The role of trophic structure in food web dynamics



The research presented in this thesis was carried out at the Department of Theoretical Life Sciences, Vrije Universiteit Amsterdam, The Netherlands. VRIJE UNIVERSITEIT

The role of trophic flows in food web dynamics

ACADEMISCH PROEFSCHRIFT

ter verkrijging van de graad van doctor aan de Vrije Universiteit Amsterdam, op gezag van de rector magnificus prof.dr. T. Sminia, in het openbaar te verdedigen ten overstaan van de promotiecommissie van de faculteit der Aard- en Levenswetenschappen op dinsdag 8 juni 2004 om 13.45 uur in de aula van de universiteit, De Boelelaan 1105

door

Lothar David Jan Kuijper

geboren te Weesp

promotoren:	prof.dr. S.A.L.M. Kooijman
	prof.dr. N.M. van Straalen
copromotor:	dr.ir. B.W. Kooi

Contents

	Intr	oductio	on	ix
1	Om	nivory	and food web dynamics	1
	Pub	lished i	n Ecological Modelling 163 (2003): 19-32	
	1.1	Introd	uction	2
	1.2	Descri	ption of the model	3
	1.3	Model	dynamics	11
		1.3.1	Model behavior typology	11
		1.3.2	Coexistence of intraguild predator and intraguild	
			prey	13
		1.3.3	Invasibility	14
		1.3.4	Complex dynamics and multiple stable states	15
	1.4	Discus	ssion and conclusions	19
n	Cor	d N ar	and growth officiancies of compand and production	
2	C al	la N gr	ing a Dynamic Energy Budget model	27
	Dub	lichod i	n Journal of Plankton Research 26 (2004): 1 15	27
	2 1	Introd	uction	28
	2.1	Model	description	30
	2.2	221	Ingestion and assimilation	30
		2.2.1	Stoichiometry	32
		2.2.3	Synthesizing Units	34
		2.2.4	Maintenance	34
		2.2.5	Egg production	36
		2.2.6	Equations of state variables	38
		2.2.7	Parameter values	38
	2.3	Result	S	39
		2.3.1	Fit to data	39
				~ /
		2.3.2	Fate of C and N: influence of algal C:N	40

	2.4	Discussion	42
	2.5	Acknowledgements	46
	2.6	Appendix I: constraints to values of ρ parameters	47
3	Stoi	chiometry and food chain dynamics	53
	Sub	mitted	
	3.1	Introduction	54
	3.2	Modeling framework	56
		3.2.1 Primary producers	56
		3.2.2 Consumers	59
		3.2.3 Decomposition and recycling	64
		3.2.4 Model summary	65
	3.3	Model dynamics	65
		3.3.1 The resource–producer system	66
		3.3.2 The producer–consumer system	68
		3.3.3 The resource–producer–consumer system	71
	3.4	Discussion	76
	3.5	Conclusions	78
			-
	3.6	Acknowledgments	79
	3.6	Acknowledgments	79
4	3.6 Mod	Acknowledgments	99 2 97
4	3.6 Moc and	Acknowledgments	79 87
4	3.6 Moc and Sub	Acknowledgments	87
4	3.6 Moc and Sub: 4.1	Acknowledgments	88 81
4	3.6 Mod and Subi 4.1 4.2	Acknowledgments	87 87 88 91
4	 3.6 Moc and Sub: 4.1 4.2 4.3 	Acknowledgments	88 91 95
4	 3.6 Moc and Sub: 4.1 4.2 4.3 	Acknowledgments	79 87 88 91 95 95
4	 3.6 Moc and Sub: 4.1 4.2 4.3 	Acknowledgments	79 87 88 91 95 99 101
4	3.6 Mod Sub: 4.1 4.2 4.3	Acknowledgments	87 88 91 95 95 99 101
4	 3.6 Moc and Sub: 4.1 4.2 4.3 4.4 	Acknowledgments	79 87 88 91 95 99 101 104
4	 3.6 Moc and Sub: 4.1 4.2 4.3 4.4 	Acknowledgments	79 87 88 91 95 99 101 104 104
4	 3.6 Moc and Sub: 4.1 4.2 4.3 4.4 	Acknowledgments	79 87 88 91 95 99 101 104 104 105
4	 3.6 Moc and Sub: 4.1 4.2 4.3 4.4 	Acknowledgments	79 87 88 91 95 99 101 104 104 104 105
4	 3.6 Moc and Sub: 4.1 4.2 4.3 4.4 	Acknowledgments	79 87 88 91 95 99 101 104 104 104 105 105
4	 3.6 Mod and Sub: 4.1 4.2 4.3 4.4 4.5 	Acknowledgments	79 87 88 91 95 99 101 104 104 105 105 106
4	 3.6 Mod and Sub: 4.1 4.2 4.3 4.4 4.5 4.6 	Acknowledgments	87 87 88 91 95 99 101 104 104 105 105 106 107
4	 3.6 Mod and Sub: 4.1 4.2 4.3 4.4 4.5 4.6 	Acknowledgments	79 87 88 91 95 99 101 104 104 105 105 106 107 110
4	 3.6 Mod and Subi 4.1 4.2 4.3 4.4 4.5 4.6 Sum 	Acknowledgments	87 87 88 91 95 99 101 104 104 105 106 107 110 117

Contents	vii
Samenvatting	121
Dankwoord	125

Introduction

Ecosystem modeling

We have merely started to understand the functioning of the many ecosystems around us, be they small-scaled micro-aggregates present in the marine waters (cf. [8]), or, for instance, the wide savanna's of the Serengeti. This is unfortunate, as changes in the world's climate, such as elevated temperature, eutrophication, enhanced levels of solar UV-B irradiation and changes in land use, are known to affect ecosystem processes, sometimes in an irreversible manner. To know which food web structures and ecological functions are most vulnerable to changes in the environment, and to understand how ecosystems are affected by these changes, would improve our ability to make predictions of how the world will change in the decades to come. In this thesis, I investigate how differently structured food webs react to changes in their environment. In that, I concentrate on food web stability (equilibrium dynamics versus oscillating population densities) and food web persistence.

The reason for our limited understanding of ecosystem dynamics lies mainly in the implicit complexity of natural ecosystems. To understand these dynamics from a theoretical point of view, one has to contemplate the underlying interactions between populations, interactions between individuals within populations, the physiology of individuals and the biochemistry behind the physiology. Putting all aspects of molecular cell biology to work in a mechanistic ecosystem model is an immense task, and we are simply not up to it. Even if we possessed all the knowledge required, the associated mathematical analysis would be far too demanding, and the model's behavior could never be traced back to a single model feature amongst the many. The art of modeling lies in the making of appropriate choices. One has to determine how much detail is reasonably required for the model to adequately grasp the problems at hand. In other words, one has to determine which details may be omitted, without getting the wrong ideas about the study objective. In this work, I will use different levels of detail in the description of the food webs that are analyzed.

When designing an ecological model, the desired resolution in the model outcomes determines the maximum allowed level of simplification. For instance, models, aiming to get insight in very general ecological phenomena, such as 'Why is the world green?' [9] or 'What is the maximum number of trophic levels' [22], will generally have little detail in the description of lower levels of organization, such as the individual or cellular level. In contrast, such detail is often inadmissible for models applied to very specific situations: to understand the dynamics of perch populations in which cannibalism occurs, requires the inclusion of details about the differences in biology between adult and juvenile individuals [3]. This gives a higher resolution in the model's outcome, but the results can rarely been extrapolated in generality. The models developed in this thesis are extended versions of simplistic food web models, traditionally used to discover general patterns in ecosystem dynamics (e.g. competitive exclusion [11], where it is shown that two species competing for the same resource cannot coexist and 'paradox of enrichment' [25], where high nutrient supplies destabilize food chains).

Trophic flow and stoichiometry

Theoretical models used to analyze the stability properties of trophic structures in variable environmental conditions concentrate on the trophic transfer of currents. In general, a single currency is used [4, 5, 18–20, 25–27], mostly energy or carbon, under the assumption that all actors in the food web, from basal resource to top predator, have a constant elemental composition (i.e. strict homeostasis). This composition is usually expressed in C-moles, where abundances of chemical elements are expressed relative to that of carbon (e.g. glucose, $C_6H_{12}O_6$ becomes CH_2O and the C-molar formula for uric acid is $CH_{0.8}O_{0.6}N_{0.8}$). However, the composition of resources, i.e. the resource quality, may vary in natural food webs. Resource quality is known to determine the assimilation and growth efficiencies of organisms [1, 2]. In turn, the biochemical composition of biota is known to change with a changing resource composition [12, 30], which affects their nutritional value to higher trophic levels [10]. Consequently, it is to be expected that changes in resource composition impact on the dynamic properties of ecosystems. Many of the changes occurring in natural ecosystems have been shown to coincide with shifts in resource composition. Eutrophication, due to anthropogenic emissions of nitrogen and phosphorous directly disturb the nutritional balance of ecosystems. Elevated levels of CO_2 and enhanced UV-B irradiation caused by stratospheric ozone depletion cause alterations in the composition of plant material [28, 29] and algae [31]. It may be concluded that using a single currency model for the assessment of potential effects of global change on ecosystem dynamics simply does not suffice.

The implementation of multiple resources requires rules for the uptake of particular resources, and rules for the merging of resources into biomass. One is forced to include more ecophysiology into a model. Generally, as in chemical reactions, the assumption is made that fixed proportions of all essential resources are required for the production of biomass. The ecological importance of the need for any organism to obtain all essential elements in the right proportions has been acknowledged only in the past decade, and, known as 'ecological stoichiometry'¹, its study has received much attention, since [30].

Dynamic Energy Budget theory

Throughout this thesis, I will use Dynamic Energy Budget theory (DEB, [14, 15]), or elements from it in stripped versions of DEB-models (in chapters 1 and 4), in the synthesis of the food web models. The DEB theory gives general rules for the uptake and utilization of resources by organisms. As the theory bases itself on conservation laws and first principles, it provides a consistent basis for modeling biological systems, and it can be applied to all organisms, without exception.

The focus of DEB-theory is on the individual organism, and effects on the population, or ecosystem level, are extrapolations of the dynamic properties of individual organisms. To keep the models simple and tractable, I use the simplest conceivable extrapolation from individuals to populations, namely the V1-morph ([14], section 2.2), which holds that for each individual the ratio between volume and surface area is equal. When all individuals are V1-morphs, the population will have a fixed surface area / volume relationship as well, which makes it possible to translate uptake, which is proportional to surface area,

¹The term stoichiometry, stoicheion for element, metron for measure, refers to the requirement that for any chemical transformation the elemental composition in the reactants is conserved

into population growth, which deals with volumes. This simplification, which negates individuality, is appropriate when individuals are small and numbers of individuals are large.

DEB theory divides individuals into permanent biomass (i.e. structural biomass) and temporary biomass (i.e. reserve biomass), which may be used for growth, reproduction or burned for maintenance². Both structural mass and reserves are a rich mixture of different compounds, but it is assumed that they obey strict homeostasis, i.e. their C-molar composition is constant, so that we may regard them as so-called 'generalized compounds'. Structure and reserves may, however, have different individual compositions. As the density of reserves may vary over time, an organism as a whole need not be constant in composition. This is a realistic property that is not well covered by models without reserves.

In assimilation, resources from the external environment are assigned to internalized reserves. Catabolism deals with the mobilization of reserves for metabolic processes. This release is a first order process with respect to the density of reserves in the organism. The resulting flux of mobilized reserves mobilized is used for maintenance, growth, development, and reproduction. Maintenance takes priority over the other processes, so that growth and reproduction come to a halt whenever the maintenance process confiscates the whole available flux of reserves³. The requirements for maintenance are proportional to the amount of structural biomass. The flux that remains after the maintenance demands are dealt with is divided over the growth, development and reproduction processes.

A DEB-modeler may designate any number of reserve pools for a particular organism. Using multiple reserve pools (for instance, 1 for each nutrient that potentially limits production) generally makes a model more realistic, and provides a higher resolution in model outcomes. However, as every reserve pool comes with an additional state variable, using multiple reserve pools might complicate model analysis severely. This is especially so when a substantial number of organisms is modeled, which is often the case in food web studies. Chapters 2 and 3, considering models of 1 and 2 populations, respectively, focus on the use of

²Unfortunately, the term 'reserve' in DEB is easily mistaken for 'material stored for later use', while a more correct interpretation would be 'internal resource for metabolic activity'

³The Droop model [6], or cell-quota model, which is often used to model algal growth is effectively a sub-model of the DEB-model under the assumption that maintenance requirements are negligible

multiple reserves. In contrast, one may also choose to refrain from using any reserve pools at all, in which case there is no temporary biomass, and assimilated resources are directly used for metabolic processes. The omission of reserves implies that total biomass becomes strictly homeostatic. What effectively remains is the Marr-Pirt model [16]. The models analyzed in chapters 1 and 4, containing 3 and 5 trophic groups, respectively, belong to this class.

DEB and stoichiometry: the synthesizing unit

When dealing with multiple essential resources, one has to make rules for the merging of these resources to create biomass and by-products. For example, suppose that a diatom species assimilates nitrogen in a mineral form and carbon in an organic form. The synthesis of biomass from reserves requires the conjunction of these two reserve types. A transformation scheme for the synthesis of biomass, can now be designed, based on nitrogen and carbon stoichiometry, and on utilization efficiencies of both compounds. A fictive example of such a scheme, in terms of C-moles, could be

CN_0	+	0.1 N	\rightarrow	$0.5 \ CN_{0.2}$	+	0.5 C
org. carbon		inorg. nitr.		biomass		inorg. waste

Here, represented as generalized compounds, organic carbon and inorganic nitrogen reserves react to form biomass and waste. The latter is formed due to a limited conversion efficiency. The production efficiency with respect to carbon is 50%, while nitrogen is used at 100% (no nitrogen is wasted). DEB uses so-called synthesizing units (SUs) to model the dynamics of such transformations. This relatively novel approach is quite similar to methods used in enzyme kinetic models, but there are a few major differences. Firstly, in enzyme kinetics models, the flux of products is based on substrate concentrations, while SU dynamics base on fluxes, exclusively. The latter seems more appropriate, as the environment at which metabolic processes occur are so typically spatially heterogeneous, that the concept of 'concentration' becomes quite cumbersome. Secondly, contrary to enzyme kinetics models, there is the assumption that substrates bind irreversibly to the SU. This simplification makes SUs much more easy to work with when complex transformations need to be modeled [13]. But more important, this simplification allows the use of SUs for modeling transformations in which generalized compounds, such as structural biomass and reserves, play a role.

In this thesis, I will make use of the SU concept for the modeling of resource acquisition and use, repeatedly. In this way, I pay due attention to the biology behind trophic transfer across ecosystems. Moreover, in the results of the work presented in this thesis, there is much focus on the differences in outcomes between SU-models and traditional ones, which generally focus on a single currency, such as nitrogen or energy.

Thesis outline

The thesis consists of four articles with each a different underlying modeling methodology. The first chapter goes back to classic ecosystem modeling, in which the food web bases on a single resource. Here, the effect of omnivory on a classic food chain in the chemostat is studied with a Marr-Pirt model, i.e. all trophic groups consist of structural components exclusively (no reserves). Basic to this study is the current view that weak trophic interactions in ecosystems restrict the potential for food web instability [7, 17, 21, 23, 24], and omnivory, causing alternative routes for trophic transfer, can impose such weak interactions on a food web.

Stoichiometry dictates that the trophic transfer of any essential element is tightly linked to the trophic transfer of others. This implies that changes in the availability of one nutrient may weakly influence the trophic transfer of others. Chapter 2 touches on this aspect of potential weak links in food chains. In this chapter a model of egg production of the copepod *Acartia tonsa* is developed and analyzed, where egg production is a function of both nutritional quantity and quality. This physiologically based model assumes three biomass components for the copepod: one for structural biomass, one for nitrogenous reserves and one for non-nitrogenous reserves.

Chapter 3 is an elaboration on chapter 2. Here, the model developed in chapter 2 is used as a population module in a dynamic food chain model, consisting of the diatom species *Thalassiosira weissflogii* feeding on mineral carbon and nitrogen, and the copepod *Acartia tonsa*, in a chemostat. The model implements nutrient recycling and decomposition, and thus comprises all basic ecosystem functions. It is analyzed with the focus on trophic transfer and stoichiometry.

In chapter 4 I aim to make the step from theoretical food web models to the ones that can be found in nature. Chapter 4 deals with stoichiometry and food web dynamics in a model of a natural forest ecosystem in Wekerom, and analyzes indirect effects of UV-B and CO_2 enhancement, and eutrophication on resource quality. This is a rather complex food web, in which trophic transfer comprises both aspects of stoichiometry, and food web connectance. For reason of the complexity of the associated ecosystem, the model used is a Monod-type model (i.e. trophic groups consist of structural components exclusively, and maintenance is neglected). In this chapter the need for putting the theoretical framework to the test in experimental ecology is highlighted.

References

- [1] Anderson TR. (1992). Modelling the influence of food C:N ratio, and respiration on growth and nitrogen excretion in marine zooplankton and bacteria. *J. Plankton Res.* 14:1645–1671.
- [2] Berg MP, De Ruiter P, Didden W, Janssen M, Schouten T, Verhoef H. (2001). Community food web, decomposition and nitrogen mineralisation in a stratified Scots pine forest soil. *Oikos* 94:130–142.
- [3] Claessen DC, De Roos AM, Persson L. (2000). Dwarfs and giants: cannibalism and competition in size-structured populations. *Am. Nat.* 155:219–237.
- [4] Diehl S. (1993). Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. *Oikos* 68:151– 157.
- [5] Diehl S, Feißel M. (2001). Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. *Ecology* 82:2977–2983.
- [6] Droop MR. (1983). 25 years of algal growth kinetics. *Botanica Marina* 26:99–112.
- [7] Fussman GF, Heber G. (2002). Food web complexity and chaotic population dynamics. *Ecology Letters* 5:394–401.
- [8] Goldman JC. (1984). Conceptual role for microaggregates in pelagic waters. *Bull. Mar. Sci.* 35:462–476.
- [9] Hairston N. G. ans Smith FE, Slobodkin LB. (1960). Community structure, population control, and competition. *Am. Nat.* 94:421–425.
- [10] Hessen DO. (1992). Nutrient element limitation of zooplankton production. Am. Nat. 140:799–814.
- [11] Hutchinson GE. (1959). Homage to Santa Roselia or why are there so many kinds of animals? *American Naturalist* 93:145–159.
- [12] Kiørboe T. (1989). Phytoplankton growth rate and nitrogen content: implications for feeding and fecundity in a herbivorous copepod. *Mar. Ecol. Prog. Ser.* 55:229–234.
- [13] Kooijman SALM. (1998). The synthesizing unit as a model for the stoichiometric fusion and branching of metabolic fluxes. *Biophysical Chemistry* 73:179–188.
- [14] Kooijman SALM. (2000). *Dynamic energy and mass budgets in biological systems*. Cambridge University Press.
- [15] Kooijman SALM. (2001). Quantitative aspects of metabolic organization; a discussion of concepts. *Phil. Trans. R. Soc. B.* 356:331–349.

- [16] Marr AG, Nilson EH, Clark DJ. (1962). The maintenance requirement of *Escherichia coli. Ann. N. Y. Acad. Sci.* 102:536–548.
- [17] McCann KS. (2000). The diversity-stability debate. *Nature (Lond.)* 405:228–233.
- [18] McCann KS, Hastings A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proc. R. Soc. Lond. B Biol. Sci.* 264:1249–1254.
- [19] McCann KS, Hastings A, Huxel GR. (1998). Weak trophic interactions and the balance of nature. *Nature (Lond.)* 395:794–798.
- [20] Mylius SD, Klumpers K, De Roos AM, Persson L. (2001). Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *Am. Nat.* 158:259–276.
- [21] Paine RT. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature (Lond.)* 355:73–75.
- [22] Pimm SL, Lawton JH. (1978). Number of trophic levels in ecological communities. *Nature (London)* 268:329–331.
- [23] Polis GA. (1998). Stability is woven by complex webs. *Nature (Lond.)* 395:744–745.
- [24] Post DM, Conners M, Goldberg DS. (2000). Prey preference by a top predator and the stability of linked food chains. *Ecology* 81:8–14.
- [25] Rosenzweig ML. (1971). Paradox of enrichment: the destabilization of exploitation ecosystems in ecological time. *Science (New York)* 171:385– 387.
- [26] Rosenzweig ML. (1973). Exploitation in three trophic levels. *Am. Nat.* 107:275–294.
- [27] Rosenzweig ML, MacArthur RH. (1963). Graphical representation and stability conditions of predator–prey interactions. *Am. Nat.* 97:209–223.
- [28] Rozema J. (1999). UV-B radiation and terrestrial ecosystems: processes, structure and feedback loops. In: Rozema J, editor. *Stratospheric ozone depletion: the effects of enhanced UV-B radiation on terrestrial ecosystems*, chapter 6. Backhuys Publishers, Leiden, The Netherlands.
- [29] Rozema J. (2000). Effects of solar UV-B radiation on terrestrial biota. In: Hester RE, Harrison RM, editors. *Issues in environmental science and technology: 14. Causes and environmental implications of UV-B radiation*, pp. 85–105.
- [30] Sterner RW, Elser JJ. (2002). *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press.
- [31] Xenopoulos MA, Frost PC, Elser JJ. (2002). Joint effects of UV radiation and phosphorous supply on algal growth rate and elemental composition. *Ecology* 83:423–435.

Omnivory and food web dynamics

Abstract

Intraguild predation is a trophic interaction in which two consumers compete for one resource and where one of the consumer species may also feed on its competitor. The intraguild predator's diet follows from the relative strength of its interactions with its potential prey. Current view holds that weak interactions between species promote the stability of food webs. To the contrary, nutrient enrichment is predicted to destabilize ecosystems. We present a theoretical analysis of the interplay between intraguild predation and nutrient enrichment in a Marr-Pirt chemostat model of a microbial food web. We perform a two-dimensional bifurcation analysis along a gradient of allochtonous nutrient levels and a gradient of one out of two biologically plausible strategies to explore the spectrum of the intraguild predator's foraging interactions. Both strategies show that intraguild predation may

- stabilize food chains
- eliminate chaos, predicted by food chain models
- give rise to multiple stable states
- be favored in systems with low turn-over rates, where the intraguild predator has a low interaction strength and a low yield on the basal resource

Keywords: Ecosystem modelling - Intraguild predation - Bifurcation analysis - Multiple stable states - Invasion - Nutrient enrichment

1.1 Introduction

Nutrient enrichment has been shown, both empirically and theoretically, to affect ecosystems in several ways [2, 11, 51]. For instance, known as the 'paradox of enrichment', it may reduce species diversity and ecosystem functioning [48]. As early as the sixties, food chain models were analysed at variable production levels [49]. Since then, a variety of modelling studies have predicted that nutrient enrichment can lead to complex dynamics, as well as extinctions of species [1, 16, 22, 28, 40, 55].

The theoretical study on the effects of nutrient enrichment has long been limited to linear food chains. The explanation lies in the history of food web modelling studies. In the late seventies, Pimm and Lawton simulated a large number of food webs including omnivorous links, as non-linear interactions [41]. They discovered that these additional interactions in general caused stable internal equilibria to become statistically rare. As stable equilibria were deemed essential for the long term survival of ecosystems, it was concluded that omnivory should be rare in natural food webs.

In the late eighties, this view became subject of debate, as renewed investigations demonstrated that, in natural systems, omnivory is the rule, rather than the exception [42, 45, 53]. As a consequence, a number of theoretical analyses of this interaction have appeared in the last few years. These studies are in general about the simplest conceivable example of omnivory, where a predator species and a consumer species compete for a single resource, while the predator species can also feed on the consumers [12, 13, 32, 33, 36, 47]. This combination of competition and predation interactions is known as intraguild predation.

One of the general results that derive from recent studies is that whenever certain conditions are met, intraguild predation can promote persistence of food webs. Firstly, the intraguild prey has to be the superior competitor for the common prey, otherwise it will be excluded from the system due to effects of competitive exclusion [44]. Secondly, the resource availability should be intermediate for coexistence of intraguild predator and intraguild prey, as hypothesized by Holt and Polis [21] and corroborated by Morin [34], Diehl and Feißel [12, 13], Heithaus [19] and Mylius et al. [36]. If the common resource is scarce, the intraguild prey may outcompete its predator. On the other hand, if it becomes too abundant, the intraguild prey may not survive the predation pressure of the omnivore. Thirdly, Bondavalli and Ulanowicz [6] showed that, due to positive effects on the basal prey, strong omnivorous predation on the intraguild prey in combination with weak predation on the common prey may foster the persistence of intraguild configurations. In Pimm and Lawton's model experiments, these conditions were not always met.

In this paper, we will present a model which lends itself to explore the complete spectrum of intraguild predation, from competitive to predacious interactions, at variable nutrient enrichment levels. As omnivorous interactions are to a large extent determined by the catching efficiencies and yields, we will focus on the particular influence of these properties on the model dynamics.

The paper is organized as follows. In the next section we present the model structure and motivate our modelling approach. In the result section we present a bifurcation analysis of the model to distinguish regions in parameter space that differ in terms of coexistence and stability. In the discussion section we put our results in context and point out implications of the study.

1.2 Description of the model

Our model describes a simple ecosystem in a chemostat environment. Although we ultimately want to gain insight in natural ecosystems, the study of less realistic, but controllable, ecosystems is a necessary first step. A chemostat system fulfills this requirement: it is spatially welldefined, input and output are known and under experimental control, and through mixing an approximately homogeneous environment can be created. The latter is a prerequisite for the type of modelling involved, in particular the use of the law of mass action to model encounters between predator and prey.

In addition to an abiotic nutrient N, the model describes three species of biota representing different trophic niches: a resource R, intraguild prey C and intraguild predator P. Figure 1.1 shows the trophic levels and interactions among these species. The resource feeds on the abiotic nutrient, and is preyed upon by both intraguild prey and predator. The latter not only predates on the resource, but also on the intraguild prey; it is not subject to predation itself. As the intraguild predator feeds on two different trophic levels, it cannot be attributed to a particular trophic level per se. For this reason we use trophic niche rather than trophic level to indicate the position of the omnivore in the food web (cf. Levine [29]).



