individuals)

# Specific abundance of traits
traitlist = c(rep("trait.1",200),
              rep("trait.2",200),
              rep("trait.3",200),
              rep("trait.4",200),
              rep("trait.5",200))

max.uptake=0.003   #nanogramm

# Temperature optimum (max.uptake) of different traits
```

```
t.opt.trait1 = 24      #Trait 1

t.opt.trait2 = 23      #Trait 2

t.opt.trait3 = 22      #Trait 3

t.opt.trait4 = 21      #Trait 4

t.opt.trait5 = 20      #Trait 5


b=5.77           # needed for Joenk equation

R1=1.3           # needed for Joenk equation

R2=1.37          # needed for Joenk equation


## Definition of temperature range


temprange = seq(from=-1, to=40, by=0.01)


**## Definition of Joenk equation**


trait1 = max.uptake*(1+b*((R1^(temprange-t.opt.trait1)-1)-(log(R1)/log(R2))*(R2^(temprange-
t.opt.trait1)-1)))

trait2 = max.uptake*(1+b*((R1^(temprange-t.opt.trait2)-1)-(log(R1)/log(R2))*(R2^(temprange-
t.opt.trait2)-1)))

trait3 = max.uptake*(1+b*((R1^(temprange-t.opt.trait3)-1)-(log(R1)/log(R2))*(R2^(temprange-
t.opt.trait3)-1)))

trait4 = max.uptake*(1+b*((R1^(temprange-t.opt.trait4)-1)-(log(R1)/log(R2))*(R2^(temprange-
t.opt.trait4)-1)))

trait5 = max.uptake*(1+b*((R1^(temprange-t.opt.trait5)-1)-(log(R1)/log(R2))*(R2^(temprange-
t.opt.trait5)-1)))


## Defintion of Plot parameter for Joenk graph


uptakes = c(trait1,trait2,trait3,trait4,trait5)
```

```
traitidentification1 = rep("trait1",length(temprange))
traitidentification2 = rep("trait2",length(temprange))
traitidentification3 = rep("trait3",length(temprange))
traitidentification4 = rep("trait4",length(temprange))
traitidentification5 = rep("trait5",length(temprange))

traitidentification = c(traitidentification1,
                        traitidentification2,
                        traitidentification3,
                        traitidentification4,
                        traitidentification5)

xachse = rep(temprange,5)  #Temperaturange für x-Achse Plot für jeden Trait

plot = data.frame(xachse,traitidentification,uptakes)


legende=c(as.character(t.opt.trait5),
          as.character(t.opt.trait4),
          as.character(t.opt.trait3),
          as.character(t.opt.trait2),
          as.character(t.opt.trait1))  #Legende für Plot: Trait1-5

mycolour=c("blue","red2","forestgreen","orange","black") #Colour coding for Plot: Trait1-5

## Code for Plot

joehnk.xlab = expression(paste("Temperature [°C]"))
joehnk.ylab = expression(paste("Maximum uptake rate",italic(" max")))
```

```
joehnk.neu <- ggplot(plot,aes(x=xachse,y=uptakes,col=traitidentification))

joehnk.neu <- joehnk.neu + ylim(0,0.0032)

joehnk.neu <- joehnk.neu + coord_cartesian(xlim = c(0, 30))

joehnk.neu <- joehnk.neu + theme_classic()

joehnk.neu <- joehnk.neu + theme(panel.grid.major = element_blank(), panel.grid.minor =
element_blank())

joehnk.neu <- joehnk.neu + scale_colour_manual(values=mycolour,

                                  labels=legende,name="Optimum \ntemperature")

joehnk.neu <- joehnk.neu + theme(axis.title.y=element_text(size=14,face="bold"),

                        axis.title.x=element_text(size=14,face="bold"),

                        axis.text.y=element_text(size=12,color="black"),

                        axis.text.x=element_text(size=12,color="black"))

joehnk.neu <- joehnk.neu + labs(x=joehnk.xlab,y=joehnk.ylab)

joehnk.neu <- joehnk.neu + guides(colour = guide_legend(override.aes = list(size=3)))

joehnk.neu <- joehnk.neu + theme(legend.title = element_text(colour="black", size=10))

joehnk.neu <- joehnk.neu + theme(aspect.ratio=3/5)

joehnk.neu <- joehnk.neu + theme(aspect.ratio=3/5)

joehnk.neu <- joehnk.neu + geom_line(size=0.2)

