Optimality and trait based approaches to sympatric speciation and sympatric co-evolution of predator and prey traits in marine plankton

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Summary

Marine microorganisms are responsible for roughly half of the Earth's primary production, circa half of the carbon dioxide sink and oxygen production on Earth. Marine plankton organisms are an important part of global biogeochemical models, which simulate the effects of current global change, e.g., increased CO_2 levels, increased temperature, or increased eutrophication on ecosystem functioning and community dynamics. However, such models rarely account for the adaptation of marine microorganisms, which are able to evolve rapidly. While some global models deal with the extinction of species and loss of biodiversity, they do not account for speciation. Due to a highly unstructured marine environment with no clear boundaries, understanding sympatric speciation, which is the speciation without geographic isolation, in plankton is particularly important. However, sympatric speciation in terrestrial systems has gained much more attention while in marine systems it was largely ignored. The most famous example of sympatric speciation are Darwin's finches, which diversified by specialisation on different resources. But despite the large number of existing speciation models, a concrete mechanism which allows for sympatric speciation via specialisation, as suggested by Darwin, has been difficult to pin down.

Therefore, in the first part of the thesis we propose a concrete mechanism of sympatric speciation via specialisation and resource partitioning allowing predators to reduce competition and create new ecological niches. The key to this mechanism are the reduced costs in the specialisation trade-off, whereby the improved ability to eat the preferred prey (gain) over-compensates the reduced ability to eat the less-preferred prey (cost). Such "plus-zero sum game" increases the grazing pressure on prey, which in turn may respond by changing traits, e.g., the specific growth rate, in order to escape the grazing pressure.

Building on this mechanism, in the second part of the thesis we explore sympatric speciation in the face of simultaneous co-evolution of a prey trait (growth rate) and a predator trait (specialisation) in a simple predator-prey interaction model. We find that the space defined by all combinations of predator and prey traits can be divided into three regions: (1) the speciation space, where the combinations of traits allow speciation leading to the establishment of two sympatric predator species; (2) the vanishing speciation space, i.e. the range of combinations allowing only ephemeral speciation and (3) the displacement space, where the resident predator is displaced by a single mutant. We also introduce and discuss some further novel concepts, e.g., evolutionary time landscape, speciation threshold and prey-equality space. We conclude that prey species can adjust traits as a response to increased predation. This raises the question of how both trophic levels would adapt to changing environmental conditions.

While some studies investigated the evolutionary response of marine plankton to increased temperature, CO_2 and acidification, changes in the marine biodiversity as a consequence of increased nutrient concentration (i.e. eutrophication) has not been intensively studied yet. Moreover, the density-independent mortality (DIM) in the ocean was largely ignored and not treated separately from the grazing mortality. Hence, in the third part of the thesis we examine the occurrence of sympatric speciation and the dynamics of a marine plankton community as a function of three changing quantities: environmental nutrient load, DIM of phytoplankton, and adaptive specialisation of zooplankton. Particularly we study the coevolution of plankton and the resource use efficiency in a four-species predator-prey interaction model at different environmental nutrient concentrations and density-independent mortalities of the prey. The results imply that increasing nutrient concentration in our model: (1) promotes biodiversity, (2) decreases the effect of DIM of phytoplankton on biodiversity, (3) changes domination from prey species to predators, and (4) decreases overall system productivity.

This thesis emphasises the importance of traits and trade-offs for understanding the adaptive behavior of marine plankton. Fast evolutionary changes and density-independent crashes of populations in marine plankton necessitate the consideration and better representation of evolutionary processes in global biogeochemical models in order to better project the impacts of climate change on marine ecosystems. Sympatric speciation deserves particular attention due to the absence of clear geographic barriers in the marine environment.

Zusammenfassung

Die marinen Mikroorganismen sind für etwa die Hälfte der Primärproduktion, circa die Hälfte der Kohlendioxid-Aufnahme und beinahe fünfzig Prozent der Sauerstoff-Produktion auf der Erde verantwortlich. Sie sind ein wichtiger Teil der globalen biogeochemischen Modellen, welche die Auswirkungen des aktuellen globalen Wandels, wie erhöhte Temperatur, erhöhter CO2-Gehalt oder Eutrophierung, auf die Ökosystemfunktionen und auf die Dynamik der marinen Gemeinschaften studieren. Jedoch berücksichtigen solche Modelle nur selten die Anpassung der marinen Mikroorganismen, die zu schnellen evolutionären Veränderungen fähig sind. Während einige globale Modelle sich mit dem Aussterben und dem Verlust der biologischen Vielfalt befassen, beschäftigen sich wenige mit der Entstehung von Arten. Da es im Meer keine klaren geographischen Grenzen gibt, gewinnt das Verständnis der sympatrischen Artbildung, die Artbildung ohne geographische Isolierung, beim Plankton besonders an Bedeutung. Sympatrische Artbildung in terrestrischen Systemen erlangte viel Aufmerksamkeit, wurde dagegen in marinen Systemen weitgehend ignoriert. Das berühmteste Beispiel für sympatrische Artbildung sind die Darwin-Finken, die durch die Spezialisierung auf verschiedene Ressourcen diversifizierten. Aber trotz der großen Anzahl der vorhandenen Modelle der Artbildung war ein konkreter Mechanismus der sympatrischen Artbildung durch Spezialisierung, wie er von Darwin gefordert wurde, bisher nicht bekannt.

Deshalb schlagen wir im ersten Teil dieser Arbeit einen konkreten Mechanismus der sympatrischen Artbildung über die Spezialisierung und Ressourcenpartitionierung vor. Dieser Mechanismus verringert die Konkurrenz zwischen den Prädatoren und ermöglicht die Entstehung von neuen ökologischen Nischen. Der Schlüssel zu diesem Mechanismus sind die reduzierten Kosten in dem Spezialisierungs-Trade-off, wobei die verbesserte Fähigkeit die bevorzugte Beute zu fressen (Gewinne) die reduzierte Fähigkeit die weniger bevorzugte Beute zu fressen (Kosten) überschreitet. So ein "Plus-Null-Summen-Spiel" erhöht den Fraßdruck auf die Beute, die dann durch die Änderung ihrer Eigenschaften, z.B. der spezifischen Wachstumsrate, darauf reagieren kann um den Fraßdruck zu verringern.

Darauf aufbauend untersuchen wir im zweiten Teil der Arbeit die sympatrische Artbildung im Angesicht der gleichzeitigen Koevolution der Beuteeigenschaft (Wachstumsrate) und der Räubereigenschaft (Spezialisierung) in einem einfachen Räuber-Beute-Interaktionsmodell. Wir finden, dass der von allen Kombinationen der Räuber-Beute-Eigenschaften definierte Raum in drei Bereiche unterteilt werden kann: (1) der Artbildungsraum, in dem die Kombinationen von Eigenschaften zu der Artbildung von zwei sympatrischen Herbivoren führen;

(2) der Raum der verschwindenden Artbildung, wo die Räuber-Beute-Kombinationen nur eine vorübergehende Artbildung erlauben und (3) der Verdrängungsraum, in dem der Resident-Prädator von einem mutierten Prädator verdrängt wird. Außerdem führen wir einige weitere Konzepte ein und definieren sie, z.B. evolutionäre Zeitlandschaft, Artbildungsschwelle und Beute-Gleichstellungsraum. Unser Fazit besagt, dass die Beutetiere ihre Eigenschaften als Reaktion auf den gestiegenen Räuberdruck anpassen können. Dies wirft die Frage auf, wie sich beide trophische Ebenen auf die verändernde Umweltbedingungen anpassen würden.

Während einige Studien die evolutionäre Reaktion des Meeresplanktons zu den erhöhten Temperaturen, CO2-Gehalt und Ozean Versauerung untersuchten, wurde die Auswirkung von erhöhten Nährstoffkonzentrationen (Eutrophierung) auf die Veränderungen der biologischen Vielfalt der Meere noch nicht intensiv untersucht. Darüber hinaus wird die dichte-unabhängige Mortalität (DUM) in dem Ozean weitgehend ignoriert und von der Grazing-Sterblichkeit in den Modellen nicht getrennt behandelt. Daher untersuchen wir in dem dritten Teil dieser Arbeit das Vorkommen der sympatrischen Artbildung und die Dynamik der marinen Planktongemeinschaft als Funktion der drei Größen: Nährstoffkonzentration, DUM von Phytoplankton und adaptive Spezialisierung von Zooplankton. Insbesondere untersuchen wir die Koevolution von Plankton und die Effizienz der Ressourcennutzung in einem Vier-Spezies-Räuber-Beute-Interaktionsmodell bei verschiedenen Nährstoffkonzentrationen und dichte-unabhängigen Mortalitäten der Beute. Die Ergebnisse deuten darauf hin, dass der Nährstoff-Anstieg in unserem Modell: (1) die biologische Vielfalt fördert, (2) die Wirkung von DUM auf die biologische Vielfalt verringert, (3) von einer Dominanz von Beutetieren zu einer Dominanz von Prädatoren ändert, und (4) die Produktivität des Gesamtsystems verringert.

Diese Arbeit betont die Bedeutung von Eigenschaften und eigenschaften-assoziierten Trade-offs für das Verständnis des adaptiven Verhaltens vom Meeresplankton. Schnelle evolutionäre Veränderungen und dichte-unabhängiges Massensterben im Meeresplankton erfordern die Berücksichtigung und bessere Darstellung der evolutionären Prozessen, z.B. Artbildung, in den globalen biogeochemischen Modellen, um die Auswirkungen des Klimawandels auf die Meeresökosysteme besser projizieren zu können. Sympatrische Artbildung verdient dabei besondere Aufmerksamkeit, weil der mariner Lebensraum keine klaren geographischen Grenzen aufweist.

1 Introduction

1.1 Motivation and aims

Motivation

A global climate change is an incontestable fact. Evolution is one way in which organisms may respond to this change via continuous adaptation. Microorganisms on land and in the ocean play a special role in response to global change because they are able to fast evolutionary adaptation to a changing environment[162,217]. Nutrient cycles in the ocean are primarily controlled by the microorganisms because they constitute more than 90 per cent of the living biomass in the sea[239]. Moreover, marine plankton is responsible for approximately half of the CO_2 sink[149] and half of the global primary production[14,67,108]. Therefore, it is crucial to understand evolutionary processes, such as speciation or extinction, occurring under global change. The nutrient cycles can be simulated in global biogeochemical models. However, despite the presence of marine planktonic organisms in these models, organisms are often represented in a pretty static way, without considering evolutionary processes. While some research has been conducted on global biodiversity loss[209], e.g. extinction, no studies account for the global biodiversity gain, e.g. speciation. And this despite the large number of existing speciation models[120,249]. The problem lies in the complexity of the evolutionary models which, being incorporated into a global model (also not an easy task), would dramatically increase the simulation time. Two approaches developed in the last decades, optimality-based[12,229] and trait-based[159,161,172], aim to decrease the complexity but in the same time increase the predictive power of the evolutionary models by applying trade-offs. Such simple yet realistic models can be built into the global models to enhance the predictive power. For instance, one of the stumbling blocks of global biogeochemical models is the over-simplified representation of zooplankton grazing. Such over-simplification may render conclusions made about the phytoplankton questionable. However, this over-simplification may be overcome by application of physiological or behavioural trade-offs in the zooplankton grazing function. These trade-offs would most likely alter the phytoplankton response to grazing, which in turn can also be examined using sensitivity analyses of the phytoplankton traits, such as specific growth rate or specific mortality.

Current global change already motivated research of evolutionary responses of marine plankton to the increased temperature[108,243], CO_2 and acidification[162]. However, changes in marine biodiversity as a consequence of increased nutrient concentration (e.g., eutrophication from fertilizers) has not been intensively studied yet. Some studies report that eutrophication may have a positive effect on the phytoplankton biomass, but decrease the biodiversity[144]. In contrast, high-nutrient ecosystems, e.g. coral reefs or coastal areas, often have high biodiversity. Thus, further investigations of mutual covariance of nutrients (e.g. nitrogen) and biodiversity are needed to fill this research gap. Moreover, it is important because ca. 40% of the world's current dietary protein comes from the synthetic fertilizers, which are keeping two billion people alive[79]. Furthermore, the antropogenic nitrogen deposition is prognosed to increase in the future[78,79,266]. Hence, changes in species composition and biodiversity in marine ecosystems are inevitable.

These changes propose another opportunity to improve current models, namely to treat the specific phytoplankton mortality as the density-independent mortality (DIM) and analyse it separately from the grazing, which is density-dependent. While grazing has a long tradition in planktonic models, DIM remains not adequately addressed. In contrast to conventional specific mortality which is usually a static parameter in models, population crashes in nature and in the laboratory indicate that DIM can be caused by multiple factors, e.g., environmental stressors (food and nutrient deprivation, pollutants, oxidative stress, intense light, darkness, seasonal cycles, catastrophes)[58], natural cell death (ageing, starvation) or PCD (altruistic response to infection in order to stop the spread, apoptosis, paraptosis)[72], and therefore can vary substantially. Understanding the effects of DIM on the plankton community is important because DIM can be responsible for more than 50 per cent of the marine microorganism's mortality[25,130] which was immensely underestimated in the past. Therefore, there is a need to conduct sensitivity analyses of the effects of different DIM on the plankton community, especially in the presence of adaptive (specialising in our case) predator.

Aims

First, this thesis aims to combine the optimality-based and trait-based approaches by defining a trade-off associated with a specific trait in zooplankton. This trade-off will then be incorporated in the zooplankton grazing definition. Specifically, we intend to mimic the adaptive specialisation of Darwin's finches which might allow speciation in sympatrically coexisting zooplankton populations. Secondly, we will investigate the response of phytoplankton to the adaptive (specialising) zooplankton grazing by allowing the evolution of phytoplankton traits, i.e. specific growth rate. Such co-evolution of predator and prey traits suggests that some combinations of traits will allow for sympatric speciation, while others will not. Will the planktonic community reorganise its structure faced with environmental change is another question we address in this part of the thesis. Finally, we aim to examine the simultaneous effects of three changing quantities (specialisation in zooplankton, density-independent mortality (DIM) in phytoplankton and different environmental nutrient concentrations) on the occurrence of sympatric speciation or extinction in zooplankton and the productivity of the system in general.

1.2 Evolution and speciation

Evolution

All life on Earth originated from a single ancestor approximately 3.8 billion years ago due to micro- and macroevolutionary processes. Microevolution (short term) can be adaptive, via natural selection, and neutral (random), via genetic drift, while macroevolution (long term) is driven by speciation and extinction[236]. The bridge between micro- and macroevolution occurs if some adaptations in organisms lead to speciation. Such bridge can be represented by adaptive dynamics or trait-based models, where evolution of traits via adaptive (natural selection) and non-adaptive (mutations, genetic drift) causes may split one population into two subpopulations.

Speciation

Speciation is defined as the establishment of new biological species. Specifically, the "biological species concept" defines speciation as the evolution of reproductive isolation between arising taxa, which means that gene flow between these taxa has stopped[249]. Reproductive isolation can occur before fertilization (prezygotic isolation) or after fertilization (postzygotic isolation), whereby the postzygotic isolation can be extrinsic (based on the environmental problems) or intrinsic (based on the developmental problems and independent of the environment)[249]. The complex nature of speciation and a very long time needed for speciation experiments greatly complicate evolutionary investigations[80,249]. Moreover, speciation depends on different genetical, ecological, environmental and other factors simultaneously in nonlinear ways[80]. Some researchers assume that understanding speciation will be enhanced by acquiring new empirical data rather than by creating new mathematical models[249]. Others assume that mathematical theory, especially analytical, instead of numerical, must play an important role in speciation research[80]. Nevertheless, both agree that theoretical studies can train our intuition, provide new insights into mechanisms of speciation, classify verbal theories of speciation and produce results beyond experimental investigations and verbal generalizations[80,249]. Following the most traditional geographic classification of speciation there are three main speciation modes: allopartic, parapatric and sympatric.

Allopatric speciation is the most common mode of speciation[168,170] and means that one population splits into two geographically isolated subpopulations. These subpopulations then experience different selective pressures, independent genetic drift and are exposed to different mutations[107]. Geographic isolation can originate through plate tectonics, formation of mountains, islands, big rivers or by accidental relocation of species creating separation by distance. In this way, Darwin's finches[92] on Galapagos Islands were separated from the original South American finches by a large ocean area and became different species.

Parapatric speciation occurs due to the isolation by distance[249], whereby two adjacent populations with slightly overlapping niches preserve some gene flow between them[226]. For example, a population of grass species living in a big forest can experience different kinds of soil, overshadowing trees and light conditions in different parts of the forest, so that individuals can develop different flowering times. Or, in the case of Darwin's finches, environmentally adjacent populations on high galapagos islands, Isabela, Santiago and Santa Cruz, could have experienced a strong divergent selection due to altitudinal gradients[93].

Sympatric speciation, which is believed to be less common and harder to demonstrate than allopatric speciation[43,215,249] is the main issue of the current thesis and therefore deserves a separate introductory chapter (see below).

1.3 Sympatric Speciation

Sympatric speciation is defined as speciation without geographic isolation[32,45,261]. Interestingly, there are two groups of different definitions of sympatric speciation: biogeographical and population-genetical[70]. The biogeographical (or ecological) definitions suggest the absence of spatial segregation and spatial divergence[61], where reproductive isolation evolves within the average dispersal distance of a single individual[43], resulting in the elimination of gene flow between two species[124]. The ecological explanation for sympatric speciation is based on the existence of discrete niches and trade-offs that create disruptive selection, whereby fitness of the intermediates (being between niches) becomes lower than fitness of the arising taxa[249]. The population genetics suggests that the evolution of reproductive isolation happens within panmictic (randomly mating)[76,80,241] interbreeding[77] populations

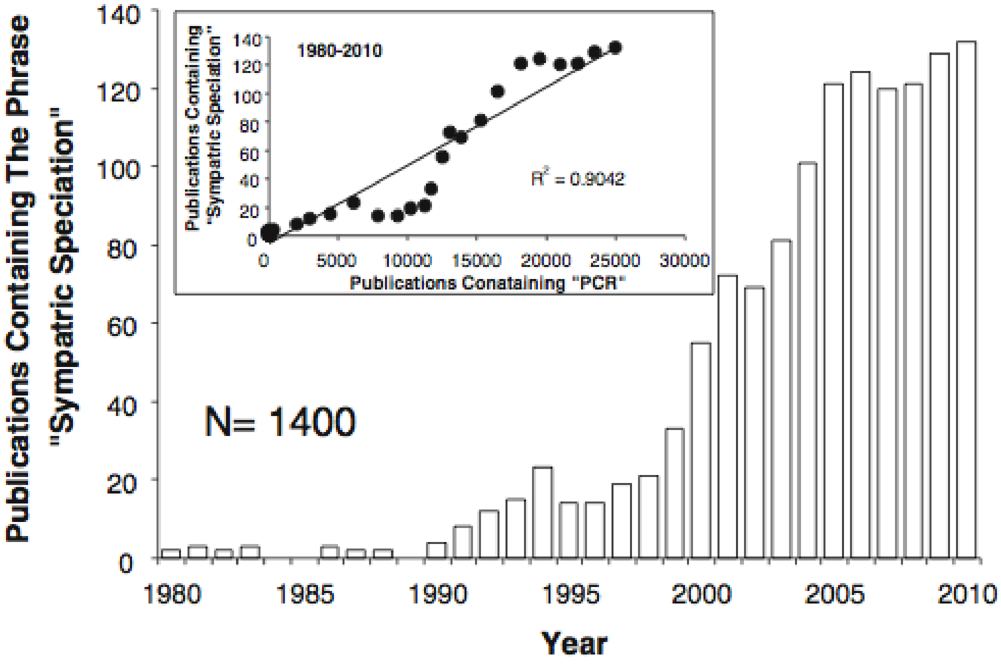

Figure 1. Publication record using the term sympatric speciation between 1980 and 2010. Source: Bird et al. (2012) published in Evolutionary Biology[27]

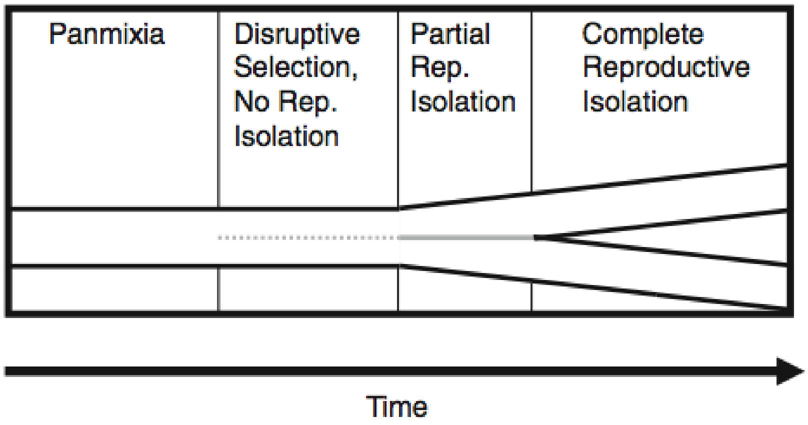

Figure 2. Conceptual diagram of sympatric speciation. The dashed grey line indicates reduced gene flow, the solid grey line shows greatly reduced gene flow between arising taxa and the splitter solid black line indicates stopping gene flow. Source: Bird et al. (2012) published in Evolutionary Biology[27]

despite high initial gene flow[76,120].