Spectrum of omnivory

Figure 1.1: Representation of the studied trophic interactions. The circles denote the different trophic niches. Abiotic resources are denoted by N, while R, C and P represent resources, consumers and predators, respectively. The architecture of the food web depends on the feeding behavior of the highest trophic level. This architecture may vary from a competition food web, where P consumes R exclusively, via a spectrum of omnivory interactions, to the linear food chain, where P only feeds on C.

The following Marr-Pirt [30] system describes the interactions among the participants:

$$\frac{d}{dt}N = (\mathbf{N}_{\mathbf{r}} - N)\mathbf{D} - \frac{a_{N,R}N}{1 + a_{N,R}b_{N,R}N}R$$
(1.1a)

$$\frac{d}{dt}R = R\left(\frac{y_{N,R}a_{N,R}N}{1 + a_{N,R}b_{N,R}N} - \mathbf{D} - m_R\right) - \frac{a_{R,C}R}{1 + a_{R,C}b_{R,C}R}C - \frac{a_{R,P}R}{1 + a_{R,C}b_{R,C}R}P$$
(1.1b)

$$\frac{d}{dt}C = C\left(\frac{y_{R,C}a_{R,C}R}{1 + a_{R,C}b_{R,C}R} - \mathbf{D} - m_C\right) - \frac{a_{C,P}C}{1 + a_{R,P}b_{R,P}R + a_{C,P}b_{C,P}C}P$$
(1.1c)

$$\frac{d}{dt}P = P\left(\frac{y_{R,P}a_{R,P}R + y_{C,P}a_{C,P}C}{1 + a_{R,P}b_{R,P}R + a_{C,P}b_{C,P}C} - \mathbf{D} - m_P\right)$$
(1.1d)

Table 1.1 summarizes the notation in the mathematical model. The parameter N_r is the reservoir density, i.e. the concentration of the nonliving nutrient in the medium supplied to the chemostat. The throughput rate **D** is the supply rate relative to the volume of the chemostat. These parameters are under control of an experimenter. They are set in bold type to distinguish them from parameters that relate to the physiology of the biota in the chemostat and can not be controlled. The parameters m_Y represent the costs for maintenance per unit of time of species Y. Parameters with two subindices separated by a comma (X, Y) involve an interaction between two species, the consumer Y and its food X. Here, $a_{X,Y}$ is the catching rate of species Y feeding on X, $y_{X,Y}$ is the corresponding yield and $b_{X,Y}$ is the handling time, characteristic for the type-II functional response [20].

When the intraguild predator is handling one type of prey, it temporarily cannot catch the other. Therefore, the functional responses that deal with the intraguild predator's consumption involve the densities of both the resource and the intraguild prey species. This two–prey functional response was first introduced by Murdoch [35] and expanded on by Cock [9] and Chesson [8]. In the model, the omnivore does not effectively select for either prey by preference. This applies well to the foraging behavior of zooplankton (Legović [27]).

We want to know how the long-term behavior of the model depends on the intraguild predation interactions as well as on the nutrient provision. To this end we will perform bifurcation analysis of system (1.1). For an introduction to bifurcation analysis the reader is referred to Guck-

Table 1.1: Parameters and state variables; t=time, m=biomass, v=volume of the reactor. The index *Y* denotes the trophic level. Some parameters, for instance the saturation constants $k_{X,Y}$, have double indices separated by a comma to emphasize that these quantities depend on two levels. Here, *Y* is the species that feeds upon *X*.

Parameter	Dimension	Units	Interpretation
D	t^{-1}	h^{-1}	Throughput rate
$\mathbf{N}_{\mathbf{r}}$	$\mathrm{m}\mathrm{v}^{-1}$	$ m mgdm^{-3}$	Substrate concentration
			in reservoir
$a_{X,Y}$	$v m^{-1} t^{-1}$	${ m dm^3mg^{-1}h^{-1}}$	Catching rate
$b_{X,Y}$	t	h	Handling time
$y_{X,Y}$	${ m m}~{ m m}^{-1}$	$mg mg^{-1}$	Mass coupling coefficient
m_Y	t^{-1}	h^{-1}	Maintenance rate
			coefficient
t	t	h	Time
N	$\mathrm{m}\mathrm{v}^{-1}$	$ m mgdm^{-3}$	Substrate density
R, C, P	$\mathrm{m}\mathrm{v}^{-1}$	$ m mgdm^{-3}$	Biomass density

enheimer and Holmes [18] and Kuznetsov [26], and to Bazykin [3] for the application to ecosystem models. Bifurcation analysis gives information about the long-term dynamic behaviour of nonlinear dynamic systems. The structural stability is studied with respect to so-called free or bifurcation parameters. When such a parameter is varied, a value at which the asymptotic dynamics changes abruptly (for instance the solution becomes a stable limit cycle instead of a stable equilibrium) is called a bifurcation point. In this study, we use two-dimensional bifurcation analysis, in which two parameters are varied simultaneously. Here, bifurcation curves separate regions in the two-dimensional parameter space, which differ in qualitative asymptotic behavior. We perform the bifurcation analyses with the computer programs AUTO [14] and LOCBIF [23].

We concentrate on two aspects of the long-term behavior, coexistence and invasibility. In correspondence to Grimm and Wissel's [17] nomenclature, we define coexistence as the potential of the intraguild predator and intraguild prey to jointly persist. Invasibility implies that a species, upon entering the system in arbitrarily small numbers, will increase in number and stays in the system. These concepts correlate but are not identical. If both intraguild predator and intraguild prey can persist at a given set of parameter values, this does not guarantee that either one can invade when it is not already present. Conversely, successful invasion of a species may not always result in coexistence. One species may also simply replace the other. To understand long-term dynamics and community assembly, both aspects must be taken into account.

The effect of an omnivory interaction depends on the foraging behavior of the intraguild predator. In the model, this behavior is controlled by the catch rates $a_{R,P}$, $a_{C,P}$ and the handling times $b_{R,P}$, $b_{C,P}$. The catch rates characterize the predation ability of the intraguild predator on the resource and intraguild prey, respectively, whereas the handling times determine the maximum ingestion rates with respect to each particular prey. In our analyses, we will use the catching rates to explore the effect of omnivory in the food chain.

As part of their study, Mylius et al. [36] performed a bifurcation analysis with the two catch rates as simultaneously varied parameters. In this way they were able to cover the complete spectrum of omnivorous interactions. They demonstrated that only in a small region of parameter space, where $a_{R,P}$ is relatively low, coexistence of the intraguild predator and intraguild prey can prevail. Their model differs from ours in that it concerns a semi-chemostat environment in which a resource species, and not a non-living nutrient, forms the base of the food chain. This implies that our model is 4-dimensional (N, R, C, P) whereas theirs is 3-dimensional (R, C, P). We will test whether their conclusions hold for our model as well.

Our aim is to weigh the effect of omnivorous interactions against the effect of nutrient enrichment. The latter is modelled through variation of the nutrient inlet density N_r in equation (1.1a), which describes the dynamics of the non-living nutrient density. Consequently we have three parameters of interest, the catch rates $a_{R,P}$, $a_{C,P}$ and the nutrient inlet concentration N_r .

A qualitative analysis of the behavior of system (1.1) using three bifurcation parameters is mathematically possible, but a graphical representation of results is cumbersome. There are a number of options to circumvent this problem, some of which brought into practice by other authors [25, 32].

In their studies, McCann and Hastings [32] and McCann et al. [33]

combine the two catch rates into a single parameter, ω , defined as

$$\omega = \frac{a_{R,P}}{a_{R,P} + a_{C,P}} \tag{1.2}$$

to specify the interaction strength of the omnivore and its prey types. When $\omega = 0$, $a_{R,P} = 0$, the highest trophic level does not feed on the resource species and effectively figures as a top predator species in a linear food chain. When $\omega = 1$, $a_{C,P} = 0$, so that the highest level ceases to feed on the consumer species. Instead, it now figures as a second consumer, competing with the other consumer for the resource species. At intermediate values of ω , the highest trophic level feeds on both species and, therefore, is an intraguild predator. Thus, $1 - \omega$ indicates the trophic distance between the intraguild predator and the consumer species [29]. In their analyses McCann and Hastings kept the sum of the two catch rates constant. The corresponding biological interpretation is that intraguild predators have a limited time-budget in which predation efforts on the one prey balance against predation efforts on the other. In our study we will extend their work by testing this approach at variable allochtonous nutrient input levels.

Recently, Kooi et al. [25] performed a bifurcation analysis of model (1.1) in which they used sets of mutually independent catch rates at variable nutrient inputs. They left out assumptions on time budgets and thus had the freedom to vary both catch rates independently. Hence, they were able to assess effects of a larger class of omnivorous interactions. However, as this setup requires two independent and unbounded parameters to determine the degree of omnivory, this approach does not lend itself to explore a spectrum of omnivorous interactions.

In pursuit of the effect of nutrient enrichment in food webs with intraguild predation, we will analyse system (1.1) at a range of N_r values, using two different biologically plausible strategies, which can be used to establish a spectrum of intraguild predation interactions. To start with, analogous to McCann and Hastings [32], we will use the time budget strategy. Here we use ω from 0 (linear food chain) to 1 (competition). To this end, system (1.1) can be rewritten into

$$\frac{d}{dt}N = (\mathbf{N}_{\mathbf{r}} - N)\mathbf{D} - \frac{a_{N,R}N}{1 + a_{N,R}b_{N,R}N}R$$
(1.3a)

$$\frac{d}{dt}R = R\left(\frac{y_{N,R}a_{N,R}N}{1+a_{N,R}b_{N,R}N} - \mathbf{D} - m_R\right) - \frac{a_{R,C}R}{1+a_{R,C}b_{R,C}R}C$$

$$- \frac{\omega R}{P} P$$
(1.3b)

$$-\frac{1}{k_{\omega} + b_{R,P}\omega R + b_{C,P}(1-\omega)C}^{P} \frac{d}{dt}C = C\left(\frac{y_{R,C}a_{R,C}R}{1 + a_{R,C}b_{R,C}R} - \mathbf{D} - m_{C}\right) - \frac{(1-\omega)C}{k_{\omega} + b_{R,P}\omega R + b_{C,P}(1-\omega)C}P$$
(1.3c)

$$\frac{d}{dt}P = P\left(\frac{y_{R,P}\omega R + y_{C,P}(1-\omega)C}{k_{\omega} + b_{R,P}\omega R + b_{C,P}(1-\omega)C} - \mathbf{D} - m_P\right), \qquad (1.3d)$$

in which $k_{\omega} = (a_{R,P} + a_{C,P})^{-1}$.

Next, we will analyze an alternative strategy in which the time budget assumption is extended with an efficiency trade-off. Here, a shift in the intraguild predator's foraging behavior in terms of catch rates is corrected for by the difference in yields on both prey types. The ecological interpretation behind this is that an omnivore feeding mainly on a less profitable resource will have to search more intensively for food than one that feeds on more profitable foods. By this extention of the time budget assumption we add a realistic property to model (1.3). In the model, we will use compound parameter ζ , which is defined as

$$\zeta = \frac{a_{R,P} y_{R,P}}{a_{R,P} y_{R,P} + a_{C,P} y_{C,P}}, \qquad (1.4)$$

and resembles ω in the sense that when $\zeta = 0$ we have a food chain en when $\zeta = 1$ we have exploitative competition. Here, $1 - \zeta$ is the trophic distance between the intraguild predator and the consumer species.

Substitution of equation (1.4) into system (1.1) yields

$$\frac{d}{dt}N = (\mathbf{N_r} - N)\mathbf{D} - \frac{a_{N,R}N}{1 + a_{N,R}b_{N,R}N}R$$
(1.5a)
$$\frac{d}{dt}R = R\left(\frac{y_{N,R}a_{N,R}N}{1 + a_{N,R}b_{N,R}N} - \mathbf{D} - m_R\right) - \frac{a_{R,C}R}{1 + a_{R,C}b_{R,C}R}C$$

$$-\frac{\frac{1}{y_{R,P}}\zeta R}{k_{\zeta} + \frac{b_{R,P}}{y_{R,P}}\zeta R + \frac{b_{C,P}}{y_{C,P}}(1-\zeta)C}P$$
(1.5b)

$$\frac{d}{dt}C = C\left(\frac{y_{R,C}a_{R,C}R}{1 + a_{R,C}b_{R,C}R} - \mathbf{D} - m_{C}\right) - \frac{\frac{1}{y_{C,P}}(1-\zeta)C}{k_{\zeta} + \frac{b_{R,P}}{y_{R,P}}\zeta R + \frac{b_{C,P}}{y_{C,P}}(1-\zeta)C}P$$
(1.5c)

$$\frac{d}{dt}P = P\left(\frac{\zeta R + (1-\zeta)C}{k_{\zeta} + \frac{b_{R,P}}{y_{R,P}}\zeta R + \frac{b_{C,P}}{y_{C,P}}(1-\zeta)C} - \mathbf{D} - m_{P}\right), \qquad (1.5d)$$

in which $k_{\zeta} = (a_{R,P}y_{R,P} + a_{C,P}y_{C,P})^{-1}$. The compound parameters ω and ζ will be referred to as interaction parameters in the rest of the paper.

In the study of trade-off mechanisms, a proper insight in the role of yields is a prerequisite. We initially conjecture the corresponding parameter values from linear food chain data, so we expect the margin of error to be large. Still, it is of ecological importance and it may well influence our model's dynamic behavior. Therefore, we will analyze the influence of the yields of the shared resource to intraguild predator biomass for both strategies.

Table 1.2 lists the values of the model parameters used in our simulations. Except for the parameters of the intraguild predator, the values are those of a microbial food chain with ciliates and bacteria, presented by Nisbet [38] and Cunningham and Nisbet et al. [10]. As an initial step, we infer the values of the intraguild predator's parameters from those of the top-predator, on the assumption that growth rate decreases with trophic distance. We quantify this idea by taking the direct biomass conversion from resource to intraguild predator $(R \rightarrow P)$ equally efficient as the indirect conversion from resource via intraguild prey to intraguild predator $(R \rightarrow C \rightarrow P)$. This approach is also followed by Diehl and Feißel [12].

parameter	unit	values					
		Y = R	Y = C	Y = P			
		X = N	X = R	X = R	X = C		
$a_{X,Y}$	$dm^3 mg^{-1} h^{-1}$	0.156	0.037	varies	varies		
$b_{X,Y}$	h	0.8	3.0	4.0	4.0		
$y_{X,Y}$	${ m mg}~{ m mg}^{-1}$	0.4	0.6	varies	0.6		
m_Y	h^{-1}	0.025	0.01	0.0075			

Table 1.2: Parameter set for bacterium-ciliate models, derived from Cunningham and Nisbet [10] and Nisbet et al. [38]. The values for the parameters m_x are given as well. The range of nutrient supplies is $0 < N_r \le 300 \text{ mg dm}^{-3}$.

1.3 Model dynamics

This section contains the bifurcation diagrams that describe the longterm qualitative behavior of system (1.3, 1.5) as a function of nutrient provision and the intraguild predator's feeding properties. We present an integrated analysis of both the time-budget and the trade-off model, and we also investigate the influence of the yield.

To start with, we will describe the different kinds of qualitative behavior we may encounter. In the paragraphs thereafter, the bifurcation diagrams will be described and compared. We will concentrate on differences in invasibility and persistence of the intraguild predator and prey, and to a lesser extent on non-equilibrium dynamics, which are well-known to emerge from food chain models.

1.3.1 Model behavior typology

The results of our analyses are presented in figures (1.2,1.3,1.5). In these figures, the concentration of the abiotic nutrient in the inflow N_r is on the horizontal axis. The omnivore's feeding strategy parameter is on the vertical axis. This parameter can be either ω or ζ , depending on which strategy is used. For comparison, both $\omega = 0$ and $\zeta = 0$ correspond with a linear food chain, whereas when $\omega, \zeta = 1$, *C* and *P* interact solely through competition for the common resource. All values in between delineate intraguild predation.

The bifurcation diagrams consist of curves that separate the parameter space into a number of regions. For each point within such an area, the qualitative asymptotic behavior of the model is identical, although the quantitative solutions may differ considerably. When we discuss the dynamics of different area's we will concentrate on the qualitative behavior, and on two aspects in particular. Firstly, we will analyse the system's persistence and analyse which trophic niches can be invaded. Secondly, we will, to some degree, analyse the attractor type. This is only done for model solutions in which all trophic niches are occupied. Moreover, we do not analyse these non-equilibrium attractors in any further detail, as this would complicate the analysis considerably, without bearing relevance to our study. We will use the term 'complex dynamics' in reference to those regions.

In the bifurcation diagrams, all regions with identical qualitative behavior are colored in the same fashion. Unpatterned regions correspond to parameter values at which the system has a single attractor; shaded regions refer to parameter values at which there are two attractors. The different colors mark the particular attractor types, in terms of resident species, as follows:

- yellow: N-R-C
- blue: N-R-P
- bright green: N-R-C-P in equilibrium
- red: N-R-C-P in non-equilibrium
- dark green: N-R-C-P in equilibrium, two attracting states

Some regions are yellow-blue shaded, which implies that either of two incompatible situations occur: the consumer outcompetes its predator and, at the same parameter values, the predator eliminates the consumer. This seems implausible, but it is not. In these regions, the system's endpoint is determined by the initial densities of all trophic niches, as is the case in all shaded regions. In this particular situation, neither the intraguild predator, nor the intraguild prey can invade a system in infinitesimal small numbers when the other species is already present. However, should either infest the system in sufficiently large numbers, it will start to take over and oust the other species. An example of this is shown if figure (1.4). Here, at some point in time, a number of consumers infests an oscillatory N-R-P system. In the left graph, the inroad of consumers is smaller (3 mg l⁻¹) than in the right graph (6 mg l⁻¹). The N-R-P system is resistant to invasion of the smaller inroad, but it collapses when the intrusion is as large as in the graph

to the right. Note that in an oscillatory system, the success of such an infestation depends on the moment of intrusion as well.

We concentrate our analyses on three main issues. These are

- effects of the growth efficiency $y_{R,P}$ on food web dynamics
- the dynamics of the time budget model versus the trade-off model
- the effects of turn-over rates

The position of the bifurcation diagrams facilitates an integrated interpretation of the modelling results is facilitated. The graphs are presented as rows of pairs, where the left diagram depicts the time budget model and the right represents the trade-off model. There is a series of such comparable graphs at four different values for $y_{R,P}$, the yield of resource biomass to omnivore biomass. When this yield is 0.60, the intraguild predator grows as efficient on producers as on consumers, i.e. $y_{R,P} = y_{C,P}$. This implies that the expressions for ω and ζ become identical (compare equations 1.2 and 1.4), so that the time budget model and the trade-off model become one and the same. Therefore, the corresponding graphs of the time budget and the trade-off approach are also identical.

Finally, we present an analysis op the model at an alternative dilution rate. This parameter can be conceived of as the turn-over rate of the ecosystem. This property affects the dynamic behavior of food chain models considerably [52, 56, 57]. In the description of model behavior we compare the diagrams pairwise and at increasing yields. We first concentrate on regions in which all trophic niches can be occupied. Later, we concentrate on mutual invasibility, and we conclude with comparing regions with multiple attracting states and complex dynamics.

1.3.2 Coexistence of intraguild predator and intraguild prey

Regions of potential coexistence of the two highest trophic niches are colored green or shaded green and another color. At the lowest yield $(y_{R,P} = 0.24)$, the regions of coexistence of the time-budget and the trade-off graphs are much alike. Still, there are some minor differences, which play a role at high nutrient levels. Firstly, there is a dark green region in which the trade-off model has two attracting equilibria with all trophic niches occupied. Secondly, there is a blue region in the trade-off model, which is not present in the time budget model. In this region

the intraguild prey species can not survive the presence of intraguild predators.

When $y_{R,P} = 0.36$, the biomass conversion from R to P is just as efficient as the conversion from R via C to P. Here, both models behave as predicted by McCann and Hastings [32], Diehl and Feißel [12] and Mylius et al. [36] in a large part of parameter space, i.e. at low nutrient inputs C outcompetes P, stable coexistence of C and P dominates at intermediate nutrient levels and P ousts C at high nutrient levels. The potential for coexistence is generally larger in the time budget model than in the trade-off model. Moreover, a relative low interaction strength between P and R (i.e. a low value of ω or ζ) proves to be beneficial for coexistence, which is in agreement with the results of Bondavalli and Ulanowicz [6].

The main difference between the bifurcation diagrams concerning $y_{R,P} = 0.36$ and $y_{R,P} = 0.48, 0.60$ is that the region of potential coexistence becomes smaller. This is because the effect of increasing $y_{R,P}$ is an enhanced competitiveness of the intraguild predator, as compared to the intraguild prey.

The simulations with increased dilution rates (0.045 instead of 0.03) pertain to $y_{R,P} = 0.36$. Compared to the corresponding graphs at $\mathbf{D} = 0.03$, there are two major differences. Firstly, stable coexistence of *C* and *P* at the higher dilution rate is bound to somewhat lower values of the interaction parameters ω and ζ . This implies that higher turnover rates favors predatory omnivores rather than competitive omnivores. Second, at the higher dilution rate the blue area, in which *C* cannot persist in the presence of *P*, originates at higher levels of enrichment. This is because the diminution of *P* due to enhanced dilution relaxes the predation pressure on *C*.

1.3.3 Invasibility

The intraguild prey, C, may invade in all regions that do not contain blue, whereas the intraguild predator, P, can invade in all regions without yellow. An increase in $y_{R,P}$ is always beneficial to P, so that such an increment enlarges the parameter region in which P can invade. Effectively, an increase in $y_{R,P}$ strengthens the interaction between R and P. The intraguild prey will not benefit from an increase in $y_{R,P}$. As a consequence, it will lose competitiveness. The regions of mutual invasibility and persistence of the intraguild configuration become smaller with increasing interaction strengths between P and R, which is in accordance with Bondavalli and Ulanowicz [6].

In general, P cannot invade if the nutrient provision is too low. This is a consequence of the assumption that C is a better competitor for the common resource than P. The effect of this superior competitiveness increases with increasing ω or ζ .

The region in which C can invade is generally smaller in the tradeoff simulations than in the time budget analyses. This is because the trade-off strategy involves a weighing of catching efforts of P on Ragainst the yield. When $y_{R,P}$ is lower than $y_{C,P}$, the trade-off strategy imposes a higher competitiveness on P than the time budget strategy. This is because a reduction in predation ability on C results in a nonsymmetrically increased catching efficiency on R; in the time budget strategy this balance is symmetric.

In line with the predictions of Bondavally and Ulanowicz [6], both strategies predict mutual invasibility (the unpatterned green regions) to be most likely at low interaction strengths between P and R, where both species can invade at the relative largest range of nutrient supply densities. This effect is most pronounced in the trade-off strategy.

An increased dilution rate brings about two marked effects. Firstly, the region of mutual invasibility generally covers a larger range of nutrient enrichment levels. Secondly, mutual invasibility is restricted to a smaller range of the interaction parameters. This result might be used as an indication that systems at high turn-over rates are less sensitive to nutrient enrichment.

1.3.4 Complex dynamics and multiple stable states

The red regions in the bifurcation diagrams correspond to parameter values, where the system's attracting state is not an equilibrium. All diagrams show such dynamics at high nutrient enrichment levels and at values of ω and ζ where the system approximates a food chain. This phenomenon has been widely used to demonstrate the 'paradox of enrichment' in food chains [2, 4]. Bifurcation analyses reveal that red regions in the right bottom positions of the diagrams comprise chaos as a result of a cascade of period doublings (unpublished data, cf. Boer et al. [4]; Kooi et al. [24]; Kooi et al. [25]). These red regions vanish rapidly when the interaction parameter changes to more competitive behavior of P. This result corroborates the current view that weak interactions stabilize food webs [22, 32]. This effect is stronger in the trade-off strategy than in the time budget strategy. This may indicate that ecological trade-off



Figure 1.2: Bifurcation diagrams of the timebudget model (left positions) and the trade-off model (right positions) at $y_{R,P} = 0.24, 0.36$. Different colors refer to differences in asymptotic qualitative behavior. Yellow: N-R-C, blue: N-R-P, bright green: N-R-C-P in equilibrium, dark-green: two attractors for N-R-C-P in equilibrium, red: N-R-C-P in non-equilibrium, dashed: two attractors of corresponding colors. Parameter values are as indicated in table (1.2), $\mathbf{D} = 0.03$. Pure competition implies $\omega, \zeta = 1$, whereas $\omega, \zeta = 0$ corresponds to a linear food chain.

strategies can reduce complex dynamics in food webs.

At low values of $y_{R,P}$ there is a second complex region in the diagrams, placed at much higher values of the interaction parameter (±0.7), although bifurcation analyses revealed that these particular regions do not contain chaotic dynamics. The combination of a relatively competitive P with a low yield on the common resource may give rise to



Figure 1.3: Bifurcation diagrams of the timebudget model (left positions) and the trade-off model (right positions) at $y_{R,P} = 0.48, 0.60$. Different colors refer to differences in asymptotic qualitative behavior. Yellow: N-R-C, blue: N-R-P, bright green: N-R-C-P in equilibrium, dark-green: two attractors for N-R-C-P in equilibrium, red: N-R-C-P in non-equilibrium, dashed: two attractors of corresponding colors. Parameter values are as indicated in table (1.2), $\mathbf{D} = 0.03$. Pure competition implies $\omega, \zeta = 1$, whereas $\omega, \zeta = 0$ corresponds to a linear food chain.

complexity. This effect is more pronounced in the trade-off strategy.

All bifurcation diagrams have regions with multiple attracting states. Alternative stable endpoints arise from tangent bifurcations and hold the potential for hysteresis loops. These loops have been demonstrated in a variety of natural ecosystems [50]. In our models, the multiple attract-



Figure 1.4: Demonstration of alternative attractors at a single parameter set. In both figures the consumer species infests a stable oscillatory producer–intraguild predator system. The moment of intrusion is marked by an arrow. In the left diagram, the inroad density (3 mg l⁻¹) is insufficient to oust the intraguild predator, which is able to recover and suppress the consumer species. In the diagram to the right, the inroad is large enough (6 mg l⁻¹) to thrive the omnivorous species to extinction. As a result, an oscillatory producer–consumer system evolves. Parameter values are $\mathbf{D} = 0.045$, $\mathbf{N}_{\mathbf{r}} = 300.0$, $\zeta = 0.7$.
ing states usually correspond to relatively large values for the interaction parameter. In general, the regions involved mark the transition from regions where P is outcompeted by C on the one side and regions where the three-trophic system persists or where P ousts C on the other side.