joehnk.neu
```

Model Simulation

```
set.seed(1)
ind = vector( mode = "list", N0)
for (i in seq(ind)){
  ind[[i]]$alive = 1
  ind[[i]]$age = sample(c(0,1,2,3,4,5),1,replace=FALSE)
  ind[[i]]$biomass = 0.01
  ind[[i]]$trait = traitlist[i]
  ind[[i]]$colour = c("red"[which(ind[[i]]$trait=="trait.1")],
                      "yellow"[which(ind[[i]]$trait=="trait.2")],
                      "green"[which(ind[[i]]$trait=="trait.3")],
                      "black"[which(ind[[i]]$trait=="trait.4")],
                      "blue"[which(ind[[i]]$trait=="trait.5")])
}



time = seq(t+1)

pop <- NaN * time # population size
pop[1] = N0

frac.blue <- NaN * time # fraction of population that is blue
cols <- sapply(ind, function(x) x$colour)
frac.blue[1] <- sum(cols  == "blue")

frac.red <- NaN * time # fraction of population that is blue
cols <- sapply(ind, function(x) x$colour)
frac.red[1] <- sum(cols  == "red")
```

```
frac.green <- NaN * time # fraction of population that is blue
cols <- sapply(ind, function(x) x$colour)
frac.green[1] <- sum(cols  == "green")

frac.yellow <- NaN * time # fraction of population that is blue
cols <- sapply(ind, function(x) x$colour)
frac.yellow[1] <- sum(cols  == "yellow")

frac.black <- NaN * time # fraction of population that is blue
cols <- sapply(ind, function(x) x$colour)
frac.black[1] <- sum(cols  == "black")

med.resource.concentration <- NaN*time
med.resource.concentration[1] <- cMed

uptake <- NaN*time
uptaketemp <- NaN*time

#################### Simulation ########################
t1 <- Sys.time()

for(i in seq(t)){ # loop for each time increment

  is.alive <- which(sapply(ind, function(x) x$alive) == 1)

  current.resource.concentration = med.resource.concentration[i]

  temp.uptake = numeric(0)
```

```
  max24 = max.uptake*(1+b*((R1^(temperature[i]-t.opt.trait5)-1)-
(log(R1)/log(R2))*(R2^(temperature[i]-t.opt.trait5)-1)))

  max23 = max.uptake*(1+b*((R1^(temperature[i]-t.opt.trait4)-1)-
(log(R1)/log(R2))*(R2^(temperature[i]-t.opt.trait4)-1)))

  max22 = max.uptake*(1+b*((R1^(temperature[i]-t.opt.trait3)-1)-
(log(R1)/log(R2))*(R2^(temperature[i]-t.opt.trait3)-1)))

  max21 = max.uptake*(1+b*((R1^(temperature[i]-t.opt.trait2)-1)-
(log(R1)/log(R2))*(R2^(temperature[i]-t.opt.trait2)-1)))

  max20 = max.uptake*(1+b*((R1^(temperature[i]-t.opt.trait1)-1)-
(log(R1)/log(R2))*(R2^(temperature[i]-t.opt.trait1)-1)))


  ind.uptake <- vector( mode="list", pop[i])

  for (l in seq(ind.uptake)){

    ind.uptake[[l]]$induptake = c(rep(NaN, length(seq(t))))

  }


  for (j in is.alive){

    if (ind[[j]]$trait=="trait.1"){


ind.uptake[[j]]$induptake[[i]]=(max24*current.resource.concentration)/(max24/2+current.reso
urce.concentration)

    }else if (ind[[j]]$trait=="trait.2"){


ind.uptake[[j]]$induptake[[i]]=(max23*current.resource.concentration)/(max23/2+current.reso
urce.concentration)

    }else if (ind[[j]]$trait=="trait.3"){


ind.uptake[[j]]$induptake[[i]]=(max22*current.resource.concentration)/(max22/2+current.reso
urce.concentration)

    }else if (ind[[j]]$trait=="trait.4"){


ind.uptake[[j]]$induptake[[i]]=(max21*current.resource.concentration)/(max21/2+current.reso
urce.concentration)
```

```
    }else if (ind[[j]]$trait=="trait.5"){

ind.uptake[[j]]$induptake[[i]]=(max20*current.resource.concentration)/(max20/2+current.reso
urce.concentration)

    }


    if (ind.uptake[[j]]$induptake[[i]] <= 0){

      ind.uptake[[j]]$induptake[[i]] = 0

    }


    temp.uptake=c(temp.uptake,ind.uptake[[j]]$induptake[[i]])

  }




  uptaketemp[i] = sum(temp.uptake)


  for (j in is.alive){

    if (uptaketemp[i]>=current.resource.concentration){

      ind.uptake[[j]]$induptake[[i]] =
ind.uptake[[j]]$induptake[[i]]/uptaketemp[i]*current.resource.concentration

      uptake[i] = current.resource.concentration


    }else{

      uptake[i] = sum(temp.uptake)

    }

  }



  med.resource.concentration[i+1] = current.resource.concentration+(D*(cMed-

                                                    current.resource.concentration)-
```

```
                                                    uptake[i])


  for(j in is.alive){


    if( ind[[j]]$biomass>=reqBM && ind[[j]]$age>=reqAge){birth=TRUE # calculate a birth
probability for each individual that is alive