The bifurcation process in sympatry occurs via the evolution of reproductive isolation[249]. Such isolation may be caused by selection against intermediate members of a population - disruptive selection[32]. Treating the reproductive isolation as a main feature of sympatric speciation, Bird (2012) broke down the general mechanism of sympatric speciation (Fig. 2) into four stages. Particularly, he separated: (1) panmixia - random mating, (2) disruptive selection, (3) partial reproductive isolation and, finally (4) complete reproductive isolation. Therefore, reproductive isolation is promoted by reducing gene flow and inhibited by increasing gene flow. However, Barton (2010) notes that weak gene flow between arising taxa may facilitate speciation[18].

Sympatric speciation remains one of the most debated and intriguing concepts in evolutionary biology[27,32,261] which has been criticized since the very beginning[66,170]. It was claimed to have little conclusive evidence in order to account for it as an evolutionary process[77]. However, the interest to sympatric speciation has increased in the last decades[27] (Fig. 1) and at present, there is enough empirical and theoretical evidence of sympatric speciation[261], showing that sympatric speciation is a plausible evolutionary process (see next subchapters).

1.3.1 Empirical Evidence of Sympatric Speciation

Despite many sceptics[43], empirical evidence of sympatric speciation is undisputable. Among numerous examples are: (1) birds - Darwin's finches[92]; (2) plants - Lord Howe Island palms[187,210]; (3) insects: Apple maggot fly (*Rhagoletis pomonella*)[38,39,64] and Pea aphid (*Acyrthosiphon pisum*)[260]; (4) fish: Crater lake cichlids[16,211] and Sticklebacks[214,242]; (5) Mollusks - snail (*Littorina saxatilis*)[119]; and (6) reptiles - Island lizards[163].

Darwin's finches is the first and probably the most famous example of speciation in sympatry. The birds colonised Galapagos islands and successfully radiated into new species by filling the existing and creating new ecological niches. While filling the existing niches happens geographically by occupying certain habitats, creating of new niches can happen via specialisation on different resources in the same habitat. The latter is often motivated by resource competition for the case of geographic impossibility to escape the competitive pressure. Thus, the finches created new niches by specialisation on different kinds of food and developing different shapes of beaks[197] (Fig. 3). They then stabilized those niches till the point of reproductive isolation via phenotypical assortative mating. However, despite the

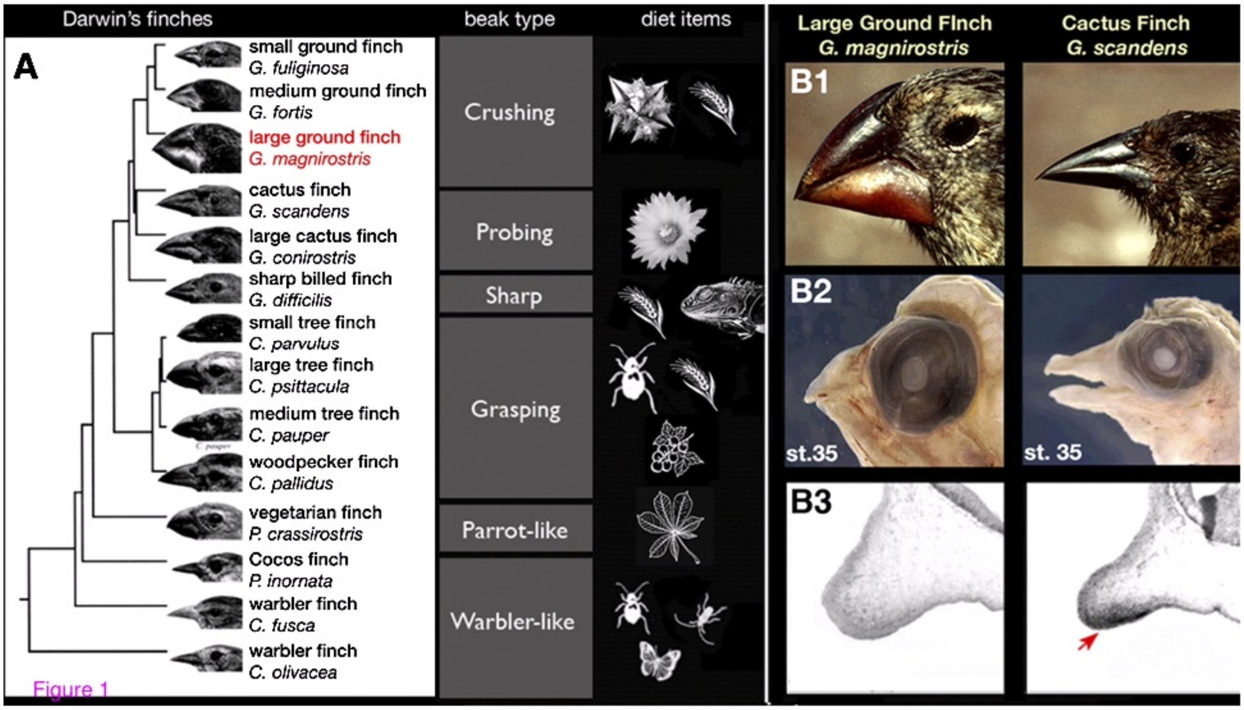

Figure 3. The beak shape diversity in Darwin's finches driven by specialisation on different kinds of food and adaptation to different feeding strategies. The figure is adopted from Rands et al. 2013 published in the BMC Genomics[197].

empirical, theoretical and genetic evidence of sympatric speciation, a concrete mechanism of speciation driven by specialisation, as suggested by Darwin, has been difficult to pin dawn.

Bolnick (2007) reports that the most compelling cases of sympatric speciation are found in small isolated environments and in ecosystems where settlement on one host plant (habitat) shifts to another plant (e.g. hawthorn flies shifted from hawthorn to apples)[65,158]. Examples of isolated environments are: oceanic islands (Lord Howe island palms)[210], postglacial lakes (Arctic char (*Salvelinus alpinus*))[89] and crater lakes (Cameroon crater lake cichlids)[211]. The representatives for sympatric Host Shifting are the Apple maggot fly (*Rhagoletis pomonella*) and the Common fruit fly (*Drosophila melanogaster*). Thus, successful laboratory experiments with Common fruit flies showed that preferences in habitat lead to strong assortative mating in 98% of flies already in the 25th generation[204]. The Host Shifting in Apple maggot fly is based on the fact that they mate on the same host on which they feed[22,123], so that accidentally changing feeding habits lead to almost immediate reproductive isolation[32]. Other notable reasons of sympatric speciation are changing flowering times in plants[210] or spawning times in fish[186,225].

Interestingly, despite the facts that (1) the ocean covers 71% of the Earth, (2) the marine environment is highly unstructured and does not have clear geographic boundaries[112], and (3) marine species have a broad geographic distribution of gene flow[272], sympatric speciation in terrestrial systems has gained much more attention while in marine systems it was largely ignored[164]. Thus, Briggs (2007) suggests that tropical reef fish diversity may be driven by strong resource competition[33]. Bird (2012) reports a collection of studies dealing with sympatric speciation of marine species. These include: tropical sea urchins[169], invertebrates and teleost fishes[272], marine gastropods[145], Tegula snails[100], Gobiodon fish[179], Halichoeres fish[206], review of reef fishes[205], Mopalia chitons[125], Hexagrammos fish[44], Littorina saxatilis snails[118] and Cellana limpets[28]. We here aim to contribute to the study of sympatric speciation in marine organisms by using phytoplankton data[189] as model parameters and constructing a model for zooplankton, which brings us to the next subchapter.

1.3.2 Theoretical Evidence of Sympatric Speciation

The mathematical modelling of sympatric speciation began in 1941 with Wright's model[278] on selection against heterozygotes indicating the fixation-probability of non-dominant modified chromosomes in a population of plants[249]. The first full model for the plausibility of sympatric speciation was presented by Maynard Smith[228] in 1966, but the conditions required for this model were not believed to be common in nature[27]. Thus, later theoretical studies investigated the conditions for the occurrence of sympatric speciation proposing two main groups: ecological and genetical conditions[261]. Among ecological conditions are: habitat shift[142,202], disruptive natural[17,50,66,120], sexual[102,190,250] and ecological selection[141,142,202,216] against intermediate hybrids[261]. Examples of genetic conditions for sympatric speciation include: genetic variation in habitat[50,120,201,202] or resource preference[17,50,66,142] and positive genetic correlation between disruptively selected traits and traits leading to assortative mating[66,142,202,203].

There were several attempts to classify sympatric speciation models. Thus, Turelli (2001) distinguish three groups of models: (1) ecological resource-based competition models, (2) sexual-selection models and (3) habitat-choice models[249]. Bolnick (2007) later distinguishes four types of assumptions for sympatric speciation models which deal with: (1) the origin of disruptive selection, (b) the mate-selection, (c) the influence of mate-selection on mating characters, and (d) the genetic one-allele versus two-allele models[32,131]. Relaxing some of these assumptions may greatly reduce the (theoretical) occurrence of sympatric specitaion, which was often shown before[31,37,82,166,271]. But, ideally sympatric speciation is promoted with strong disruptive selection, strong assortative mating, low assortative-costs, low recombination rate and high mutation rates[81].

Sympatric speciation is driven by disruptive selection[45,249] while the latter can be triggered by competition. The competition for resources or habitat between individuals within a single population may lead to adaptations for the alternative resource or habitat. Such adaptations may cause disruptive selection against intermediates and assortative mating of extreme individuals within a population. It has been shown that competition can be stronger between more similar individuals, so that newly arising and therefore rare taxa may experience less competition[20,30,212,233,240]. The best example showing that disruptive selection due to resource-competition can lead to sympatric speciation is probably the model of Dieckmann and Doebeli (1999)[48]. Reduced competition via disruptive selection may occur because different ecological niches exist and can be filled[52,249]. Most of the current models of sympatric speciation assume the existence of such niches. However, niche differentiation alone, or disruptive selection alone, does not necessarily stop the gene flow[32,249]. Thus, disruptive selection has to result in reproductive isolation, e.g. via assortative mating[249], in order for speciation to complete.

Assortative mating can be seen as a by-product of niche differences[261]. Bolnick (2007) distinguishes two types of models dealing with mating: assortment and trait-preference models. While in the assortment models females select for males similar to themselves in some traits, in the trait-preference models females select for a specific trait in males independent of the state of this trait in females themselves. The assortative mating works because there is an advantage of reduced recourse or habitat competition. However, there is no such thing as a free lunch[59], indicating the existence of costs for assortativeness. Indeed, Bolnick (2007) reports that disruptive selection is insufficient for sympatric speciation if assortative mating is coupled with the significant costs. In turn, low (or absent) costs of being choosy promote sympatric speciation[80]. The choosiness of females can be greatly reduced if resources are limited[185,199] or predation-risk is high[91].

The verbal theory outlined above is supported by many sympatric speciation models. Earlier classifications of sympatric speciation models are also widely accepted. Hovewer, we here discuss two main schools of sympatric speciation modeling: population genetics and adaptive dynamics models. The model presented in the current thesis is very similar to the adaptive dynamics framework, but has some significant distinctions (for details see introductions to chapters 2 and 3). In the following subchapters we briefly introduce the two schools of speciation modelling which shaped the theoretical research of sympatric speciation: population genetics and adaptive dynamics.

1.3.3 Population Genetics Models of Sympatric Speciation

According to Gavrilets (2003) the usual geographic definition of sympatric speciation was not precise enough for population genetics modelling purposes because one would need a clear definition of geographic separation. Therefore, most of the population genetics models define sympatric speciation as the emergence of new species from a randomly mating population in a particular birth place[80]. The founders of population genetics are Fisher, Wright, Haldane and Kimura[80], followed by Dickinson and Antonovics (1973)[47], Udovic (1980)[251], Felsenstein (1981)[66] and continuing by Kondrashov[138–142], Higashi[102] and Gavrilets[80,83] to name a few.

Thus, Higashi et al. (1999) created a model showing that disruptive sexual selection alone is sufficient for sympatric speciation of the African cichlids. Particularly, female cichlids split up into choosy individuals, selecting red or blue males, and non-choosy ones, mating randomly. This leads to the divergence of a single population into two subpopulations via disruptive sexual selection. In this way, extreme male phenotypes gain an advantage, because choosy females mate only with red or blue males, while intermediate (e.g. purple) males gain no advantage, because non-choosy females mate randomly[32]. Bolnick (2007) summarizes the flaws of Higashi's model: missing costs, unexplained origin of polymorphism and high sensitivity to changes in the model, which immediately results in directional instead of disruptive sexual selection. Therefore, it can be concluded, that sexual selection alone might not be sufficient for the occurrence sympatric speciation[13,43,80,255]. Thus, sexual conflict[84], male-male competition[255], opposing sexual and natural selection[250], and meiotic drive genes affecting the sex ratio and secondary sexual traits[146] or, in most cases, simply the recourse competition can help to enhance disruptive selection and compensate the costs of female-choosiness[32].

Trying to explain the causes of disruptive selection, Felsenstein (1981), offered one-allele and two-allele models[32]. In one-allele models a single new allele (m allele) causes the AA individuals to mate with AA, and aa with aa. Like in the example with the cichlid fish shown above, the m allele that conferred to the random mating produces less-fit heterozygotes (intermediates). In the two-allele models females might be polymorphic, resulting in selection of MA preferring AA and Ma preferring aa genotypes.

Despite the advances in understanding sympatric speciation, population genetics models have some critical issues. One of them, to our opinion, is that they pre-define two niches by different characteristics, such as geography, habitat, coloration, behavior, ploidy etc., in order to show the occurrence of reproductive isolation[27]. We suppose that niches should be created but not pre-defined. Another problem is the assumption that mutation and random genetic drift alone are sufficient for sympatric speciation to occur. Calling mutation and drift a null model of speciation[80], population genetics imply that no selection is needed for speciation, but "the principal evolutionary mechanism in the origin of species must . . . be an essentially nonadaptive one [Wright 1932, p. 364]"[277]. The number of incompatible genes can then increase in different populations, which develop into reproductive isolation as a by-product[80].

However, the adaptive dynamics framework did not agree with Wright's idea of essentially nonadaptive principal evolutionary mechanism.

1.3.4 Adaptive Dynamics Models of Sympatric Speciation

Primarily the adaptive dynamics framework equates the word adaptive to sympatric, because adaptive speciation assumes ecological contact between individuals[55]. Interactions within a population, especially resource competition may lead to divergence as an adaptive response to disruptive selection. The modeling of adaptive speciation began in 1960s[55], but the first models were not very realistic. Rosenzweig (1978) improved previous studies by suggesting that competition for continuously distributed resources could lead to adaptive diversification[207]. Later Seger (1985)[219], Doebeli (1996)[51], Christiansen (1991)[42], Brown and Pavlovic (1992)[34], and Abrams et al. (1993)[7] continued this line of research. The focus of the earlier adaptive dynamics models[49,87,88,174,175] was on the emergence of disruptive selection. Thereby, the system somehow experienced disruptive selection via directional ecological or sexual selection. The next step in the development of adaptive dynamics models was the introduction of the concept of evolutionary branching, which indicated the protected dimorphism[55]. We suppose that the protected dimorphism is the analog to reproductive isolation described by the population genetics framework. Eventually, adaptive dynamics theory has shown sympatric speciation to be a plausible evolutionary process for different ecological selection scenarios[48,51–54,56,86,88,102,122,132,133,141,148,173,175,178,255]. In contrast to the population genetics framework, claiming the unimportance of selection, adaptvie dynamics theory states, that "Understanding how these selective scenarios emerge from biological interactions is as important as understanding how the ensuing split into reproductively isolated subunits unfolds genetically"[55].

1.4 Optimality and trait based approach

Trait-based approach

Current nutrient-phytoplankton-zooplankton (NPZ) ecosystem models are problematic in many ways[10]. They are overly complicated and therefore provide a low degree of predictability[127], but at the same time not sophisticated enough to reflect the complexity of the real world. NPZ models mechanistically describe particular species, group the organisms into functional types (e.g. zooplankton, fish), classify the size (e.g. micro-, nanozooplankton) or diet (e.g. herbivores, carnivores), which leads to countless parameters[127]. Thus, the main problem lies in using many fixed characteristics (parameters) while fewer adaptive ones (variables), which represents the reality in a pretty static way[172]. In contrast, organisms and ecosystems are highly adaptive entities, able to respond to changing environmental conditions by adjusting behavior or changing physiological traits.

An alternative modelling approach is based on the physiological or behavioral functional traits of individual organisms[160]. Trait-based models aim to reduce the complexity of current models by considering trade-offs associated with specific traits. This means that a particular trait, e.g. body size, will be beneficial for the organism in one environment (gain), but harmful in the other (cost). The traits in such models are able to adapt to changing conditions by altering their values, while trade-offs protect the traits from becoming unrealistic, via balancing gains and costs[172]. The adaptation is due to the maximization of Darwinian fitness as a main survival mechanism[127,161]. Applying traits and trade-offs reduces the number of parameters in the model, which decreases the amount of information needed (input), but at the same time increases the number of interconnected variables, which increases the amount of information obtained (output). Moreover, some traits (size, nutrient acquisition) and trade-offs (competitive ability vs. predator susceptibility) are universal and can be applied to different communities. Thus the trait-based approach allows a better representation of reality and might help to predict the responses of ecosystems to current global change more correctly.

The trait-based approach has been successfully applied in terrestrial ecology[193], to microbes[270], marine phytoplankton[35,71,160], zooplankton[127,161] and fish[73]. One of the first

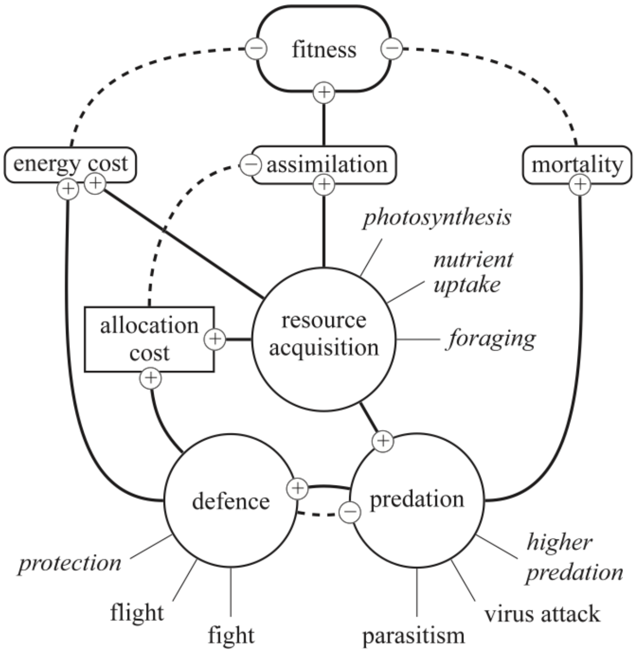

Figure 4. Major individual processes (tasks) and associated trade-offs. Solid lines with plusses indicate gains, while dotted lines with minuses indicate energetic costs. Source: Smith et al. (2011)[229].

less-static models considered the zooplankton feeding preferences[63]. A trait-based approach has also been applied to study global phytoplankton distribution[71].

Optimality-based approach

Another alternative to NPZ models is an optimality-based approach[12,135,180–184,229,231,232,275]. The basic assumption of optimality models is that through natural selection only organisms with the most efficient strategies can survive and reproduce in the continuous competition for resources[229]. The organisms are viewed as the carriers of countless optima, which can be calculated mathematically. The optimality-based approach is very similar to the trait-based approach, because trade-offs are also central to it. The process of optimization needs a goal function (e.g. N:Chl ratio, or nutrient uptake[180,231]), and a trade-off maximizing this goal function by balancing gains and costs[229]. While the trait-based approach focuses on traits, the optimality-based approach deals with processes (Fig. 4) which redistribute the energy assimilated and utilised. The latter makes it similar to the Dynamic Energy Budget theory[143]. The example of optimization in plankton is the maximization of the growth rate

$$G = A - L, \tag{1}$$

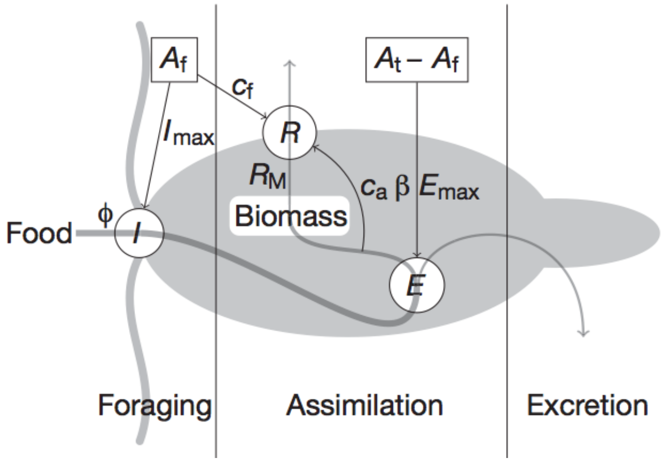

Figure 5. Optimal current feeding of zooplankton, where the ingestion rate I and the assimilation efficiency E are the gains and the respiration R is the cost. A_f is the foraging efficiency, I_{max} is the maximum specific ingestion rate, ϕ is the prey capture coefficient, c_f are the foraging costs. Assimilation efficiency is a function of digestion (coefficient β). A_t is the total specific activity, c_a are the costs of assimilation coefficient and R_M are the specific maintenance energy requirements. Source: Pahlow (2010)[184]

where G is net growth rate, A gross assimilation, and L loss, which may comprise respiration (energetic cost) as well as predation mortality (Fig. 4). Zooplankton can also maximize the growth rate as a measure of fitness, which also balances the gains versus costs:

$$g = EI - R \tag{2}$$

where E is the assimilation efficiency, I is the specific ingestion rate and R is the respiration (Fig. 5,[184]). Optimality-based models describe adaptive behavior of organisms and therefore increase the predictive power and realism of the models, compared to the current NPZ approach[101,232,273]. Due to the optimality condition, the number of parameters can also be reduced[180,182,231]. And even if the organisms are not perfectly optimal, seeking optimality in the physiology and behavior will improve our understanding of adaptation[188]. Optimality-based approaches have been applied to terrestrial systems[258], bacteria[253], phytoplankton[12,135,180–183,231,232] and zooplankton[184].