In the time budget model at $y_{R,P} = 0.24, 0.36$ and the trade-off model at $y_{R,P} = 0.36$, $\mathbf{D} = 0.045$, the yellow-green dashed regions mark parameter values at which both the N-R-C-P and the N-R-C assemblages attract. In these regions, loss of the intraguild predator would cause the system to shift towards a state in which it cannot re-invade.

In the trade-off model at $y_{R,P} = 0.24$, there are two attracting states in which all trophic niches are occupied at high nutrient enrichment levels and $\zeta = \pm 0.06$. Here, a catastrophic event may cause a permanent change in biomass distributions in the system, but there is no extinction of species. The persistent web is bi-stable at this set of parameters.

In all graphs where $y_{R,P} > 0.24$, there exists a yellow–blue dashed region. In these regions both the N-R-C and the N-R-P assemblages are structurally stable. Both assemblages are resistant to invasion. Should, however, the system be infested by large numbers of the non-resident species, the system undergoes a drastic change, after which the infesting species replaces the resident species.

The model simulations at $\mathbf{D} = 0.045$ yield larger regions of multiple stable states. This indicates that high turn-over rates might promote the occurrence of hysteresis loops in ecosystems. This result emerges from both the time budget and the trade-off model.

1.4 Discussion and conclusions

Our study concentrated on the influence of nutrient enrichment in an ecosystem with intraguild predation. We used two strategies for modelling the intraguild predation interaction, including a time budget assumption and an efficiency trade-off for the omnivore's foraging behavior.

The predictions of both modelling approaches are similar for the largest part of the explored parameter space. However, the models may behave different at interaction parameter values roughly between $0.6 < \omega, \zeta < 0.8$. So, far, this parameter range has received little theoretical attention, as McCann and Hastings [32] were primarily interested in the parameter range $0 < \omega < 0.5$. However, Navarette et al. [37] showed that this more competitive type of intraguild preda-



Figure 1.5: Bifurcation diagrams of the timebudget model (left) and the trade-off model (right) at $\mathbf{D} = 0.045$ and $y_{R,P} = 0.36$. Different colors refer to differences in asymptotic qualitative behavior. Yellow: N-R-C, blue: N-R-P, bright green: N-R-C-P in equilibrium, dark-green: two attractors for N-R-C-P in equilibrium, red: N-R-C-P in non-equilibrium, dashed: two attractors of corresponding colors. Parameter values are as indicated in table (1.2). Pure competition implies $\omega, \zeta = 1$, whereas $\omega, \zeta = 0$ corresponds to a linear food chain.

tion can play a dominant role in natural ecosystems. Our analyses show that intraguild predation close to competition yields a rich repertoire of ecologically plausible dynamic behaviors.

Our results are consistent with the findings of Huxel and McCann [33], Boer et al. [5] and Persson et al. citePeHaBr01 in that the models predict the paradox of enrichment for food chains, i.e. complex behavior occurs at high nutrient inlet densities. However, this complex behavior is readily eliminated when a weak interaction between the intraguild predator and the resource species is established. Therefore, our results support the view that weak interactions promote stability and persistence of food webs [6, 7, 15, 31, 33, 39, 43, 46]. We find this phenomenon to be more demonstrative in the trade-off model than in the time budget model. Under the assumption that the trade-off approach adds realism, our results further substantiate the current view. If complex dynamics, as often found in theoretical food chain studies, are so easily eliminated by weak interactions, and intraguild predation in nat-

ural ecosystems is widespread, the predicted complex dynamics might be artefactual, rather than realistic.

Mylius et al. [36] find that coexistence of P and C requires a relatively low attack rate of P on R. In general terms, such behavior corresponds to low values of interaction parameters ω, ζ . Our results corroborate this finding to a large extent, as we find the largest regions of coexistence in the lower parts of the bifurcation diagrams. In addition, we find that both the yield $y_{R,P}$ and dilution rate **D** are important modifiers in determining the scope of potential coexistence of C and P.

We find that intraguild predation in the vicinity of exploitative competition ($\zeta, \omega \to 1$) results in extinction of the intraguild predator. This result is in agreement with the competitive exclusion principle. However, at somewhat lower values for ω or ζ , the existence of multiple stable states in which both the N-R-C system as the N-R-P system are resistant to invasion, is a common phenomenon in our analyses. Both endpoints are equivalent in the sense that both C and P figure as consumer guilds. According to Tilman's R^* -rule [54], the better competitor will always oust his opponent. In our models the consumer is the better competitor for the resource species. Resistance of the N-R-P system to invasion of C suggests that a weak interaction between P and C can be a good defence mechanism for inferior competitors.

At high nutrient enrichment levels and intermediate interaction strengths between P and R our model predicts exclusion of C. This finding corresponds with current theory [12, 13, 21, 32]. This effect depends on the intraguild predator's growth efficiency on the resource species. Moreover, it acts more dominantly in the trade-off model than in the time budget model. It appears that a modestly competitive intraguild predator bearing a low yield on the common resource, in combination with a low system turn-over rate provides the best environment for a persistent food web with omnivory.

As a final result, our model predicts regions of multiple attracting in all of the simulations. At $\mathbf{D} = 0.045$, the corresponding regions contribute significantly to the overall dynamics. The regions involved cover a transition trajectory between two extremes, for instance at the one end of the region P goes extinct, whereas at the other end C is eliminated. The existence of multiple stable states in natural systems has received increasing interest in the past years [50], and an increasing amount of cases have been reported. If omnivory is a potential cause for the emergence of multiple stable states, and it is widespread in natural systems, it might be one of the explanations for the ubiquitousness of multiple stable states.

Acknowledgements

The authors thank Nico van Straalen, Matty Berg and Tineke Troost for their valuable comments on the paper.

References

- [1] Abrams PA. (1993). Effect of increased productivity on the abundances of trophic levels. *Am. Nat.* 141:351–371.
- [2] Abrams PA, Roth JD. (1994). The effect of enrichment of three-species food chains with nonlinear functional response. *Ecology* 75:1118–1130.
- [3] Bazykin AD. (1998). *Nonlinear dynamics of interacting populations*. World Scientific, Singapore.
- [4] Boer MP, Kooi BW, Kooijman SALM. (1998). Food chain dynamics in the chemostat. *Math. Biosci.* 150:43–62.
- [5] Boer MP, Kooi BW, Kooijman SALM. (2001). Multiple attractors and boundary crises in a tri-trophic food chain. *Math. Biosci.* 169:109–128.
- [6] Bondavalli C, E. UR. (1999). Unexpected effects of predators upon their prey: the case of the american alligator. *Ecosystems* 2:49–63.
- [7] Borrvall C, Ebenmann B, Jonsson T. (2000). Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters* 3:131–136.
- [8] Chesson J. (1983). The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297–1304.
- [9] Cock MJW. (1978). Assessment of preference. J. Anim. Ecol. 47:805-816.
- [10] Cunningham A, Nisbet RM. (1983). *Transients and oscillations in continuous culture*. Academic Press, London.
- [11] DeAngelis DL. (1992). *Dynamics of nutrient cycling and food webs*. Chapman & Hall, London.
- [12] Diehl S, Feißel M. (2000). Effects of enrichment on three-level food chains with omnivory. *Am. Nat.* 155:200–218.
- [13] Diehl S, Feißel M. (2001). Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. *Ecology* 82:2977–2983.
- [14] Doedel EJ, Champneys AR, Fairgrieve TF, Kuznetsov YA, Sandstede B, Wang X. (1997). Auto 97: Continuation and bifurcation software for ordinary differential equations. Technical report, Concordia University, Montreal, Canada.
- [15] Fussman GF, Heber G. (2002). Food web complexity and chaotic population dynamics. *Ecology Letters* 5:394–401.
- [16] Ghosh D, Sarkar AK. (1998). Stability and oscillations in a resourcebased model of two interacting species with nutrient cycling. *Ecol. Modell*. 107:25–33.

- [17] Grimm V, Wissel C. (1997). Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding discussion. *Oecologia (Berlin)*. 109:323–334.
- [18] Guckenheimer J, Holmes P. (1985). *Nonlinear Oscillations, Dynamical Systems and Bifurcations of Vector Fields*, volume 42 of *Applied Mathematical Sciences*. Springer-Verlag, New York, 2 edition.
- [19] Heithaus MR. (2001). Habitat selection by predators and prey in communities with asymetrical intraguild predation. *Oikos* 92:542–554.
- [20] Holling CS. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45:3–60.
- [21] Holt DH, Polis GA. (1997). A theoretical framework for intraguild predation. Am. Nat. 149:745–764.
- [22] Huxel G, McCann K. (1998). Food web stability: the influence of trophic flows across habitats. *Am. Nat.* 152:460–469.
- [23] Khibnik AI, Kuznetsov YA, Levitin VV, Nikolaev EV. (1993). Continuation techniques and interactive software for bifurcation analysis of odes and iterated maps. *Physica D* 62:360–371.
- [24] Kooi BW, Boer MP, Kooijman SALM. (1998). Consequences of population models on the dynamics of food chains. *Math. Biosci.* 153:99–124.
- [25] Kooi BW, Kuijper LDJ, Boer MP, Kooijman SALM. (2002). Numerical bifurcation analysis of a tri-trophic food web with omnivory. *Math. Biosci.* 177-178:201–228.
- [26] Kuznetsov YA. (1998). *Elements of Applied Bifurcation Theory*, volume 112 of *Applied Mathematical Sciences*. Springer-Verlag, New York, 2 edition.
- [27] Legović T. (1989). Predation in food webs. Ecol. Modell. 48:267-276.
- [28] Leibold MA, Chase JM, Shurin JB, Downing AL. (1997). Species turnover and the regulation of trophic structure. Ann. Rev. Ecol. Syst. 28:467–494.
- [29] Levine S. (1980). Several measures of trophic structure applicable to complex food webs. *J. theor. Biol.* 83:195–207.
- [30] Marr AG, Nilson EH, Clark DJ. (1962). The maintenance requirement of *Escherichia coli. Ann. N. Y. Acad. Sci.* 102:536–548.
- [31] McCann KS. (2000). The diversity-stability debate. *Nature (Lond.)* 405:228–233.
- [32] McCann KS, Hastings A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proc. R. Soc. Lond. B Biol. Sci.* 264:1249–1254.

- [33] McCann KS, Hastings A, Huxel GR. (1998). Weak trophic interactions and the balance of nature. *Nature (Lond.)* 395:794–798.
- [34] Morin P. (1999). Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology* 80:752–760.
- [35] Murdoch WW. (1973). The functional response of predators. J. Appl. *Ecol.* 10:335–342.
- [36] Mylius SD, Klumpers K, De Roos AM, Persson L. (2001). Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *Am. Nat.* 158:259–276.
- [37] Navarette SA, Menge BA, Daley BA. (2000). Species interactions in intertidal food webs: prey or predation regulation of intermediate predators? *Ecology* 81:2264–2277.
- [38] Nisbet R, Cunningham A, Gurney WSC. (1983). Endogenous metabolism and the stability of microbial prey-predator systems. *Biotechnol. Bioeng*. 25:301–306.
- [39] Paine RT. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature (Lond.)* 355:73–75.
- [40] Persson A, Hansson C, Brönmark P, Lundberg P, Pettersson LB, Greenberg L, Nilsson PA, Nyström P, Romare P, Tranvik L. (2001). Effects of enrichment on simple aquatic food webs. *Am. Nat.* 157:654–669.
- [41] Pimm SL, Lawton JH. (1978). On feeding on more than one trophic level. *Nature (Lond.)* 275:542–544.
- [42] Polis GA. (1991). Complex trophic interactions in deserts: an empirical critique of food web theory. *Am. Nat.* 138:123–155.
- [43] Polis GA. (1998). Stability is woven by complex webs. *Nature (Lond.)* 395:744–745.
- [44] Polis GA, Myers C, Holt R. (1989). The ecology and evolution of intraguild predation: potential predators that eat each other. *Ann. Rev. Ecol. Syst.* 20:297–330.
- [45] Polis GA, Strong DR. (1996). Food web complexity and community dynamics. Am. Nat. 147:813–846.
- [46] Post DM, Conners M, Goldberg DS. (2000). Prey preference by a top predator and the stability of linked food chains. *Ecology* 81:8–14.
- [47] Revilla T. (2002). Effects of intraguild predation on resource competition. *J. Theor. Biol.* 214:49–62.
- [48] Rozenzweig ML. (1971). Paradox of enrichment: the destabilization of exploitation ecosystems in ecological time. *Science (New York)* 171:385– 387.

- [49] Rozenzweig ML, MacArthur RH. (1963). Graphical representation and stability conditions of predator–prey interactions. *Am. Nat.* 97:209–223.
- [50] Scheffer M, Carpenter SR, Foley JA, Folke C, Walker B. (2001). Catastrophic shifts in ecosystems. *Nature (Lond.)* 413:591–596.
- [51] Scheffer M, Hosper SH, Meijer ML, Moss B. (1993). Alternative equilibria in shallow lakes. *Trends Ecol. & Evol.* 8:352–356.
- [52] Smith HL, Waltman P. (1994). *The theory of the chemostat*. Cambridge University Press.
- [53] Sprules WG, Bowerman JE. (1988). Omnivory and food chain length in zooplankton food webs. *Ecology* 69:418–426.
- [54] Tilman D. (1990). Constraint and trade-offs: towards a predictive theory of competition and succession. *Oikos* 58:3–15.
- [55] Vayenas DV, Pavlou S. (1999). Chaotic dynamics of a food web in a chemostat. *Math. Biosci.* 162:69–84.
- [56] Vayenas DV, Pavlou S. (1999). Coexistence of three microbial populations competing for three complementary nutrients in a chemostat. *Math. Biosci.* 161:1–13.
- [57] Vayenas DV, Pavlou S. (2001). Chaotic dynamics of a microbial system of coupled food chains. *Ecol. Modell.* 136:285–295.

2

C and N gross growth efficiencies of copepod egg production studied using a Dynamic Energy Budget model

Abstract

Simple stoichiometric models based on the principle that limiting elements are used with high efficiency have been unable to capture the apparently constant and low nitrogen gross growth efficiency that characterizes egg production in marine copepods. A new model of egg production is presented based on Dynamic Energy Budget theory. The model splits substrates between nitrogenous and non-nitrogenous compounds, distinguishes between structural and reserve components of animal biomass, and requires that assimilated substrates are utilized to meet maintenance costs prior to allocation for egg production. Carbon and nitrogen gross growth efficiencies of egg production by Acartia in response to food C:N are predicted realistically. Production tends to be maximized when consuming N-rich food, indicating a general N-limitation, the benefits being greatest at high intake rates. However food carbon also plays a role in regulating egg production by supporting protein-sparing biochemical pathways. The model indicates that zooplankton are unable to utilize dietary N efficiently for egg production, even when it is scarce in the diet, because of the N demands for maintenance by the adult. The work emphasizes the need to consider the C and N requirements for maintenance in order to understand dietary constraints to mesozooplankton production.

2.1 Introduction

The ability to quantify the efficiency with which grazers utilize ingested prey items for growth and reproduction is central to the development of mathematical models for studying the flows of carbon and nutrients in ecosystems. Quantifying growth efficiency requires an understanding of the nutritional aspects of food which limit production. Evidence to support nutrient element limitation of freshwater zooplankton is strong, particularly for Daphnia spp. where the potential for phosphorus limitation is well documented [15, 33]. The situation is less clear in the case of marine zooplankton. Strong correlations between egg production of copepods and food N have been shown in laboratory experiments [12, 24]. At first sight such results support the case for N limitation in these organisms. However correlation does not of itself conclusively demonstrate a causal limitation by the nutrient element [9].

The potential limiting effects of C and N in marine zooplankton can be examined using simple stoichiometric models [1, 4]. In these models, the limiting element is identified as the one in least supply relative to demand. A threshold elemental C:N ratio in food items, ϕ_F^* , can then be defined, below which C limits production, and above which N limits:

$$\phi_F^* = \frac{\phi_Z \, K_N^*}{K_C^*} \tag{2.1}$$

where K_N^* and K_C^* are the maximum (upper bound) efficiencies with which N and C (respectively) can be used for production of eggs, and ϕ_Z is the C:N ratio of zooplankton biomass. The limiting element is assumed to be used with maximum efficiency, with excesses of other elements released as waste products. Deciding on an appropriate values for K_N^* and K_C^* is however not easy. Previous studies have assumed that N and P can be used with a high maximum efficiency, e.g. 1.0 [1, 38], whereas K_C^* is lower because catabolic processes necessarily result in the evolution of CO₂. The maximum C growth efficiency based solely on the energetic costs of converting food substrates to biomass is 0.75 [11]. However K_C^* also needs to take into consideration other C requirements of organisms, such as the energetic costs of locomotion and the maintenance costs of existent structures. In the instance of zooplankton consuming food with a typical C:N for marine seston (e.g. the Redfield ratio, 6.625), C-limitation of zooplankton is indicated if values for K_C^* as low as 0.2-0.3 are inserted into equation (2.1). Stoichiometric theory would however require that N growth efficiency increases with increasing food C:N under C-limiting conditions. The experimental evidence shows Acartia using N for egg production with a low and constant efficiency of 0.4 [12, 24] and an even lower efficiencies contrast strongly with the high efficiencies which might, at least in theory, be expected for limiting elements. Protein sparing is a well known phenomenon in a range of organisms (e.g. McGoogan and Gatlin, [29]; Roxburgh and Pinshow [32]; Arnould et al. [6]) as a means of maximizing the utilization of limiting elements for growth. So if marine copepods are limited by elemental N, why do they utilize it with such low efficiency?

Justus von Liebig's 'Law of the Minimum', upon which stoichiometric theory is based, has been repeatedly invoked in plankton ecology [14]. However the simplicity and empirical nature of the stoichiometric approach, e. g. the difficulty in prescribing values for K_N^* and K_C^* , renders it difficult to apply when examining C versus N limitation of marine copepods. New approaches to modeling resource use by consumers need to consider in greater detail the complex interplay between elements, biochemical arguments and physiology [3, 27]. One such approach is Dynamic Energy Budget (DEB) theory which provides a theoretical framework that is conceptually applicable to all organisms [28]. Substrates assimilated from food items are directed to reserve pools which in turn are used for processes such as maintenance, growth, development and reproduction. An important concept incorporated into the DEB approach is the 'synthesizing unit' (SU). Enzymatic processes that handle a range of potentially limiting substrates and form one or more products are represented on the basis of probability theory of substrates being attached to binding sites on SUs. In this way smooth transitions between states between different dominant limiting factors can be represented [27].

Here we use a DEB model which includes SUs to investigate how the production of marine copepods is influenced by C:N ratio in food (phytoplankton). Carbon is divided between nitrogenous substrates (proteins, nucleic acids: P) and non-nitrogenous substrates (carbohydrates, lipids: H) [1]. Substrates are firstly utilized for maintenance of the adult, with those remaining being available for egg production. Utilization follows

two pathways, a *P*-only pathway in which energetic demands are met using *P*, and a *PH* pathway in which energetic demands are met using *H*, thereby sparing *P*. The relative dominance of the two pathways depends on the availabilities of *P* and *H* and the kinetics of the SUs. The limiting roles of C and N in egg production thus manifest themselves in this advanced treatment of *P* and *H* utilization, rather than on the basis of elemental ratios as in simple stoichiometric models. The model is calibrated to fit the experimental data of [24], and results discussed in context of the ongoing debate regarding the roles of C and N in the nutrition of marine zooplankton.

2.2 Model description

The model (Figure 2.1) is based on DEB theory [26]. Assimilated food is passed to the reserve pools, from where it is available for use by SUs to meet the demands for maintenance and egg production by the organism. A list of model variables and parameters is provided in Table 1. DEB notation is used throughout.

2.2.1 Ingestion and assimilation

Carbon is ingested at a constant rate $j_{C,I}$ (mol C (mol C)⁻¹ h⁻¹). This C is divided between nitrogenous substrates (proteins, nucleic acids: P) with a fixed C:N ratio, ϕ_P , and non-nitrogenous substrates (carbohydrates, lipids: H). The biochemical composition of phytoplankton (the food) is variable in nature depending on growth conditions. Nitrogendeficient cells usually exhibit low protein to carbohydrate ratios (high C:N ratios) reflecting accumulation of storage carbohydrates [7]. These compounds are assimilated by the predator much more easily than structural carbohydrates [2]. The application of a single assimilation efficiency for C in a model being used to examine the influence of food C:N on growth is therefore inappropriate. We employ the model of Anderson [2] which, based on data for diatoms, divides C into four fractions, soluble (storage) and insoluble (structural) carbohydrates, lipids and proteins $(H_1, H_2, L, P$ respectively), with assimilation efficiencies of 0.881, 0.487, 0.373 and 0.688 respectively. Non-nitrogenous substrates, H, incorporate the sum of H_1 , H_2 and L. Equations for these



Figure 2.1: Flow diagram of model illustrating how ingested proteins (P) and carbohydrates (H) are passed to reserve pools, and subsequently utilized by SUs for maintenance and egg production.

components as fractions of total cell C, $\theta_{F,P}$, $\theta_{F,H1}$, $\theta_{F,L}$, $\theta_{F,H2}$, are [2]:

$$\theta_{F,P} = \frac{\phi_P}{\phi_F} \tag{2.2a}$$

$$\theta_{F,H1} = 0.0232 \,\phi_F + 0.0118$$
 (2.2b)

$$\theta_{F,L} = 0.141 (1 - \theta_{F,H1})$$
 (2.2c)

$$\theta_{F,H2} = (1 - \theta_{F,H1}) (1 - 0.141) - \theta_{F,P}$$
, (2.2d)

where ϕ_F is the total C:N of ingested food. Amounts of *P* and *H* assimilated $(j_{P,A}, j_{H,A}, \text{ mol C} (\text{mol C})^{-1} \text{ h}^{-1})$, are then:

$$j_{P,A} = 0.688 \,\theta_{F,P} \, j_{C,I}$$

$$j_{H,A} = (0.881 \,\theta_{F,H1} + 0.487 \,\theta_{F,H2} + 0.373 \,\theta_{F,L}) \, j_{C,I} .$$

$$(2.3a)$$

These empirical relationships break down for $\phi_F < 5$. Assimilated substrates enter reserve pools, m_P and m_H , quantified as densities normalized to structure. A novel feature of the model is that it includes separate reserve pools for P and H, unlike previous DEB models which have only a single reserve (e. g. Muller et al. [30]). The two reserve pools are subsequently mobilized to meet the requirements for maintenance and egg production at constant rates k_E (h⁻¹). Unassimilated substrates are egested as pellets.

2.2.2 Stoichiometry

DEB theory divides the biomass of organisms between structure and reserves. Structure is permanent and has an associated maintenance cost, which is met using reserves. A similar concept is embraced by Droop cell quota models, in which the minimum subsistence quota represents structural material, the remainder operating as an active pool available for growth [16, 40]. It is common to think of the primary reserves in animals as carbohydrates and lipids, such as triacylglycerol in high-latitude copepods (e. g. Swadling et al. [35]). However reserves of protein also play major functional roles in organisms, particularly for reproduction (e. g. MacCluskie and Sedinger [10]; Telang et al. [36]). Moreover the very fact that organisms such as marine zooplankton typically have high N excretion rates reflects the extensive use of metabolically-active nitrogenous compounds for respiration.

The model is set up here for egg production of adult Acartia tonsa. Zero growth of female structure is assumed, and so structural biomass is not explicitly included as a state variable in the model. Available substrates are allocated to reproduction after maintenance costs have been met. Changes in body weight of adult females can occur in reality [21]. Such changes are possible in the model due to changes in the size of reserve pools. Eggs, although composed largely of reserve material, typically show little variation in C:N (e. g. Anderson and Pond [5]) and so egg production can be treated in the same way as production of structure in other DEB models. We therefore assume that maintenance and

egg production (biomass products denoted X in our terminology) both conform to the same elemental stoichiometry (i. e. both have C:N ϕ_X). The magnitudes of P and H are specified by normalizing to structural biomass of the females, i. e. with units mol C (mol C)⁻¹. The maintenance term in DEB represents not only the production of biomass to replace that lost through protein turnover, but also other costs to the organism such as the energetic expenditure associated with locomotion, filtration, defense mechanisms, membrane transports and the maintenance of osmotic potential. However by giving maintenance the same stoichiometry as egg production, we have assumed that protein turnover and associated costs dominate maintenance. The costs of movement and other feeding-related costs in animals have indeed generally been shown to be low [17, 23, 25]. The energetic costs of egg production and maintenance can be met using either H or P as substrates; the former are expected to be the preferred option, thereby sparing P. The following two reactions are possible:

$$n_P^{PH} P + n_H^{PH} H \rightarrow X + n_{CO_2}^{PH} CO_2$$
 (2.4a)

$$n_P^P P \rightarrow X + n_{\mathrm{NH}_4^+}^P \mathrm{NH}_4^+ + n_{\mathrm{CO}_2}^P \mathrm{CO}_2$$
, (2.4b)

where the parameters *n* are the yield coefficients which must stoichiometrically balance. The first equation (2.4a) is the '*PH* reaction', i. e. both *P* and *H* are reactants, whereas the second (2.4b) is the '*P* reaction'. If the efficiencies with which carbon is used to make structure are known for each of the above reactions (efficiencies ψ_{PH} in the *PH*-reaction, and ψ_P for the *P* reaction, respectively), then the yield coefficients are:

$$n_P^P = \frac{1}{\psi_P} \tag{2.5a}$$

$$n_{\rm CO_2}^P = \frac{1}{\psi_P} - 1$$
 (2.5b)

$$n_{\mathrm{NH}_{4}^{+}}^{P} = \frac{1}{\psi_{P} \phi_{P}} - \frac{1}{\phi_{X}}$$
 (2.5c)

$$n_H^{PH} = \frac{1}{\psi_{PH}} - \frac{\phi_P}{\phi_X}$$
(2.5d)

$$n_P^{PH} = \frac{\phi_P}{\phi_X} \tag{2.5e}$$

$$n_{\rm CO_2}^{PH} = \frac{1}{\psi_{PH}} - 1$$
 (2.5f)

2.2.3 Synthesizing Units

The PH and P reactions (equations 2.4a, b) are controlled by synthesizing units, which merge potentially limiting substrates, in this case proteins and carbohydrates, into metabolic products. SUs are enzymes for which the dissociation rate of enzymes-substrate complexes without transformation is taken to be negligibly small, simplifying their mathematical formulation. Moreover, the kinetics of SUs are based on fluxes rather than concentrations. Using the latter is cumbersome, as they tend to be ill-defined in spatially structured environments, such as living cells. SUs can be used to predict rates of macro-biochemical reactions, depending on the supply rates of substrates. They may also be used to assess contributions of simultaneous metabolic pathways when substrates can be used in different functions. For a detailed description of the SU concept, we refer to Kooijman [27].