    }else{birth=FALSE}

    if(birth){

      len.ind <- length(ind)

      ind[[len.ind+1]] <- list(alive=1, age=0, biomass=ind[[j]]$biomass/2, trait=ind[[j]]$trait,

                               colour=ind[[j]]$colour) # create offspring, inherits half biomass of parent

      ind[[j]]$biomass=ind[[j]]$biomass/2

      ind[[j]]$age=0

    } else if (ind[[j]]$age<=reqAge && ind[[j]]$biomass<=reqBM) { #else, advance age + 1

      ind[[j]]$age = ind[[j]]$age + 1

      ind[[j]]$biomass=ind[[j]]$biomass + ind.uptake[[j]]$induptake[[i]]*c# advance age +
biomass of parent

    }else if (ind[[j]]$age>=reqAge && ind[[j]]$biomass<=reqBM) { #else, advance age + 1

      ind[[j]]$age = ind[[j]]$age + 1

      ind[[j]]$biomass=ind[[j]]$biomass + ind.uptake[[j]]$induptake[[i]]*c# advance age +
biomass of parent

    }else{

      ind[[j]]$age = ind[[j]]$age + 1

    }

  }


  death <- pop[i]*D

  # death <- round(pop[i]/(1+D))   #######das macht nur eine gerade Linie

  ind=sample(ind, length(ind)-death)
```

```
  is.alive <- which(sapply(ind, function(x) x$alive) == 1)
  pop[i+1] <- length(is.alive)

  cols <- sapply(ind, function(x) x$colour)
  frac.blue[i+1] <- sum(cols[is.alive]  == "blue")
  cols <- sapply(ind, function(x) x$colour)
  frac.red[i+1] <- sum(cols[is.alive]  == "red")
  cols <- sapply(ind, function(x) x$colour)
  frac.green[i+1] <- sum(cols[is.alive]  == "green")
  cols <- sapply(ind, function(x) x$colour)
  frac.yellow[i+1] <- sum(cols[is.alive]  == "yellow")
  cols <- sapply(ind, function(x) x$colour)
  frac.black[i+1] <- sum(cols[is.alive]  == "black")


}


t2 <- Sys.time()
dt <- t2-t1
dt
```

Eidesstattliche Erklärung gemäß §7 Abs. 8

„Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation selbstständig und ohne die Benutzung anderer als der angegebenen Hilfsmittel und Literatur angefertigt habe. Alle Stellen, die wörtlich oder sinngemäß aus veröffentlichten und nicht veröffentlichten Werken dem Wortlaut oder dem Sinn nach entnommen wurden, sind als solche kenntlich gemacht. Ich versichere an Eides statt, dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie - abgesehen von unten angegebenen Teilpublikationen und eingebundenen Artikeln und Manuskripten - noch nicht veröffentlicht worden ist sowie, dass ich eine Veröffentlichung der Dissertation vor Abschluss der Promotion nicht ohne Genehmigung des Promotionsausschusses vornehmen werde. Die Bestimmungen dieser Ordnung sind mir bekannt. Darüber hinaus erkläre ich hiermit, dass ich die Ordnung zur Sicherung guter wissenschaftlicher Praxis und zum Umgang mit wissenschaftlichem Fehlverhalten der Universität zu Köln gelesen und sie bei der Durchführung der Dissertation zugrundeliegenden Arbeiten und der schriftlich verfassten Dissertation beachtet habe und verpflichte mich hiermit, die dort genannten Vorgaben bei allen wissenschaftlichen Tätigkeiten zu beachten und umzusetzen. Ich versichere, dass die eingereichte elektronische Fassung der eingereichten Druckfassung vollständig entspricht."

Teilpublikationen:

Pietsch, T., Nitsche, F., & Arndt, H. **2022**. High molecular diversity in the functional group of small bacterivorous non-scaled chrysomonad flagellates. *European Journal of Protistology*, 125915. https://doi.org/10.1016/j.ejop.2022.125915

Werner, J., **Pietsch, T.**, Hilker, F. M., & Arndt, H. **2022**. Intrinsic nonlinear dynamics drive single-species systems. *Proceedings of the National Academy of Sciences*, *119*(44). https://doi.org/10.1073/pnas.2209601119

Zum Zeitpunkt der eingereichten Dissertation als Manuskript eingebundene Publikation:

Pietsch, T. & Arndt, H., **2024**. Comparison of mixotrophic and heterotrophic chrysomonads of similar size regarding bacterivory and growth rate. *European Journal of Protistology*, 126109. https://doi.org/10.1016/j.ejop.2024.126109.

20.03.2023, Pietsch Tobias