Optimality and trait based approach

Here we combine trait-based and optimality-based approaches by defining and optimizing the specialization of zooplankton as a trait. We also derive a specialization trade-off as part of the zooplankton grazing function which may enable to partition the resources and thus to reduce the resource competition. With that we aim to mimic the adaptive specialization of Darwin's finches[45,92,93] and gain new insights in evolutionary and population dynamics within a marine plankton community.

1.5 Traits and trade-offs

Traits

The most comprehensive collection of traits by this time (2014) was accomplished by Elena Litchman for both phytoplankton (Fig. 6 top[159]) and zooplankton (Fig. 6, bottom[161]) species. She classifies four types of traits: morphological, physiological, behavioral and life-history traits. These types are divided in three groups describing ecological functions. In phytoplankton these groups are: reproduction, resource acquisition and predator avoidance; in zooplankton: feeding, growth and reproduction, survival. But not all traits are equally important and general. Therefore, the trait-based modeling approach is seeking for key (or principal) traits, enabling the best possible representation of fitness[161] and the characterisation of broad spectrum of organisms. Key phytoplankton traits would be the cell size or resource utilisation[159]. For zooplankton such key traits would be body size, feeding mode or diel vertical migrations. Of particular interest are the combinations of characteristics, expressed as ratios (e.g. size ratio of P:Z = 1:10, or stoichiometric C:N:P ratio)[161]. Because the stoichiometric ratios are not really traits, they can be better described by optimality-based models. Such ratios show that traits or trait-similar entities in the organisms are mostly interrelated[161] and influence (depend on) each other. Thus, several characteristics of an organism can be calculated simultaneously, e.g. co-limitation by P, N and light in phytoplankton[182], which allows for more benefits from observational and empirical data compared to mechanistic NPZ models.

This thesis aims to enrich Fig. 6 with a further zooplankton trait - specialization. Fitness will be maximized in order to show which strategy, specialists or generalists, is selected for during the evolution of specialisation. We assume a certain incentive for becoming a specialist, because specialization always implies costs. The majority of organisms are generalists because it is more safe to have several resource-options, e.g. brown bear (*Ursus arctos*). But there are also a few very specialized organisms, e.g. coala (*Phascolarctos cinereus*) or panda bear (*Ailuropoda melanoleuca*). Therefore, there is a fundamental trade-off, as it was shown for microbial taxa (Fig. 7,[270]).

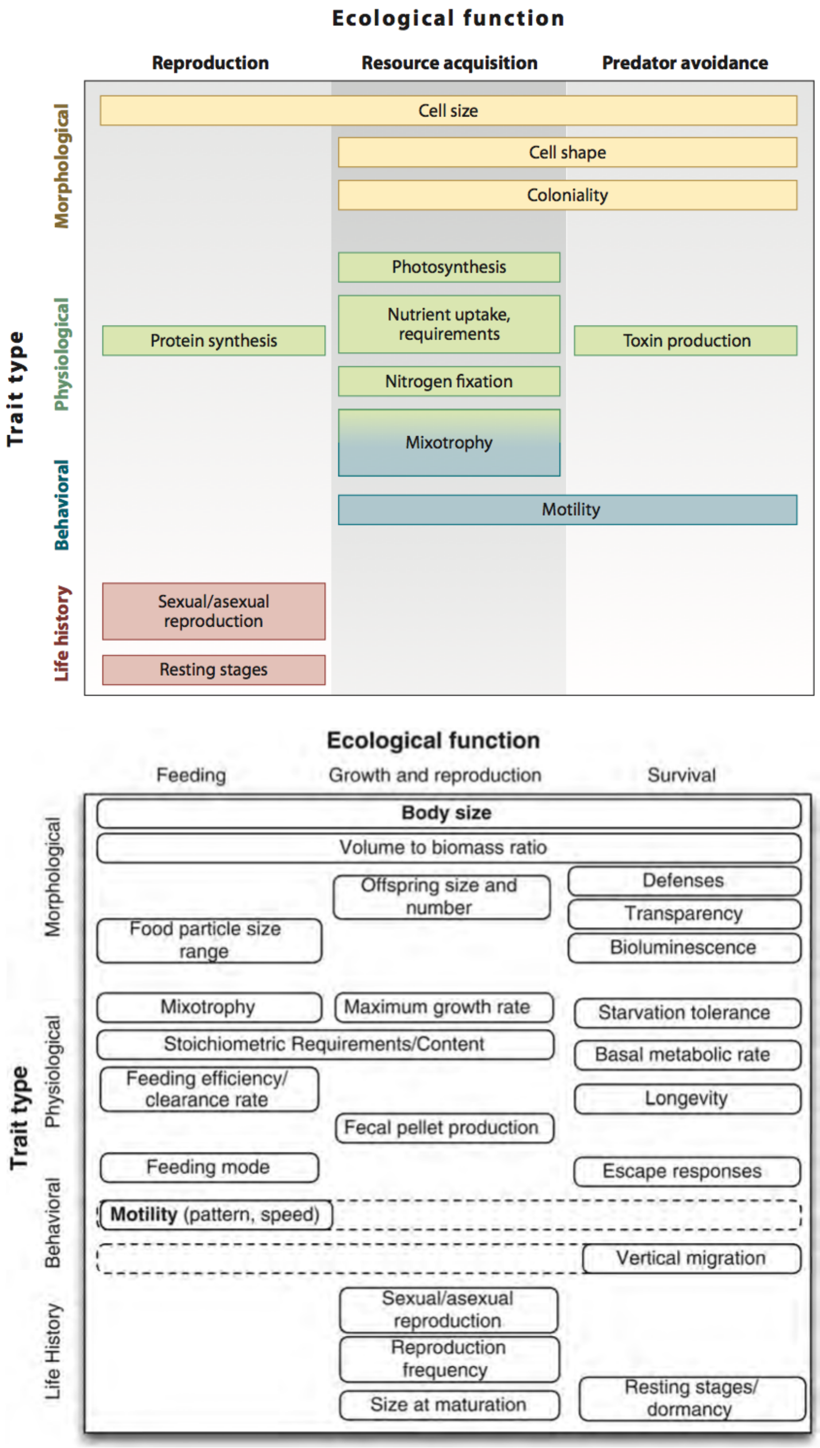

Figure 6. Collections of phytoplankton (top)[159] and zooplankton (bottom)[161] functional traits by Elena Litchman.

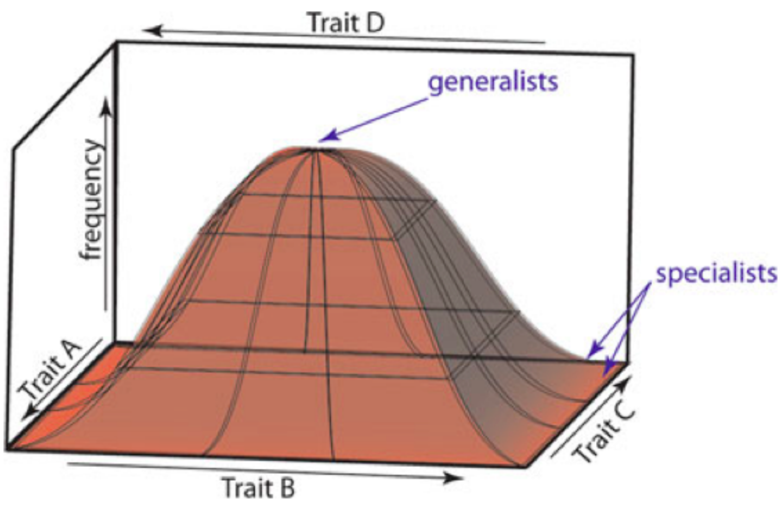

Figure 7. A fundamental specialist-generalist trade-off, showing that improved performance in one trait is countered by decreased performance in another trait. Source: Wallenstein (2012)[270]

Trade-offs

"You can't have everything. Where would you put it?"
Steven Wright

This quote represents the concept of trade-off. Trade-offs are inescapable physical or physiological constraints in feeding, survival, growth and reproduction, explaining why not everything can be maximised at the same time[161,229]. For example, nutrient uptake in phytoplankton is correlated with the size, whereby small cells prevail in low-nutrient environments while big cells dominate high-nutrient environments[40,154]. Increasing cell size in phytoplankton decreases the ability to gain nutrients because the ratio of the surface area, needed for nutrient uptake, to volume decreases. However, bigger cell size increases survival chances against predation[200]. This phytoplankton trade-off between competitive ability vs. predator susceptibility is one of the most studied[95,96,117,150,151,246]. The best studied trade-off in zooplankton species is associated with the diel vertical migrations[9,68] of zooplankton into deeper less lit waters. Such migrations allow zooplankton to escape predation at the daytime with the cost of lost feeding opportunities zooplankton would have at the surface.

Trade-offs often connect functional traits[29,94,245]. Therefore, energy gained from feeding (or nutrient acquisition) is redistributed between different processes, such as growth, maintenance, protection and reproduction[161]. Investing in one process, trades off against the others (zero-sum game), which limits organisms on one hand, but provides a certain resilience and a possibility to adapt to changing conditions on the other. Similar to the co-limitation in traits, trade-offs may explain the coexistence of species[160]. While gains in trade-offs are often obvious, the correct identification of costs is a difficult task[229,275].

Foraging activity in zooplankton aims to maximize the goal function, often taken to be net growth rate. To maximize net growth, an organism must not only balance gains (ingestion) and costs (respiration, excretion and mortality)[265], but also switch from one feeding mode to the other[127]. In general, feeding efficiency is traded off against feeding-related metabolic costs, predation risk and mating success[127]. The necessity of switching, and therewith the existence of trade-offs, can be shown in the following examples: (1) a non-motile ambush feeder has low metabolic costs[127], but will never meet the mate unless it moves and neglects feeding[126]; (2) searching for a mate not only increases the encounter rate with predators[127], but also reduces the energy investments in growth rate[161] because moving requires energy; (3) daily vertical migrations decrease encounter rate with predators, but imply costs of lost feeding opportunities[127]; (4) reducing predator mortality in ambush feeders is traded off against slower feeding rate; (5) tunicates invest more in grow rate and therefore grow faster then copepods, while copepods invest more in the development of jumping-muscles and therefore are exposed to lower predation risk[161] etc.

There are several attempts to classify trade-offs. One classification of trade-offs, based on the optimal processes in individual organisms, was offered by Lan Smith[229] (Table 1). Trade-offs can be also categorized into functional groups, such as physiological or behavioural trade-offs. Physiological trade-offs often occur during resource acquisition[160]. Behavioral trade-offs may result from the competitive ability for one vs. another nutrient[244], nutrient vs. light[110,134,152], or nutrient vs. grazer resistance[152]. Another trade-off classification was suggested by Visser (2013)[264]. He singled out four kinds of trade-offs: allocation, consonance, conflict and dichotomy trade-offs. Allocation trade-offs show limitation of traits by some finite recourse whereby the gains in one trait are equal to costs in the other. Consonance trade-offs allow the combination of two traits to gain more fitness than each of them alone. Conflict trade-offs result in a lower fitness for the combination of two traits compared to each of them alone. And finally, the dichotomy trade-offs describe competing effects of two elements of fitness within a single trait.

In this thesis we would like to propose a new kind of trade-off, describing one element of fitness (steady state population biomass) within a single trait (specialisation). It is similar

Table 1. Trade-offs based on different processes in organisms[229]

Trade-offs	References
Adaptive dynamics of communities	
Max. growth rate vs. edibility	274
Growth (minus cost of defense) vs. defense against grazers	75
Max. growth rate vs. assimilation of nitrate	71
Half-sat. value for ammonium vs. ability to use nitrate	71
Half-sat. value for nutrient vs. resistance to grazing	172
Half-sat. value for ammonium vs. ability to use nitrate	101
Half-sat. value for nutrients vs. optimal temp. for growth	101
Regulation of autotrophic growth	
Energy requirements vs. inverse growth rate	224
Iron for light harvesting vs. iron for N assimilation	11
Competitive ability for light vs. competitive ability for P	134
Energy for nutrient uptake vs. energy for biosynthesis	180
Energy for nutrient uptake vs. energy for biosynthesis	182
N for biosynthesis vs. N for photosynthesis	182
P for nucleus and membranes vs. P for N uptake, biosynth.	182
Energy for nutrient uptake vs. energy for C aquisition	275
Energy for light harvesting vs. energy for Calvin cycle	275
N for light reactions vs. N for dark reactions	12
Uptake and grazing	
Accumulating energy stores vs. avoiding predation	69
Half-sat. value for substrate vs. max. growth rate	273
Energetic cost of predation vs. energy gained from prey	248
Opportunity to capture prey vs. risk of being preyed upon	248
Affinity for nutrient vs. max. uptake rate	230
Affinity for nutrient vs. max. uptake rate	232
Energy used swimming vs. energy gained from prey	184

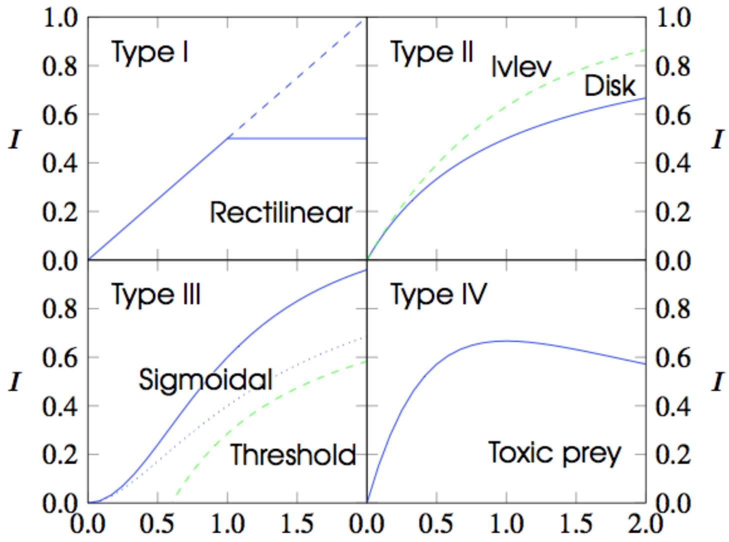

Figure 8. Holling functional responses. Picture by M.Pahlow

to the allocation trade-off, but in a single trait, and with the plus-zero sum game, whereby gains can become higher than costs (for more details, see Chapter 2).

1.6 Zooplankton feeding

Zooplankton is a group of nearly ubiquitous aquatic organisms[126]. Compared to terrestrial systems, where plant biomass greatly exceeds animal biomass, the marine zooplankton has roughly the same biomass as marine phytoplankton[276]. A close relationship and interdependence of both plankton groups make studying zooplankton as important as studying phytoplankton. Thus, phytoplankton primary production is supported by the CO_2 respired and nutrients excreted (remineralized) by zooplankton. Moreover, by consuming phytoplankton, zooplankton transfers the energy from lower to higher trophic levels (fish, humans). Zooplankton also exports carbon to the deep ocean via fecal pellets, which might have an effect on the global change. The interplay between these two trophic levels is often characterised by predator-prey interaction models. Particularly, the transfer of the energy (or biomass) from phytoplankton to zooplankton is described by the ingestion rate in the form of Holling functional responses[104].

The Type I functional response shows a rectilinear increase in the ingestion rate of the predator as a function of prey density up to the certain maximum. Afterwards ingestion rate remains constant (Fig. 8 top left). The Type I functional response assumes that food processing time (or handling time) needed by predator to handle one prey item is negligible. It also implies that processing one prey item does not interfere with the searching for the next prey item[116]. This functional response is applicable for some filter feeders[74] and can be described by Eq. 3 (M.Pahlow):

$$I = min(g\ P,\ I_{max}) \tag{3}$$

where g is the prey preference, P is the prey concentration and I_{max} is the maximum ingestion rate.

The Type II functional response implies both handling and search for an item of prey as mutually exclusive predator activities. It is described by the "Disk equation" (Eq. 4[105]) and has a hyperbolic shape showing decelerating ingestion rate (Fig. 8 top right).

$$I = \frac{aP}{1 + ahP} \tag{4}$$

where a is the search rate (or encounter rate) and h is the handling time. This type of response is more realistic because it often fits the results of empirical experiments[116] and therefore is commonly used in modelling studies. It implies that the saturation of a predator (I_{max}) is more likely achieved at high concentration of prey (P), because most of the time is used to process the prey (h) and very little time to find the prey (a). Mathematically equivalent equations are derived for enzymatic reactions (Michaelis-Menten) and growth of microorganisms (Monod)[85]. Another equation which can describes Type II prey-dependent functional response is the Ivlev equation[114], which is likewise able to show the saturation of the predator (Fig. 8 top right). However, despite the very similar form, it has different underlying assumptions and different explicit mathematical structure.

The Type III functional response also describes the saturable ingestion rate, but, compared to the Type II, in two different forms: sigmoidal and threshold forms (Fig. 8 bottom left). **The Threshold response** implies that no feeding occurs below a certain feeding threshold[85]. Thus, searching feeding activity might be interrupted in order to reduce metabolic expenses if the prey concentration becomes to low[184,194]. Threshold Type III functional response can be described by following equation[105]:

$$I = I_{max} \frac{P - P_{th}}{P + K} \tag{5}$$

where K is a half-saturation constant. **The Sigmoidal response** may occur if a predator can select between multiple prey species and specialise on one or the other prey depending on the prey density. It can be caused by learning and prey switching (or feeding strategy switching). Learning means increasing the foraging efficiency due to the increasing prey density. Prey switching appears if the prey density of the preferred prey falls below the prey density of the less-preferred prey, which has been shown in several empirical studies[90,121,129,147]. The prey-preference g_i of a predator for prey i is described as a quadratic dependence of prey i of the total available food[63] and is represented in the following equation:

$$I = I_{max} \frac{g_i P_i^2}{\sum_{i=1}^{n} g_i P_i^2} \tag{6}$$

The Type IV functional response describes the reduction of ingestion rate at the higher prey density for the case of toxic prey (Fig. 8 bottom right), which might be relevant for the cases of toxic phytoplankton blooms:

$$I = I_{max} \frac{gP}{gP + K + \theta P^2} \tag{7}$$

where θ is the toxicity of a prey.

Functional responses describe the zooplankton feeding mechanistically. They are formulated for a single predator and a single (Type I, II, III, IV) or multiple (Type III) prey species. The most advanced functional response, in our opinion, is the Type III, which can have two forms: either threshold (in case of the feeding threshold) or sigmoidal form (in case of prey preferences). However, non of them is realistic enough to be able to describe zooplankton feeding correctly. The current mechanistic description of the zooplankton feeding can be effectively improved via the integration of traits, trade-offs and different feeding modes, as described in Kiørboe (2010)[127], into models of zooplankton feeding behaviour. One such attempt was successfully carried out by Pahlow & Prowe (2010)[184] describing the optimal current feeding in zooplankton. We here continue the optimality-based description of zooplankton feeding and introduce an alternative Type of functional response by defining it for two predators and two prey species. Particularly, we extend the Type II response with the new non-quadratic definition of the prey preference (specialisation) and with a feeding threshold simultaneously. Moreover, we have embedded a specialisation trade-off between the improved ability to eat the preferred prey and the reduced ability to eat the less-preferred prey (for more details see Chapter 2).

1.7 Overview of the thesis and author contributions

Chapter 2 introduces the optimality-trait based mechanism of the sympatric speciation in a marine predator-prey interaction model. The specialisation, as an adaptive trait of zooplankton, is defined and iteratively optimised to the point of stabilisation. The presented model enriches the Holling II functional response of zooplankton with the feeding threshold and the specialisation trade-off between the improved ability to eat the preferred prey (gain) and the reduced ability to eat the less-preferred prey (cost). An increase in gains is coupled to some loss in costs. This coupling is quantified with the help of the cost coefficient, which can allow gains to become higher than costs (plus-zero sum game). The latter may lead to disruptive selection and resource partitioning, which creates two niches based on two available resources (phytoplankton species) and, in case of niche stabilisation, to sympatric speciation. This mechanism agrees well with adaptive specialisation of Darwin's finches as a classical example of sympatric speciation. This chapter is a submitted manuscript entitled: "Sympatric speciation by optimal specialisation" by Y.Zablotski, M.Pahlow and A.Oschlies. Y.Zablotski has developed the concept of the specialisation trade-off based on the initial idea of M.Pahlow. He translated the concept in computer language (MATLAB), produced explanatory diagrams, calculated and graphically represented the results and prepared the manuscript, with guidance provided by both co-authors.