The SUs for maintenance and production have the same properties, such that the underlying reactions are stoichiometrically identical. Each SU has two binding sites, the first binding P and the second binding H (Figure 2.2) A reaction proceeds as soon as P is bound to the P binding site. If at that instant the H binding site has already been filled, then the PH reaction proceeds. Conversely, if the H binding site is empty, then the P reaction takes place. Binding of P and H to their respective binding sites is controlled by affinity parameters, ρ ($0 \le \rho \le 1$). *H* is bound with affinity ρ_{H}^{PH} . The protein-sparing PH reaction is favored over the P reaction in the model by setting parameter ρ_P^P , the affinity for *P* if *H* has not yet been bound to the SU, to be lower than parameter, ρ_{P}^{PH} , the affinity for P if H has already been bound. It is assumed that any one organism has a very large number of SUs, such that their binding states can be calculated on a probabilistic basis. Four binding states are possible: θ_{P} (neither site filled), θ_{P} (first site filled: P reaction proceeds), θ_{H} (second binding site filled), θ_{PH} (both sites filled: PH reaction proceeds).

2.2.4 Maintenance

There is a continuous requirement for substrates to meet the ongoing requirements of maintenance. These requirements are met first in the model, and any remaining substrates are then used for egg production. Let the cost of maintenance be k_M (mol C (mol C)⁻¹ h⁻¹). Maintenance products are formed when maintenance SUs in binding state θ_P or θ_{PH}



Figure 2.2: Conceptual diagram showing binding of P and H by synthesizing units. Products (biomass: X, NH⁺₄, CO₂) are formed as soon as P is bound. Thus if P is bound without H being present then the P pathway is followed (energetic demands met using P), otherwise the protein-sparing PH pathway proceeds (energetic demands met using H).

release their substrates and revert to $\theta_{..}$. Differential equations for the four binding states are:

$$\frac{d}{dt}\theta_{..} = k_M - \left(\frac{\rho_P^P}{n_P^P}k_E m_P + \frac{\rho_H^{PH}}{n_H^{PH}}k_E m_H\right)\theta_{..}$$
(2.6a)

$$\frac{d}{dt}\theta_{.H} = \frac{\rho_H^{PH}}{n_H^{PH}} k_E m_H \theta_{..} - \frac{\rho_P^{PH}}{n_P^{PH}} k_E m_P \theta_{.H}$$
(2.6b)

$$\frac{d}{dt}\theta_P = \frac{\rho_P^P}{n_P^P} k_E m_P \theta_{..} - k_M \frac{\theta_P}{\theta_P + \theta_{PH}}$$
(2.6c)

$$\frac{d}{dt}\theta_{PH} = \frac{\rho_P^{PH}}{n_P^{PH}} k_E m_P \theta_{.H} - k_M \frac{\theta_{PH}}{\theta_P + \theta_{PH}}.$$
(2.6d)

In this model the total dissociation rate (of θ_P and θ_{PH}) is fixed, because the maintenance requirements, k_M are fixed. The relative contributions of the *P* and *PH* routes in meeting k_M are proportional to the relative magnitudes of θ_P and θ_{PH} at steady state:

$$\theta_P^* = \frac{\rho_P^P}{n_P^P} m_P \tag{2.7a}$$

$$\theta_{PH}^{*} = \frac{\rho_{H}^{PH}}{n_{H}^{PH}} m_{H} .$$
(2.7b)

The quantities of P and H consumed in maintenance are then:

$$j_{P,M} = k_M \left(n_P^{PH} \,\Omega_{PH} + n_P^P \,\Omega_P \right) \tag{2.8a}$$

$$j_{H,M} = k_M n_H^{PH} \Omega_{PH} , \qquad (2.8b)$$

where:

$$\Omega_P = \frac{\theta_P^*}{\theta_P^* + \theta_{PH}^*}$$
(2.9a)

$$\Omega_{PH} = \frac{\theta_{PH}^*}{\theta_P^* + \theta_{PH}^*}. \qquad (2.9b)$$

Amounts of X produced (h^{-1}), ammonium excreted and CO₂ (mol (mol C)⁻¹ h^{-1}) respired as products of maintenance (normalized to structure) are:

$$j_{X,M} = k_M \tag{2.10a}$$

$$j_{\rm NH_4^+,M} = k_M n_{\rm NH_4^+}^P \Omega_P$$
 (2.10b)

$$j_{{\rm CO}_2,M} = k_M \left(n_{{\rm CO}_2}^P \,\Omega_P + n_{{\rm CO}_2}^{PH} \,\Omega_{PH} \right) \,.$$
 (2.10c)

2.2.5 Egg production

The fluxes of P and H assigned to the production SUs are the remainders of the catabolic flux after maintenance is paid:

$$j_{P,C}^g = k_E m_P - j_{P,M}$$
 (2.11a)

$$j_{H,C}^g = k_E m_H - j_{H,M}$$
 (2.11b)

The production SUs have the same properties as the maintenance SUs. Products are formed as soon as P is bound, whether or not H is present. The fractions of SUs in binding states θ_P and θ_{PH} therefore remain at zero. Contrary to the maintenance SUs, the production SUs dissociate

at a rate proportional to the abundance of the substrate-SU complexes. Equations for the $\theta_{..}$ and $\theta_{.H}$ binding combinations are:

$$\frac{d}{dt}\theta_{..} = \frac{\rho_P^{PH}}{n_P^{PH}} j_{P,C}^g \theta_{.H} - \frac{\rho_H^{PH}}{n_H^{PH}} j_{H,C}^g \theta_{..}$$
(2.12a)

$$\frac{d}{dt}\theta_{.H} = \frac{\rho_{H}^{PH}}{n_{H}^{PH}} j_{H,C}^{g} \theta_{..} - \frac{\rho_{P}^{PH}}{n_{P}^{PH}} j_{P,C}^{g} \theta_{.H} , \qquad (2.12b)$$

giving rise to steady-state fractions:

$$\theta_{..}^{*} = \frac{\frac{\rho_{P}^{PH}}{n_{P}^{PH}} j_{P,C}^{g}}{\frac{\rho_{P}^{PH}}{n_{P}^{PH}} j_{P,C}^{g} + \frac{\rho_{H}^{PH}}{n_{P}^{PH}} j_{H,C}^{g}}$$
(2.13a)

$$\theta_{.H}^{*} = \frac{\frac{\rho_{H}^{PH}}{n_{H}^{PH}} j_{H,C}^{g}}{\frac{\rho_{P}^{PH}}{n_{P}^{PH}} j_{P,C}^{g} + \frac{\rho_{H}^{PH}}{n_{H}^{PH}} j_{H,C}^{g}}.$$
 (2.13b)

The amount of X produced as eggs, and the amounts of ammonium excreted and CO2 respired as products of egg production are:

$$j_{X,G} = j_{P,C}^{g} \left(\frac{\rho_{P}^{P}}{n_{P}^{P}} \theta_{..}^{*} + \frac{\rho_{P}^{PH}}{n_{P}^{PH}} \theta_{.H}^{*} \right)$$
(2.14a)

$$j_{\mathrm{NH}_{4}^{+},G} = j_{P,C}^{g} \frac{\rho_{P}^{t} n_{\mathrm{NH}_{4}^{+}}^{t}}{n_{P}^{P}} \theta_{..}^{*}$$
 (2.14b)

$$j_{\rm CO_2,G} = j_{P,C}^g \left(\frac{\rho_P^P \, n_{\rm CO_2}^P}{n_P^P \, \theta_{..}^*} + \frac{\rho_P^{PH} \, n_{\rm CO_2}^{PH}}{n_P^{PH} \, \theta_{.H}^*} \right) \,.$$
(2.14c)

Quantities of protein and carbohydrate used in egg production are:

$$j_{P,G} = j_{P,C}^{g} \left(\rho_{P}^{P} \theta_{..}^{*} + \rho_{P}^{PH} \theta_{.H}^{*} \right)$$
 (2.15a)

$$j_{H,G} = \frac{\rho_H^{PH} n_H^{PH}}{n_P^{PH}} j_{P,C}^g \theta_{.H}^*$$
 (2.15b)

Fraction κ of activated P and H left after maintenance and egg production is returned to the reserve pools. Remaining substrates, $j_{P,R}, j_{H,R}$ for P and H respectively, are rejected and assumed to be respired as CO₂ or excreted as ammonium:

$$j_{P,R} = (1-\kappa) \left(k_E m_P - j_{P,M} - j_{P,G} \right)$$
 (2.16a)

$$j_{H,R} = (1-\kappa) \left(k_E m_H - j_{H,M} - j_{H,G} \right)$$
 (2.16b)

2.2.6 Equations of state variables

The model is configured for a copepod with a fixed structural biomass (e. g. an adult female) ingesting C at a continuous rate $j_{C,I}$. The only state variables required in order to study the fate of C and N in ingested food are therefore those of the reserve pools, m_P and m_H . Equations for these variables are:

$$\frac{d}{dt}m_P = j_{P,A} + \kappa \left(k_E m_P - j_{P,M} - j_{P,G}\right) - k_E m_P \quad (2.17a)$$

$$\frac{d}{dt}m_H = j_{H,A} + \kappa \left(k_E m_H - j_{H,M} - j_{H,G}\right) - k_E m_H \quad (2.17b)$$

At steady state the total assimilated C and N are balanced by the sum of the products of the SUs and rejected substrates:

C:
$$j_{P,A} + j_{H,A} = j_{X,M} + j_{CO_2,M} + j_{X,G} + j_{CO_2,G} + j_{P,R} + j_{H,R}$$
 (2.18a)
N: $\frac{j_{P,A}}{\phi_P} = \frac{j_{X,M} + j_{X,G}}{\phi_X} + j_{\mathrm{NH}_4^+,M} + j_{\mathrm{NH}_4^+,G} + \frac{j_{P,R}}{\phi_P}$. (2.18b)

2.2.7 Parameter values

Where possible, model parameters are derived for the copepod Acartia tonsa consuming diatoms, permitting comparison of our results with the experimental results of Kiørboe [24].

A C:N ratio for nitrogenous substrates (proteins), ϕ_P , of 3.7 mol C (mol N)⁻¹ was used [39]. The ratio in eggs, ϕ_X , was set at 5.9 mol C (mol N)⁻¹, based on the C:N in eggs of Acartia [25]. The stoichiometric coefficients in the *PH* and *P* reactions (equations 2.5a-f) are then determined from parameters ψ_{PH} , ψ_P , i. e. the efficiencies with which C is used in these reactions. We expect the efficiency with which *P* and *H* are used to produce eggs to be close to the theoretical maximum of 0.75 [11] and have accordingly used this value when setting ψ_{PH} , ψ_P . Equations 2.4a,b can accordingly be rewritten as:

$$0.63 P + 0.71 H \rightarrow X + 0.33 \text{ CO}_2$$
 (2.19a)

$$1.33 P \rightarrow X + 0.19 \text{ NH}_4^+ + 0.33 \text{ CO}_2$$
, (2.19b)

Costs of maintenance are highly variable between organisms and environments, tending to be highest for small organisms experiencing high temperatures. We tuned the cost of maintenance (parameter k_M) to fit Kiørboe's [24] data (see below), obtaining a value of 0.0041 h⁻¹ which is reasonable for Acartia at 17° C (the temperature of Kiørboe's experiments).

A high affinity, 0.95 was set for the binding efficiency of P to SUs in state $\theta_{.H}$ (parameter ρ_P^{PH}), thereby allowing the favored PH reaction to proceed

readily. Setting values for the binding probabilities of P and H to SUs in state $\theta_{...}$, parameters ρ_P^P and ρ_H^{PH} respectively, is more problematic. One might expect the binding of H to $\theta_{...}$ to have a high affinity, setting up the PH route, and of P to $\theta_{...}$ to have a lower affinity, suppressing the P route, i. e. $\rho_P^P < \rho_H^{PH}$. However, if it is assumed that copepods can in principle fulfil maintenance requirements solely using protein reserves, a constraint in the model is that $\rho_P^P \ge \rho_H^{PH}$ (Appendix I). For simplicity we therefore assume that the two parameters have the same value, minimising this dichotomy. The value was tuned by fitting to data (see below), giving $\rho_P^P = \rho_H^{PH} = 0.66$.

The reserve mobilisation rate, k_E , was set to 0.1 h⁻¹. The fates of C and N at steady state in the model, the focus of the work here, are not affected by these parameters, although the sizes of the *P* and *H* reserve pools are. Predicted total (structure plus storage) C:N ratios of zooplankton are 6.2 when ϕ_F is 6.625 (the Redfield ratio), increasing to 10.5 for ϕ_F of 35. The fractions of substrates rejected by the maintenance and production SUs returned to the reserve pools, parameter κ , was set to 0.5. This setting gives realistic predicted total body compositions (structure plus reserves) for zooplankton.

2.3 Results

The model is used to study the fate of algal C and N for copepods ingesting food items with a wide range of C:N ratios. Results are then compared with those of the egg production experiments of Kiørboe [24]. In these experiments adult female Acartia tonsa were fed the diatom Thalassiosira weissflogii with C:N ratios manipulated through the concentration of nutrient in the algal growth medium. Carbon ingestion by Acartia was independent of algal C:N at ~0.06 mol C (mol C)⁻¹ h⁻¹ and so we use this value for I_C in the model. This intake rate appears to be near the maximum for this species which may be ~ 0.08 mol C (mol C)⁻¹ h⁻¹, based on a maximum intake of 0.333 μ g C ind⁻¹ h⁻¹ and an individual weight of 4 μ g C [8]. We show only steady-state solutions of the model, obtained numerically.

2.3.1 Fit to data

Parameters for maintenance and SU binding affinities, k_M , ρ_P^P and ρ_H^{PH} , were tuned in order to fit the model to the data for C and N gross growth efficiency (K_C, K_N) of egg production versus algal C:N as found by Kiørboe [24]. Noting the constraint that $\rho_P^P \ge \rho_H^{PH}$ (Appendix I), these two parameters were assumed to be equal in value, effectively fitting them together. A least-squares fit to the K_C and K_N data was carried out, with a weighting (factor 10) toward matching K_C which shows a clear relationship with ϕ_F . The agreement between model and data is shown in Figure 2.3, achieved with $k_M = 0.0041$ h^{-1} and $\rho_P^P = \rho_H^{PH} = 0.66$. A close fit is achieved for K_C . The model predicts that K_N declines at high algal C:N because an increasing proportion of food N has to be used for maintenance purposes (see below). The data do not support this decline, although only a single point is in marked disagreement with the trend.



Figure 2.3: Model fit (line) to the data of Kiørboe [24]: gross growth efficiencies for C and N, K_C and K_N , versus algal C:N ratio (molar). Fitted parameters: $k_M = 0.0041 \text{ h}^{-1}$ and $\rho_P^P = \rho_H^{PH} = 0.66$.

2.3.2 Fate of C and N: influence of algal C:N

The predicted fate of algal C and N in the fitted model, for algal C:N, ϕ_F , 5-35, is shown in Figure 2.4a. Nitrogen in food is assumed to be solely in the form of proteins which are assimilated with a fixed efficiency of 0.688, so that the fraction of N allocated to pellets is constant at 0.312. The fraction of C egested as pellets declines at high ϕ_F because of the increasing proportion of storage carbohydrates in the algae which are easily assimilated [2]. Fractions of C and N allocated to egg production correspond to K_C and K_N as shown in Figure 2.3. These fractions are consistent with the observations of other studies involving Acartia [12, 25, 31]. The fractions of intake respired (C) or excreted (N) compare favourably with fractions of 0.15 respired and 0.25 excreted observed by Kiørboe et al. [25] for Acartia tonsa feeding on Rhodomonas baltica with a C:N of 5.75 (at high food concentration). Several processes contribute to respiration and excretion. Production of structure through maintenance to replace of degrading tissues does not contribute to egg production and hence K_C and K_N . This production is assumed to be balanced by equivalent losses of CO_2 or ammonium from the organism, i. e. the degrading material. The C and N requirements for maintenance in terms of production of X are proportional to the structural biomass of the zooplankter, which is held constant in the model. The fraction of ingested C required for maintenance therefore remains constant proportion of C intake. Production of CO₂ associated with maintenance is also a constant fraction of C intake because the PH and P reactions both yield the same amount of CO₂ (equations 2.19a,b). However production of CO₂ associated with the energetic costs of egg production decline with increasing ϕ_F in line with decreasing carbon gross growth efficiency.



Figure 2.4: Predicted fate of C and N in food for algal C:N 5-35: (a) constant intake of C of 0.06 mol C (mol C)⁻¹ h⁻¹, (b) constant intake of N of 0.01 mol N (mol C)⁻¹ h⁻¹. Respiration and excretion are subdivided into three components (from the bottom up): maintenance (production of biomass for maintenance is assumed to be balanced by an equivalent loss of CO₂ or NH₄⁺ of material turned over), energetic costs of egg production, and energetic costs of maintenance.

A fixed maintenance requirement means that an increasing proportion of N

in food must be allocated for this purpose as ϕ_F increases (for a fixed C intake, in which case N intake declines). This increasing allocation decreases the N available for egg production, resulting in lower K_N . The fraction of N needed to meet the energetic costs of egg production and maintenance decreases with increasing ϕ_F because the increased availability of H relative to P favours the PH route (equation 2.3a) rather than the P route (equation 2.3b) thereby sparing N. Perhaps the most striking asymmetry in the modelled fates of C and N is in the fluxes rejected by SUs. ϕ_F the SU binding sites for H rapidly become saturated. A fraction $(1 - \kappa)$ of the excess C arriving at these binding sites is rejected, the remainder being returned to reserves. In contrast, N is always in short supply relative to the demands for maintenance and egg production, and so is effectively bound by SUs, with little rejection.

The fates of C and N predicted by the model for an animal ingesting a constant N ration are shown in Figure 2.4b. The main difference with the results described above is that K_N , the fraction of N allocated to production, now increases with increasing ϕ_F . There is no longer a requirement for an increasing proportion of N to be allocated to maintenance because the availability of N remains fixed. The N in food is used more efficiently for egg production at high ϕ_F because there is a ready supply of *H* to favour the *PH* route (which has a N efficiency of 100% for producing *X*: equation 2.19a) rather than the *P* route (which has an efficiency of 47%: equation 2.19b).

2.3.3 Fate of C and N: influence of food ration

The influence of food intake on the predicted fate of C and N, for an algal C:N of 15, is shown in Figure 2.5. Lower intake increases the cost of maintenance as a fraction of assimilated substrates, and so decreases growth efficiencies for C and N. Indeed if ϕ_F is below 0.0162 then there is insufficient C to meet the requirements for maintenance and zero egg production (the minimum ration depends on ϕ_F , increasing at high values). Results are consistent with experimental observations (Kiørboe et al. [25]) showing increasing production, and decreasing respiration and excretion, as fractions of intake, as intake increases.

2.4 Discussion

Laboratory experiments in which copepods were fed food with varying C:N showed egg production being proportional to intake of N [24], apparently indicating limitation by that element. Previous models based on classical stoichiometric theory [4] have been unable to capture the decreasing carbon gross growth efficiency (K_C), and apparently low (~0.4) and constant K_N , of egg production with increasing food C:N observed in these experiments. Here we used a new model based on DEB theory to examine the roles of food C and N in controlling zooplankton egg production. The model splits substrates between



Figure 2.5: Predicted fate of C and N in food for algal C:N of 15, C intake 0.02-0.06 mol C (mol C)⁻¹ h⁻¹. Fractions as in Figure 2.4.

nitrogenous and non-nitrogenous compounds [1], distinguishes between structural and reserve components of animal biomass, and requires that assimilated substrates are utilised to meet maintenance costs prior to allocation for egg production. Conversion of substrates to products is controlled by synthesising units. The model is able to realistically capture the trend of decreasing K_C of egg production with increasing food C:N, ϕ_F , observed by Kiørboe [24]. It also captures the relatively low K_N , but predicts a decrease at high ϕ_F , although only a single data point is in obvious disagreement with the model (Figure 2.3).

Before discussing the implications of the results regarding the nutrition of marine zooplankton, it is worth commenting on the parameterisation of the model. Many of the model parameters were set based directly on experimental data for Acartia, or on a sound theoretical basis. The main unknown parameters are the maintenance requirement, k_M , and the affinity parameters of the SUs, ρ_P^P , ρ_P^{PH} , ρ_H^{PH} . With the exception of ρ_P^{PH} (which was given a theoretical value), these parameters were assigned values by fitting to data (Kiørboe [24]). The model is sensitive to k_M which is therefore well constrained by the data, but less so to the affinity parameters. Alternative values for these affinities, in combination with small adjustments to k_M , can result in other parameter combinations that also provide a good fit to the data. However the basic patterns of C and N utilisation exhibited by the model remain unchanged, and so we argue that the insight into zooplankton nutrition thus provided is real.

Classical stoichiometric theory dictates that limiting elements are used with high efficiency, with non-limiting elements being recycled to the environment (e. g. Hessen [20]). Indeed previous modelling studies have assumed that N can be used with a maximum efficiency of 100% [1, 38]. Models of this type are therefore unable to predict the low K_N of ~0.4 that is seen in egg production experiments. This inconsistency led Anderson and Hessen [4] to conclude

that 'stoichiometric models do not support the view of a predominant N limitation in marine copepods'. An important difference between these previous models and the DEB model described here is that the latter has a significant N requirement for maintenance. The new model successfully generated the low K_N seen in the laboratory experiments, the maintenance demand for N playing a key role. Although it may appear self-evident that maintenance should feature as a component in the N budget, the advantage of our model is that it provides a quantitative evaluation of this process in context of the N budget as a whole, based on physiological principles. Nitrogen gross growth efficiency in the model depends not only on food C:N, but also the ration. So if N becomes scarce in food then what little there is is allocated to maintenance, and K_N is low, not high (Fig. 2.5). The maintenance parameter in the model, k_M , was estimated by fitting to data. The resulting value for k_M of 0.0041 h⁻¹ is slightly higher than the respiration rate measured by Thor [37] for Acartia during star-vation of 0.003 h^{-1} (0.4 nl O₂ individual⁻¹ min⁻¹, converted assuming 4 μ g C individual⁻¹, respiratory quotient of 1, 1 mole gas occupies 24 L at 18° C). Published estimates of N turnover in marine crustaceans are scarce. Fry and Arnold [19] noted rapid carbon turnover during growth of brown shrimp (Penaeus aztecus). Frazer et al. [18] found that larval krill reared at 1.5°C replaced 13-22% of body N during 8-10 week experiments. The egg production experiments to which the model is fitted were however carried out at 17° C, in which instance a considerably higher protein turnover rate would be expected. In general, improved estimates of N turnover are needed for zooplankton, as well as other organisms (Frazer et al. [18]).

Carbon gross growth efficiency of copepods is typically low, between 0.2 and 0.3, in common with other planktonic consumers [34]. We have already discounted 'obligatory' respiration as a major C sink in copepods. The model indicates that less than 20% of food C is respired due to maintenance and the energetic costs of maintenance and egg production (Fig. 2.4). The relative demands for C and N by the modelled copepods are reflected in the extent to which substrates are bound by the SUs. Very little N is rejected by SUs, whereas the low K_C in the model is due to high rejection of C by SUs. In other words, the predicted low carbon gross growth efficiency is due to stoichiometric regulation, effectively N limitation (see below), and not energetic demands for C-rich compounds. One can speculate about the ultimate fate of this rejected material. One possibility is that it is simply respired or excreted, or it could be egested in pellets [13].

Low rejection of N by SUs is consistent with the idea that zooplankton are N-limited. Predicted egg production is inversely related to food C:N for animals ingesting a constant carbon ration (Fig. 2.4a). A feature of the model is however that it is not restricted to the simple Liebig-type C or N limitation. The simple stoichiometric models which do operate on Liebig principles would show zero sensitivity to C in food under conditions of N-limitation. Yet the DEB model shows that an animal ingesting a food item with a fixed quantity of C and N would increase production if extra C is added to that food (Fig. 2.4b). This extra C increases the prevalence of the PH reaction pathway relative to the P pathway, permitting protein sparing for egg production. Simple stoichiometric models predict the fate of C and N based only on the relative elemental ratios of consumer and prey, and assumed growth efficiencies. The fate of C and N in the model described here depends on both quantity and quality of the food, demands for maintenance and egg production, and the dynamic action of the SUs. The separate influences of C and N in ingested food on production, as predicted by the new model, is shown in Figure 2.6. At high C:N ratios (> 20) production appears to be strongly N-limited, with little or no response to further supplements of C in the diet. At low C:N ratios, and particularly when total intake of C is also low, production is stimulated by addition of either C or N to the diet.



Figure 2.6: Production as predicted by the model, as influenced by quantities of C and N in ingested food. Dotted line indicates food C:N = 20 (higher C:N to right, lower to left).

As a further examination of the relationship between intake and food C:N, the former can be quantified in terms of dry weight, i. e. it is assumed that copepods are obtaining a certain ration on a per gram basis. It is possible to convert the biochemical fractions used in the model to a per unit weight scale by assuming fixed elemental compositions for these fractions: $C_{59}N_{16}H_{94}O_{19}S_{0.5}$ for protein [39] and $C_{18}H_{36}O_2$ and CH_2O for lipid and carbohydrate respectively [1]. The relative dominance of these fractions is related to food C:N



(equations 2.2a-d). On this basis, the production versus intake and algal C:N is shown in Figure 2.7. These results confirm that egg production is maximised by consuming as much as possible, and by selecting food items rich in nitrogen.