Chapter 3 applies the introduced optimality-trait approach to a four-species marine ecosystem model with co-evolving traits: adaptive specialisation in zooplankton and growth rate in phytoplankton. The study investigates the combinations of predator and prey traits which allow for sympatric speciation in predators and combinations which do not. This approach allowed to introduce several novel concepts: speciation space, displacement space, vanishing speciation, evolutionary time landscape, speciation threshold and prey-equality space. Our rather unusual definition of fitness as a steady state population biomass allows the direct simultaneous comparison of coexisting populations of all species on the fitness landscape as a function of two changing quantities: specialisation cost-coefficient of the zooplankton and the specific growth rate of the phytoplankton. The evolutionary time is then defined as the number of evolutionary iterations needed for the stabilisation of the niches or for the displacement of one predator. The results reveal three main evolutionary outcomes in predators: displacement, stable and vanishing speciation. It also shows that prey species can reduce grazing pressure by either reducing the growth rate at low specialisation costs (passive strategy) or by increasing the growth rate at high specialisation costs (active strategy). This chapter is a manuscript in preparation entitled: "Sympatric co-evolution of predator and prey traits" by Y.Zablotski, M.Pahlow and A.Oschlies. Y.Zablotski conceived the idea, introduced novel concepts and performed the simulation experiments. Comprehensible representation of results and preparation of the manuscript was accomplished by Y.Zablotski with the participation of both co-authors.

Chapter 4 builds directly upon both previous studies and examines the co-evolution of traits (DIM in phytoplankton vs. adaptive specialisation in zooplankton) at different nutrient loads. Particularly, the model explores the community dynamics, occurrence of sympatric speciation and ecosystem productivity. The results of this study reveal that increasing environmental nutrient concentration: (1) increases the occurrence of sympatric speciation; (2) lowers the effect of DIM on biodiversity; (3) changes the domination (higher biomass) of the prey over predator in low-nutrient environments to the domination of the predator over prey in high-nutrient environments; and (4) decreases the overall productivity of the system, due to a faster accumulation of nutrients in the water than assimilation by the organisms. This chapter is also a manuscript in preparation entitled: "Sympatric speciation of marine zooplankton along nutrient and density-independent phytoplankton mortality gradients” by Y.Zablotski, M.Pahlow, A.Oschlies. Y.Zablotski proposed the idea, performed simulation experiments and analysed the results. He also wrote the manuscript, with comments provided by both co-authors.

Summarising, this study presents a novel optimality-trait based zooplankton grazing definition, aiming to provide the current global biogeochemical models with the evolutionary (adaptive) properties of the plankton organisms. Therefore, the fifth chapter proposes future work.

2 Sympatric speciation by optimal specialisation

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Abstract

Sympatric speciation is one of the most debated and intriguing concepts in evolutionary biology, because in contrast to allopatric speciation it happens without geographic isolation[27,32,261]. Speciation can reduce resource competition[32] via niche partitioning. It can result from disruptive selection and assortative mating, leading to reproductive isolation, e.g., by divergent mate timing or habitat choice[32,251]. However, a concrete mechanism which allows for sympatric speciation has been difficult to pin down. Here we define a specialisation trade-off between the improved ability to eat the preferred prey (gain) and the reduced ability to eat the less-preferred prey (cost). Specialisation of predators can lead to sympatric speciation, provided that sufficient ability is retained to eat the less-preferred prey. We find that the degree of specialisation strongly depends on specialisation cost and that high costs can prevent speciation. Low and intermediate specialisation costs produce disruptive selection and, for two prey species, create two niches via resource partitioning. Our model suggests that omnivory can lead to sympatric speciation in predators.

2.1 Introduction

Investigating the machinery of speciation is crucial for understanding evolution. Sympatric speciation, defined as speciation without geographic isolation[45,170], is the most intriguing case and is believed to be less common and harder to show than allopatric speciation, which is the speciation owing to geographic isolation[249]. Despite clear evidence for the occurrence of sympatric speciation[27,32,261], its significance is often considered controversial[27,32]. Previous studies have examined sympatric speciation in specific cases, e.g., plants[210], insects[39], fish[16] and birds[45]. Speciation models of adaptive dynamics[48,49,53,88,141,175] have revealed sympatric speciation in different types of ecological interactions, e.g., coevolution[49], competition, mutualism, or predator-prey interactions[53]. Models of population genetics[80,138–140,142,251] have studied the non-adaptive causes of sympatric speciation, e.g., mutations, gene flow and genetic drift. Nearly all models of sympatric speciation make the core assumptions of the presence of two externally prescribed ecological niches (maxima in the fitness landscape) and of the existence of disruptive selection (simultaneous selective pressure in two directions)[32]. The adaptive dynamics framework goes one step further and generates niches by letting the system "experience disruptive selection"[53]. However, adaptive dynamics does not provide an explanation of how disruptive selection can be experienced because it still needs a predefined fitness landscape. We here use a specialisation trade-off aiming to explain how such a fitness landscape may be created by the process of evolution itself and how this can then initiate disruptive selection.

The abstract nature of previous approaches makes it difficult to pin down mechanisms of speciation. Here we define a concrete trade-off associated with a specific trait, specialisation, from which we derive a concrete mechanism for speciation. While advantages (gains) of a certain trait are often quite obvious, related costs are less easily recognised[229,275]. Whereas sexual speciation models have considered the costs of choosiness[80,115,192] or mate-search costs in females[176], trait-associated costs have not been explicitly accounted for in asexual sympatric speciation models. We here define specialisation as a trait, and explicitly define and balance both costs and gains in a specialisation trade-off in order to optimize predator fitness in a simple asexual predator-prey interaction model. Our optimal-trait approach suggests that mutations reducing the costs of specialisation can generate disruptive selection. Thereby, our study provides new insights into the still not fully understood evolutionary process of sympatric speciation.

2.2 Model

2.2.1 Predator-prey model

In order to introduce our concept of optimal specialisation, we first construct a predator-prey interaction model (Table 2 and Fig. 9) to represent a simple closed ecosystem with two primary producers (prey species, P_1 and P_2) and two initially identical herbivores (predators, Z_1 and Z_2). We assume asexual reproduction in both prey and predator species. The two prey species are nutritionally identical, but can potentially be discerned by the predators.

The model describes the dynamics of phytoplankton (prey), zooplankton (predator), and a single nutrient (N) representing nitrogen. The net rate of phytoplankton change is expressed as the difference between phytoplankton net growth rate and grazing losses. Zooplankton net growth is the difference between zooplankton grazing and an assumed linear zooplankton mortality. We use nitrogen concentration as the common currency for all model compartments and assume constant carbon to nitrogen (C:N) composition of all predator and prey species. Thus, N is consumed by phytoplankton and regenerated by mortality of both phytoplankton and zooplankton:

$$\frac{\mathrm{d}P_j}{\mathrm{d}t} = \mu_j P_j - \sum_{i=1}^{2} g_{i,j} Z_i \qquad j \in \{1,2\} \tag{8}$$

$$\frac{\mathrm{d}Z_i}{\mathrm{d}t} = \sum_{j=1}^{2} g_{i,j} Z_i - m_i Z_i \qquad i \in \{1,2\} \tag{9}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -\sum_{j=1}^{2} \mu_j P_j + \sum_{i=1}^{2} m_i Z_i \tag{10}$$

where μ_j is net growth rate of phytoplankton type j (P_j), $g_{i,j}$ is specific grazing rate of predator type i (Z_i) on phytoplankton type j (P_j), and m_i is mortality of zooplankton type i (Z_i). Phytoplankton net growth rate is the difference between nutrient uptake and phytoplankton specific mortality:

$$\mu_j = \mu_{\max,j} \frac{N}{N + K_{N,j}} - d_j \tag{11}$$

where $K_{N,j}$ and d_j are the half-saturation concentration and the specific mortality, respectively, of phytoplankton type j. We define the specific grazing rate ($g_{i,j}$) of predator i on prey j as a function of search rate (a_i), handling time (h_i) and foraging efficiency ($e(S)$ see below):

$$g_{i,1} = \frac{a_i e(-S_i)\max(P_1 - P_{\mathrm{th}},\ 0)}{1 + a_i h_i[e(-S_i)(P_1 - P_{\mathrm{th}}) + e(S_i)(P_2 - P_{\mathrm{th}})]} \tag{12}$$

$$g_{i,2} = \frac{a_i e(S_i)\max(P_2 - P_{\mathrm{th}},\ 0)}{1 + a_i h_i[e(-S_i)(P_1 - P_{\mathrm{th}}) + e(S_i)(P_2 - P_{\mathrm{th}})]} \tag{13}$$

where P_{th} is a feeding threshold and S_i is the degree of specialisation of predator Z_i.

2.2.2 Specialisation trade-off

We consider two prey species ($j \in \{1, 2\}$) and define the degree of specialisation in the range $S_i \in [-1; 1]$ as an adaptive trait of predator species i, where $S_i = 0$ indicates no specialisation (omnivory or generalism as opposed to specialism, Fig. 10). The sign of S determines which is the preferred and which is the less-preferred prey, so for $S < 0$ P_1 is preferred and for $S > 0$ P_2 is preferred. Specialisation is assumed to affect the foraging efficiency of the predator (e, the ability to capture and eat prey). Gains and costs of specialisation define a trade-off associated with prey preference: gains are due to an improved foraging efficiency of the preferred prey, $e(S) > 0.5$, and costs are owing to the reduced foraging efficiency of the less-preferred prey, $e(S) < 0.5$ (Fig. 10). This definition allows to use S_i and $-S_i$ to characterise effects of specialisation with respect to both prey types: $e(-S)$ describes the effect of specialisation on the foraging efficiency on P_1 and $e(S)$ is the effect of specialisation on the foraging efficiency on P_2 (Fig. 9). $S < 0$ indicates specialisation on only the first prey, since in this case $e(-S)$ is a gain (Fig. 10 blue) and $e(S)$ is a cost (Fig. 10 green). Specialisation is only on the second prey for $S > 0$, where $e(-S)$ is a cost (Fig. 10 blue) and $e(S)$ is a gain (Fig. 10 green).

We assume that an increase in gains is coupled to some loss in costs. The coupling is quantified with the help of the cost-coefficient (ζ_{S}, Fig. 10, all symbols are defined in Table 2). A cost of $\zeta_{\mathrm{S}} = 1$ implies that any gain in foraging efficiency of the preferred prey is offset by an equal loss in foraging efficiency of the less-preferred prey (Fig. 10 and Fig. 11 left). A cost of $\zeta_{\mathrm{S}} = 0$ indicates that the foraging efficiency of the less-preferred prey is not affected by specialisation, while the foraging efficiency of the preferred prey increases due to specialisation (Fig. 10 and Fig. 11 right). This behaviour is described by:

$$e(S) = 0.5[1 + \max(S,\ 0) + \zeta_{\mathrm{S}} * \min(S,\ 0)] \tag{14}$$

where $\max(S,\ 0)$ represents the gain and $\zeta_{\mathrm{S}} * \min(S,\ 0)$ the cost of specialisation. Thus, foraging efficiencies on the preferred and less-preferred prey species define the trade-off associated with specialisation. Thereby the cost-coefficient (ζ_S in Eq. 14) relates the possible gains by an improved foraging efficiency of the preferred prey to the possible costs by a reduced foraging efficiency of the less-preferred prey.

2.2.3 Model implementation

We start out with a single ecological niche inhabited by one perfectly omnivorous predator population ($S_i = 0$) and, using Eq. 9, determine the fitness of an assumed mutant Z_2, with specialisation $S_2 \in [-1; 1]$ as its steady-state abundance in the presence of a resident population Z_1, with $S_1 = 0$. The resulting fitness landscape for Z_2, as a function of S_i, is initially symmetric and may have one or two maxima ($S_2^{\mathrm{opt,j}}$) depending on the specialisation costs (ζ_S, Fig. 12a-c). A maximum in the fitness landscape represents a (local) optimum in the degree of specialisation, which characterises a niche and hence forms an evolutionary attractor. Highest costs ($\zeta_S = 1$, Fig. 12a) produce one optimum at $S_2^{\mathrm{opt}} = 0$, which means no specialisation and therefore no niche creation. Intermediate costs ($0.37 < \zeta_S < 1$) result in two optima (e.g., $S_2^{\mathrm{opt,1}} = -0.21$ and $S_2^{\mathrm{opt,2}} = 0.21$ for $\zeta_S = 0.5$ in Fig. 12b), which represent selective pressure towards specialisation to either prey type. The steep trough in between indicates strong disruptive selection.

Evolution is initialised by displacing the original resident with either of the two fittest mutants, i.e., we set $S_1 = S_2^{\mathrm{opt,1}}$ from the initial fitness landscape for Z_2, so that the mutant becomes the new resident. Holding the degree of specialisation of Z_1 constant at $S_1 = -0.21$, we re-calculate the fitness landscape for a new mutant Z_2 in terms of $S_2 \in [-1; 1]$, which now becomes asymmetric and displays a global maximum close to the initial $S_2^{\mathrm{opt,1}} = -0.21$ and a secondary (local) maximum close to the initial $S_2^{\mathrm{opt,2}} = 0.21$ (Fig. 12b). We assume that evolution proceeds in small steps, so that the trough between the two fitness maxima (at $S_i = 0$) cannot be crossed, because the direction of the selective pressure is determined by the local slope of the fitness landscape around the previous $S_2^{\mathrm{opt,2}}$. Therefore, only the second (local) maximum is approached by evolution. The small steps are implemented via determining the maxima on two separate fixed intervals of a fitness landscape, $S_1 \in [-1; 0]$ for Z_1 and $S_2 \in [0; 1]$ for Z_2. The trough is essential for the stabilisation of the two niches because selection against intermediates is a prerequisite for reproductive isolation[262]. The conditions, $S_1 < 0$ and $S_2 > 0$, ensure that the fitness landscape for Z_1 is mirroring the fitness landscape of Z_2 (Fig. 9). This allows to calculate just the fitness landscape for Z_2 (Fig. 12b) to trace the evolution of specialisation in mutant and resident. Thus, the local maximum $S_2^{\mathrm{opt,2}} = 0.21$, which is a gain of Z_2, is equal to the $S_1^{\mathrm{opt,1}} = -0.21$, which is a gain of Z_1, where the negative sign indicates the specialisation of Z_1 on P_1. Stabilisation of the two niches is then demonstrated by repeatedly (1) evaluating the fitness landscape of a new mutant predator Z_2 and (2) assigning the local optimum $S_2^{\mathrm{opt},1}$ close to the previous $S_1^{\mathrm{opt},1}$ until both $S_2^{\mathrm{opt,j}}$ stop changing and converge to two separate and stable niches (blue curve in Fig. 12b). In the following, we term one cycle of steps (1) and (2) as one evolutionary iteration. The number of evolutionary iterations in our model was limited to one hundred. Niches are considered stabilised if the total of the last three changes in the population biomass is less than 0.001 mmol/l. The stabilisation of niches in reality would represent a long evolutionary process of many small steps from the occurrence of a new degree of specialisation in a few individuals to the establishment and reproductive isolation of two new populations.

2.3 Results and Discussion

Whether speciation occurs and how far it develops depends strongly on the cost of specialisation (ζ_{S}, Fig. 12). Speciation can occur only if the loss of the ability to eat the less-preferred prey costs less than the gain in the ability to eat the preferred prey (Fig. 10 and Fig. 11). The relation between costs and gains can be illustrated with the help of fitness landscapes. A fitness landscape with one central maximum, which results from high costs ($\zeta_{\mathrm{S}} = 1$, Fig. 11 left, Fig. 12a), does not allow for speciation since there is no incentive for specialisation. The initial fitness landscape for $\zeta_{\mathrm{S}} < 1$ has two maxima and a local minimum, at $S_i = 0$ (Fig. 12b). Specialisation on either prey type is then rewarded, providing a strong incentive for specialisation.

Initially, the omnivorous zooplankton population is not specialised on either prey species, so that differential feeding is only due to behavioural food preferences. This always results in a zero-sum game (high costs: $\zeta_{\mathrm{S}} = 1$) where the single niche (evolutionary attractor) is located at the fitness maximum at $S_i = 0$ (Fig. 12a). Random mutations causing specialisation on one (preferred) prey species then may reduce to some degree the predator's ability to consume the other (less-preferred) prey species. If the gain in ability to eat the preferred prey is more than the loss in ability to eat the less-preferred prey, the specialisation has a lower cost, $\zeta_{\mathrm{S}} < 1$, than a behavioural food preference, which is always associated with $\zeta_{\mathrm{S}} = 1$. This results in a plus zero-sum game (gains are higher than costs), which turns the initial fitness maximum into a fitness minimum and produces two new (local) fitness maxima. Assuming the mutationally induced specialisation is inheritable, the ability to specialise on different prey species with $\zeta_{\mathrm{S}} < 1$ allows zooplankton individuals in one population to reduce intraspecific competition.

The two (local) maxima can be interpreted as two ecological niches occupied by two mutants whose fitnesses are higher than the fitness of a resident situated in the fitness minimum (Fig. 12b). The locations of the maxima, and hence the niches, depend on both ζ_S and the current degrees of specialisation of the resident and the mutant, but the stabilised niches never lie very far away from the initial maxima, due to our assumption that evolution proceeds in small steps. In our model, the iterative evolutionary cycle converges rapidly, so that the niches usually assume their final positions within a few evolutionary iterations. The cost of specialisation determines not only the heights of the fitness maxima, but also the distance between them (Fig. 12b,d). Both height and distance are important factors affecting the possibility of speciation. The height of the maxima relative to $S_i = 0$ determines the strength of the selective pressure against intermediates, which is required to drive the sub-populations apart. The distance between the maxima diminishes with increasing costs indicating decreasing chances for speciation to occur, which agrees with the suggestion that "costs of being choosy ... act against sympatric speciation"[82]. In reality, some minimum distance between niches near $\zeta_S = 1$ will also be necessary to allow reproductive isolation (because of genetic variability), but the exact nature of the threshold difference is beyond the scope of the present study. Low costs ($\zeta_S < 0.37$) also result in two niches with both predators fully specialised on either kind of prey (Fig. 11 right and Fig. 12c). In this model niches stabilise for all values of low and intermediate specialisation costs tested ($\zeta_S < 1$, Fig. 12d) within 100 evolutionary iterations.

Our model describes an adaptive trait and therefore is conceptually similar to models of adaptive dynamics. However, there are several critical distinctions between adaptive dynamics and our optimal-trait approach. The first major difference is the definition of fitness. While adaptive dynamics defines the invasion fitness of a mutant as the long-term per capita growth rate of a rare mutant[53,88], we calculate fitness in terms of steady-state population biomass. Adaptive dynamics requires that both the fitness of the resident and its first derivative with respect to mutant's strategy are zero at evolutionary stable states and branching points, which complicates the fitness-comparison of coexisting species. Contrarily, fitness is represented by population biomass in our model and therefore allows a quantitative comparison of coexisting species. In addition, our definition of the specialisation trade-off results in a non-differentiable fitness landscape at the evolutionary attractor $S_i = 0$ (singular point, Fig. 12a-c). This makes the application of adaptive dynamics in our case difficult because the adaptive dynamics requires that the fitness landscape is differentiable at the fitness extrema.

Compared to the "classical optimization models of evolution ... [in which] ... the evolutionary attractors only occur at fitness maxima", in the adaptive dynamics an evolutionary attractor can occur at a fitness minimum where the system experiences disruptive selection[53]. However, adaptive dynamics does not provide any concrete incentive for disruptive selection or trait-associated costs. In our optimization model reduced specialisation costs in the specialisation trade-off transform the initial fitness maximum at $S_i = 0$ into a fitness minimum and thus generate disruptive selection and evolutionary branching. Reduced costs provide predators with an evolutionary advantage to consume more of the preferred prey while not loosing part of the ability to consume the less-preferred prey. This makes sense intuitively, because specialising predators are able to partition resources and therefore reduce intraspecific competition, which results in higher mutant fitness compared to the branching point. Reduced specialisation costs allow the predator to escape from the fitness minimum and lower resource competition via specialised feeding, similar (not mathematically, but conceptually) to the assortative mating in models of adaptive dynamics[53]. Thus, we introduce the term assortative feeding to describe the non-random nature of specialisation in our model. The idea that resource competition was likely the main reason for sympatric speciation via evolutionary branching has been confirmed by several empirical studies[53], e.g. in intertidal snails[119], Anolis lizards[163] and senecio trees[136].

Apart from adaptive dynamics, previous models of sympatric speciation depended on preexisting niches[228,251], e.g., different habitats: maggot flies (*Rhagoletis pomonella*) which occupy new fruits to reside and reproduce[39], and crater lake cichlids occupying new lake areas and consuming different amounts of the same food[16,211]. Contrarily, single species of Darwin finches specialised on different sizes of seed on Galapagos[92], where the seed consumed could not be related to habitat. Evolution of optimal specialisation in our model mimics Darwin's case and shows that natural selection can create niches by resource partitioning via specialisation. Thus, in contrast to previous sympatric speciation models, where available ecological niches create feeding preferences, in this study it is the feeding preferences which create ecological niches.

Despite the fact that specialists in our model tend to consume the preferred prey, they do not entirely lose the ability to eat the less-preferred prey for $\zeta_\mathrm{S} < 1$, which implies a certain degree of generalist behaviour even for $S_i = -1$ and $S_i = 1$ (Fig. 11). The degree of generalist behaviour is determined by both the cost (ζ_S) and the degree of specialisation (S_i): the higher ζ_S the more generalist behaviour will be retained (Fig. 12). This means that the kind of specialisation produced by our model generates different degrees of omnivory. The strongest omnivory appears at the highest costs $\zeta_S = 1$, as no specialisation occurs for $S_i = 0$ (Fig. 12a), hence predators remain generalists. The weakest omnivory appears at the lowest costs $\zeta_S = 0$ where even the highest degree of specialisation does not reduce the ability to eat the less-preferred prey (Fig. 11 right). Reduced costs of specialisation generate an increased biomass in zooplankton (Fig. 12a-c) because of the increased prey consumption. Thus, reduced resource competition and higher prey consumption are the advantages of specialisation allowing speciation of predators in sympatry. The retained ability to eat the less-preferred prey could be interpreted as an evolutionary insurance mechanism for the case that the preferred prey becomes scarce or goes extinct. Otherwise, complete specialisation on a single prey could cause the extinction of the predator. On the other hand, optimal specialisation could be an evolutionary mechanism allowing predators to respond to the evolution of their prey.

Our model demonstrates the plausibility of sympatric speciation for the example of specialisation to certain prey species in predators. In this example, our model reveals that omnivory can be a prerequisite for sympatric speciation and explicitly considers the costs of the specialisation trait. Compared to previous models, which explain the origin of sympatric speciation using fitness landscapes, our model goes one step further and explains how a fitness landscape can originate from a specialisation trait. It also goes one step further in allowing the analysis of evolution after evolutionary branching via iterative optimisation to the point of niche-stabilisation. Considering disruptive selection by partial specialisation as a main driver for sympatric speciation[249], our results imply that sympatric speciation could be much more common in nature than previously suggested[43]. Thus, the analysis of both gains and costs within trade-offs in optimal-trait models may provide a new tool to study evolution.

2.4 Acknowledgments

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2.5 Figures and Tables

Table 2. Variables and Parameters of the model

Symbol	Definition	Unit	Value	Reference
	Variables			
P_j	Population abundance of phytoplankton	mmol/l	-	-
Z_i	Population abundance of zooplankton	mmol/l	-	-
N	Environmental nutrient concentration	mmol/l	-	-
S_i	Specialisation of Z_i	-	[-1; 1]	this study
ζ_{S}	Cost of specialisation of Z_i	-	[0; 1]	this study
	Parameters			
$\mu_{\max,j}$	Maximum specific growth rate of P_j	l/d	1.9	[189]
d_j	Specific mortality rate of P_j	l/d	0.01	this study
$K_{N,j}$	Half-saturation concentration of P_j	mmol/l	9.32	[189]
P_{th}	Grazing threshold	mmol/l	4.08	this study
h_i	Handling time per prey item of Z_i	d	0.055	[57]
a_i	Search rate of Z_i	L/mmol*d	0.14	[128]
m_i	Specific mortality rate of Z_i	1/d	0.1	[103]
	Functions			
$e(S)$	Foraging efficiency	-	[0; 1]	calculated
$S_i^{opt,j}$	Optimal specialisation of Z_i	-	[-1; 1]	derived
μ_j	Net growth rate of P_j	1/d	-	calculated
$g_{i,j}$	Specific grazing rate of Z_i on P_j	1/d	-	calculated

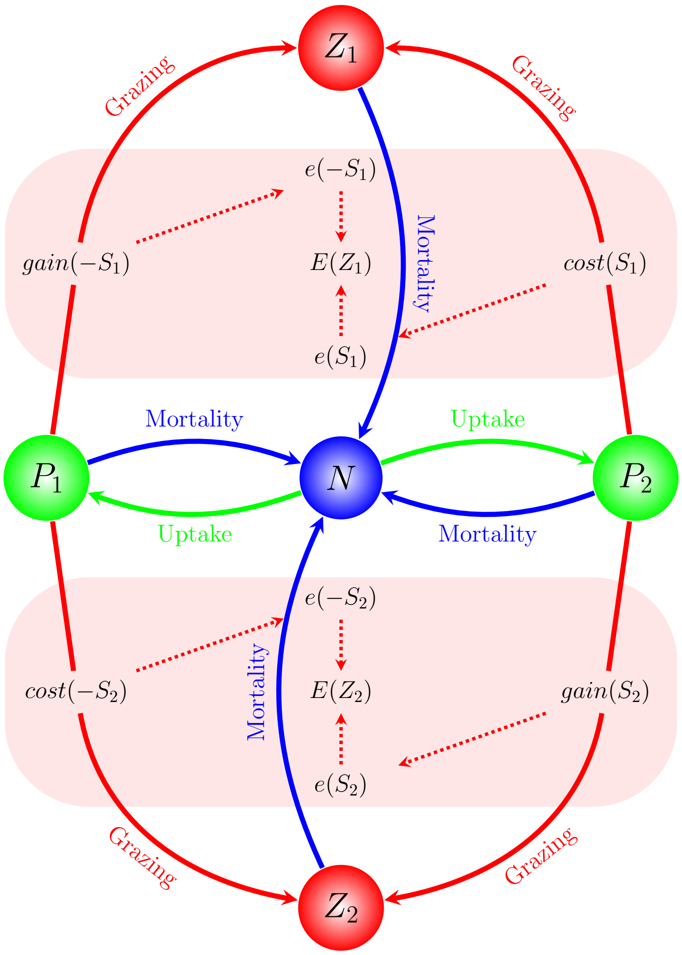

Figure 9. Conceptual representation of the specialisation trade-off. Blue indicates nutrients (N), green phytoplankton (P) and red zooplankton (Z). Costs and gains of specialisation define a trade-off (pink) in terms of foraging efficiency $e(S_i)$ as a function of specialisation S_i of predator Z_i, here illustrated for the case of two predators, Z_1 and Z_2, specialising on two prey species, P_1 and P_2, respectively. $S_1 < 0$ and $S_2 > 0$, is the condition for coexistence. Gains from specialising in one prey are coupled to the costs in the other prey. $E(Z_i)$ - compound foraging efficiency in zooplankton is composed of the foraging efficiency of the preferred prey, $e(-S_1)$ and $e(S_2)$, and the foraging efficiency of the less-preferred prey, $e(S_1)$ and $e(-S_2)$, see Fig. 11.

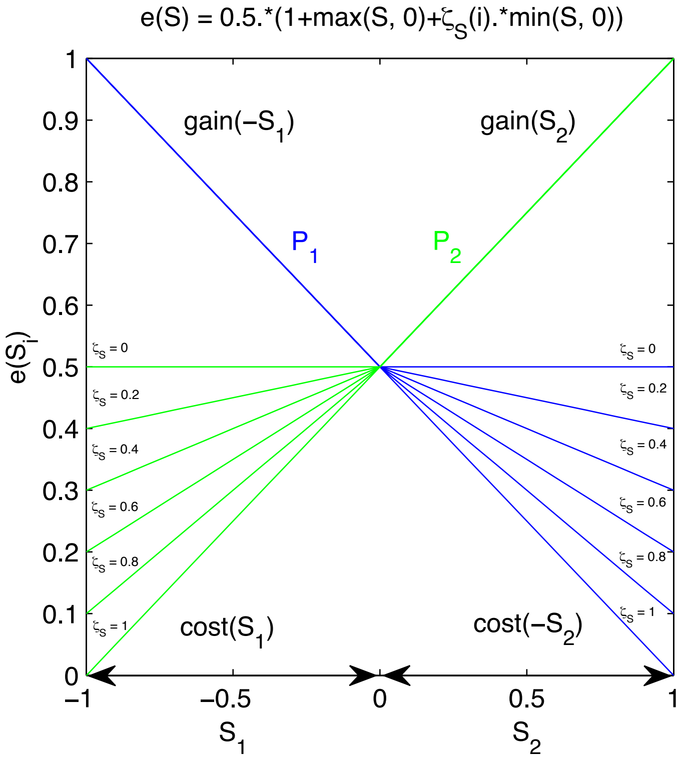

Figure 10. Effect of the specialisation (S_i) on the foraging efficiency ($e(S_i)$) for both predators consuming both prey species. $S_1 \in [-1;0]$ is the specialisation of the first predator Z_1 on the first prey species P_1 (blue) where: $e(-S_1) \in [1;0.5]$ is a foraging efficiency of Z_1 on the preferred prey P_1 (gain) and $e(S_1) \in [0;0.5]$ is a foraging efficiency of Z_1 on the less-preferred prey P_2 (cost). $S_2 \in [0;1]$ is the specialisation of the second predator Z_2 on the second prey species P_2 (green), where: $e(S_2) \in [1;0.5]$ is a foraging efficiency of Z_2 on the preferred prey P_2 (gain) and $e(-S_2) \in [0;0.5]$ is a foraging efficiency of Z_2 on the less-preferred prey P_1 (cost). Thus, specialisation produces gains if $e(S) > 0.5$ and costs if $e(S) < 0.5$. $\zeta_{\mathrm{S}} \in [0;1]$ is the cost-coefficient indicating costs of specialisation.

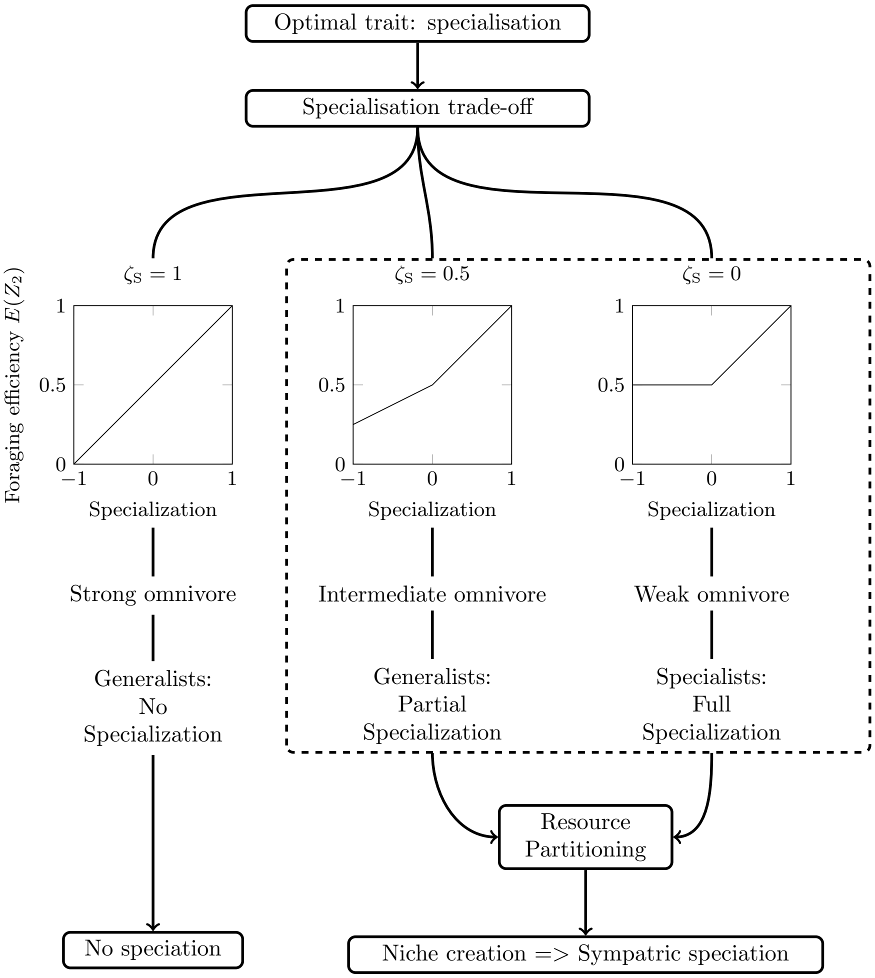

Figure 11. Mechanism of the trade-off between costs and gains for optimal specialisation. The cost of specialisation is described by the cost coefficient $\zeta_S \in [0;1]$. The relationship between costs and gains of specialisation for predator i is given by $\frac{\partial e(S_i)}{\partial S} = -\zeta_S \frac{\partial e(-S_i)}{\partial S}$ (Fig. 10). Left, $\zeta_S = 1$ produces a zero-sum game, which corresponds to the food preferences in many ecosystem models. Middle and right, $\zeta_S < 1$ result in plus zero-sum games indicating the advantage in foraging efficiency caused by specialisation on the preferred prey owing to the retained ability to eat the less-preferred prey. Corresponding fitness landscapes are shown in Fig. 12a for no specialisation, Fig. 12b for partial specialisation and Fig. 12c for full specialisation. The dashed box highlights cases which result in disruptive selection and resource partitioning.

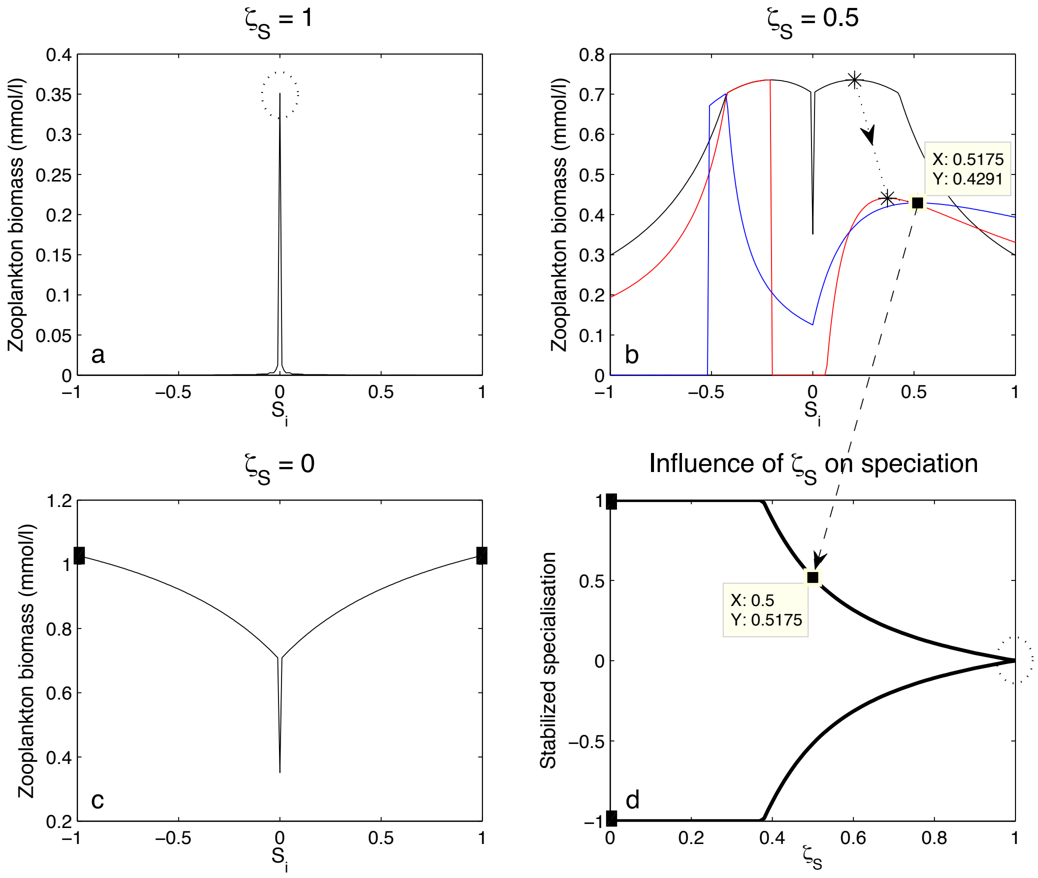

Figure 12. Influence of specialisation costs (ζ_S) on speciation and resource use efficiency. a-c, zooplankton population biomass as a function of specialisation ($S_i \in [-1; 0]$ - means specialisation on the first prey, $S_i \in [0; 1]$ - means specialisation on the second prey). *a*, no niche creation at highest costs. *b*, creating two niches with intermediate costs. The black curve shows the initial symmetric fitness landscape and the development of two niches after the first evolutionary iteration. The red curve displays one of the consecutive evolutionary steps on the way to niche-stabilisation. The blue curve shows the stabilised niches. The dotted line indicates the stabilisation process. *c*, creating two niches with no costs. *d*, stabilised specialisation as a function of specialisation costs. Small filled squares in *b* and *d* and the dashed arrow show a stabilised niche for $\zeta_S = 0.5$. Both curves hit the specialisation axis at costs ≈ 0.37 for the parameter values in Table 1. Large filled squares in *c* and *d* indicate a full specialisation at lowest costs. Dashed circles in *a* and *d* indicate no specialisation and no niche creation at highest costs.

3 Sympatric co-evolution of predator and prey traits

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Abstract

Sympatric speciation is the establishment of new species without geographic isolation[27,32,261]. One of the possible mechanisms of sympatric speciation is resource partitioning by specialisation on a preferred prey which allows predators to reduce the competition via creation and stabilisation of new ecological niches. This increases grazing pressure on prey. Prey in turn may respond by changing traits. Here, we explore sympatric speciation in the face of simultaneous co-evolution of a prey trait (growth rate) and a predator trait (specialisation) in a simple predator-prey interaction model. We find that the space defined by all combinations of predator-prey traits can be divided into three regions: (1) the speciation space, where the combinations of traits allow speciation leading to the establishment of two sympatric predator species; (2) the vanishing speciation space, i.e. the range of combinations allowing only ephemeral speciation and (3) the displacement space, where the resident predator is displaced by a single mutant. Changes in growth rate of one prey result in the increase in prey fitness and decrease in predator fitness with the prey fitness maxima and predator fitness minima on the borders of the speciation space, which we call speciation thresholds. The evolution of prey towards speciation thresholds drives one of the predators to extinction directly after the crossing the threshold, which potentially opens a new opportunity for resource partitioning for the remaining predator. Thus, our results reveal conditions needed for the appearance of sympatric speciation and show that the co-evolution of traits can lead to the evolutionary cycles in predator-prey interactions as described in the "Red Queen theory"[256].

3.1 Introduction

Darwin's 'On the Origin of Species by Means of Natural Selection'[45] set the stage to understanding sympatric speciation, which is speciation without geographic isolation. The famous Darwin finches colonised the Galapagos islands and developed different phenotypes (beak forms, body size) by specialisation on different kinds of food. Being often too time expensive for laboratory experiments, evolution in general, and sympatric speciation in particular, is best studied using mathematical models. The first mathematical representations of sympatric speciation was by Maynard Smith in 1966 applying population genetics[228]. Later, population genetics extended sympatric speciation to other non-adaptive causes of evolution, e.g., mutations, genetic drift, strength of disruptive selection, recombination rate etc.[80,83,138–140,142,251]. The main problems with these models were that they required the existence of predefined ecological niches and assumed disruptive selection against intermediates. This problem was first solved by the adaptive dynamics approach, which studied the adaptive causes of sympatric speciation in both sexual and asexual populations[48,49,53,88,141,175]. However, in spite of the abundance of models dealing with sympatric speciation and ample evidence in, e.g., plants[210], insects[39] and fish[16], a concrete mechanism for sympatric speciation via specialisation on different resources as suggested by Darwin was proposed only recently by an optimal-trait approach[280]. In this study we showed that reduced specialisation-costs can generate disruptive selection and cause evolutionary branching, which may lead to sympatric speciation in predators for the case of static prey traits. One of the findings of that study was that speciation of the predator increased the grazing pressure on prey.

Most organisms are either predators or prey[3] and are subject to some form of predator-prey interaction[6]. Planktonic evolution is dominated by protection, not competition[227], thus predation strongly influences the evolution of algae[223,259]. Several studies have shown that the introduction of a new predator[62], or evolutionary change in the predator, may produce an evolutionary response in the traits of the prey[4], also called "anti-predator effort"[1] or "anti-predator behaviour"[156]. For instance, a predator may influence the immediate per capita growth rate of a prey[5]. Predators in turn will readapt to the changes in prey traits[155]. This is in line with Van Valen's "Red Queen" hypothesis, which predicts the continuous co-evolution of coexisting species[4,256].

Therefore, in the present study we allow a prey species to adjust its growth rate in response to increasing grazing pressure. The goal of this paper is to explore evolutionary and population dynamics in a four-species Optimality-Trait based Sympatric Speciation Model (OTSSM[280]) during the co-evolution of two traits: specialisation in predators and growth rate in prey species. We use a sympatric speciation model because the marine environment has no clear geographic boundaries. Particularly, we examine different combinations of traits in a predator-prey interaction model of the marine plankton community in order to find combinations of traits allowing speciation (and coexistence) in predators and combinations which do not. We suggest that a set of combinations exists where speciation (and coexistence) is possible and threshold combinations beyond which it is impossible.

3.2 Methods

In order to explore sympatric co-evolution of traits, we employ a predator-prey interaction model[280] representing a simple ecosystem with two primary producers (prey species, P_1 and P_2) and two herbivores (predators, Z_1 and Z_2) undergoing evolutionary dynamics. We assume a closed system with plus- or minus zero-sum games between the trophic levels within this system. We consider specialisation $S_i \in [-1; 1]$ as the evolving trait in the two predators and maximum specific growth rate $\mu_{max,1} \in [0.05; 5.05]\,\mathrm{d}^{-1}$ as the evolving trait in the first prey species P_1 (Fig. 13), whereas the maximum specific growth rate of the second prey P_2 remains constant at $\mu_{\mathrm{max},2} = 2\,\mathrm{d}^{-1}$. Evolution is assumed to favour the trait associated with the greatest fitness, whereby fitness is defined here as steady-state population biomass[280].

$S_1 \in [-1; 0]$ is the specialisation of the first predator (Z_1) on the first prey (P_1), $S_2 \in [0; 1]$ is the specialisation of the second predator (Z_2) on the second prey (P_2) and $S_i = 0$ indicates no specialisation (omnivory or generalism as opposed to specialism). The sign of S determines which is the preferred and which is the less-preferred prey, so for $S < 0$ P_1 is preferred and for $S > 0$ P_2 is preferred. Specialisation is assumed to affect the foraging efficiency of the predator (e, the ability to capture and eat prey). Gains and costs of specialisation define a trade-off associated with prey preference: gains are due to an improved foraging efficiency of the preferred prey, $e(S) > 0.5$, and costs are owing to the reduced foraging efficiency of the less-preferred prey, $e(S) < 0.5$ (Fig. 14). This definition allows to use S_i and $-S_i$ to characterise effects of specialisation with respect to both prey types: $e(-S)$ describes the effect of specialisation on the foraging efficiency on P_1 and $e(S)$ is the effect of specialisation on the foraging efficiency on P_2 (Fig. 14). $S < 0$ indicates specialisation on only the first prey, since in this case $e(-S)$ is a gain and $e(S)$ is a cost. Specialisation is only on the second prey for $S > 0$, where $e(-S)$ is a cost and $e(S)$ is a gain.