Figure 2.7: Production as predicted by the model, as influenced by food intake (in units of dry weight) and food C:N.

2.5 Acknowledgements

TRA is funded by the Natural Environment Research Council, UK. The authors would like to thank Bob Kooi and Tineke Troost for their valuable discussions and comments on the manuscript. We wish to thank two anonymous referees for their comments on the manuscript.

2.6 Appendix I: constraints to values of ρ parameters

When there is insufficient supply of reserves to fulfill maintenance demands, the copepods will die. Equations 2.8a,b quantify the amounts of reserves used for maintenance. After some rearranging, they read as follows:

$$j_{P,M} = k_M \frac{\rho_P^P j_{P,C} + \frac{n_P^{PH}}{n_H^{PH}} \rho_H^{PH} j_{H,C}}{\frac{\rho_P^P}{n_P^{P}} j_{P,C} + \frac{\rho_H^{PH}}{n_H^{PH}} j_{H,C}}$$
(2.20a)

$$j_{H,M} = k_M \frac{\rho_H^{PH} j_{H,C}}{\frac{\rho_H^{PH}}{n_H^{PH}} j_{H,C} + \frac{\rho_P^{P}}{n_P^{P}} j_{P,C}}, \qquad (2.20b)$$

in which $j_{H,C} = k_E m_H$ and $j_{P,C} = k_E m_P$. It is assumed that copepods can potentially fulfill maintenance requirements by respiration of protein reserves solely. The organisms are at the brink of starvation when all proteins and all carbohydrates are invested in maintenance. This is the case when $j_{P,C} = j_{P,M}$ and $j_{H,C} = j_{H,M}$. Using equations (2.20a,2.20b), this gives

$$j_{H,C} = n_H^{PH} k_M - \frac{\rho_P^P n_H^{PH}}{\rho_H^{PH} n_P^P} j_{P,C}$$
 (2.21a)

$$j_{H,C} = \frac{\rho_P^P n_H^{PH} j_{P,C} \left(k_M - \frac{j_{P,C}}{n_P^P} \right)}{\rho_H^{PH} \left(j_{P,C} - k_M n_P^{PH} \right)} .$$
(2.21b)

Substitution of these two gives, after some algebra, the starvation boundary of $j_{P,C}$, which is the amount of proteins that is just sufficient for survival. The quantity of protein used when all available proteins and carbohydrates are invested in maintenance is

$$j_{P,C}^{*} = \frac{\rho_{H}^{PH} n_{P}^{PH} k_{M}}{\rho_{H}^{PH} + \rho_{P}^{P} \frac{n_{P}^{PH}}{n_{P}^{P}} - \rho_{P}^{P}}.$$
(2.22)

In the absence of carbohydrates, the quantity of required proteins can be derived from equation (2.20a) with $j_{H,C} = 0$, giving $j_{P,M} = k_M n_P^P$. If $j_{P,C}^* < k_M n_P^P$, a certain amount of carbohydrates is required to produce enough $j_{X,M}$. This violates the assumption that copepods can potentially survive in the absence of carbohydrates. Therefore, we need $j_{P,C}^* \ge k_M n_P^P$, which translates into the constraint

$$\rho_{H}^{PH} \left(n_{P}^{PH} - n_{P}^{P} \right) \geq \rho_{P}^{P} \left(n_{P}^{PH} - n_{P}^{P} \right) .$$
(2.23)

As the *PH* route is more efficient with respect to the usage of nitrogen than the *P* route (see equations 4a, 4b), we have $n_P^P \ge n_P^{PH}$, so that $\rho_P^P \ge \rho_H^{PH}$. To obtain a preference for the *PH* route, ρ_H has to be as large as possible and, therefore, we use $\rho_P^P = \rho_H^{PH}$.

Symbol	Description	Value	Units
Н	carbohydrates reserve biomass	variable	$mol C (mol C)^{-1}$
$j_{C,I}$	carbon intake	variable	$mol C (mol C)^{-1} h^{-1}$
$j_{\rm CO_2,M}$	CO_2 produced in maintenance	variable	mol C (mol C) $^{-1}$ h $^{-1}$
$j_{CO_2,G}$	CO_2 produced in egg production	variable	mol C (mol C) $^{-1}$ h $^{-1}$
$j_{H,A}$	assimilated H	variable	$mol C (mol C)^{-1} h^{-1}$
j_{H}^{g}	H assigned to egg production	variable	mol C (mol C) $^{-1}$ h $^{-1}$
$j_{H,G}$	H used for egg production	variable	$mol C (mol C)^{-1} h^{-1}$
ĴН.М	H used for maintenance	variable	mol C (mol C) $^{-1}$ h $^{-1}$
$j_{H,R}$	H rejected by production SUs	variable	mol C (mol C) $^{-1}$ h $^{-1}$
$j_{\rm NH^+,G}$	NH_4^+ produced in egg production	variable	mol N (mol C) $^{-1}$ h $^{-1}$
$j_{\mathrm{NH}^+,M}$	NH_4^+ produced in maintenance	variable	mol N (mol C) $^{-1}$ h $^{-1}$
ĴP.A	assimilated P	variable	$mol C (mol C)^{-1} h^{-1}$
j_{PG}^{g}	P assigned to egg production	variable	$mol C (mol C)^{-1} h^{-1}$
1P G	P used for egg production	variable	$mol C (mol C)^{-1} h^{-1}$
ј <u>р</u> м	P used for maintenance	variable	mol C (mol C) $^{-1}$ h $^{-1}$
jp R	P rejected by production SUs	variable	mol C (mol C) $^{-1}$ h $^{-1}$
i_{X} G	X produced in egg production	variable	mol C (mol C) $^{-1}$ h $^{-1}$
іх м	X replaced in maintenance	variable	mol C (mol C) $^{-1}$ h $^{-1}$
k_E	reserve mobilization rate	0.10	h^{-1}
k_M^{\perp}	maintenance turnover rate	0.0041	h^{-1}
K_C	carbon gross growth efficiency	variable	mol C (mol C) $^{-1}$
$\overline{K_N}$	nitrogen gross growth efficiency	variable	mol N (mol N) ⁻¹
m_H	reserve carbohydrate density	variable	mol C (mol C) $^{-1}$
m_P	reserve protein density	variable	mol C (mol C) $^{-1}$
n_{CO}^{P}	CO_2 formed per X produced in P-route	0.33	mol C (mol C) $^{-1}$
n_{CO}^{PH}	CO_2 formed per X produced in PH-route	0.33	mol C (mol C) $^{-1}$
n^{PH}_{PH}	H used per X formed in PH -route	0.71	mol C (mol C) $^{-1}$
$n_{\rm NIII}^{H}$	NH_4^+ formed per X produced in P-route	0.19	mol N (mol C) $^{-1}$
n_P^P	P used per X formed in P-route	1.33	mol C (mol C) $^{-1}$
n_P^{PH}	P used per X formed in PH -route	0.63	mol C (mol C) $^{-1}$
P	protein reserve biomass	variable	mol C (mol C) $^{-1}$
X	biomass: structure, eggs	variable	mol C (mol C) $^{-1}$
β_N	average assimilation efficiency of N	variable	mol N (mol C) $^{-1}$
β_C	average assimilation efficiency of C	variable	mol C (mol C) $^{-1}$
ϕ_F	C:N of food	variable	mol C (mol N) $^{-1}$
ϕ_P	C:N of proteins	3.7	mol C (mol N) $^{-1}$
ϕ_X	C:N of structural biomass, eggs	5.9	mol C (mol N) $^{-1}$
κ	fraction H and P returned to reserves	0.5	-
$\theta_{F,L}$	lipid carbon fraction of diatoms	variable	mol C (mol C) $^{-1}$
$\theta_{F,H1}$	soluble carbohydrate fraction of diatoms	variable	mol C (mol C) $^{-1}$
$\theta_{F,H2}$	insoluble carbohydrate fraction of diatoms	variable	mol C (mol C) ^{-1}
$\theta_{F,P}$	protein fraction of diatoms	variable	mol C (mol C) $^{-1}$
θ_{xy}	fraction of SUs in state xy	variable	-
θ^*_{xy}	steady state fraction of SUs in state xy	variable	-
ρ_{P}^{P}	binding probability of P to θ_{\perp}	0.66	-
ρ_{P}^{PH}	binding probability of P to θ_{H}	0.95	-
$ ho_{H}^{PH}$	binding probability of H to θ_{\perp}	0.66	-
ψ_P	C yield efficiency: reaction P	variable	mol C (mol C) $^{-1}$
ψ_{PH}	C yield efficiency: reaction <i>PH</i>	variable	mol C (mol C) $^{-1}$
Ω_P	steady state binding state for reaction P	variable	-
Ω_{PH}	steady state binding state for reaction PH	variable	-

Table 2.1: List of variables and parameters

References

- [1] Anderson TR. (1992). Modelling the influence of food C:N ratio, and respiration on growth and nitrogen excretion in marine zooplankton and bacteria. *J. Plankton Res.* 14:1645–1671.
- [2] Anderson TR. (1994). Relating C:N ratios in zooplankton food and faecal pellets using a biochemical model. *J. Exp. Mar. Biol. Ecol.* 184:183–199.
- [3] Anderson TR, Boersma M, D. R. (2004). Stoichiometry: linking elements to biochemicals. *Ecology* p. in press.
- [4] Anderson TR, Hessen DO. (1995). Carbon or nitrogen limitation in marine copepods? *J. Plankton Res.* 17:317–331.
- [5] Anderson TR, Pond DW. (2000). Stoichiometric theory extended to micronutrients: comparison of the roles of essential fatty acids, carbon, and nitrogen in the nutrition of marine copepods. *Limnol. Oceanogr.* 45:1162–1167.
- [6] Arnould JPY, Green JA, Rawlins DR. (2001). Fasting metabolism in Antarctic fur seal (*Arctocephalus gazella*) pups. *Comp. Biochem. Physiol.* A 129:829–841.
- [7] Barlow RG. (1982). Phytoplankton ecology in the southern benguela current, i. biochemical composition. *J. Ecp. Mar. Biol. Ecol.* 63:209–227.
- [8] Besiktepe S, Dam HG. (2002). Coupling of ingestion and defecation as a function of diet in the calanoid copepod *Acartia tonsa*. *Mar. Ecol. Prog. Ser.* 229:151–164.
- [9] Brett MT. (1993). Comment on 'possibility of N and P limitation for planktonic cladocerans: an experimental test' (Urabe and Watanabe) and 'nutrient element limitation of zooplankton production' (Hessen). *Limnol. Oceanogr.* 38:1333–1337.
- [10] C. MM, Sedinger JS. (2000). Nutrient reserves and clutch-size regulation of Northern Shovelers in Alaska. *Auk* 117:971–979.
- [11] Calow P. (1977). Conversion efficiencies in heterotrophic organisms. *Biol. Rev.* 52:385–409.
- [12] Checkley DM. (1980). The egg production of a marine copepod in relation to its food supply: laboratory studies. *Limnol. Eceanogr.* 25:430–446.
- [13] Checkley DM, Entzeroth LC. (1985). Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen cycle. *J. Plankton Res.* 7:553–568.
- [14] De Baar HJW. (1994). Von Liebig Law of the minimum and plankton ecology (1899-1991). *Prog. Oceanogr.* 33:347–386.

- [15] DeMott WR, Gulati RD, Siewertsen K. (1998). Effects of phosphorousdeficient diets on the carbon and phosphorous balance of *Daphnia magna*. *Limnol*. *Oceanogr*. 43:1147–1161.
- [16] Droop MR. (1983). 25 years of algal growth kinetics. *Botanica Marina* 26:99–112.
- [17] Flood PR. (1991). Architecture of, and water circulation and flow rate in, the house of the planktonic tunicate *Oikopleura labradoriensis*. *Mar. Biol.* 111:95–111.
- [18] Frazer TK, Ross RM, Quetin LB, Montoya JP. (1997). Turnover of carbon and nitrogen during growth of larval krill, *Euphausia superba* Dana: a stable isotope approach. *J. Exp. Mar. Biol. Ecol.* 212:259–275.
- [19] Fry B, Arnould C. (1982). Rapid ¹³C/¹²C turnover during growth of brown shrimp *Penaeus aztecus*. *Oecologia* 54:200–204.
- [20] Hessen DO. (1992). Nutrient element limitation of zooplankton production. *Am. Nat.* 140:799–814.
- [21] Hirst AG, McKinnon AD. (2001). Does egg production represent adult female copepod growth? A call to account for body weight changes. *Mar. Ecol. Prog. Ser.* 223:179–199.
- [22] Jones RH, Flynn KJ, Anderson TR. (2002). Effect of food quality on carbon and nitrogen growth efficiency in the copepod *Acartia tonsa*. *Mar. Ecol. Prog. Ser.* 235:147–156.
- [23] Karasov WH. (1992). Daily energy expenditure and the cost of activity in mammals. *Am. Zool.* 32:238–248.
- [24] Kiørboe T. (1989). Phytoplankton growth rate and nitrogen content: implications for feeding and fecundity in a herbivorous copepod. *Mar. Ecol. Prog. Ser.* 55:229–234.
- [25] Kiørboe T, Møhlenberg F, Hamburger K. (1985). Bioenergetics of the planktonic copepod *acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. *Mar. Ecol. Prog. Ser.* 26:85–97.
- [26] Kooijman SALM. (1995). The stoichiometry of animal energetics. J. *Theor. Biol.* 177:139–149.
- [27] Kooijman SALM. (1998). The synthesizing unit as a model for the stoichiometric fusion and branching of metabolic fluxes. *Biophysical Chemistry* 73:179–188.
- [28] Kooijman SALM. (2001). Quantitative aspects of metabolic organization; a discussion of concepts. *Phil. Trans. R. Soc. B.* 356:331–349.

- [29] McGoogan BB, Gatlin DM. (1999). Dietary manipulations affecting growth and nitrogenous waste prroduction of red drum *Sciaenops ocellatus*. I. Effects of dietary protein and energy levels. *Aquaculture* 178:333–348.
- [30] Muller EB, Nisbet RM, Kooijman SALM, Elser JJ, McCauley E. (2001). Stoichiometric food quality and herbivore dynamics. *Ecology Lett.* 4:519– 529.
- [31] Pagano M, Saint-Jean L. (1994). *In situ* metabolic budget for the calanoid copepod *Acartia clausi* in a tropical brackish lagoon (Ebrié Lagoon, Ivory Coast). *Hydrobiologia* 272:147–161.
- [32] Roxburgh L, Pinshow B. (2000). Nitrogen requirements of an old world nectarivore, the orange tufted sunbird *Nectarinia osea*. *Physiol. Biochem. Zool*. 73:638–645.
- [33] Sterner RW, Hessen DO. (1994). Algal nutrient limitation and the nutrition of aquatic herbivores. *Annu. Rev. Ecol. Syst.* 25:1–29.
- [34] Straile D. (1997). Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group. *Limnol. Oceanogr.* 42:1375–1385.
- [35] Swadling KM, Nichols PD, Gibson JAE, Ritz DA. (2000). Role of lipid in the life cycles of ice-dependent and ice-independent populations of the copepod *Paralabidocera antarctica*. *Mar. Ecol. Prog. Ser.* 208:171–182.
- [36] Telang A, Buck NA, Wheeler DE. (2002). Response of storage protein levels to variation in dietary protein levels. J. Insect. Physiol. 48:1021– 1029.
- [37] Thor P. (2003). Elevated respiration rates of the neritic copepod *Acartia tonsa* during recovery from starvation. *Journal of Experimental Marine Biology and Ecology* 283:133–143.
- [38] Urabe J, Watanabe Y. (1992). Possibility of N or P limitation for planktonic cladocerans: an experimental test. *Limnol. Oceanogr.* 37:244–251.
- [39] Vollenweider RA. (1985). Elemental and biochemical composition of plankton biomass; some comments and explorations. *Arch. Hydrobiol*. 105:11–29.
- [40] Zonneveld C. (1996). Modelling the kinetics of non-limiting nutrients in microalgae. J. Mar. Syst. 9:121–136.

Stoichiometry and food chain dynamics

Abstract

Traditional models of chemostat systems looking at interactions between predator, prey and nutrients have used only a single currency, such as energy or nitrogen. In reality growth of autotrophs and heterotrophs may be limited by various elements, e.g. carbon, nitrogen, phosphorous or iron. In this study we develop a dynamic energy budget (DEB) model chemostat which has both carbon and nitrogen as currencies, and examine how the dual availibility of these elements affects the growth of phytoplankton, trophic transfer to zooplankton, and the resulting stability of the chemostat ecosystem. Both species have two reserve pools to obtain a larger metabolic flexibility with respect to changing external environments. Mineral nitrogen (DIN) and carbon (DIC) form the base of the food chain, and they are supplied at a constant rate. In addition, the biota in the chemostat recycle nutrients by means of respiration and excretion, and organic detritus is recycled at a fixed rate. We use numerical bifurcation analysis to assess the model's dynamic behavior. In the model, phytoplankton is nitrogen limited, and nitrogen enrichment can lead to oscillations and multiple stable states. Moreover, we found that recycling has a destabilizing effect on the food chain due to the increased repletion of mineral nutrients. We found that both carbon and nitrogen enrichment stimulate zooplankton growth. Therefore, we conclude that the concept of single element limitation may not be applicable in an ecosystem context.

Keywords: Ecosystem modeling - Food chain - Multiple nutrient limitation - Dynamic Energy Budgets - Nitrogen - Nutrient enrichment

3.1 Introduction

Food web models in which a set of ordinary differential equations describe the dynamics of trophic groups are ubiquitous in theoretical ecology. They have been commonly used to study the stability and potential coexistence of species assemblages and predict ecologically realistic phenomena, such as the competitive exclusion principle and the 'paradox of enrichment' [18, 44], where high nutrient provisions cause an equilibrated food chain to become unstable and oscillations occur. Furthermore, these models may predict the occurrence of multiple stable states and associated hysteresis loops, which have been shown to occur in nature as well [48].

Over the past decades, global change has drawn attention to the understanding of environmental carbon and nutrient cycles. These involve the transfer of matter through the trophic niches within ecosystems. A proper understanding of element cycling involves a modelling strategy in which massbalance of all elements is satisfied, such that the whereabouts of elements can be precisely followed. Traditional models are however simplistic and they do not always correctly handle mass-balance [27]. Furthermore, they usually focus on a single currency, mostly energy, rather than a spectrum of potentially important elements, such as carbon, nitrogen, phosphorous and iron. In this study we aim for a model, which traces the trophic flow of nitrogen and carbon through a simple marine food chain, using a mass-balance formulation.

The co-occurrence of multiple currencies requires rules for merging multiple resources into biomasses. When homeostasis for biota is assumed, biomass has a fixed elemental ratio or stoichiometry, while the availability of substrates may be variable. The classic approach here is to apply 'Liebig's law of the minimum' [21, 23, 24, 34, 36]. This law states that the availability of the limiting element determines the rate at which a population grows, exclusively. This implies that at some point in the availability of nutrients, limitation switches from the one nutrient to another. This switching behavior is generally modelled using a minimum operator in the description of the growth rate [51]. Simulation of a minimum model can be done without experiencing any trouble, however, if one is interested in a bifurcation analysis, this approach leads to elements of discontinuity in the Jabobian matrix with respect to parameter values associated with resource availability where limitation switches from one resource to another. To circumvent this problem, so-called synthesizing units (SUs) can be used [30]. Their dynamics relate to classic enzyme kinetics. The latter map substrate concentrations to product fluxes. In contrast, SU's merge fluxes of substrates, rather than concentrations, into biomass and by-products. The SU production rate is a smooth function of substrate availability and a maximum production rate.
Many models dealing with multiple nutrient limitation assume homeostasis for total biomass for each species [13]. Although this assumption is convenient for many purposes, the elemental composition of biomass appears to be dependent on the nutritional conditions for many species [5, 10, 31, 53]. Organisms may store nutrients that are provided in excess quantities, hence their nutritional value to the next trophic level may change. Quota models [12] allow for such deviations of whole-body homeostasis, by dividing biomass into permanent (structural) and non-permanent (reserve) components, each with their own composition. Although both components themselves obey homeostasis, total biomass composition need not be constant as reserve densities may vary over time. The implementation of this biological detail comes at the cost of an extra ODE for each reserve pool in the model, which makes numerical analysis more time-consuming. However, current computer power compensates for this drawback. Grover used a quota model on Liebig Law principles to analyse effects of stoichiometry on predator-prey systems.

Muller et al. (2001) abandoned the Liebig approach and used synthesizing units in the context of a dynamic energy budget model (DEB, Kooijman, 2000) to investigate effects of stoichiometry on the dynamics of a producer–consumer system. DEB provides consistent rules for the uptake and use of substrates and can be applied to all organisms. In DEB, assimilated materials are passed to reserve pools, which are mobilized for metabolic processes such as maintenance and growth. The SU's govern these processes in which multiple types of substrates may figure, and the fate of compounds which are in excess provision for metabolic transformations, i.e. non-limiting substrates, can be conveniently determined. This facilitates the formulation of a mass-balance model, in which storage and recycling are implemented.

Recently, Kuijper et al. (2004) demonstrated that a multiple reserve DEB model, employing SU's, could adequately predict egg-production and metabolic mineral release in the copepod *Acartia tonsa*, while a single reserve model was unable to do so. Essential to this study was the dual role of nitrogenous organic reserves that could be preferentially used as building blocks for egg-production, or for energization of metabolic processes. Here, an SU-complex with rules for preferential use of substrates determines the fate of reserves. This approach substantially increases the metabolic flexibility imposed on the consumer model in a physiologically plausible manner.

We expand on the work of Muller et al. (2001) by developing a DEB model where the producer and consumer both possess particular reserve pools for energy and nutrients, where Muller used a single reserve for the producer and no reserve for the consumer species. The model in this paper considers a simple food chain of copepods and diatoms in a chemostat, a setup which lends itself in principle for experimental testing. The diatom population, modelled after *Thalassiosira weissflogii* uses nitrogen (DIN), carbon (DIC) and light, which are supplied to the chemostat at fixed rates. In turn, the copepod population, *Acartia tonsa*, feeds on diatoms. Dead biomass and fecal pellets are stored in nitrogenous and non-nitrogenous detritus pools, from which they are mineralised. These recycled minerals, plus the minerals excreted by the copepods and the diatoms themselves can be assimilated again by the diatoms. The volume of the chemostat is constant, and all constituents are washed out at a fixed rate. We study the combined effects of resource enrichment and recycling in this setup on the qualitative behaviour of the food chain and compare them to predictions of traditional food chains.

We are aware that taking the step from very simple stoichiometric models to biologically detailed ones comes with a few drawbacks. For instance, it becomes increasingly difficult to assess the effect of any particular model parameter on model dynamics when there are many candidate parameters that can be varied simulteneously. Moreover, one requires more biological knowledge and experimental data to validate a more complex model. On the other hand, traditional simplistic stoichiometric models have been unable to correctly capture element limitation in zooplankton production [3, 32, 39], while a DEB-based model could [32]. One can question whether simple stoichiometric models are able to adequately describe food web dynamics if their use in population studies is limited. We address this question by comparing results of a stoichiometric multiple-reserve DEB model using synthesizing units with results of models following a traditional approach.

The paper is organized as follows. The next section holds a detailed introduction to the modelling framework, in which we motivate our modelling decisions. In the section thereafter, we present a summary of the chemostat model as used in this study. In the results section, we present a bifurcation analysis of the model, in which we vary the availability of resources. In the discussion, we will compare the model results to classic studies and point out implications of this study.

3.2 Modeling framework

3.2.1 Primary producers

assimilation

For simplicity's sake, we assume that producers may only be limited either by light, mineral carbon or mineral nitrogen. While iron has been shown to be a potential limiting factor in phytoplankton [15, 16, 46], this currency is not included in the basic structure of the model. Iron limitation can be implemented without loss of consistency, but this makes model formulations considerably more complex, thereby compromising the aim of this study. For now, we assume ad libitum availability of iron.

In addition to structural volume, we assume have two reserve pools for the diatoms, one consisting of non-nitrogenous organic materials (hydrocarbons) and one consisting of mineral nitrogen. Assimilation of minerals into these

reserves follows the biochemical reaction

$$N \rightarrow E_N^A$$
 (3.1a)

$$C + light \rightarrow E_H^A , \qquad (3.1b)$$

where N and C stand for inorganic sources of nitrogen and carbon. Autotroph inorganic nitrogen and organic carbon reserves are represented by E_N^A and E_H^A , respectively.

Algal acquisition of minerals and energy is a complex process, and we simplify the modelling thereof considerably to maintain a certain degree of simplicity. Firstly, we assume a spatially homogeneous environment, which implies that the model does not allow for light gradients, caused by photon-scattering and self-shading, which occur in natural aquatic ecosystems. However, our focus is on the effects of more metabolic flexibility, and this can best be studied in a spatially homogeneous environment. This is due to the metabolic memory; in a spatially heterogeneous environment the travelling path of individuals then becomes important. Secondly, we simplified the speciation of non-living resources in the environment to a large extent. As for carbon uptake, we omit the complex carbon chemistry of marine systems, and its impact on diatom production [38]. Instead, we use a single carbon currency (DIC).