We assume that an increase in gains is coupled to some loss in costs. The coupling is quan-

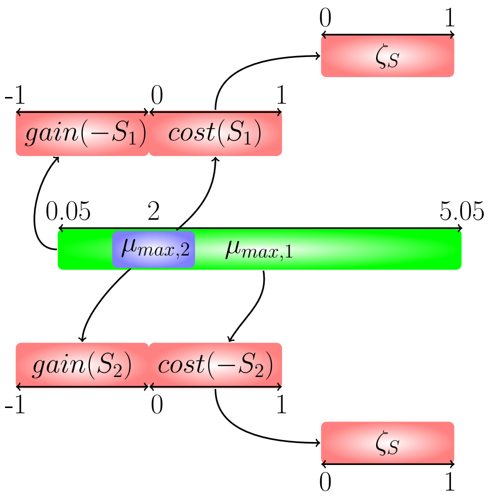

Figure 13. Conceptual representation of the adaptive traits of the model. Red indicates the specialisation trait (S_i) of predators (Z_1, Z_2), green - the evolving growth rate ($\mu_{max,1} \in [0.05; 5.05]\,\mathrm{d}^{-1}$) of the first prey ($P_1$) and blue - the (constant) stable growth rate ($\mu_{max,2} = 2\,\mathrm{d}^{-1}$) of the second prey ($P_2$). $-S_i \in [-1; 0]$ is the specialisation of the predator on the first prey and $S_i \in [0; 1]$ is the specialisation of the predator on the second prey. $\zeta_\mathrm{S} \in [0; 1]$ - is the cost-coefficient as a part of costs in the specialisation trade-off.

tified with the help of the cost-coefficient (ζ_S, Fig. 13, all symbols are defined in Table 1 of the OTSSM). A cost of $\zeta_\mathrm{S} = 1$ implies that any gain in foraging efficiency of the preferred prey is offset by an equal loss in foraging efficiency of the less-preferred prey. A cost of $\zeta_\mathrm{S} = 0$ indicates that the foraging efficiency of the less-preferred prey is not affected by specialisation, while the foraging efficiency of the preferred prey increases due to specialisation (Fig. 14).

Changes in the foraging efficiency of the predator via adaptive specialisation may cause reciprocal changes in the growth rate of the prey. Therefore, in a series of simulation experiments, prey mutants are introduced as new species of the first prey, P_1, which can have different maximum growth rates, $\mu_{max,1}$. The growth rate of the first prey was varied between 0.05 and 5.05 d^{-1} and the specialisation cost-coefficient ζ_S between 0 and 1, while the growth rate of the second prey, $\mu_{max,2} = 2\,\mathrm{d}^{-1}$, was held constant (Fig. 13). Simulations of the OTSSM for each combination of ζ_S and $\mu_{\mathrm{max},1}$ allowed to construct fitness landscapes for both predator and prey species (Figs. 17, 18, 19).

For each simulation experiment, we start out with a single ecological niche inhabited by one omnivorous predator population and two populations of different prey species. We define the fitness of an assumed mutant Z_2, with specialisation $S_2 \in [-1; 1]$ as its steady-state

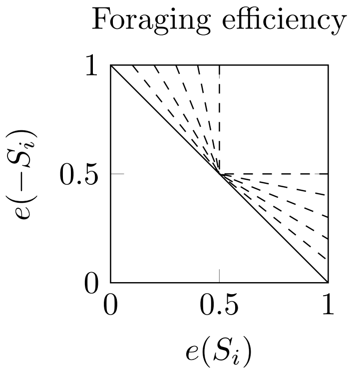

Figure 14. Effect of the specialisation (S_i) on the foraging efficiency ($e(S_i)$) for both predators, with specialisation cost-coefficient $\zeta_\mathrm{S} \in [0;1]$, $\frac{\mathrm{d}e(S_i)}{\mathrm{d}S} = -\zeta_\mathrm{S}\frac{\mathrm{d}e(-S_i)}{\mathrm{d}S}$, consuming both prey species. $e(-S_1) \in [1;0.5]$ is a foraging efficiency of Z_1 on the preferred prey P_1 (gain) and $e(S_1) \in [0;0.5]$ is a foraging efficiency of Z_1 on the less-preferred prey P_2 (cost), $e(S_2) \in [1;0.5]$ is a foraging efficiency of Z_2 on the preferred prey P_2 (gain) and $e(-S_2) \in [0;0.5]$ is a foraging efficiency of Z_1 on the less-preferred prey P_1 (cost). Our concept of foraging efficiency at $\zeta_\mathrm{S} = 1$ corresponds to the classical concept of food preferences, where the sum of the foraging efficiencies e is always equal to 1 (zero-sum game, solid line). For $\zeta_\mathrm{S} < 1$, the sum of the foraging efficiencies becomes greater than 1 (plus zero-sum game, dashed lines).

abundance in the presence of a resident population Z_1 with $S_1 = 0$. The resulting two-dimensional fitness landscape for Z_2 is initially symmetric and can have one (for $\zeta_\mathrm{S} = 1$) or two (for $\zeta_\mathrm{S} < 1$) optima ($S_2^{\mathrm{opt,j}}$)[280].

Evolution is initialised by replacing one of the original residents with either of the two fittest mutants, so that one of the mutants becomes the new resident. For example, for $\zeta_\mathrm{S} = 0.5$, we find two optima at $S_2^{\mathrm{opt,1}} = -0.21$ and $S_2^{\mathrm{opt,2}} = 0.21$. We then assign one of the optimal degrees of specialisation to the new resident, e.g., $S_1 = S_2^{\mathrm{opt,1}} = -0.21$ and re-evaluate the fitness landscape for Z_2 with specialisation $S_2 \in [-1;1]$ (for details refer to Zablotski et al., (2014)[280]). Stabilisation of the two niches is then demonstrated by repeatedly (1) evaluating the fitness landscape of a new mutant predator Z_2 and (2) assigning the local optimum close to the previous one until both $S_2^{\mathrm{opt,j}}$ stop changing and converge to two separate and stable niches. In the following, we term one cycle of steps (1) and (2) as one evolutionary iteration. Niches are considered created after the appearance of one minimum (branching point) and two maxima on the fitness landscape. Niches are considered stabilised if the total of the last three changes in the population biomass is less than 0.001 mmol/l. The iterative optimisation was stopped and the number of evolutionary iterations, which we call

evolutionary time, was recorded if (1) one of the predators had gone extinct (no speciation) or (2) the niches stabilised (speciation). Otherwise, optimisation was limited to one hundred evolutionary iterations.

To account for the fact that speciation can occur on vastly different time scales[60,137,171,218,221], we compare the evolutionary time needed for speciation under different conditions. We plot the evolutionary time to extinction (Fig. 16a) or niche stabilisation for all trait combinations of $\mu_{max,1} \in [0.05; 5.05]\,\mathrm{d}^{-1}$ and $\zeta_\mathrm{S} \in [0; 1]$ in an **evolutionary time landscape** (Fig. 16b). We define the **speciation space** as containing all combinations of traits which allow speciation after the stabilisation of created niches or do not cause extinction after 100 evolutionary iterations. The set of all combinations which cause the displacement of one of the predators after the initial creation of transitory new niches, we call the **vanishing speciation space**. Finally, the combinations which result in displacement of one predator by the other after the first evolutionary iteration, we call the **displacement space**. We define the border of the speciation space as the **speciation threshold** (Fig. 17). Population biomasses of primary producers and herbivores are displayed as fitness landscapes: merged (Fig. 17), separate (Fig. 18) and superimposed (Fig. 19). The nutrients in our closed system are found only in the organisms and in the surrounding medium. Thus, we can also define a **nutrient landscape** which solely mirrors the change in the environmental nutrient concentration during the evolution of the prey growth rate, $\mu_{max,1}$, simulated for all specialisation costs, ζ_S (Fig. 15).

3.3 Results and Discussion

Several studies have shown prey to evolve in response to the presence of a predator[6]. Thus, the core of this study is the change of a trait in a prey species (phytoplankton) as an evolutionary response to increased predation (zooplankton). The increased predation results from sympatric speciation via evolutionary branching in the OTSSM. Several empirical studies have verified the existence of evolutionary responses to predation, e.g., development of various ornamentations[153,238,254], body shapes[269], sizes, the foundation of colonies, the production of spines[111], release of toxins or repellents[191], or a change in the growth rate[5]. Our main results are: (1) sympatric speciation can occur under different combinations of predator-prey traits, summed up in the speciation space (Fig. 16) and (2) sympatric coevolution of predator and prey traits can lead to evolutionary change in one species as a response to the evolutionary change in the other species (Fig. 19) as suggested by "Red

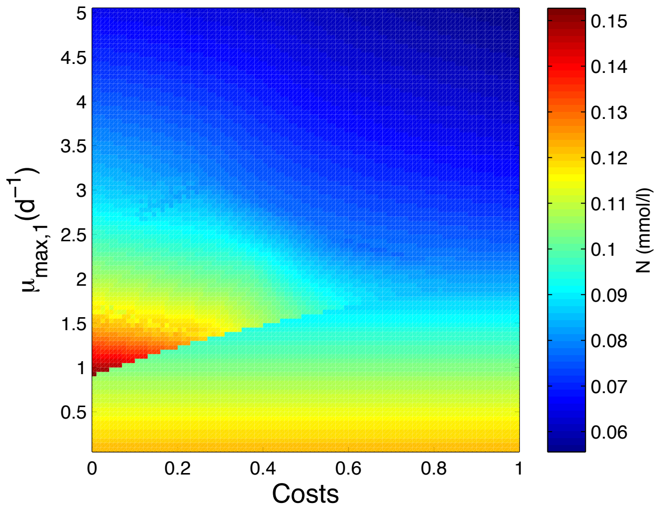

Figure 15. Nutrient landscape displays changes in nutrient concentration of surrounding medium as a function of the cost-coefficient, $\zeta_S \in [0;1]$, and the evolving trait of the first prey species, $\mu_{max,1} \in [0.05; 5.05]\,\mathrm{d}^{-1}$.

Queen" hypothesis[256].

The evolution is driven either bei (1) occupation of the new habitats, or (2) competitively induced specialisation within communities[208]. The marine diversity compared to the terrestrial diversity is highly saturated[15], so that speciation most probably happens via creating new niches in the formed marine communities rather than via occupation of the new habitats. Thus, unclear geographic boundaries in the marine environment and highly saturated communities make sympatric speciation via specialisation a suitable explanation for the evolution of marine organisms.

Our model shows that the increase in $\mu_{max,1}$ and ζ_S result in higher nutrient assimilation by the organisms (Fig. 19). Consequently, less nutrients remains in the environment (Fig. 15). However, a reduction by ca. $0.1 (mmol/l)$ is not critical compared to ca. $10.28 (mmol/l)$ nutrients contained in the organisms. Therefore, the nutrients in our model system are used effectively and are redistributed between the organisms in terms of biomass on the fitness-landscape (Fig. 19). The nutrients are used by the organisms independently of whether speciation in the predators occurs or not.

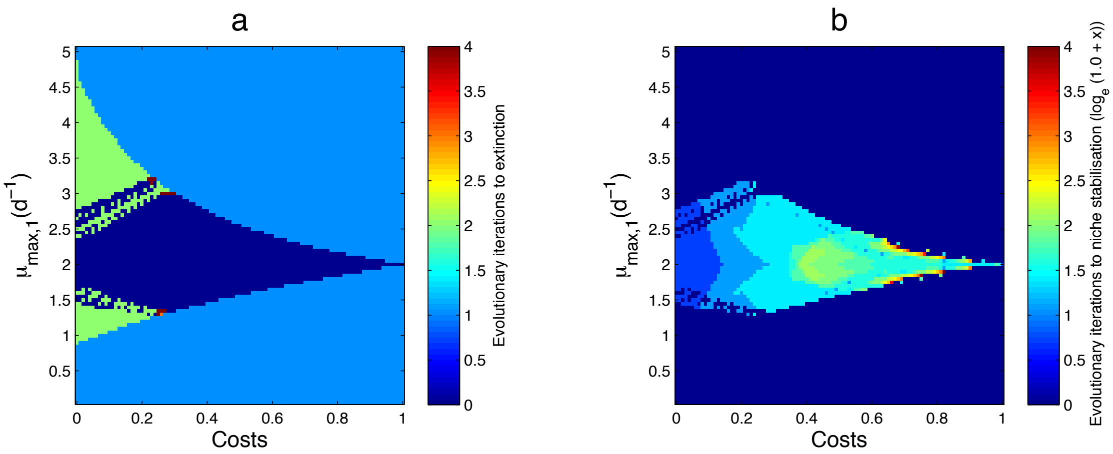

Figure 16. Speciation space displays the occurrence or the absence of sympatric speciation (a). Evolutionary time landscape displays the number of evolutionary iterations needed for speciation (b). Both, speciation space and evolutionary time are functions of the cost-coefficient, $\zeta_{\mathrm{S}} \in [0;1]$, on the x-axes and the evolving trait of the first prey species, $\mu_{max,1} \in [0.05; 5.05]\,\mathrm{d}^{-1}$ on the y-axes.

3.3.1 Speciation space and Evolutionary time

Fig. 16 shows the occurrence of sympatric speciation or the displacement in zooplankton (Fig. 16a) and evolutionary time needed for stable speciation to occur (Fig. 16b) for different combinations of predator and prey traits. All combinations of traits in (Fig. 16a) result in a surface showing three evolutionary outcomes in the predator: (1) the region where two ecological niches are created and stabilised is the **stable speciation space** (dark blue color in Fig. 16a); (2) the region where niches are created but not stabilised because one of the predators goes extinct is the **vanishing speciation space** (yellow and red colors in Fig. 16a) and (3) the region where no niches are created because one of the predators is displaced by the other after the first evolutionary iteration is the **displacement space** (light blue color in Fig. 16a). While speciation occurs in both the stable and the vanishing speciation spaces, we will refer to the speciation space as the stable speciation space because only in this area the speciation remains evolutionarily stable. For a few combinations of ζ_{S} and $\mu_{\mathrm{max},1}$ ecological niches are created with stable (not-overlapping) oscillations. They can be called **stable oscillating speciation**, because despite the oscillations the two niches are retained.

One of the prerequisites of speciation is the evolutionary branching. The evolutionary branching in our study is derived in a different mathematical way compared to the adaptive dynamics, mainly because of the distinctive definition of fitness. While in the adaptive dynamics fitness is defined as the long-term growth rate[87], we here define fitness as a steady-state population biomass. Our definition allows the direct comparison of coexisting populations while fitness in the adaptive dynamics is always equal to zero at steady state, i.e. fitnesses of the coexisting populations are equal[87] and thus not directly comparable.

The two unequal peaks on a fitness landscape in our approach do not lead to the displacement of one of the predators if the two maxima (two ecological niches) are stabilised via iterative optimisation (Fig. 12 in the OTSSM). In this case sympatric speciation is evolutionarily stable for two species with different fitnesses. This works against the "survival of the fittest" principle[235] but for the survival of the coexisting (speciation space in Fig. 16). We suggest that nature has a variety of successfully coexisting populations with non-identical fitness, otherwise current diversity would be reduced to a very few species. Thus, the comparability of fitness of the co-evolving species was one of the main goals of the fitness definition in this study.

The cases where one of the predators displaces the resident (displacement space in Fig. 16a) and where one of the predators displaces the other after initial speciation (one of the unequal peaks disappears during the optimisation, vanishing space in Fig. 16a) both confirm the "survival of the fittest" principle. Thus, our model shows that both coexistence and competitive exclusion are the driving forces of evolution occurring at different ecological conditions (combinations of traits).

Every particular specialisation cost is associated with a different range of trait values in $\mu_{\mathrm{max},1}$ allowing speciation (Fig. 16a). The higher the specialisation costs, the narrower the range allowing speciation, so that one would expect wider speciation ranges at lower costs. Our model results confirm this expectation and agrees with the suggestion that "costs of being choosy ... act against sympatric speciation"[82]. Interestingly, the lowest costs $\zeta_{\mathrm{s}} \in [0; 0.30]$ allow speciation in a wide range of $\mu_{\mathrm{max},1}$, but the niches do not stabilise throughout this wide range, hence invaders disappear after few evolutionary iterations when the difference between prey species becomes too large (yellow and red colors in Fig. 16a). We call this vanishing speciation because two species (two maxima on the fitness landscape) occur initially but only one of them remains after iterative optimisation. As a result, the stable speciation range initially widens as costs increase. In the beginning, the fitness of both mutants in the vanishing speciation space is higher than the fitness of the resident. But one of the mutants is then displaced because the fitness of the second mutant greatly exceeds the fitness of the first. Vanishing speciation needs just several (2-4) evolutionary iterations until one of the predators becomes extinct (color bar in Fig. 16a).

The evolutionary time landscape shows the number of evolutionary iterations needed for the stabilisation of niches within the stable speciation space along both cost and trait gradients (Fig. 16b). Our results show that the more costly the specialisation, the more evolutionary time is needed to stabilise the niches. The cost $\zeta_s = 1$ is an exception, because there is no speciation and therefore nothing to stabilise. There are only a few (among all 10201 model simulations) damped oscillations (not shown) which could stabilise after more than one-hundred evolutionary iterations, but because of the very low number we consider them irrelevant.

The line cutting the stable speciation space in half along the cost gradient, where growth rates of both prey species are identical, $\mu_{max,i} = 2\,\mathrm{d}^{-1}$, we call the **prey-equality line**. The evolutionary time landscape on the prey-equality line resembles a bell curve, with the top of the bell at intermediate costs, $\zeta_s \in [0.4; 0.6]$. The middle part of the bell shows the largest evolutionary time for the stabilisation of niches. In turn, lower and higher costs allow faster speciation. This indicates that strong and weak cost-reducing mutations favour speciation, while intermediately strong mutations hamper speciation. The evolutionary time on the edges of speciation space looks like a bell curve shifted to the right, with the top of the bell at higher costs, $\zeta_s \in [0.55; 0.9]$. The evolutionary time along the trait gradient does not change with $\mu_{max,1}$ in the area of low costs, $\zeta_s \in [0; 0.35]$, looks like a bell curve at intermediate costs $\zeta_s \in [0.35; 0.55]$ and like an upside-down bell curve at high costs, $\zeta_s \in [0.55; 0.9]$. This implies that the bigger the difference between prey species, the more time at high costs and the less time at intermediate costs is needed for sympatric speciation to stabilise. Differences between the prey species do not influence evolutionary time at low costs.

In this way our model shows that evolutionary branching and subsequent sympatric speciation possess a certain flexibility because they require different durations to create and stabilise new niches given different combinations of predator-prey traits. This is similar to the suggestion from the adaptive dynamics framework that "evolutionary branching is a generic and robust phenomenon ... [and can occur] ... under a wide range of different ecological conditions"[53]. The evolutionary time is important for understanding speciation because the more evolutionary time is needed to stabilise the niches, the more risk exists that something like restored gene flow, hybrids, or altered environmental conditions might hinder or prevent stable speciation.

Considering the width of the speciation space and the height of the evolutionary time land-

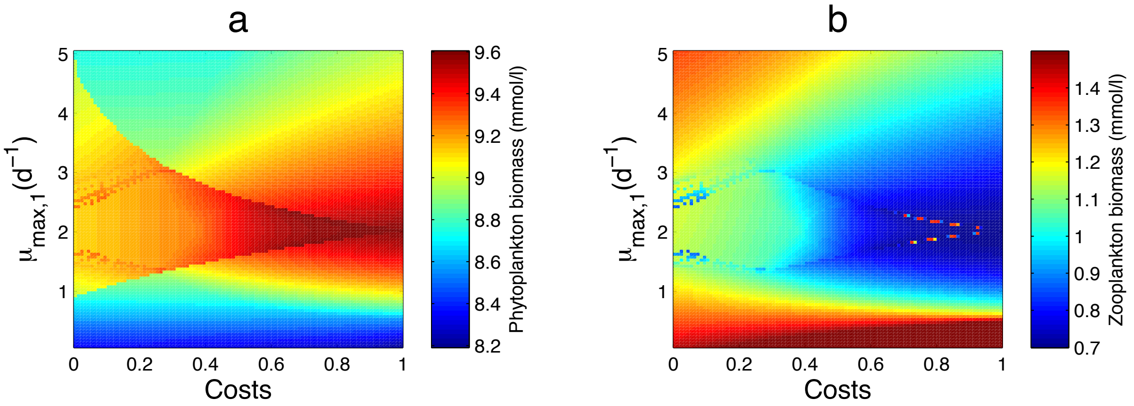

Figure 17. Merged fitness landscapes for both prey species (a) and merged speciation landscapes for both predators (b). Both graphs display population biomasses as a function of the cost-coefficient, $\zeta_S \in [0;1]$, and the evolving trait of the first prey species, $\mu_{max,1} \in [0.05; 5.05]\,\mathrm{d}^{-1}$.

scape we can conclude that the most favorable conditions for sympatric speciation are: (1) low specialisation costs (strong cost-reducing mutations), (2) big differences in growth rate of prey species at intermediate costs and (3) small differences in growth rate at high specialisation costs (weak cost-reducing mutations). The shortest evolutionary time (Fig. 16b) corresponds to the highest predator biomass (Fig. 17b) within the speciation space, while the longest evolutionary time is associated with low biomass in zooplankton.