We use a type-II functional response to model the assimilation of inorganic nitrogen. Although light impacts on the enzymatic activity of nitrogen reductase, which is important in the assimilation of nitrogen [4], it appears that nitrogen uptake rates can be described by a simple saturating function [14]. Carbon assimilation is modelled by a complementary SU, which requires both light and carbon. Data from Riebesell et al. (1993) shows that, provided that pH is constant and CO_2 is therefore a constant percentage of total inorganic carbon, carbon assimilation can be described with a saturating function of DIC availability. For the mathematical derivation of SU dynamics, we refer to Kooijman (1998). The assimilated fluxes, scaled to structural biomass, are

$$j_{N,A}^{A} = I_{N}^{A} f_{N}^{A} = I_{N}^{A} \frac{N}{N + K_{N}^{A}}$$
 (3.2a)

$$j_{H,A}^{A} = I_{C}^{A} f_{C}^{A} = I_{C}^{A} \left(1 + \frac{K_{L}^{A}}{j_{L}} + \frac{K_{C}^{A}}{C} - \frac{1}{\frac{j_{L}}{K_{L}^{A}} + \frac{C}{K_{C}^{A}}} \right)^{-1}$$
, (3.2b)

where $I_{\rm N}^A$, $I_{\rm C}^A$ are the maximum structure specific assimilation rates of mineral nitrogen and carbon dioxyde, respectively, $f_{\rm N}^A$, $f_{\rm C}^A$ are the corresponding scaled functional responses, in which $K_{\rm N}^A$, $K_{\rm C}^A$ are the half-saturation concentrations of minerals, K_L^A is the half-saturation flux of photons, and j_L is the photon flux.

growth

We use an extended Droop-model [12] with two reserve pools for the diatom species, by which we assume that costs associated with basal metabolism are negligible. The transformation of reserves into biomass and by-products is described by the following macro-biochemical process

$$y_{E_N^A, X^A} E_N^A + y_{E_H^A, X^A} E_H^A \longrightarrow X^A + y_{N, X^A} N + y_{C, X^A} C$$
, (3.3)

where E_N^A , E_H^A are the autotroph's nitrogen and carbon reserves, respectively, X^A represents autotroph structural biomass and C and N are minerals excreted into the environment. The coefficients y couple substrates and by-products to structural biomass stoichiometrically. Their values are determined by using the maximum attainable production efficiencies per substrate and on the C:N ratios of the compounds involved in the transformation. Here,

$$y_{E_N^A, X^A} = \frac{1}{\phi_{X^A} \ \psi_{N,G}^A} \qquad (3.4a) \qquad \qquad y_{N,X^A} = \frac{1 - \psi_{N,G}^A}{\phi_{X^A} \ \psi_{N,G}^A} \qquad (3.4c)$$

$$y_{E_{H,X^{A}}^{A}} = \frac{1}{\psi_{H,G}^{A}}$$
 (3.4b) $y_{C,X^{A}} = \frac{1 - \psi_{H,G}^{A}}{\psi_{H,G}^{A}}$, (3.4d)

where ϕ 's refer to the C:N ratio of the particular compound and ψ 's are production efficiencies on the corresponding substrate.

A fundamental principle of DEB-theory is that reserves are mobilised as a first order process in reserve density. Hence, reserve dynamics are described by

$$\frac{d}{dt}[E]_{N}^{A} = j_{N,A}^{A} - k_{E}^{A} [E]_{N}^{A}$$
(3.5a)

$$\frac{d}{dt}[E]_{H}^{A} = j_{H,A}^{A} - k_{E}^{A} [E]_{H}^{A} , \qquad (3.5b)$$

where k_E^A is the turnover rate of reserves. Throughout this paper, bracketed variables indicate that the associated compound is expressed in units per unit of structural biomass. The structure-specific fluxes of mobilized reserves amount to

$$j_{N,C}^{A} = [E]_{N}^{A} \left(k_{E}^{A} - r^{A}\right)$$
 (3.6a)

$$j_{H,C}^{A} = [E]_{H}^{A} \left(k_{E}^{A} - r^{A} \right) ,$$
 (3.6b)

in which r^A is the structure specific growth rate $\frac{1}{X^A} \frac{d}{dt} X^A$. The two reserves are merged to form biomass at a complementary synthesizing unit. Biomass specific growth equals

$$r^{A} = \left(\frac{y_{E_{N}^{A}, X^{A}}}{j_{N,C}^{A}} + \frac{y_{E_{H}^{A}, X^{A}}}{j_{H,C}^{A}} - \frac{y_{E_{N}^{A}, X^{A}} y_{E_{H}^{A}, X^{A}}}{y_{E_{H}^{A}, X^{A}} j_{N,C}^{A} + y_{E_{N}^{A}, X^{A}} j_{H,C}^{A}}\right)^{-1} . (3.7)$$

Note that $j_{N,C}^A$ and $j_{H,C}^A$ now figure in both the left-hand side and right-hand side of Eq. 3.6, by which the biomass specific growth rate, r^A , is implicitly defined and must be solved numerically. The growth SU differs from the assimilation SU which merges carbon and photons, in that growth is not bounded by a maximum transformation rate, such as I_C^A in Eq. 3.2b. Rather, the growth rate is limited by the boundedness of the reserve fluxes, mobilized from the reserve pools.

excretion

Excreted materials are recycled back into the environment, from which they become available again to the producer population. Metabolic by-products are excreted in mineral form, so that they become directly available again. Organic materials must be decomposed before they are available in mineral form, and they are stored in organic detritus pools.

Growth comes with overhead costs. The evolution of by-products amounts to

$$y_{N,G}^{A} = y_{N,X^{A}} r^{A}$$
 (3.8a)

$$j_{C,G}^A = y_{C,X^A} r^A$$
 (3.8b)

Imbalances between supply rates and growth requirements may result in rejection of the non-limiting susbtrate at the SU. Excess substrates are only partly excreted and partly returned to their orinigal reserve pools (fraction κ^A). This enables non-limiting reserves to dam up within the algae, which effects on the total biomass composition, and the associated nutritional value to the next trophic level. The biomass specific fluxes of excreted NH₃ and D_H are

$$j_{N,R}^{A} = (1 - \kappa^{A}) \left(j_{E_{N}^{A},C}^{A} - y_{E_{N}^{A},X^{A}} r^{A} \right)$$
 (3.9a)

$$j_{D_{H},R}^{A} = (1 - \kappa^{A}) \left(j_{E_{H}^{A},C}^{A} - y_{E_{H}^{A},X^{A}} r^{A} \right) .$$
(3.9b)

The total amount of excreted compounds by the producers is

$$j_{N,E}^{A} = j_{N,G}^{A} + j_{N,R}^{A}$$
 (3.10a)

$$j_{C,E}^{A} = j_{C,G}^{A}$$
 (3.10b)

$$j_{D_H,E}^A = j_{D_H,R}^A$$
 (3.10c)

3.2.2 Consumers

assimilation

Food composition for consumers can be expressed in terms of structural volume X^A , nitrogen reserves E_N^A and carbohydrate reserves E_H^A of the diatoms. The

producer's structural mass X^A comprises proteins, carbohydrates and unassimilable materials. Homeostasis dictates that each of them has a fixed contribution to structural mass. The consumer species can assimilate the structural proteins directly with efficiency $y_{E_P^C,X^A}$. It is known that low C:N-foods enhance copepod production [9, 25]. In the model, the reserve densities largely determine the C:N of diatoms. We assume that the producer's nitrogen reserves can, in conjunction with carbohydrates, also be transformed into protein reserves, thus modelling a positive copepod response to ingesting low C:N diatoms. The associated carbohydrates derive from either the producer's reserves E_H^A or structural components X^A . The biochemical transformations involved are

$$\begin{array}{rccc} X^{A} & \to & y_{E_{P}^{C},X^{A}} \ E_{P}^{C} + y_{H,X^{A}} \ H + & & \\ & & y_{D_{P},X^{A}} \ D_{P} + y_{D_{H},X^{A}} \ D_{H} \end{array} \tag{3.11a}$$

$$E_H^A \to H$$
 (3.11b)

$$H \rightarrow y^{H}_{E^{C}_{H},H} E^{C}_{H} + y^{H}_{\mathsf{C},H} \mathsf{C}$$
(3.11c)

$$H + y_{E_{N}^{N}, E_{P}^{C}}^{NH} E_{N}^{A} \to y_{E_{P}^{C}, H}^{NH} E_{P}^{C} + y_{C, H}^{NH} C, \qquad (3.11d)$$

where H is the hydrocarbon precursor formed from autotroph structure and reserves, D_P and D_H represent nitrogenous and non-nitrogenous detritus formed, respectively. The coefficients y balance the transformations stoichiometrically. We base their values on assimilation efficiencies of carbon and nitrogen, such that

$$y_{E_{P}^{C},X^{A}} = \psi_{P,A}^{C} \frac{\phi_{P}}{\phi_{X^{A}}}$$
(3.12a) $y_{E_{H}^{C},H}^{H} = \psi_{H_{E},A}^{C}$ (3.12e)

٦

$$y_{D_{P},X^{A}} = \left(1 - \psi_{P,A}^{C}\right) \frac{\phi_{P}}{\phi_{X^{A}}} \quad (3.12c) \qquad \qquad y_{E_{P}^{C},H}^{NH} = \psi_{H_{E},A}^{C} \qquad (3.12h)$$

We assume that unassimilable producer structure is egested as pellets, which contribute to the carbohydrate and protein detritus pools, D_H and D_P , respectively. A SU governs the transformations (3.11c,3.11d), which occur simultaneously, i.e. carbohydrates may be used for production of either carbohydrate or protein reserves, of which the latter occurs in association with the diatoms nitrogen reserves. The SU resembles the production SU of Kuijper et al. (2004) (cf. auxiliary SU as introduced in Kooi et al., 2004). When carbohydrates bind

to an empty SU, reaction (3.11c) takes place and carbohydrate reserves are produced, while reaction (3.11d), and the associated production of protein reserves, occurs when carbohydrates bind to a SU that is already saturated with E_N^A . Net assimilation of copepod reserves is

$$j_{P,A}^{C} = I_{X^{A}}^{C} f_{X^{A}}^{C} \left(y_{E_{P}^{C},X^{A}} + y_{E_{P}^{C},H}^{NH} \left(y_{H,X^{A}} + [E]_{H}^{A} \right) \theta \right)$$
(3.13a)

$$j_{H,A}^{C} = I_{X^{A}}^{C} f_{X^{A}}^{C} y_{E_{H}^{C},H}^{H} \left(y_{H,X^{A}} + [E]_{H}^{A} \right) \left(1 - \theta \right) , \qquad (3.13b)$$

in which $I_{X,A}^C$ is the maximum copepod ingestion rate with respect to diatoms and θ is the fraction of assimilation SU's saturated with diatom nitrogen reserves

$$\theta = \frac{[E]_N^A}{[E]_N^A + \frac{y_{H,X^A} + [E]_H^A}{y_{E_N^A, E_P^A}^{NH}}} .$$
(3.14)

Furthermore, $f_{X^A}^C = \frac{X^A}{K_{C,X^A} + X^A}$, and this models the functional response of copepod feeding on algae.

maintenance and growth

For maintenance and growth, we employ the model for *Acartia* egg production by Kuijper et al. (2004). Reserves can be transformed into structural biomass in one of two production routes. We will name a P-route, in which proteins are processed exclusively, and a PH-route, where merging of proteins and carbohydrates takes place. The transformations are

$$y_{E_{P}^{C},X^{C}}^{PH} E_{P}^{C} + y_{E_{H}^{C},X^{C}}^{PH} E_{H}^{C} \to X^{C} + y_{C,X^{C}}^{PH} C$$
 (3.15a)

$$y_{E_P^C,X^C}^P E_P^C \longrightarrow X^C + y_{C,X^C}^P C + y_{N,X^C}^P$$
 N (3.15b)

in which the stoichiometric couplers are defined in terms of maximum growth efficiencies and C:N ratios of the substrates

$$y_{E_{P}^{C},X^{C}}^{PH} = \frac{\phi_{P}}{\phi_{X^{C}}}$$
 (3.16a) $y_{E_{P}^{C},X^{C}}^{P} = \frac{1}{\psi_{C,P}}$ (3.16d)

$$y_{E_{H}^{C},X^{C}}^{PH} = \frac{1}{\psi_{C,PH}} - \frac{\phi_{P}}{\phi_{X^{C}}} \quad (3.16b) \qquad y_{\mathsf{C},X^{C}}^{P} = \frac{1 - \psi_{C,P}}{\psi_{C,P}} \quad (3.16e)$$

$$y_{C,X^{C}}^{PH} = \frac{1 - \psi_{C,PH}}{\psi_{C,PH}}$$
 (3.16c) $y_{N,X^{C}}^{P} = \frac{1}{\phi_{P} \ \psi_{C,P}} - \frac{1}{\phi_{X^{C}}}$. (3.16f)

Analogous to the modelling of Thalassiosira, the copepod reserve dynamics are

$$\frac{d}{dt}[E]_{P}^{C} = j_{P,A}^{C} - k_{E}^{C}[E]_{P}^{C}$$
(3.17a)

$$\frac{d}{dt}[E]_{H}^{C} = j_{H,A}^{C} - k_{E}^{C}[E]_{H}^{C}, \qquad (3.17b)$$

and, accordingly, the catabolic fluxes are

$$j_{P,C}^{C} = [E]_{P}^{C} \left(k_{E}^{C} - r^{C}\right)$$
 (3.18a)

$$j_{H,C}^{C} = [E]_{H}^{C} (k_{E}^{C} - r^{C}) , \qquad (3.18b)$$

Maintenance and production require building blocks and energy to meet the associated costs. Protein reserves serve as building blocks, whereas carbohydrates are the preferred substrate for respiration to avoid wasting proteins. However, when the supply of carbohydrates is short, the copepods may respire proteins instead. Costs for maintenance are proportional to structural volume. Biomass specific costs for maintenance are subtracted from the catabolic flux by an auxiliary SU. For an elaborate derivation of SU dynamics, the reader is referred to Kuijper et al. (submitted). Maintenance costs are

$$j_{P,M}^{C} = k_{M}^{C} \frac{\rho_{P}^{P} j_{P,C}^{C} + \frac{y_{E_{C}^{C},X^{C}}^{P}}{y_{E_{H}^{P},X^{C}}^{P}} \rho_{H}^{PH} j_{H,C}^{C}}{\frac{\rho_{P}^{P}}{y_{E_{D}^{C},X^{C}}^{P}} j_{P,C}^{C} + \frac{\rho_{H}^{PH}}{y_{E_{H}^{C},X^{C}}^{P}} j_{H,C}^{C}}$$
(3.19a)

$$j_{H,M}^{C} = k_{M}^{C} \frac{\rho_{H}^{PH} j_{H,C}^{C}}{\frac{\rho_{P}^{P}}{y_{E_{P}^{C},X^{C}}^{P}} j_{P,C}^{C} + \frac{\rho_{H}^{PH}}{y_{E_{H}^{C},X^{C}}^{PH}} j_{H,C}^{C}}, \qquad (3.19b)$$

where k_M^C is the maintenance rate coefficient. The ρ 's stand for the probability of binding a substrate-molecule that is directed to a SU, ρ_P^P is the probability of protein binding to an empty SU and ρ_H^{PH} is the binding probability of carbohydrates to an available binding site on the SU. The remainder of the catabolic flux after maintenance is paid is the growth directed flux

$$j_{P,B}^C = j_{P,C}^C - j_{P,M}^C$$
 (3.20a)

$$j_{H,B}^C = j_{H,C}^C - j_{H,M}^C ,$$
 (3.20b)

and these two fluxes are used for biomass production. The SU which governs the associated transformations resembles the maintenance SU in that it completes exactly the same transformation, however, the production rate is not fixed here; the growth rate depends on the availability of proteins and carbohydrates (Kuijper et al. submitted). The biomass specific growth rate amounts to

$$r^{C} = j^{C}_{P,B} \frac{\frac{y^{P_{H}^{H}}_{E_{P}^{C},X^{C}} \rho^{P_{H}}_{P}}{y^{P}_{E_{P}^{C},X^{C}} \rho^{P_{H}}_{H}} j^{C}_{P,B} + j^{C}_{H,B}}{\frac{y^{P_{H}^{H}}_{E_{H}^{L},X^{C}}}{\rho^{P_{H}}_{H}} j^{C}_{P,B} + \frac{y^{P_{H}^{H}}_{E_{P}^{C},X^{C}}}{\rho^{P_{H}}_{P}} j^{C}_{H,B}}, \qquad (3.21)$$

with ρ_P^{PH} as the binding probability of protein reserves on SUs that have al-

ready bound carbohydrates. The associated use of reserves is

$$j_{P,G}^{C} = j_{P,B}^{C} \frac{\frac{y_{E_{H,X^{C}}}^{P,R} \rho_{P}^{P,H}}{y_{E_{P,X^{C}}}^{P,R} \rho_{H}^{P,H}} j_{P,B}^{C} + j_{H,B}^{C}}{\frac{y_{E_{P,X^{C}}}^{P,R} \rho_{H}^{P,H}}{y_{E_{P,X^{C}}}^{P,R} \rho_{H}^{P,H}} j_{P,B}^{C} + j_{H,B}^{C}}$$

$$j_{H,G}^{C} = j_{H,B}^{C} \frac{\rho_{H}^{P,H} j_{P,B}^{C}}{\frac{y_{E_{P,X^{C}}}^{P,H} \rho_{H}^{P,H}}{y_{E_{H,X^{C}}}^{P,R} \rho_{H}^{P,H}} j_{H,B}^{C} + j_{P,B}^{C}}$$
(3.22a)
$$(3.22b)$$

Reserves unable to bind to the growth SU are partly restored into the corresponding reserve pools with fraction κ^C . The fraction $1 - \kappa^C$ is excreted as minerals.

excretion and defecation

Fecal pellets and the dead biomass contribute to the detritus pools. Egestion of pellets, i.e. unassimilated materials, amounts to

$$j_{D_{P},A}^{C} = I_{X^{A}}^{C} f_{X^{A}}^{C} \left(1 - \psi_{P,A}^{C}\right) \frac{\phi_{P}}{\phi_{X^{A}}}$$
(3.23a)

$$j_{D_{H},A}^{C} = I_{X^{A}}^{C} f_{X^{A}}^{C} \left(1 - \psi_{H,X^{A}}^{C}\right) \left(1 - \frac{\phi_{P}}{\phi_{X^{A}}}\right) .$$
(3.23b)

The overhead of assimilation quantifies as the difference between ingestion and assimilation (Eq. 3.13) and fecal production (Eq. 3.23). The associated biomass specific excretion of minerals is

$$j_{N,A}^{C} = I_{X^{A}}^{C} f_{X^{A}}^{C} \left(\frac{1}{\phi_{X^{A}}} + [E]_{N}^{A}\right) - \frac{j_{P,A}^{C} + j_{D_{P},A}^{C}}{\phi_{P}}$$
(3.24a)

$$j_{\mathsf{C},A}^C = I_{X^A}^C f_{X^A}^C \left(1 + [E]_H^A\right) - j_{P,A}^C - j_{H,A}^C - j_{D_P,A}^C - j_{D_H,A}^C$$
(3.24b)

We assume that all metabolic products of the consumer species are in mineral form. The excretion of maintenance products is a weighted sum of the products of the P and the PH-route

$$j_{N,M}^{C} = \frac{j_{P,M}^{C}}{\phi_{P}}$$
 (3.25a)

$$j_{C,M}^C = j_{P,M}^C + j_{H,M}^C$$
 (3.25b)

Growth overhead giving rise to excretion quantifies as

$$j_{N,G}^{C} = j_{P,B}^{C} \frac{\frac{y_{N,X}^{P}}{y_{E_{P}^{C},X}^{P}} \rho_{P}^{P} j_{P,B}^{C}}{\frac{y_{E_{P}^{C},X}^{P}}{y_{E_{P}^{C},X}^{P}} \rho_{P}^{P} j_{P,B}^{C}}$$

$$j_{C,G}^{C} = j_{P,B}^{C} \frac{\frac{y_{C,X}^{C}}{y_{E_{P}^{C},X}^{P}} \rho_{P}^{P} j_{P,B}^{C} + \frac{y_{C,X}^{P}}{y_{E_{P}^{C},X}^{P}} \rho_{H}^{P} j_{H,B}^{C} + j_{P,B}^{C}}{\frac{y_{E_{P}^{C},X}^{P}}{y_{E_{P}^{C},X}^{P}} \rho_{H}^{P} j_{H,B}^{C} + \frac{y_{C,X}^{P}}{y_{E_{H}^{C},X}^{P}} \rho_{H}^{PH} j_{H,B}^{C}}{\frac{y_{E_{P}^{C},X}^{P}}{y_{E_{P}^{C},X}^{P}} \rho_{H}^{PH} j_{H,B}^{C} + j_{P,B}^{C}}}.$$
(3.26b)

To our knowledge, copepods do not excrete organic substances. Therefore, excretion as a consequence of rejection at the growth SU is also assumed to be in mineral form. It amounts to

$$j_{N,R}^{C} = \frac{(1 - \kappa^{C}) (j_{P,B}^{C} - j_{P,G}^{C})}{\phi_{P}}$$
(3.27a)

$$j_{C,R}^{C} = (1 - \kappa^{C}) (j_{P,B}^{C} + j_{H,B}^{C} - j_{P,G}^{C} - j_{H,G}^{C})$$
 (3.27b)

The total excretion of consumers amounts to

$$j_{N,E}^{C} = j_{N,A}^{C} + j_{N,M}^{C} + j_{N,G}^{C} + j_{N,R}^{C}$$
 (3.28a)

$$j_{C,E}^{C} = j_{C,A}^{C} + j_{C,M}^{C} + j_{C,G}^{C} + j_{C,R}^{C}$$
 (3.28b)

death

For simplicity, we assume that the consumers have a constant death rate. Death results in the production of detritus species. Biomass specific contributions to the detritus pools amount to

$$j_{D_P,H}^C = k_H^C \left(\frac{\phi_P}{\phi_{X^C}} + [E]_P^C \right)$$
(3.29a)

$$j_{D_H,H}^C = k_H^C \left(1 - \frac{\phi_P}{\phi_{X^C}} + [E]_H^C \right) .$$
 (3.29b)

3.2.3 Decomposition and recycling

Excreted minerals are in the form of utilizable nutrients for the producer species. However, organic materials must be decomposed first. For reasons of simplicity, we have chosen to model the biodegradation of detritus as a first order process.

3.2.4 Model summary

1

The structure of the complete model is

$$\frac{d}{dt}\mathbf{N} = \left(j_{\mathbf{N},E}^{A} - j_{N,A}^{A}\right)X^{A} + j_{\mathbf{N},E}^{C}X^{C} + k_{D}\frac{D_{P}}{\phi_{P}} + D\left(X_{r,\mathbf{N}} - \mathbf{N}\right)$$
(3.30a)

$$\frac{d}{dt}\mathbf{C} = (j_{\mathbf{C},E}^{A} - j_{H,A}^{A}) X^{A} + j_{\mathbf{C},E}^{C} X^{C} + k_{D} (D_{H} + D_{P}) + D (X_{r,\mathbf{C}} - \mathbf{C})$$
(3.30b)

$$\frac{d}{dt}[E]_{N}^{A} = j_{N,A}^{A} + \kappa^{A} \left(j_{N,C}^{A} - y_{E_{N}^{A},X^{A}} r^{A} \right) - k_{E}^{A}[E]_{N}^{A}$$
(3.30c)

$$\frac{d}{dt}[E]_{H}^{A} = j_{H,A}^{A} + \kappa^{A} \left(j_{H,C}^{A} - y_{E_{H}^{A},X^{A}} r^{A} \right) - k_{E}^{A}[E]_{H}^{A}$$
(3.30d)

$$\frac{d}{dt}X^{A} = (r^{A} - D) X^{A} - I^{C}_{X^{A}} f^{C}_{X^{A}} X^{C}$$
(3.30e)

$$\frac{d}{dt}[E]_{P}^{C} = j_{P,A}^{C} + \kappa^{C} \left(j_{P,B}^{C} - j_{P,G}^{C} \right) - k_{E}^{C}[E]_{P}^{C}$$
(3.30f)

$$\frac{d}{dt}[E]_{H}^{C} = j_{H,A}^{C} + \kappa^{C} \left(j_{H,B}^{C} - j_{H,G}^{C} \right) - k_{E}^{C}[E]_{H}^{C}$$
(3.30g)

$$\frac{d}{dt}X^C = \left(r^C - D - k_H^C\right)X^C \tag{3.30h}$$

$$\frac{d}{dt}D_P = \left(j_{D_P,H}^C + j_{D_P,A}^C\right)X^C - (k_D + D)D_P$$
(3.30i)

$$\frac{d}{dt}D_H = j_{D_H,E}^A X^A + \left(j_{D_H,H}^C + j_{D_H,A}^C\right) X^C - (k_D + D) D_H .$$
(3.30j)

The currencies for structural biomasses are X^A and X^C , however, carbonous reserves alse contribute to the C-molar volume of biomass. Total C-molar biomasses are

$$\mathcal{A} = X^A \left(1 + [E]_H^A \right) \tag{3.31a}$$

$$\mathcal{C} = X^{C} \left(1 + [E]_{H}^{C} + [E]_{P}^{C} \right) .$$
(3.31b)

Table 1.1 lists the model notation, and table 1.2 holds referenced parameter values as used in the model.

3.3 Model dynamics

In this section we analyze the model's long-term behavior. We will concentrate on the influence of the nutritional conditions, on the role of increased metabolic flexibility with respect to variable nutritional conditions, and on effects of recycling. To facilitate the analysis, we follow a stepwise approach in which we deal with subsections of the model before we analyse the complete model as given in Eq. (3.30). We start with the analysis of the resource– producer system, in which the consumer level is absent. We continue with the analysis of a producer–consumer system, in which both the composition of the producer species and the supply rate of producers act as input parameters, i.e. in this analysis, the dynamics of the diatoms are not modeled explicitly. In this way, the model effectively becomes a static model, comparable to that of Anderson and Hessen (1995) and Kuijper et al. (2004). We conclude this section with the analysis of the resource–producer–consumer system. To study the effect of recycling, we will compare results to analyses, in which we omitted the recycling of nutrients.

As default environmental conditions for the system to run, we chose an inorganic carbon $(X_{r,C})$ and nitrogen $(X_{r,N})$ supply concentration of 2 mM and 10 μ M, respectively. These are realistic values for the upper layers of those marine waters where nitrogen is likely to be the limiting factor. Both minerals are supplied at a fixed throughput rate of D = 0.001 h⁻¹. The default light flux (j_L) is set constant to 600 μ mol m⁻² s⁻¹, at which light is abundant. This simplification has been done to facilitate the model analysis. The default recycling rate for organic matter, k_D , was set to 0.005 h⁻¹ [17].

3.3.1 The resource–producer system

Figure (3.1) contains the analysis of the resource–producer system. This system is a subsection of system 3.30, where the consumer is absent ($X^C = 0$). The diatom biomass is plotted against resource density for the resources light, inorganic carbon and inorganic nitrogen. Recycling effectively complements the resource supply, so that biomasses are lower when this process is excluded from the model (fig. 3.1, lower row). For the same reason, the reserve densities of non-limiting reserves are also higher when recycling takes place. The qualitative behavior of the model does not depend on recycling.