3.3.2 Speciation threshold

Speciation thresholds are the narrow bands in speciation space along the cost gradient which separate the space of stable speciation from the two adjacent spaces of displacement. Speciation thresholds are displayed in the Figure 17 which represents the summed biomasses of the two prey species (Fig. 17a) and the two predators (Fig. 17b). Fitness landscapes show that in general phytoplankton biomass is high and zooplankton biomass is low in the speciation space. In contrast, phytoplankton biomass is low and zooplankton biomass is high in displacement spaces. This implies that speciation in the predator is more advantageous for the prey species than for the predator itself (except of prey-equality line).

The shape of the prey fitness landscape within speciation space is slightly concave, while the shape of the predator speciation landscape is slightly convex. This agrees with the suggestion that changing a trait value from "most vulnerable", which in our case would be the prey-equality line, enables the first prey to reduce predatory pressure and increase its

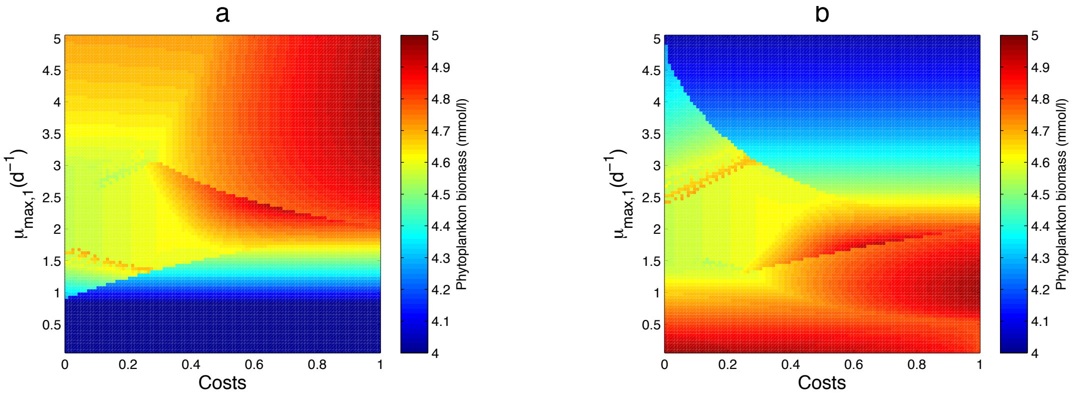

Figure 18. Separate fitness landscapes for both first (a) and second (b) prey species, both display population biomasses as a function of the cost-coefficient, $\zeta_S \in [0; 1]$, and the evolving trait of the first prey species, $\mu_{max,1} \in [0.05; 5.05]\,\mathrm{d}^{-1}$.

own biomass[6]. Moreover, hillocks in the phytoplankton fitness landscape showing the maximal biomasses of prey and valleys in zooplankton fitness landscape showing the minimal biomasses of predator species are located exactly on the speciation thresholds (Fig. 17). Thus, the movement of the prey from the prey-equality line towards the speciation thresholds shows the prey's strategy to escape the grazing pressure with the optimum on the speciation thresholds for each particular cost value. After passing the threshold one of the predators goes extinct. This relieves the remaining predator from interspecific competition, which immediately results in the increase of the predator biomass (displacement spaces in Fig. 17b). Such increase may reinforce intraspecific competition and, along with the two available resources, opens the single remaining predator a new opportunity for potential resource partitioning which would close the evolutionary cycle of continuous mutual co-adaptation in predator-prey interactions suggested by the "Red Queen" hypothesis[256]. Except the prey-equality line, where speciation increases fitness of the predator and decreases fitness of the prey, allowing speciation in the predator within a speciation space seems to be positive for the prey because it keeps the interspecific competition in predators high. Predator also might need to develop some offensive adaptations in response to the anti-predator changes in prey-traits, simply because adaptation requires energy and therefore has costs[3].

Speciation thresholds of prey species on the merged fitness landscapes could be considered their optimal lines because the thresholds display the highest biomass values of prey species for any particular cost within the speciation space (Fig. 17a). Interestingly, the optimal line for a particular prey species is not just one of the speciation thresholds. The optimal line of the first (evolving) prey species consists of two segments: (1) **the low-cost segment** at costs $\zeta_{\mathrm{s}} \in [0; 0.27]$ (below the prey-equality line along the trait gradient) where the first prey species grows more slowly compared to the second prey species and (2) **the high-cost segment** at costs $\zeta_{\mathrm{s}} \in [0.28; 1]$ (above the prey-equality line) where the first prey species grows faster (Fig. 18a) than the second prey species.

The low-cost segment of the optimal line could be explained with a **passive competitive strategy** of the first prey species against the second prey species, because if the second prey species grows faster, the second predator can easily specialise on it due to low specialisation costs and keep the population biomass of the second prey species low. Moreover, the competitive success of the second predator against the first predator will also reduce the grazing pressure on the first prey species. This agrees with the concept of "evolution along genetic lines of least resistance"[213]. Vice versa, increasing growth rate at low specialisation costs is not advantageous for the first prey species because the first predator, which specialises on the first prey species, will also increase its abundance and hence will keep the first prey species from outcompeting the second. The high-cost segment of the optimal line could be called an **active competitive strategy**, where the first prey species is able to outgrow the second, because specialisation of the first predator becomes too costly. The latter means that mutation indicated reduction in specialisation costs is not strong enough to allow predators to adjust their behaviour in the response to the anti-predator change in the prey. Thus, increasing the growth rate for the evolving first prey species is disadvantageous at low costs and profitable at intermediate and high costs.

The fitness landscape of the second prey species (Fig. 18b) does not represent a strategy, but just a response to the evolution of the first prey species, because the growth rate of the second (not-evolving) prey species is held constant while the growth rate of the first (evolving) prey species changes. This change in the evolving prey species indirectly affects the not-evolving prey species via the specialisation trade-off in predators thus influencing the shape of the fitness landscape of the second prey species. In this way, an evolving prey species is able to actively escape predation and passively compete with the second prey species by adjusting its specific growth rate.

3.3.3 Prey-equality space

Superimposing separate fitness landscapes for both prey species (P_1 vs P_2, Fig. 19) uncovers a region on the fitness landscape where both prey species have identical biomass (except for the speciation thresholds) but different trait values (except for the prey-equality line, where

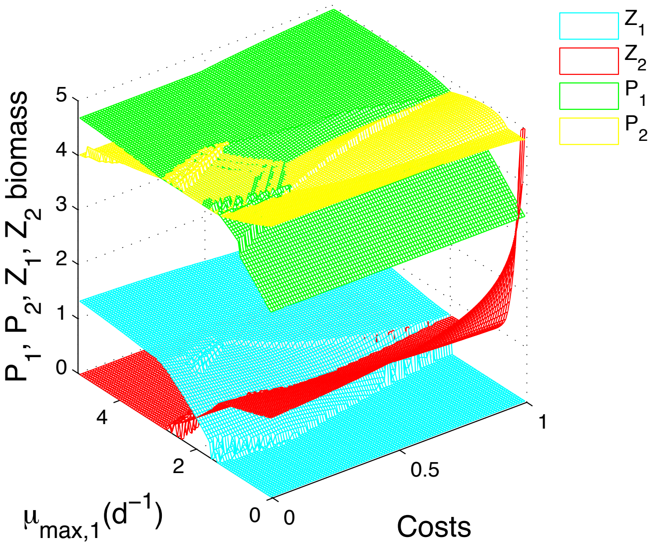

Figure 19. Superimposed fitness landscapes for both predators (blue and red) and both prey species (green and yellow) display population biomasses as a function of the cost-coefficient, $\zeta_S \in [0; 1]$, and the evolving trait of the first prey species, $\mu_{max,1} \in [0.05; 5.05]\,\mathrm{d}^{-1}$.

$\mu_{max,i} = 2\,\mathrm{d}^{-1}$) at low specialisation costs. In the following we refer to this region as the **prey-equality space**. The prey-equality space repeats the contours of the speciation space at lower costs forming a pentagon on the fitness landscape with two angles starting on a line of cost $\zeta_s = 0$. Two border lines of the prey-equality space coincide with the speciation thresholds from the cost of $\zeta_s = 0$ to the costs $\zeta_s = 0.24$ ending at the two other angles of the pentagon. Then both lines turn towards the prey-equality line and hit it at the cost of $\zeta_s = 0.36$ thus forming the last angle of the pentagon. While the biomasses of both prey species in the prey-equality space stay the same, predators respond with changing biomass. Thus, the prey-equality space could be seen as a manifestation of an indirect not-intentional mutualism in prey. Increasing costs, nevertheless, allow the first prey species to dominate over the second, whereby the prey-equality space vanishes and the fitness landscapes cross each other at the prey-equality line (Fig. 19).

Together, prey-equality space and prey-equality line show a steady increase in biomass along the cost gradient from $4.6(mmol/l)$ at a cost of $\zeta_s = 0$ to $4.8(mmol/l)$ at a cost of $\zeta_s = 1$. The equality line, where fitness landscapes of predators cross, show a decrease of predator biomass from $0.58(mmol/l)$ at a cost of $\zeta_s = 0$ to $0.35(mmol/l)$ at a cost of $\zeta_s = 0.99$ (Fig. 19). This shows that the stronger the cost-reducing mutations in zooplankton are, the more fitness do predators gain. The last point on the prey-equality line of predator fitness landscapes, at a cost of $\zeta_\mathrm{s} = 1$, shoots up to a predator biomass $0.53(mmol/l)$, where two predators stop specialising on the different prey species and fuse to one purely omnivorous population. This fusion does not affect prey biomass. The biomass of a single predator population at highest costs $\zeta_\mathrm{s} = 1$ is lower than added population biomasses after speciation at all the other costs, which indicates that speciation has a positive effect on the predator populations.

A higher growth rate of the first prey in comparison to the second increases the competitive ability in resource acquisition of the first predator due to a larger prey population. That is why the fitness of the first predator is always higher than the fitness of the second (even in the prey-equality space) as soon as the growth rate of the first prey exceeds the growth rate of the second (Fig. 19). The displacement space above the prey-equality line shows that a faster growing first prey (active competitive strategy) allows the first predator to survive and displace the second. In turn, the displacement space below the prey-equality line shows that if prey species lower their growth rate (passive competitive strategy) they can drive the first predator to extinction. Because Z_1 specialises on P_1, one would expect a positive effect of such exclusion for P_1. However, after crossing the lower speciation threshold, the biomass of P_1 continuous to decline due to increased abundance of the second predator.

Superimposing the separate fitness landscapes of both predators (Z_1 vs Z_2, Fig. 19) can be seen as mutual invasibility plots, showing not only sympatric speciation with coexistence, competition and resource partitioning within the speciation space, but also the competitive exclusion in the displacement spaces where only one predator survives. The fact that both prey species survive and even can drive one of the predators to extinction shows a stronger response of prey to predation than vice versa. This is similar to the suggestion made by Abrams (2000)[6] and is in line with "life-dinner" principle, which states that predator only runs for the dinner, while the prey runs for the life[46].

3.4 Conclusions

The current study shows that prey species are able to partly escape a grazing pressure by adapting the specific maximum growth rate. Decreasing growth rate is beneficial for the first prey at low costs (green hillocks at low costs in Fig. 19) and disadvantageous at high costs. Vice versa, increasing growth rates is disadvantageous for the first prey at low costs and beneficial at high costs. Similarly to Van Valens "Red Queen” hypothesis of co-evolution[256], our model shows a potential co-evolutionary change of coexisting species, consisting of the following steps: (1) sympatric speciation in predators along the prey-equality line in order to reduce intraspecific competition, (2) the evolution of the prey-trait as a response to the increased grazing pressure which moves the trait values from the "most vulnerable" value, on the prey-equality line, towards speciation (coexistence) thresholds and finally, (3) the displacement of one of the predators, which may provide the surviving predator with a new opportunity for resource partitioning and potential sympatric speciation, because of the growing intraspecific resource competition and two available resources. The third step is a hypothesis and would need a reformulation of the current model. Along with the finding of expected results, such as speciation and displacement spaces, we revealed some unexpected results, including the vanishing speciation space, the prey-equality space, the optimal lines and the passive and active competitive strategies of prey species. Different combinations of traits in our model determine whether "survival of the fittest” or survival of the coexisting is the driving principle of evolution. Our model offers insights into how sympatric co-evolution of traits can affect the occurrence of sympatric speciation and population dynamics in four-species predator-prey interaction system.

4 Sympatric speciation of marine zooplankton along nutrient and density-independent phytoplankton mortality gradients

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Abstract

Current global change motivated research into the evolutionary response of marine plankton to increased temperature[108,243], CO_2 and acidification[162]. However, changes in marine biodiversity as a consequence of increased nutrient concentration, e.g., eutrophication, have not been intensively studied yet. While density-dependent mortality (DDM) of phytoplankton, e.g., grazing and aggregation, was intensively studied, density-independent mortality (DIM), e.g., programmed cell death (PCD), starvation or oxidative stress, in planktonic models has not been adequately addressed. Here we use a four-species predator-prey interaction model to explore the occurrence of sympatric speciation in marine zooplankton, the coevolution of plankton, and the resource utilisation efficiency as a function of three changing quantities: environmental nutrient load (N), DIM of phytoplankton (d), and adaptive specialisation of zooplankton (S). We find that increasing environmental nutrient concentration: (1) increases the occurrence of sympatric speciation and thus promotes biodiversity; (2) lowers the effect of DIM on biodiversity; (3) changes the domination (higher biomass) of the prey over the predator in a low-nutrient environment to the domination of the predator over the prey in a high-nutrient environment; and (4) decreases overall productivity of the system, with nutrients accumulating faster in the water than they can be assimilated by the organisms, which might lead to a higher pollution level.

4.1 Introduction

Nutrient cycles in the ocean are primarily controlled by microorganisms because they constitute more than 90 per cent of the living biomass in the sea[239]. Marine microorganisms are responsible for roughly half of the Earth's primary production[14,67,108], circa half of the carbon dioxide sink[149] and produce approximately half of the Earth's oxygen[239]. Due to the high importance of the microorganisms for the global nutrient cycles, it is crucial to understand their evolutionary processes, e.g., speciation and extinction. Because of the unstructured marine environment[112] which has no clear geographic barriers, understanding sympatric speciation[45], which is speciation without geographic isolation, in plankton becomes particularly important, compared to allopatric (geographic) speciation[167,170]. Sympatric speciation in the marine environment may be caused by resource competition, which first generates disruptive selection[178], then motivates resource partitioning and finally leads to reproductive isolation of sympatric species[48,86,219]. However, despite the fact that the ocean covers 71% of the Earth, sympatric speciation in terrestrial systems has gained much more attention while in marine systems it was largely ignored[164].

The survival of marine microorganisms strongly depends on the availability of nutrients and the mortality rate. Nutrient inputs stem from non-anthropogenic (e.g., remineralisation, N_2 fixation) and anthropogenic (e.g., synthetic fertiliser addition) sources. While eutrophication may increase the phytoplankton biomass, it can reduce the number of genera in a sample[144]. Too low or too big nutrient inputs can influence the productivity of the system and change the biodiversity or the composition of marine plankton[14]. For instance, nitrogenous fertiliser of agricultural origin can cause massive toxic phytoplankton blooms[19,234]. Around 40% of the world's dietary protein has been produced using the Haber-Bosch process for synthetic fertilisers, which are keeping two billion people alive[79]. Moreover, nitrogen deposition is prognosed to increase in the future[78,79,266]. Therefore, it is important to understand the effects of increasing environmental nutrient concentration on biodiversity.

Although phytoplankton growth was intensively studied, phytoplankton death received relatively little attention[25,72]. However, population crashes in the laboratory and nature indicate that mortality of phytoplankton is not solely density-dependent (DDM), e.g., grazing or aggregation, but also density-independent (DIM)[72]. For instance, cell death by lysis can exceed 50% of the phytoplankton population[25,130]. Sheldrake (1974) reports that even exponentially growing populations contain dividing, non-dividing and dying cells[222]. This implies that both grazing and DIM may be present in growing or crashing populations. While both grazing and DIM have been included in plankton models since the very beginning, DIM remains not adequately addressed. DIM of phytoplankton can be caused by environmental stressors (nutrient deprivation, pollutants, oxidative stress, intense light, darkness, seasonal cycles)[58], natural cell death (ageing, starvation) or programming cell death (PCD, e.g., altruistic response to infection in order to stop the spread, apoptosis, paraptosis)[72]. For instance, unexplained population crashes were registered for dinoflagellates[98,99,157,252]. Bidle (2005) reports that viral infection in coccolithophore *Emiliania huxleyi* played a role in the establishment and maintenance of PCD[26]. Here we vary DIM of phytoplankton (d) independently of grazing (g) aiming to investigate the influence of DIM on the occurrence or absence of speciation in zooplankton and the competition between phytoplankton and zooplankton populations.

Phytoplankton and zooplankton are two major players in marine biogeochemical cycles. Marine phytoplankton is bottom-up controlled by nutrients and top-down controlled by DDM and DIM. This necessitates the analysis of the interplay between phytoplankton, zooplankton and environmental nutrient concentration (N). However, state-of-the-art models of sympatric speciation do not consider the combined effects of nutrient availability and DIM in prey on the evolution of specialising predators.

Here we first investigate the simultaneous effect of different nutrient loads and different DIM on the occurrence of sympatric speciation in marine zooplankton using an optimality and trait based sympatric speciation model (OTSSM[280]). Secondly, we investigate how the amount of nutrients in the system may change the effect of DIM on plankton. Thirdly, we consider whether changes in nutrient concentrations might influence survival and cause a shift in the dominating (highest fitness) species in the community. Finally, we trace the changes in the productivity of the system by comparing nutrient concentrations in organisms with the nutrient concentrations in the surrounding water at different nutrient loads.

4.2 Methods

Coexistence and evolutionary dynamics between populations in a four-species predator-prey interaction model of marine plankton (OTSSM[280]) is considered for environmental nutrient concentrations ranging from 9.41 to 30 mmol·L^{-1} and DIM values between 0.001 and 0.025 d^{-1} (Fig. 20). One run of the OTSSM is considered to be one simulation experiment. We assume no nutrients light co-limitation, no change in the stoichiometry or in nutrient uptake of the phytoplankton (P_1 and P_2) with increasing nutrient concentration. Fitness is defined

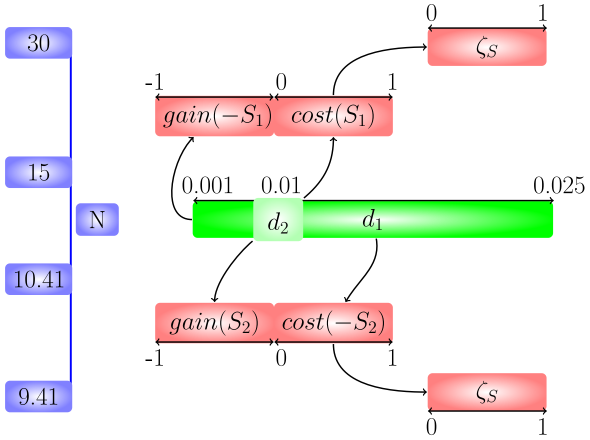

Figure 20. Conceptual representation of the changing quantities of the model: $d_1 \in [0.001; 0.025]\,\mathrm{d}^{-1}$ - is DIM of the first prey species, $S_1 \in [-1; 0]$ - specialisation of the first predator on the first prey and $S_2 \in [0; 1]$ - specialisation of the second predator on the second prey, $\zeta_S \in [0; 1]$ - is a cost-coefficient determining the degree of specialisation on the preferred or less-preferred prey, $N = [9.41, 10.41, 15, 30]$ mmol·L^{-1} - environmental nutrient concentrations. Blue indicates nutrients (N), green - phytoplankton (P) and red - zooplankton (Z).

as a steady state population biomass. Zooplankton species (Z_1 and Z_2) adjust their feeding behaviour via adaptive specialisation. The specialisation cost-coefficient, $\zeta_S \in [0; 1]$, determines the optimal degree of specialisation, $S_i \in [-1; 1]$, on the preferred or less-preferred prey. The ζ_S value is determined by cost-reducing mutations[280]. The occurrence of sympatric speciation is then studied as a function of three changing quantities (ζ_S, d_1 and N). DIM changes of the prey species alter its population biomass and therefore may cause an adaptive response in the predator. Hence, we consider DIM as a trait of prey species.

25 DIM values, $d_1 \in [0.001; 0.025]\,\mathrm{d}^{-1}$, were applied to the first phytoplankton species (P_1) while the DIM rate of the second phytoplankton (P_2) was held constant at $d_2 = 0.01\,\mathrm{d}^{-1}$ (Fig. 20). Each DIM of P_1 was then combined with 11 values of the zooplankton's specialisation cost-coefficient $\zeta_S = [0; 1]$ resulting in 275 simulation experiments (runs of the OTSSM). This allowed to construct fitness landscapes for both predators and prey species (Fig. 23, for details on the evolution of specialisation see Zablotski et al. (2014)[280]) to study evolutionary and population dynamics. We suggest that there are combinations of traits, $d_1 \in [0.001; 0.025]\,\mathrm{d}^{-1}$ and $\zeta_S \in [0; 1]$, which result in sympatric speciation (speciation space) and combinations which do not (vanishing speciation and displacement spaces, for details see Zablotski et. al., (2014)[279]). Each combination of quantities resulted in different numbers of evolutionary iterations until reaching stabilisation of the niches or extinction of

one of the predators[279] (Fig. 21).