The effect of light is shown in the left graphs of figure (3.1). When light intensity is too low, the producer population cannot survive. There appears to be a threshold intensity at which the population suddenly reaches a considerable biomass. Although the sharp angle in the curves (fig. 3.1, left panel) might suggest a switch in survivability, light dependency is continuous. When light intensity is increased further, the total producer biomass increases, although the structural biomass is seemingly unaffected by light enhancement. Increased light intensity facilitates carbohydrate assimilation through higher photosynthesis rates. However, excess carbohydrate reserves cannot be used for production when nitrogen is scarce, so that they will effectively dam up.

Carbon dependency is shown in the center diagrams of figure (3.1). Carbon limitation occurs at supplies roughly between 100 and 500 μ M, below which the producers cannot survive and above which further enrichment has no effect on the structural biomass density of the producers. This result is similar to the predictions of Liebig's law. When carbon is limiting, the associated reserve



Figure 3.1: Algal total biomass as a function of light intensity (left), inorganic carbon supply (center), or nitrogen supply (right) when excreted compounds are recycled (upper row) or not (lower row). When kept constant, $X_{r,N} = 50 \ \mu$ M, $X_{r,C} = 2 \ m$ M and the photon flux is 600 μ mol m⁻² s⁻¹. Biomasses, as well as the densities of the non-limiting reserve are higher when recycling is included in the model.

density is small, as carbon is then efficiently used for growth. However, further carbon enhancement causes carbohydrate reserve accumulation and the associated growth of total biomass.

The diagrams on the right-hand side of figure (3.1) show the effect of nitrogen on diatom production. Over the whole plotting range of $X_{r,N}$ nitrogen is the limiting nutrient. The relative contribution of structural biomass to total biomass decreases with increasing nitrogen provision. This is due to a decrease in carbohydrates reserve density. The reduction of carbohydrate accumulation with increasing $X_{r,N}$ can be attributed to the lesser extent to which nitrogen is the limiting factor.

3.3.2 The producer–consumer system

In the analysis, the effect of the diatom's composition on the copepod's growth is investigated. For this reason we left out the explicit modelling of producer dynamics. Inert producers are supplied to the chemostat, where consumers feed on them. This corresponds to an experimental setup where a two-stage chemostat is used [6] and compares to the theoretical approach followed by Anderson and Hessen (1995) and Kuijper et al. (2004). Here, algae are grown under controlled conditions in one vessel and then supplied to a second vessel, in which grazers are present, at a fixed rate. In the associated model, the density of diatoms in the supply to the second chemostat, as well as their composition in terms of reserve densities act as model parameters.

Figure (3.2) gives contourlines of consumer densities when producer supply rates and either of their reserve densities are varied. It is to be expected that the density of the reserve associated with the limiting nutrient will be generally low. Therefore, the density of the reserve that does not appear on the vertical axis is kept at zero, thereby simulating limitation of the corresponding nutrient. The contourline marked zero indicates the survival boundary of the consumer species. Higher diatom reserve densities facilitate invasion of the copepod, more so for nitrogen reserves than for carbohydrate reserves.

Figure (3.3) shows the effect of balancing the producers reserve densities. Here, the total reserve density is kept constant at 0.5 (in molar ratio to biomass). The graph gives contourlines of copepod densities, and the zerocontourline indicates the consumer survival boundary. The figure shows that a relatively even distribution of producer nitrogen and carbohydrate reserves promotes consumer survivability ($E_N^A/(E_N^A + E_H^A) \approx 0.6$). Producers are generally low in reserves that limit their production and high in reserves that are non-limiting. As a consequence, an even distribution in reserve densities is only achievable when the producer species experiences a proper nutrition. It appears that grazers profit from a proper nutrition of the primary producers.

Consumer biomass densities as function of supplied producer structure are presented in figure (3.4). Here, five scenario's are compared, in which diatoms of different compositions, in terms of reserve densities, are supplied to the copepods in the chemostat. The diagrams show that the composition of the



Figure 3.2: Contourplots of the consumer's structural mass at variable algal structure concentrations and variable $[E]_{H}^{A}$ (left) and $[E]_{N}^{A}$ (right). The density of the alternative reserve is kept at zero, which corresponds to severe limitation of the associated nutrient. The contourline marked zero indicates the invasion boundary of the consumer species. High producer reserve densities facilitate consumer persistence. This effect is stronger for nitrogen than for carbohydrate reserves.



Figure 3.3: Contourplots of the consumer's structural mass when the structure specific density of total producer reserves is held constant at 0.5, while the quantity of producer structure (x-axis) and the composition of its reserves (y-axis) are varied. A properly balanced composition of net producer biomass facilitates survival of the consumer species.



Figure 3.4: Biomass densities of consumers (left: structural only, right: structural + reserves) when producers of different nutritional quality are supplied. \mathbf{N}^+ , \mathbf{H}^+ : E_N^A , E_H^A fixed at 1; \mathbf{N}^- , \mathbf{H}^+ : E_N^A = 0 and E_H^A = 1; \mathbf{N}^+ , \mathbf{H}^- : E_N^A = 1 and E_H^A = 0; \mathbf{N}^- , \mathbf{H}^- : E_N^A , E_H^A fixed at 0; \mathbf{N}^{\pm} , \mathbf{H}^{\pm} : E_N^A , E_H^A fixed at 0.5. The producers benefit when both producer reserves are abundant (\mathbf{N}^+ , \mathbf{H}^+). The absence of both reserves results in a significant growth reduction (\mathbf{N}^- , \mathbf{H}^-). The (\mathbf{N}^{\pm} , \mathbf{H}^{\pm})-curve is always above the (\mathbf{N}^- , \mathbf{H}^+) and (\mathbf{N}^+ , \mathbf{H}^-)-curves, which indicates that a proper balance in the presence of the producers reserves facilitates growth. The (\mathbf{N}^+ , \mathbf{H}^-)-scenario results in higher structural biomasses than the reversed situation, (\mathbf{N}^- , \mathbf{H}^+). However, the total biomass of the (\mathbf{N}^- , \mathbf{H}^+)-scenario increases faster with increasing food supply. This can be attributed to the damming up of non-limiting hydrocarbon reserves.

producers significantly affects the consumer density. When producer reserves are both high, the consumers can persist at a lower supply of food, and their population size is largest. Nitrogen-limited diatoms (N^-, H^+) lead to lower structural copepod biomasses than carbon-limited ones (N^+, H^-) . When both producer reserves are evenly abundant, (N^{\pm}, H^{\pm}) , consumer biomasses are higher then when producers are limited by either resource, which again suggests that copepods may benefit from a well-balanced nutrition of the lower trophic level. The model predicts that the total biomass of copepods, living on nitrogen limited algae, exceeds that of copepods, living on carbon limited ones. This can be attributed to the damming up of carbohydrates in the copepods themselves.

3.3.3 The resource-producer-consumer system

Here we analyse the complete food-chain, where both the diatom and the copepod species are modeled explicitly. The result so far predict that under ambient conditions, nitrogen is the model's limiting factor for diatom growth. Therefore, we concentrate mainly on nitrogen supply as input parameter.

Figure (3.5) contains a one-parameter bifurcation analysis of the food web, when the concentration of the nitrogen supply, $X_{r,N}$, is varied. The upper graphs concern the biomass densities of producers and consumers in the absence of recycling. All excretes and decomposed organic matter is lost from the system, which is a common feature of traditional models [33, 37, 40, 44]. In the graphs in the middle panel, the recycling rate, k_D , is held at the ambient value of 0.005 h^{-1} , and the bottom row contains graphs of the food-chain when recycling of organic matter is infinitely fast. The vertical lines indicate values for $X_{r,N}$ where the qualitative behavior of the system changes, i.e. bifurcation points. Table 3.3 gives the nomenclature of the bifurcations involved. The transcritical bifurcation indicates the invasion boundary of the copepods.

When nitrogen enrichment is increased beyond the vertical line indicating the Hopf bifurcation, the stable equilibrium of coexisting producers and consumers breaks down, and limit cycles originate. The amplitudes (maxima and minima) are indicated in the bifurcation diagrams, dashed curves represent unstable states and solid curves are stable states. The model's behavior at high nitrogen inflow resemble Rosenzweig's 'paradox of enrichment' [44] in that it leads to destabilization of the system. However, this phenomenon is usually associated with the occurrence of a supercritical Hopf bifurcation. Our model predicts that in the absence of recycling, or when the recycling rate is sufficiently low, the system's destabilization is caused by a subcritical Hopf bifurcation. Here, an unstable limit cycle originates, which forms a separation between two stable states in complex systems has been pointed out by Scheffer et al. (2001), and our model demonstrates that it is possible even in a simple short food chain.

There is a range of nitrogen provisions at which the producer and con-



Figure 3.5: Biomass densities of producers (left) and consumers (right) as function of nitrogen provision when recycling is absent (upper row), ambient (middle row) or infinitely fast (lower row). The consumer's invasion boundary is marked TC. At a supercritical Hopfbifurcation (H^-), the stable steady state becomes unstable and a stable limit cycle originates. However, at a subcritical Hopf-bifurcation (H^+), an unstable limit cycle originates, which marks the separation between a stable limit cycle and a stable steady state. The region in which these two stable states co-occur is bounded by the subcritical Hopf and the saddle-node bifurcation (T).



Figure 3.6: Two-dimensional bifurcation diagram which demonstrates the influence of the recycling rate of organic detritus in conjunction with nitrogen enrichment. At the Bautin-point, the Hopf-bifurcation changes from sub-critical (low \dot{k}_D) into super-critical (higher \dot{k}_D). In the region bounded by the sub-critical Hopf curve and the saddle-node curve, there exist multiple stable states. These are a stable steady state and a limit cycle.

sumer can coexist in equilibrium. The exploitation ecosystem hypothesis (EEH) predicts that over this range the producer species should have a constant population density [40]. This result is, however, debated, as primary producer biomass has been shown to increase with nutrient enrichment [7, 22]. Our model predicts an increasing mass of the primary producer with increasing nitrogen availability. Grover (2003) links such an increase to the resource replenishment associated with recyling by the consumer species. Indeed, the slope of the producer population is steeper when recycling is implemented. However, in the absence of recycling, the slope is still positive (left upper graph), so that the effect can not be attributed to nutrient recycling exclusively, and must be attributed to the metabolic flexibility of the consumer species.

From figure (3.5) it appears that the occurrence of multiple stable states depends on the recycling rate of organic detritus. Figure (3.6) presents a 2-dimensional bifurcation curve in which the nitrogen supply $X_{r,N}$ and the decomposition rate k_D are varied simultaneously. The position of the Hopf bifurcation decreases with increasing $X_{r,N}$. This implies that the stable regions of the system become smaller with increasing k_D , and thus, increased recycling rates may destabilize the food chain. The dashed curve indicates the position of the saddle-node, or tangient, bifurcation. The distance between the two bifurcation curves gives the region where multiple stable states exist. At the point where the saddle node and the Hopf bifurcations intersect, the Hopf bi-



Figure 3.7: Biomass densities as function of inorganic carbon provision (left) and light (right). Solid lines denote the diatom population size, whereas dashed lines are used for the copepod population. The two supercritical Hopf bifurcations mark the region where oscillations occur, in this case at low resource inputs. When light is used as bifurcation parameter, the Hopf and transcritical bifurcation almost coincide. Due to limited space, the transcritical bifurcation point for the invasion of the consumer is omitted in the left diagram.

furcation switches from supercritical (lower part) to subcritical (upper part). This point is called a Bautin point and above it, the system's behavior follows the classical paradox of enrichment.

Figure (3.7) contains the one-parameter bifurcation diagrams of the food chain when the inorganic carbon supply, $X_{r,C}$ (left), and the light intensity, j_L (right panel), are varied under otherwise ambient conditions. When the light flux or the carbon supply is low (i.e. far beneath ambient conditions) the system oscillates in a region bounded by two supercritical Hopf bifurcations. When light figures as bifurcation parameter (right panel), the invasion boundary of the copepod almost coincides with the Hopf bifurcation, although close inspection revealed that the two bifurcation points do not intersect. The cycling behavior is caused by the relatively high supply of nitrogen in this region of the parameter space. The paradox of enrichment is usually associated to absolute values of nutrient concentrations. In contrast, our results suggest that food chain destabilization may also follow from imbalances in the relative supply of particular resources. From figure (3.1) it can be observed that the diatoms are limited by light ($j_L \leq 30$) or carbon ($X_{r,C} \leq 500$) in only a small region of the analysed parameter space. However, figure (3.7) shows that the copepod population continues to increase with increasing light and carbon supplies. This implies that limitation of the lowest trophic levels not necessarily restrict the production of higher trophic niches.



Figure 3.8: Biomass densities as function of inorganic carbon provision (left) and light (right). Solid lines denote the diatom population size, whereas dashed lines are used for the copepod population. The two supercritical Hopf bifurcations mark the region where oscillations occur, in this case at low resource inputs. When light is used as bifurcation parameter, the Hopf and transcritical bifurcation almost coincide. Due to limited space, the transcritical bifurcation point for the invasion of the consumer is omitted in the left diagram.

We conclude our analyses by studying the effect of varying resources supplies simulateneously. Figure (3.8) shows the 2-dimensional bifurcation diagrams from which the pairwise effect of nitrogen and carbon (left), nitrogen and light (center), and carbon and light (right) can be studied. The unchanged resource supply is fixed at the default value. The solid curves mark the invasion boundary of the copepod species, which can invade in the regions to the right of this curve. When nitrogen and carbon, or nitrogen and light are varied simultaneously, the food-web persists in steady state in the region between the transcritical and the Hopf bifurcation. This region generally becomes larger with increasing carbon and light. This supports the hypothesis that a proper balance in the provision of nutrients may facilitate food-web persistence. However, the range of $X_{r,N}$, where the steady state is stable is largest at very low carbon inputs. In that region, the potential for nitrogen to destabilize the food chain is small, whereas a small enhancement in carbon provision will make the system cross the Hopf bifurcation and become unstable. When carbon and light are varied simulataneously there is a region confined by two supercritical Hopf bifurcations, in which the food chain is unstable. To the right of this region, the food chain is stable, but this region becomes smaller when $X_{r,N}$ is increased. This is not shown in the diagram, but it follows from the $X_{r,N}$ - j_L and the $X_{r,N}$ - $X_{r,C}$ plots, where nitrogen enrichment in the vicinity of a Hopf bifurcation promotes food chain destabilization.

3.4 Discussion

We investigated the effect of resource availability in combination with metabolic flexibility on the dynamic properties of a marine microbial food chain, in which we modelled stoichiometry explicitly. Furthermore, we assessed the effect of recyling by decomposition and excretion of non-limiting nutrients and metabolic products by living biota. We used the SU construct for modelling stoichiometric requirements as an alternative for classic Liebig models. Although the model holds more biological detail than traditional stoichiometric food chain models, it produces, to a large extent, similar results. This finding can be used as a validation of simple models in most cases.

SU's have a range, rather than a point, over which limitation changes gradually from one nutrient to another. This range may be very small, in which case results of an SU-model resemble results of Liebig's minimum law. Indicated by the kink in the associated curve (fig. 3.1), switching from carbon to nitrogen limitation in the resource–producer system is very similar to Liebig limitation. However, numerical bifurcation analysis did not cause any problems, as it may do in minimum models.

Liebig's law does not dictate what happens to non-limiting resources. We used a mass-balance model, where it is inevitable to explicitly model the fate of any compound. SU's mathematically translate substrate fluxes into product fluxes and rejected fluxes. The rejected fluxes comprise non-limiting elements, of which the fate can be addressed conveniently to model mass-balance, which is a necessity for assessing effects of stoichiometry in food webs [20, 36].

The model predicts that, under default conditions, nitrogen and not energy, limits diatom production, although our model does not include other nutrients such as iron or phosophorous. Moreover, while our focus was on the effect of an increased metabolic flexibility, we modeled potentially limiting nutrients in a very simplistic manner and neglected effects of carbon speciation into HCO_3 and CO_2 , as well as the effect of self-shading, which may influence light versus element limitation. This may explain why there is a very small parameter range for light inputs where this resource is limiting the resource–producer system. Nevertheless, our findings with respect to nitrogen limitation are in agreement with Graziano et al. (1996) and Tomasky et al. (1999). Carbon enrichment results in carbohydrate accumulation in the diatom, but the structural biomass remains unaffected in the absence of copepods. A detailed representation of inorganic carbon dynamics and light gradients was beyond the scope of this paper, but may be included in future work. This omission causes limitations in the applicability of the model.

When copepods are present in the system, their structural density increases with both the inorganic carbon (fig. 3.7) and nitrogen supply (fig. 3.5) to the system. Copepods thus benefit from enhancement of minerals, which they cannot assimilate themselves. The effect of nitrogen enrichment on copepod production can be understood, as it stimulates diatom growth, which in turn, will effect on the copepod population size. However, while carbon is non-limiting

to the diatoms, carbon enrichment also effectively promotes the copepod population growth (see fig. 3.7). This effect can be attributed to the change in diatom biomass composition following upon carbon enrichment, i.e. the accumulation of carbohydrate reserves in diatoms. This leads to a change in their nutritional value to copepods. Here, the effect of multiple reserves for the description of population dynamics becomes clear. As both carbon and nitrogen stimulate the growth of the copepod population, it seems that these animals are not limited by either element. Non-linearities in the description of trophic interactions make it difficult to predict how enrichment with nutrients that are non-limiting to the lowest trophic level will affect the dynamics of larger systems. Our results demonstrate that nutrient limitation as applied to single organisms might not be applicable to whole ecosystem functioning. Metabolic flexibility leads to efficient use of limiting resources and allows for sloppier use of non-limiting ones. As each trophic level has its own mode of resource acquisition and use, it is to be expected that whole ecosystems will generally comprise multiple limitations.

In our results, copepods influence the dynamics of the diatom population, a property commonly featured in stoichiometric models [13, 36]. EEH predicts that grazing effectively nullifies effects of nutrient enrichment on the producer population size [40, 41]. However, our model predicts that in the presence of grazers, nitrogen enrichment stimulates the diatom population, while light and carbon enrichment cause a decline in the producer's population size. Deviations from the EEH may be caused by storage strategies of herbivores [21]. According to Grover, the sequestration of resources by a consumer species may cause a reduction in primary production when the associated nutrient is enriched. In our model, diatoms have a high C:N when nitrogen is limiting, due to the damming up of carbohydrates. When copepods ingest carbon-rich diatoms, they will use nitrogen more efficiently, as transformation (3.15a) will then prevail over transformation (3.15b). Consequently, less DIN is formed and excreted as by-product of a biomass synthesis process, which corresponds to lower recycling. Enrichment with nitrogen causes exactly the opposite effect. The C:N of diatoms then becomes lower and copepods will be less efficient with respect to this mineral, thereby recycling it more efficiently and promoting algal growth. Our results are therefore in line with Grover's observations.

We found that nitrogen enrichment can destabilize the food chain (fig. 3.5), which is in agreement with the classic results of Rosenzweig (1971). The classic result concerns the crossing of a supercritical Hopf bifurcation, so that the stable internal equilibrium becomes unstable and a stable limit cycle comes into existence [1, 40, 45]. The same happens in our model when the recycling rate of organic matter is sufficiently high. However, many of the classical studies do not take into account the recycling of any nutrient. Another important difference between our study and classic studies on nutrient enrichment is the use of SU's for the description of biomass production, rather than Holling's disc equation. Muller found a richer repertoire of dynamic behaviors for simple food chain models due to the use of SUs [39]. In the absence of recycling,

our model predicts the existence of a subcritical, instead of a supercritical Hopf bifurcation, an effect that can be attributed to the use of SU's. At a subcritical Hopf bifurcation point, a stable equilibrium becomes unstable and an unstable limit cycle occurs, forming the separatrix between the stable steady state and an alternative stable state. When the recycling of organic matter is set at a biologically plausible value of 0.005 h^{-1} [17], the multiple stable states still exist, although the parameter range at which they occur is narrow. Scheffer et al. (2001) have shown that multiple stable states are common in nature. In correspondence to the results of Muller et al. (2001), our results suggest that they might also occur in food webs as simple as a resource–producer–consumer system.

In addition to high nitrogen input, low carbon input or light availability can also destabilize the food chain in our model. This suggests that destabilization can also be caused by imbalances in the availability of essential resources, as was also found by Loladze et al. in a simple stoichiometric model. This result corresponds to the finding of Muller and co-workers (2001) that a high level of nutrients reduces persistance of the consumer. Indeed, when nitrogen levels are high, the model is more stable when light and carbon are also high. This can be observed in figure (3.8), where the range of values at which a stable internal equilibrium exists becomes larger with increasing light and carbon. In real aquatic systems, nitrogen enrichment can cause algal blooms [42], which, in turn, reduce light penetration in the water. The combined effects of reduced light and enhanced nitrogen may promote the destabilization of aquatic ecosystems, which corresponds to the findings of Lima et al. (2002).

Recycling appears to be a destabilizing factor in the model. With higher decomposition rates, equilibria destabilize at lower nitrogen provisions. This result goes well with the findings of Kooi et al. (2002). However, a word of caution is needed, here. Decomposition in nature is a complex process in which different organic materials are decomposed at different rates. Furthermore, the role of bacteria in the breakdown of dissolved organic matter is significant. As our main interest was in the application of SU's for the modelling of ecological stoichiometry, we simplified the decomposition process to a large extent, i.e. we assigned only two detritus components and we chose not to explicitly model decomposer species.

3.5 Conclusions

We designed an aquatic food chain model, capable of assessing effects of organismal metabolic flexibility with respect to ecological stoichiometry, modeled according to the Dynamic Energy Budget theory using synthesizing units.

With the parameters used in the analysis, the model predicted that the lowest trophic level is limited by nitrogen. The model confirmed the paradox of enrichment, although the repertoire of dynamic behaviors is augmented with the presence of multiple stable states for biologically plausible decomposition rates. Our results show realistic responses of population densities in response to nutrient enrichment. However, the model incorporates nutrients in a simplistic manner, and in forthcoming work, a more detailed description of nutrient chemistry is recommended.

While working well for single species, we found that the concept of single element limitation may not be applicable when used in an ecosystem context, because the consumer population benefits both from carbon and nitrogen enrichment. The model demonstrates that not only nutrient enrichment, but also an improper balance in the availability of essential resources may destabilize the food chain.

The model shows that accumulation of non-limiting resources on the one trophic level may affect population densities of other trophic levels. It is therefore to be expected that on the ecosystem level, where multiple trophic levels coexist, multiple resource limitations may occur simultaneously.

Finally, our results suggest that recycling, which replenishes minerals, thereby enriching the nutritional state of the system, will generally be a destabilizing factor in food web dynamics. We conclude that our approach allows for bringing more ecological detail in food chain models, while still being numerically tractable.

3.6 Acknowledgments

Tom Anderson is funded by the Natural Environment Research Council, UK. The authors would like to thank Tineke Troost, Cor Zonneveld and Herman Verhoef for their valuable discussions and comments on the manuscript.

symbol	interpretation			
	species			
A	producer			
C	consumer			
compounds				
С	mineral carbon			
D_H	carbohydrate detritus			
D_P	protein detritus			
E_x^z	reserves x of species z			
H	carbohydrates			
Ν	mineral nitrogen			
P	proteins			
X^z	structural mass of species z			
	processes			
A	assimilation			
B	catabolism after maintenance			
C	catabolism			
E	excretion			
G	growth			
H	mortality			
Ι	ingestion			
M	maintenance			
R	rejection			
	other			
f_x^z	Scaled functional response of z feeding on x			
$j_{x,y}^z$	Flux of x in process y of species z			
k_D	Decomposition rate of organic matter			
k_E^z	Reserve mobilization rate of species z			
k_H^z	Mortality rate of species z			
\dot{k}_M^z	Maintenance rate of species z			
\dot{r}^z	Structure specific growth rate of species z			
$y^{p}_{x_{1},x_{2}}$	Mass coupler $x_2 \rightarrow x_1$ in pathway p			
\dot{D}	Dilution rate			
$[E]_x^z$	Reserve density x of species z			
L	light			
I_x^z	Maximum specific ingestion rate of species z on x			
K_x^z	Half saturation value of species z utilizing x			
κ^{z}	Fraction of unused reserves directed back to reserves of species z			
$ heta_{s_1s_2}$	fraction of SUs in state s_1, s_2			
$ ho_x^p$	SU binding probability of x for pathway p			
ϕ_x	C:N ratio of compound <i>x</i>			
$\psi^z_{x,y}$	Transformation efficiency of x in process y of species z			

Table 3.1: Interpretation of symbols

parameter	value	units	reference
\dot{k}^A_E	0.36	h^{-1}	[55]
$\dot{k}_{E}^{\overline{C}}$	0.1	h^{-1}	[32]
$\dot{k}_{H}^{ar{C}}$	0.008	h^{-1}	[50]
$\dot{k}_{M}^{\widehat{C}}$	0.0041	h^{-1}	[32]
\dot{k}_D^m	0.005	h^{-1}	[17]
$I^A_{ m C}$	0.01	\mathbf{h}^{-1}	[43]
$I_{ m N}^{ar{A}}$	0.01	h^{-1}	[11]
$I_{X^A}^{\hat{C}}$	0.06	h^{-1}	[25]
K^A_{C}	750.0	$\mu \mathbf{M}$	after [8, 43]
K_L^A	210	$\mu \mathrm{mol} \ \mathrm{m}^{-2} \ \mathrm{s}^{-1}$	[55]
K^A_N	2.5	$\mu \mathbf{M}$	[14]
K_{C,X^A}	20.0	$\mu {f M}$	fitted after [26]
κ^A	0.98	-	Kooijman, pers. comm.
κ^{C}	0.5	-	[32]
$ ho_{H}^{PH}$	0.66	-	[32]
$ ho_P^P$	0.66	-	[32]
$ ho_P^{PH}$	0.95	-	[32]
ϕ_P	3.7	#/#	[54]
ϕ_{X^A}	10.0	#/#	[49]
ϕ_{X^C}	5.9	#/#	[26]
$\psi^C_{H_E,A}$	0.881	-	[2]
$\psi^{A^{'}}_{H,G}$	0.8	-	-
$\psi_{H_{X},A}^{\tilde{C}^{-,-}}$	0.553	-	[2]
$\psi^{\hat{A}}_{N.G}$	0.8	-	-
$\psi^{C, lpha}_{P, A}$	0.688	-	[2]

Table 3.2: Parameter values

Table 3.3: Bifurcations

symbol	type	interpretation
H^{-}	supercritical Hopf	stable equilibrium becomes unstable
		a stable limit cycle originates
H^+	subcritical Hopf	stable equilibrium becomes unstable
		an unstable limit cycle originates
T	saddle-node	stable and unstable state coincide
		and disappear
TC	transcritical	unstable and stable state coincide
		and exchange stability properties

References

- [1] Abrams PA, Roth JD. (1994). The responses of unstable food chains to enrichment. *Evolutionary Ecology* 8:150–171.
- [2] Anderson TR. (1994). Relating C:N ratios in zooplankton food and faecal pellets using a biochemical model. J. Exp. Mar. Biol. Ecol. 184:183–199.
- [3] Anderson TR, Hessen DO. (1995). Carbon or nitrogen limitation in marine copepods? J. Plankton Res. 17:317–331.
- [4] Berges JA, Harrison P. (1995). Relationships between nitrate reductase activity and rates of growth and nitrate incorporation under steady-state light or nitrate limitation in the marine diatom *Thalassiosira pseudonana* (bacillariophyceae). J. Phycol. 31:85–95.
- [5] Boersma M, Kreutzer C. (2002). Life at the edge: is food quality really of minor importance at low quantities. *Ecology* 83:2552–2561.
- [6] Boraas ME. (1983). Population dynamics of food-limited rotifers in twostage chemostat culture. *Limnol. Oceanogr.* 28:546–563.
- [7] Brett MT, Goldman CR. (1997). Consumer versus recource control in freshwater pelagic food webs. *Science* 275:384–386.
- [8] Burkhardt A, Amoroso G, Riebesell U, Sultemeyer D. (2001). CO₂ and HCO₃-uptake in marine diatoms acclimated to different CO₂ concentrations. *Limnol. Oceanogr.* 46:1378–1391.
- [9] Checkley DM. (1980). The egg production of a marine copepod in relation to its food supply: laboratory studies. *Limnol. Eceanogr.* 25:430–446.
- [10] Cross WF, Benstead JP, Rosemond AD, Wallace JB. (2003). Consumer resource stoichiometry in detritus-based streams. *Ecology Letters* 6:721– 732.
- [11] Davidson K, Gurney WSC. (1999). An investigation of non-steady-state algal growth. II. Mathematical modelling of co-nutrient limited algal growth. *Journal of Plankton Research* 21:839–858.
- [12] Droop MR. (1983). 25 years of algal growth kinetics. *Botanica Marina* 26:99–112.
- [13] Elser JJ, Urabe J. (1999). The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. *Ecology* 80:735–751.
- [14] Eppley RW, Rogers JN, McCarthy JJ. (1969). Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. *Limnol. Oceanogr.* 14:912–920.
- [15] Erdner DL, Anderson DM. (1999). Ferredoxin and flavodoxin as biochemical indicators of iron limitation during open-ocean iron enrichment. *Limnol. Oceanogr.* 44:1609–1615.