275 simulation experiments, $d_1 \in [0.001; 0.025]\,\mathrm{d}^{-1}$ and $\zeta_\mathrm{S} \in [0; 1]$, were conducted for four environmental nutrient concentrations, $N = [9.41, 10.41, 15, 30]$ mmol·L^{-1}, resulting in 1100 simulations of the OTSSM (Fig. 21). Thus, every combination of the three quantities d_1,ζ_S and N results in a single point in a three-dimensional space. The nutrients in our closed system are found only in the organisms and in the surrounding medium. The speciation spaces for different nutrient loads were compared in order to investigate the effect of nutrient enrichment on sympatric speciation in predators.

The effectiveness of nutrient assimilation by the organisms, which we call the productivity of the system, was studied by comparing the ratio of nutrients in the environment to the nutrients in the organisms for four nutrient loads (Fig. 24). Added biomasses off all organisms (P_1, P_2, Z_1, Z_2) for all 275 combinations of predator and prey traits were averaged for each of the four nutrient concentrations to a single number, resulting in four values on the blue curve in Fig. 24. Nutrients in the water for all combinations of predator and prey traits were also averaged to a single number for each of the four nutrient concentrations resulting in four values on the green curve in Fig. 24.

4.3 Results and discussion

4.3.1 Occurrence of sympatric speciation

The occurrence of sympatric speciation in a zooplankton population increases with growing nutrient loads and with decreasing costs of specialisation (Fig. 21). This result agrees with the higher biodiversity in habitats with high nutrient availability, e.g., coral reefs or coastal areas, and low biodiversity in habitats with low nutrient availability, such as the open ocean. However, our result contradicts cases where high nutrient availability increases biomass but not the biodiversity, e.g., plankton blooms, or where a nutrient-poor environment indicates high biodiversity, e.g. some tropical rain forest areas. The degree of the positive effect of nutrient enrichment on the occurrence of sympatric speciation in our study declines with increasing specialisation costs at low nutrient loads ($N = [9.41, 10.41]$ mmol·L^{-1}, Fig. 21). In contrast, high nutrient loads ($N = [15, 30]$ mmol·L^{-1}, Fig. 21) allow for sympatric speciation even at highest costs, except $\zeta_\mathrm{S} = 1$, where speciation is not possible[280]. This indicates that nutrient-poor environments require very strongly cost-reducing mutations for speciation to occur ($N = 9.41$ mmol·L^{-1}, Fig. 21), whereas in nutrient-rich environments even a weakly

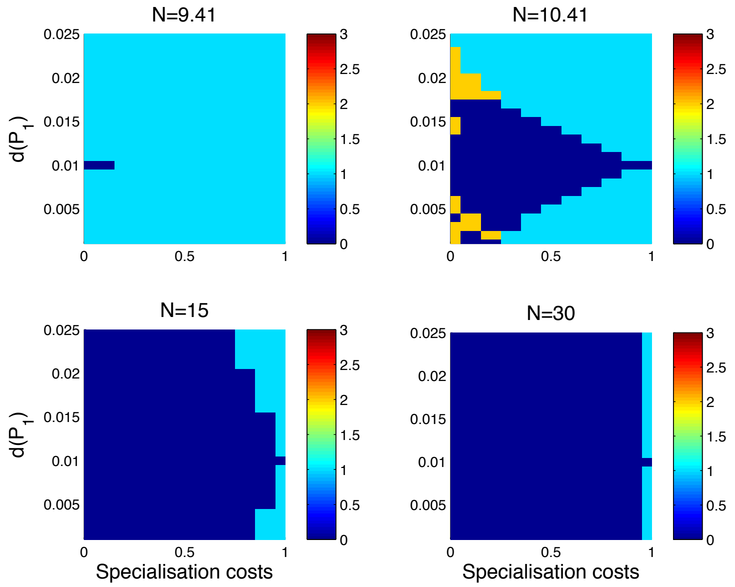

Figure 21. Speciation space (dark blue), vanishing speciation space (yellow) and displacement space (light blue) for four different environmental nutrient loads, as a function of the cost-coefficient, $\zeta_S \in [0;1]$, and the varying DIM of the first prey species, $d_1 \in [0.001; 0.025]\,\mathrm{d}^{-1}$. Color bar shows a number of evolutionary iterations needed to extinction of one of the predators.

cost-reducing mutation leads to speciation ($N = 30$ mmol·L^{-1}, Fig. 21). Thus, our model suggests that nutrient-rich systems may have a faster evolution rate (speciation rate), are more adaptable and therefore less vulnerable to changes, than nutrient-poor systems.

There are to our knowledge no studies of sympatric speciation along nutrient and DIM gradients. But a nutrient enrichment experiment in grasslands showed a decrease in biodiversity with increasing nutrient level[113], which contradicts our findings, and a decrease of ecosystem productivity, which is in line with our study (see below). However, a direct comparison of our study to nutrient enrichment experiments is not possible because nutrient enrichment experiments use gradually increasing nutrient concentrations in a short period of time, while our study examines a given state of the system at different nutrient concentrations without explicit consideration of time between the different nutrient concentrations.

On one hand, nutrient enrichment experiments[113] suggest that eutrophication or any other change in nutrient composition will inevitably decrease biodiversity. On the other hand, our model implies that high nutrient amounts in the ecosystem can benefit biodiversity. This seems to be a contradiction. But a major difference between the two above cases is the rate

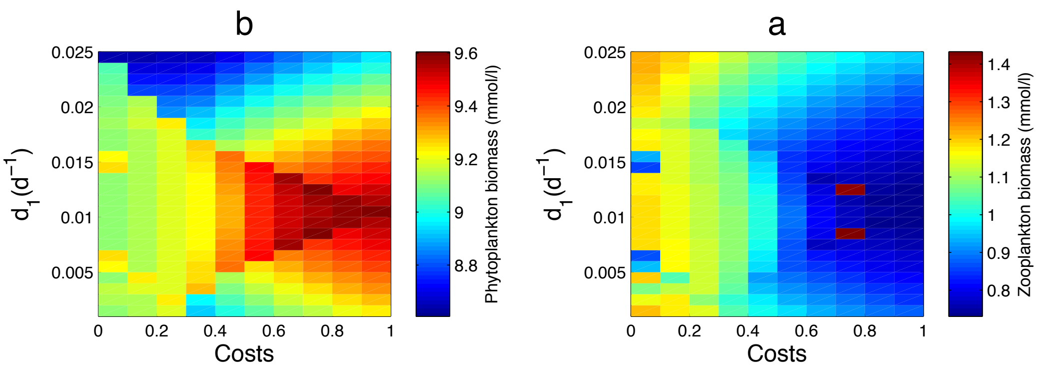

Figure 22. Merged fitness landscapes for both prey species (a) and for both predators (b) for $N = 10.41$. Both graphs display population biomasses as a function of the cost-coefficient, $\zeta_S \in [0; 1]$, and the varying DIM of the first prey species, $d_1 \in [0.001; 0.025]\,\mathrm{d}^{-1}$. The two red rectangles for costs of 0.75 in the right panel are due to a stable oscillation of the zooplankton biomass, whereby niches are stabilised by slightly varying fitness.

of nutrient enrichment. We suggest that fast nutrient enrichment reduces resource competition and allows some species to benefit more than the others, and displace them before new species appear, thus causing biodiversity loss. Extinction can be very fast, while speciation needs more time than is feasible for nutrient enrichment experiments. Therefore, decrease in biodiversity (and absence of speciation) in nutrient enrichment experiments might be viewed as a consequence of the relatively short duration of these experiments. In contrast, slow nutrient enrichment keeps resource competition high, which in the long term may create new niches and thus stimulate biodiversity as suggested by the OTSSM[280].

Fig. 21 shows that the extent of the speciation space grows fast at low nutrient loads and more slowly for high nutrient loads. Thus, adding 1 mmol·L^{-1} to the lowest nutrient loads in our model of $N = 9.41$ mmol·L^{-1} fills almost the half of the graph with speciation space (Fig. 21, $N = 10.41$ mmol·L^{-1}), while adding another 4.5 mmol·L^{-1} which should have filled the whole graph with speciation space, still leaves some displacement areas (Fig. 21, $N = 15$ mmol·L^{-1}). Nevertheless, after a certain amount of added nutrients, somewhere in between $N = 15$ mmol·L^{-1} and $N = 30$ mmol·L^{-1}, the graph is filled completely with speciation space (except $\zeta_S = 1$, Fig. 21, $N = 30$ mmol·L^{-1}).

4.3.2 Effects of DIM on plankton at different nutrient loads

Empirical evidence of DIM in the form of PCD in phytoplankton includes multiple examples. Particularly, diatoms *Ditylum brightwellii* and *Thalassiosira weissflogii* were subjected to lysis in response to nitrogen and phosphorus limitation[21,36], the dinoflagellate *Peridinium gatunese* initiated PCD due to inorganic carbon limitation[257], a green algae induces PCD under prolonged darkness[220], the cyanobacterium *Trichodesmium* activated PCD after exposure to light for more than 7 hours[24] or due to ageing[23]. The effects of DIM on competition and coexistence were studied between ecologically similar species within one trophic level, e.g., protozoan bacterivores[237], or zooplankton[177]. Different mortality levels were applied in previous studies to all competing species simultaneously, whereas our study varies DIM of one phytoplankton species while DIM of the second remains constant (see Methods). In contrast to previous empirical studies, which show the reduction of competition between coexisting species by increasing DIM levels, and in contrast to most theoretical studies, which predict no effect of varying DIM on competition[2,106], our results indicate two different effects of varying DIM levels on competition of coexisting phytoplankton species (Fig. 22). Firstly, the zooplankton community biomass decreases and the phytoplankton community biomass increases within speciation space when DIM of P_1 moves away from the line where mortalities of both phytoplankton species are equal to 0.01 (prey-equality line). This indicates reduced competition between prey species and therefore increased prey availability per predator. However, it also indicates increased competition between predators, an unexpected effect of increasing resource availability, which might be due to the potential adaptive effort needed by predators to react to a changed abundance of the prey. The competition between predators continues to grow (because the zooplankton community biomass continues to decline) until DIM hits a speciation threshold (line separating the speciation space from the displacement space) and one of predators goes extinct. Secondly, moving further away from the prey-equality line and passing the speciation threshold for zooplankton, altering DIM of the first prey indicates a decrease in the phytoplankton community biomass and the increase in the zooplankton community biomass (represented now by a single species due to the extinction of the other). The increase of the zooplankton biomass is then due to the absence of interspecific competition, which allows the remaining zooplankton species to prosper and therefore suppress the biomass of both prey species. The first effect weakens and the second effect strengthens along the specialisation-cost gradient (Fig. 22).

The coexistence, which in our case follows sympatric speciation, or the occurrence of extinction in zooplankton depends on the availability of nutrients in the system (Fig. 23). Thus, increasing nutrient concentrations reduce the susceptibility of plankton to variations in DIM of phytoplankton. Particularly at the lowest nutrient concentrations, small changes in DIM cause extinction on both trophic levels, predators and prey species. Even the slightest increase in DIM of P_1 causes extinction of P_1 and, consequently, Z_1, while the

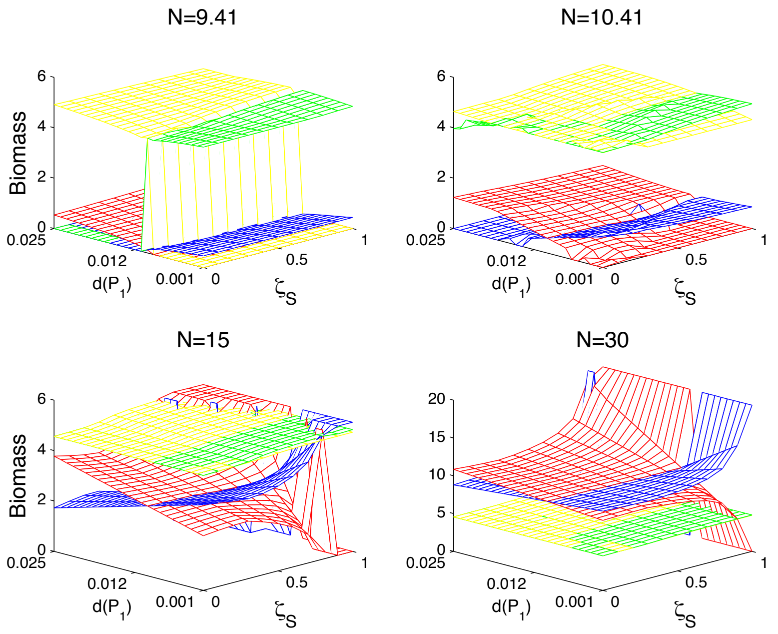

Figure 23. Superimposed fitness landscapes of all four species presented in the model for different nutrient concentrations. P_1 is green, P_2 is yellow, Z_1 is blue and Z_2 is red. All graphs display population biomasses as a function of the cost-coefficient, $\zeta_S \in [0;1]$, and the varying DIM of the first prey species, $d_1 \in [0.001; 0.025]\,\mathrm{d}^{-1}$

slightest decrease in DIM of P_1 causes extinction of P_2 and, consequently, Z_2 (Fig. 23, $N = 9.41$ mmol·L^{-1}). The $N = 9.41$ mmol·L^{-1} concentration is so low that the grazing threshold ($P_{th} = 4.08\,\mathrm{mmol{\cdot}L^{-1}}$ [280]) does not prevent phytoplankton extinction. A small increase in environmental nutrient concentration dramatically diminishes the effect of DIM on both trophic levels. Thus, an increase from $N = 9.41$ mmol·L^{-1} to $N = 10.41$ mmol·L^{-1} allows both phytoplankton species to survive, while one of the zooplankton species still goes extinct at high specialisation costs or large DIM differences between the prey species (Fig. 23, $N = 10.41$ mmol·L^{-1}). However, at higher nutrient concentration (Fig. 23, $N = [15; 30]$ mmol·L^{-1}) both trophic levels can have more that one species, except for $\zeta_S = 1$, where speciation and coexistence is not possible[280]. Our result that some DIM levels allow for coexistence and some do not is in line with a similar suggestion made by Chesson (1994)[41]

4.3.3 Domination

Another important result is that the system shifts from dominance of phytoplankton (the biomass of prey species is higher than the biomass of predators) at low environmental nu-

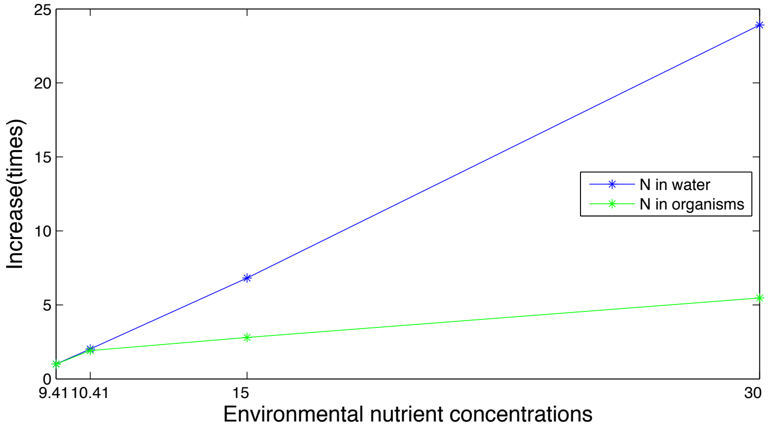

Figure 24. The productivity of the system is displayed by the comparison of nutrient concentrations assimilated by the organisms to the nutrient concentrations accumulated in the water (y axis) for four nutrient loads (x axis).

trient concentrations to a dominance of zooplankton (predator biomass is higher than prey biomass, Fig. 23). This shift in dominance happens only at high nutrient concentrations ($N = [15; 30]$ mmol·L^{-1}). Thus, at $N = 15$ mmol·L^{-1} the zooplankton is dominant over the phytoplankton provided that interspecific competition is absent, which means that one of the predators goes extinct. The nutrient richest environment $N = 30$ mmol·L^{-1} allows Z to dominate the community even in the presence of interspecific competition (Fig. 23). Besides, increasing nutrient concentration in the water column means not only more resources for the phytoplankton, but also an increase in environmental pollution and turbidity levels, which might decrease fitness of the phytoplankton. Moreover, a growing density of plankton in the water column will also increase the competition for light in phytoplankton[109]. In turn, predators do not depend on light, but gain more prey, and therefore more fitness, with increasing nutrient concentration, which could explain the switch in domination from phytoplankton to zooplankton.

4.3.4 System productivity

The system productivity is defined as the conversion rate of available resources to biomass[268]. Fig. 24 shows that increasing nutrient concentrations decrease system productivity, despite increasing primary and secondary production. This means that nutrient accumulation in the water is grater than nutrient assimilation by the organisms. Particularly, low-nutrient environments ($N = [9.41; 10.41]$ mmol·L^{-1}) indicate similar nutrient accumulation in both organisms and surrounding water, while rich-nutrient environments ($N = [15; 30]$ mmol·L^{-1})

demonstrate less nutrient accumulation by the organisms compared to the surrounding water. Thus, the increase in nutrient concentration is 7-fold at $N = 15$ mmol·L^{-1} and 24-fold at $N = 30$ mmol·L^{-1} in the water, while only 3-fold and 5.5-fold in the organisms (Fig. 24).

Isbell (2013) reports that (1) nutrient addition studies showed decreased biodiversity associated with increased productivity[198,267], (2) biodiversity experiments indicated decreased plant diversity leading to lower productivity[97,247], and finally, (3) one study did not find any connection between biodiversity and productivity[8]. Isbell (2013) suggested covariation of biodiversity and productivity across space and time. The results of our model agree with the nutrient addition studies, showing decrease in productivity coupled with the increase in biodiversity.

4.4 Conclusions

We conclude that nutrient increase in our model: (1) promotes biodiversity (Fig. 21), (2) decreases the effect of DIM on biodiversity (Fig. 23), (3) changes domination from prey species to predators (Fig. 23), and (4) decreases the overall system productivity (Fig. 24). There is experimental evidence of a positive effect of fish on phytoplankton via a trophic cascade, which indicates increased zooplankton mortality[144]. Thus, increased levels of the zooplankton mortality raise the following questions for future research: (1) how common is speciation in zooplankton under predatory pressure? (2) how will the community dynamics, the phytoplankton fitness, and the system productivity change in response to the increased mortality of zooplankton? Our results suggest that knowing the effects of changes in the environmental nutrient concentration and DIM levels of phytoplankton on biodiversity can be essential to understanding the long-term impacts of different nutrient and mortality levels on ecosystem functioning and species composition. Because global nitrogen deposition is prognosed to increase in the future[78,79] and DIM will remain an unpredictably changing value, there is a need for long-term nutrient enrichment/addition experiments (as described by Isbell (2013)[113]) and DIM experiments (as suggested by Franklin (2006)[72]) in marine plankton.

5 Outlook

The current thesis shows that traits and trade-offs can substantially improve our understanding of ecological and evolutionary processes in zooplankton. Therefore, one of the possible future directions of research would be to define more traits and to derive more trade-offs associated with these traits. Kiørboe's (2010)[127] exhaustive review of zooplankton feeding contains enough traits and trade-offs derived from data and observations. However, they are not yet used in modelling studies. Therefore, the next step would be a further incorporation of traits and trade-offs into new mathematical analytical models. The beginning of this path has already been made by the work of Pahlow[184], Visser[263,265] and Mariani[165]. The current thesis also aims to contribute to the development of traits and trade-offs in models using adaptive types of modelling rather than population genetics.

Which is why our model can also be improved in the population genetics direction by considering microbiological processes, e.g selection, drift, genetics and development[236], or be extended to one-allele or two-allele models.

Existing optimality-based and trait-based models should be build into current global biogeochemical models. This aims to increase the predictive power of the global models via application of trade-offs. The best examples of using trade-offs on a global scale are the studies of Follows[71] and Prowe[195,196]. We suggest that a specialisation trade-off can also be built into the global models because it is part of a simple grazing function, which is used in many global models. Such an improved global model would most likely be the first model investigating global speciation patterns in the marine environment. Moreover, the combination of existing studies, which indicate a decrease in biodiversity, with the model which provides a speciation component, might provide new insights on the global marine biodiversity.

Building more trophic levels into the sympatric speciation model, introduced by the current thesis, is another path of possible future research. Thus, the sensitivity analysis of density-dependent zooplankton mortality might simulate the zooplankton predation caused by fish. Moreover, similar to the sensitivity analyses of the specific phytoplankton mortality (DIM in Chapter 4) presented here, specific (density-independent) zooplankton mortality can be introduced and studied separatly from the predatory fish mortality. The grazing of larger zooplankton on smaller zooplankton could became an additional source of mortality for the smaller zooplankton. Such combination might provide insights about trophic cascades in the plankton community with adaptive (specialising) zooplankton.

Interesting results might be provided by the current optimality-based models of phytoplankton[181,183] in case where they experience a specialising predation by zooplankton as presented here.

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Eidesstattliche Erklärung

Hiermit erkläre ich, dass die vorliegende Arbeit mit dem Titel: **"Optimality and trait based approaches to sympatric speciation and sympatric co-evolution of predator and prey traits in marine plankton”** von mir selbstständig angefertigt wurde. Bis auf zitierte Referenzen und Beratung meiner Betreuer wurden keine weiteren Quellen verwendet. Diese Arbeit ist unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft entstanden. Sie wurde weder im Rahmen eines Prüfungsverfahrens an anderer Stelle vorgelegt noch veröffentlicht. Ich erkläre mich einverstanden, dass diese Arbeit an die Bibliothek des GEOMAR und die Universitätsbibliothek der CAU weitergeleitet wird.

Kiel, den July 22, 2014

Yury Zablotski