- [16] Erdner DL, Price NM, Doucette GJ. (1999). Characterization of ferredoxin and flavodoxin as markers of iron limitation in marine phytoplankton. *Mar. Ecol. Prog. Ser.* 184:43–53.
- [17] Fujii M, Murashige S, Ohnishi Y, Yuzuwa A. Miyasaka H, Suzuki Y, Komiyama H. (2002). Decomposition of phytoplankton in seawater part I: Kinetic analysis of the effect of organic matter concentration. J. Oceanography 58:433–438.
- [18] Fussmann GF, Ellner SP, Shertzer KW, Hairston Jr NG. (2000). Crossing the Hopf bifurcation in a live predator-prey system. *Science* 290:1358– 1360.
- [19] Graziano LM, Geider LJ, Li WKW, Olaizola M. (1996). Nitrogen limitation of North Atlantic phytoplankton: analysis of physiological condition in nutrient enrichment experiments. *Aquatic Microbial Ecology* 11:53–64.
- [20] Grover JP. (2002). Stoichiometry, herbivory and competition for nutrients: simple models based on planktonic systems. *J. Theor. Biol.* 214:599– 618.
- [21] Grover JP. (2003). The impact of variable stoichiometry on predator–prey interactions: a multinutrient approach. *American Naturalist* 162:29–43.
- [22] Hansson LA. (1992). The role of food chain composition and nutrient availability in shaping algal biomass development. *Ecology* 73:241–247.
- [23] Huisman J, Weissing FJ. (1999). Biodiversity of plankton by species oscillations and chaos. *Nature* 402:407–410.
- [24] Huisman J, Weissing FJ. (2001). Fundamental unpredictability in multispecies competition. *American Naturalist* 157:488–494.
- [25] Kiørboe T. (1989). Phytoplankton growth rate and nitrogen content: implications for feeding and fecundity in a herbivorous copepod. *Mar. Ecol. Prog. Ser.* 55:229–234.
- [26] Kiørboe T, Møhlenberg F, Hamburger K. (1985). Bioenergetics of the planktonic copepod *acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. *Mar. Ecol. Prog. Ser.* 26:85–97.
- [27] Kooi BW, Boer MP, Kooijman SALM. (1998). On the use of the logistic equation in food chains. *Bull. Math. Biol.* 60:231–246.
- [28] Kooi BW, Kuijper LDJ, Kooijman SALM. (2004). Consequences of symbiosis for food web dynamics. *J. Math. Biol.* In press.
- [29] Kooi BW, Poggiale JC, Auger P, Kooijman SALM. (2002). Aggregation methods in food chains with nutrient recycling. *Ecol. Modell*. 157:69–86.

- [30] Kooijman SALM. (1998). The synthesizing unit as a model for the stoichiometric fusion and branching of metabolic fluxes. *Biophysical Chemistry* 73:179–188.
- [31] Kooijman SALM. (2000). Dynamic energy and mass budgets in biological systems. Cambridge University Press.
- [32] Kuijper LDJ, Anderson TR, Kooijman SALM. (2004). C and N gross growth efficiencies of copepod egg production studied using a dynamic energy budget model. *Journal of Plankton Research* 26:1–15.
- [33] Kuijper LDJ, Kooi BW, Zonneveld C, Kooijman SALM. (2003). Omnivory and food web dynamics. *Ecol. Modell*. 163:19–32.
- [34] Liebig J. (1840). *Chemistry and its application to agriculture and physiology*. Taylor and Walton, London.
- [35] Lima ID, Olson DB, Doney SC. (2002). Intrinsic dynamics and system stability properties of size-structured pelagic ecosystem models. *Journal* of Plankton Research 24:533–556.
- [36] Loladze I, Kuang Y, Elser JJ. (2000). Stoichiometry in producer–grazer systems: linking energy flow with element cycling. *B. Math. Biol.* 62:1137–1162.
- [37] McCann KS, Hastings A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proc. R. Soc. Lond. B Biol. Sci.* 264:1249–1254.
- [38] Morel FMM, Cox EH, Kraepiel AML, Lane TW, Milliga AJ, Schaperdoth I, Reinfelder JR, Tortell PD. (2002). Aqcuisition of inorganic carbon by the marine diatom *Thalassiosira weissflogii*. *Funct. Plant Biol*. 29:301–308.
- [39] Muller EB, Nisbet RM, Kooijman SALM, Elser JJ, McCauley E. (2001). Stoichiometric food quality and herbivore dynamics. *Ecology Lett.* 4:519–529.
- [40] Oksanen L, Fretwell SD, Arruda A, Niemela P. (1981). Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118:240.
- [41] Oksanen L, Oksanen T. (2000). The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist* 155:703–723.
- [42] Paerl HW. (1997). Coastal eutrophication and harmful algal blooms: importance of atmospheric deposition and groundwater as "new" nitrogen and other nutrient sources . *Limnol. Oceanogr.* 42:1154–1165.
- [43] Riebesell U, Wolf-Gladrow DA, Smetacek V. (1993). Carbon dioxide limitation of marine phytoplankton growth rates. *Nature (London)* 361:249– 251.
- [44] Rosenzweig ML. (1971). Paradox of enrichment: the destabilization of exploitation ecosystems in ecological time. *Science (New York)* 171:385– 387.

- [45] Rosenzweig ML. (1973). Exploitation in three trophic levels. *Am. Nat.* 107:275–294.
- [46] Scharek R, Van Leeuwe MA, DeBaar HJW. (1997). Responses of Southern ocean phytoplankton to the addition of trace metals. *Deep Sea Res. pt. II* 44:1239–1253.
- [47] Scheffer M, Carpenter SR, Foley JA, Folke C, Walker B. (2001). Catastrophic shifts in ecosystems. *Nature (Lond.)* 413:591–596.
- [48] Scheffer M, Hosper SH, Meijer ML, Moss B. (1993). Alternative equilibria in shallow lakes. *Trends Ecol. & Evol.* 8:352–356.
- [49] Strzepek RF, Price NM. (2000). Influence of irradiance and temperature on the iron content of the marine diatom *Thalassiosira weissflogii* (Bacillariophyceae). *Mar. Ecol. Prog. Ser.* 206:107–117.
- [50] Takahashi T, Ohno A. (1996). The temperature effect on the development of calanoid copepod, *Acartia tsuensis*, with some comments to morphogenesis. *Journal of Oceanography* 52:125–137.
- [51] Tilman D. (1982). *Resource competition and community structure*. Princeton University Press.
- [52] Tomasky G, Barak J, Valiela I, Behr P, Soucy L, Foreman K. (1999). Nutrient limitation of phytoplankton growth in Waquoit Bay, Massachusetts, USA: a nutrient enrichment study. *Aquatic Ecology* 33:147–155.
- [53] Villar-Argaiz M, Medina-Sanchez JM, Carrillo P. (2002). Linking life hisotry strategies and ontogeny in crustacean zooplankton: implications for homeostasis. *Ecology* 83:1899–1914.
- [54] Vollenweider RA. (1985). Elemental and biochemical composition of plankton biomass; some comments and explorations. *Arch. Hydrobiol*. 105:11–29.
- [55] Zonneveld C, Van Den Berg HA, Kooijman SALM. (1997). Modeling carbon cell quota in light-limited phytoplankton. *J. theor. Biol.* 188:215–226.

4

Model predictions of global change effects on the structure and functioning of a soil food web

Abstract

Global change may affect the structure and functioning of decomposer food webs through qualitative changes in freshly fallen litter. We analyzed the predicted effects of a changing environment on a dynamic model of a donor-controlled natural decomposer ecosystem near Wekerom, The Netherlands. This system consists of fungi, bacteria, fungivores, bacterivores and omnivores feeding on microbiota and litter as well. The model concentrates on carbon and nitrogen flows through the trophic niches that define this decomposer system, and is designed to predict litter masses and abundances of soil biota. For modeling purposes, the quality of freshly fallen leaf litter is defined in terms of nitrogenous and nonnitrogenous components, of which refractory and labile forms are present. The environmental impacts of elevated CO_2 , enhanced UV-B and eutrophication, each with their own influence on leaf litter quality, are studied. The model predicts steady-state dynamics exclusively, for all three scenario's. Environmental changes impact most demonstratively on the highest trophic niches, and affect microbiotic abundances and litter decomposition rates to a lesser extent. We conclude that the absence of trophic cascade effects and non-equilibrium dynamics may be attributed to weak trophic links occurring in the system. We set out a number of experimentally testable hypotheses that may improve understanding of ecosystem dynamics.

4.1 Introduction

Although the earth has continuously changed since its origin, we have become aware that alterations in the earth system are now occurring at an accelerated pace [17, 24, 78]. Ozone depletion leading to enhanced UV-B levels, increases in atmospheric greenhouse gases, elevated temperature, and changes in the use of natural resources have been experimentally shown to affect biological systems in many ways [81]. However, from a theoretical point of view, their effect on the structure of communities and long-term functioning of ecosystems is only moderately understood.

Element cycling, and the role of global change therein, is a central theme in ecology. Different aspects of global change impact on the quality of litter, and litter decomposition plays a key role in the cycling of resources in terrestrial donor-controlled ecosystems. The decomposition rate of detritus depends on its nutritional quality to decomposer organisms [14, 23, 53]. In turn, the dynamics of soil food webs depend on interactions between decomposers and higher trophic levels [2, 21, 76]. Therefore, it is to be expected that the functioning of such donor-controlled ecosystems depends on the composition of the litter provided.

Temperature and soil humidity directly influence the activity of soil decomposers and play a key role in litter decomposition [5]. Other environmental factors influence this process indirectly. Enhanced levels of UV-B have been shown to alter the chemical composition of fresh plant litter into more recalcitrant forms [28, 39, 40, 71, 72]. Furthermore, increased levels of atmospheric CO_2 potentially increase the carbon content of leaf litters, and their lignin:N ratio's [15, 16, 27, 57, 58]. In contrast, although eutrophication with nitrogen has toxic effects on soil microflora [82], it enhances the nitrogen content of leaf litters [25, 68], and so potentially augments soil species with nutrients that were originally limiting their activity and this may increase decomposition rates [26]. Antagonistic effects on the quality of litters make it hard to predict the effects of global change on the functioning of donor-controlled ecosystems.

In the past decades, our understanding of the physiology and function of soil micro-organisms has increased rapidly [56]. Moreover, there has been an increased knowledge of trophic channels along which energy and nutrients are transferred in natural ecosystems [13, 51]. Therefore, currently, many natural ecosystems have been successfully charted. At this stage it may have become possible to make the step from empirically based descriptive models, which have successfully outlined the basic structure and functioning of food webs, but are limited in their use for understanding long-term ecosystem dynamics, to mechanistic models of natural food webs, which may be used to discover general patterns in ecosystem dynamics and functioning. In this paper, we develop such a mechanistically based food web model, and we will use it to predict how different scenario's of global change might affect soil ecosystems both quantitatively (changes in net litter composition and masses of litter and soil functional groups) and qualitatively (changes in community structure, sta-

bility, top-down versus bottom-up regulation). Our goal is to put forward experimentally testable predictions on long-term effects of global change on soil communities, and to point out gaps in knowledge required to advance in the understanding of dynamics of soil ecosystems.

In this study we employ a dynamic model of a Scots pine forest soil ecosystem in Wekerom, The Netherlands, which has been described in detail by Berg et al. [8] and Berg and Verhoef [10]. Due to the large number of functional groups (sensu Moore et al.) involved, this web is essentially beyond the complexity at which a complete analysis is still feasible. Therefore, we have reduced the total number of groups by lumping species that belong to the same trophic group. This leaves groups of bacteria, fungi, bacterivores, fungivores and omnivores feeding on both detritus and microflora. Figure 4.1 shows the simplified trophic structure of the forest soil. Fresh litter supplied to the system is divided into nitrogenous and carbonous components, which are, in turn, split up in refractory and labile parts. The abundance of the four resulting components in the regular litter fall is affected by several aspects of global change. In this study we will analyze the effect of alterations in litter composition on the dynamics of the Wekerom food web. We will concentrate on eutrophication, UV-B enhancement and elevated CO₂ levels in this study, as these aspects of global change have been shown to affect the composition of leaf material. Litter is generally biochemically degraded by fungi and bacteria, although enchytraeids are also known to decompose litter [18]. Bacterivores and fungivores graze on the soil microflora, in which they find competitors in the enchytraeids, which can use both detritus and microbial biomass for growth [18]. Litter degradation comprises both chemical decomposition and fragmentation. In this study, we will model the upper litter layer, as this is the layer in which the majority of decomposition takes place [9]. We assume that fragmented materials, as well as the biota that live on them, are physically transported to the fragmentation layer, which is out of the scope of this study.

Litter quality is usually defined in terms of nitrogen and energy availability, and litter C:N-ratio's have traditionally been used as a measure for litter quality. Here, lower C:N-ratio's usually refer to a higher nutritional quality of litter. However, some nitrogenous compounds are recalcitrant (e. g. lignin) while soluble nitrogen-deficient hydrocarbons can generally be easily degraded, which obscures the concept of litter quality [4, 11]. We pay due attention to the characteristics of the particular chemical substances in the litter, by using a compound-based, rather than an element-based stoichiometric model. We model the biota's acquisition and utilization of potentially limiting resources using a model module, called the Synthesizing Unit (SU). Mathematically, this method connects closely to enzyme kinetics where concentrations of substrates transform into products. In this study, synthesizing units model the flows of carbon and nitrogen, in their different forms, through the food web. This theoretical approach was earlier used by Kooijman [32], Muller et al. [54], Kuijper et al. [35], Kuijper et al. [36] and Kooi et al. [31]. Using this approach, we augment classic food chain theory with aspects of nutritional physiology of soil



Figure 4.1: Conceptual model of trophic flows in the Wekerom Scots pine forest ecosystem. Arrows refer to flows of resources, rectangles are litter components, large circles are trophic guilds and the small hexagon represents the function of exogenous fungal enzymes that transform stable components into labile components, which may be used by fungi. Table 4.1 summarizes the notation.
biota, based on field biology data [7].

The paper's organization is as follows. In the next section, we set out the model philosophy and assumptions in some detail. In the results section, we show model predictions as to how changes in litter quality, caused by nutrient enrichment and enhanced UV-B and CO_2 , affect the dynamics of the litter layer. Here, we discuss these model predictions in detail, and put forward a number of experimentally testable ecological hypotheses, instilled by the results of the dynamic model. In doing so, we emphasize the need for collaborations between experimentalists and theoreticians. Furthermore, we concentrate on the dynamic behavior of the model, and compare it to theoretical predictions from theoretical ecology. We conclude by pointing out implications of using a mechanistic modeling approach in the analysis and understanding of soil ecosystems.

4.2 Model setup and assumptions

The model is about energy and nutrient flows across the soil ecosystem. This requires the characterization of transformations of litter components into biota and transformations of prey into predators. We assume homeostasis for all components, i.e. the stoichiometry of all biota and particular litter components is constant. We use C-moles per square meter as unit of mass. Table 4.1 contains the assumed biochemical composition of the food web components in terms of their C:N-ratio's. The C:N ratio of the labile nitrogenous litter is based on average C:N of proteins (\approx 3, [79]), while the C:N of stable nitrogen is typical for lignin (≈ 20 , [1]). Biota are given a biologically realistic C:N (5-10 cf. [75]), where fungi have a somewhat lower C:N than other biota. Biochemical transformations are listed in Box 4.1. The stoichiometry of these transformations follows from literature assimilation and production efficiencies [8] and the C:N ratio's of the forest ecosystem's participants. The model parameters are listed in table 4.2. Maximum production rates, which can be regarded as the intrinsic growth rates of the associated populations, have been given a biologically plausible value. Degradation rates of stable litter are conjectured from Minderman [50]. The litter input rate and composition are based on local observations [7]. For simplicity, the natural residence time of litter components is taken one year precisely, hence the value of D = 1/365 per day. Unfortunately, there is no data available for estimating the parameters of interactions between soil organisms and substrates. Therefore, we used a standardized biologically plausible value for all searching rates and substrate affinities. Appendix I contains the mathematical expressions for the dynamic interactions in the top litter layer. Note that plants are not included in the model, as our focus is on the top litter layer, in which plant roots are virtually absent in the Wekerom system [7].

Fungi. In the Wekerom soil ecosystem, fungi dominate the degradation of recalcitrant litter components. In this process, using exogenous enzymes, brown-rot fungi release and utilize energy rich resources from the matrix of

soil component	notation	composition
stable nitrogen	S_N	$CN_{0.05}$
stable carbon	S_C	CN_0
labile nitrogen	L_N	$CN_{0.35}$
labile carbon	L_C	CN_0
fungi	F	$CN_{0.1}$
bacteria	B	$CN_{0.2}$
fungivores	C_F	$CN_{0.2}$
bacterivores	C_B	$CN_{0.2}$
omnivores	0	$CN_{0.2}$
	•	•

Table 4.1: Actors in the upper litter layer and their biochemical representations as C:N ratio's

Table 4.2: Environmental constants and parameters of interactions between soil biota and their resources

		1	1
parameter	interpretation	dimension	value
$j_{L_N,D}$	max. degradation rate of S_N	d^{-1}	$7.14 10^{-3}$
j_{L_C} ,D	max. degradation rate of S_C	d^{-1}	$4.0 \cdot 10^{-3}$
$j_{F,Gm}$	max. fungal specific growth rate	d^{-1}	5.0
$j_{B,Gm}$	max. bacterial specific growth rate	d^{-1}	10.0
$j_{C_F,G}$	max. fungivore specific growth rate	d^{-1}	$3.0 \cdot 10^{-1}$
$j_{{C}_{\boldsymbol{B}}}$, $_{G}$	max. bacterivore specific growth rate	d^{-1}	$5.0 \cdot 10^{-1}$
$j^O_{L_C,I}$	max. omnivore ingestion rate of L_C	d^{-1}	1.0
$a_{S_N}^{F}$	fungal enzymatic affinity for S_N	d^{-1}	5.0
$a_{S_C}^{F'}$	fungal enzymatic affinity for S_C	d^{-1}	5.0
$a_{L_N}^{F^{\odot}}$	fungal affinity for L_N	d^{-1}	5.0
$a_{L_C}^{F''}$	fungal affinity for L_C	d^{-1}	5.0
$a_{L_N}^{B^{\odot}}$	bacterial affinity for L_N	d^{-1}	5.0
$a_{L_C}^{B}$	bacterial affinity for L_C	d^{-1}	5.0
$a_F^{C_F}$	fungivorous food searching rate	d^{-1}	5.0
$a_B^{\overline{C}_B}$	bacterivorous food searching rate	d^{-1}	5.0
$a_{L_C}^{O}$	omnivorous food searching rate	d^{-1}	5.0
$J_{C_{\mathrm{in}}}$	litter input rate	C-mole d^{-1}	$5.0 \cdot 10^{-2}$
D	loss rate	d^{-1}	$\frac{1}{365}$
varied par.	interpretation	dimension	default value
θ_{S_N}	fraction of S_N in supplied litter	-	0.20
θ_{S_C}	fraction of S_C in supplied litter	-	0.45
θ_{L_N}	fraction of L_N in supplied litter	-	0.05
θ_{L_C}	fraction of L_C in supplied litter	-	0.30

no.	transformation	biochemical reaction
1	stable litter breakdown by fungi	$S_N ightarrow rac{1}{7}L_N + rac{6}{7}\mathrm{CO}_2$
		$S_C ightarrow rac{1}{5}L_C + rac{4}{5}CO_2$
2	fungal growth	$\frac{2}{7}L_N + 3\frac{5}{7}L_C \rightarrow F + 3 \operatorname{CO}_2$
3	bacterial growth	$\frac{4}{7}L_N + 2\frac{3}{7}L_C \to B + 2 \text{ CO}_2$
4	fungivore growth	$F \rightarrow \frac{3}{20}C_F + \frac{7}{100}NH_3 + \frac{17}{20}CO_2$
5	bacterivore growth	$B \rightarrow \frac{1}{4}C_B + \frac{3}{20}NH_3 + \frac{3}{4}CO_2$
6	omnivore assimilation	$L_C \rightarrow \frac{9}{50}H + \frac{4}{5}L_C + \frac{1}{50}CO_2$
		$L_N \rightarrow \frac{7}{20}P + \frac{1}{2}L_N + \frac{21}{400}NH_3 + \frac{3}{20}CO_2$
		$B \rightarrow \frac{12}{35}P + \frac{5}{35}H + \frac{2}{25}\text{NH}_3 + \frac{14}{35}\text{CO}_2$
		$F \rightarrow \frac{6}{35}P + \frac{3}{7}H + \frac{2}{50}NH_3 + \frac{14}{35}CO_2$
7	omnivore growth	$\frac{4}{7}P + \frac{16}{21}H \rightarrow O + \frac{1}{3}CO_2$

Table 4.3: Biochemical transformations occurring in the top litter layer

stable components [29]. White-rot fungi may metabolize refractory materials directly [30]. We use Michaelis-Menten kinetics to model this process of excision. We assume that the production of labile organic nitrogen is efficient, so that no nitrogen is lost in mineral form. The process rate of persistent litter degradation is slow, as compared to other transformation processes. Fungi have prior access to the labile components released from the persistent matrix and they can use them in addition to other labile components in the litter to form biomass. This process of merging soil substrates for growth is modeled with a complementary SU [32], which describes the process rate of a biochemical transformation in which two or more resources are required (see appendix I). The availability of nitrogen and energy determines the growth rate of fungi, which models the influence of resource quality. We assume that the maximum carbon growth efficiency of fungi is approximately 25% (using 45% production efficiency [8] and a biologically plausible 75% uptake efficiency, rounded off downward in contrast to bacteria which need less complex structures and may therefore be more efficient). Furthermore, as nitrogen is generally considered to be the limiting nutrient in the initial phase of litter degradation, we assume that nitrogen can be used at a potential 100% efficiency.

Bacteria. Although many species of bacteria are capable of lignin and holo-cellulose degradation under anaerobic circumstances, these species are deemed to comprise only a small fraction of the total soil bacterial biomass, especially in the rarely waterlogged top litter layer. Therefore, in the model bacteria can only use labile components in the litter, including labile organic matter released from persistent litter, but left unused by fungi. Bacteria effectively compete with fungi for labile components of litter. As bacterial structural components are less complex than eukaryote fungal structures, we assume 33% maximum carbon growth efficiency for bacteria (approximately 45% production efficiency [8] and 75% uptake efficiency), which is slightly higher than

the fungal efficiency with respect to carbon, and gives bacteria a slight competitive advantage. Hence, we model a slow degradation route dominated by fungi and a fast route dominated by bacteria, sensu Moore et al. [51]. We assume that bacteria can use nitrogen 100% efficiently. Analogous to fungal production, a complementary SU conducts the merging process of nitrogenous and carbonous substrates for bacterial growth. For simplicity, we assume that bacteria and fungi can access labile litters equally efficient. This translates into identical values for uptake affinities in table 4.2.

Fungivores. In the model, fungivores comprise the group of animals that feed on fungi. These are collemboles, oribatids, prostigmatids and fungivorous nematodes. Although many species are known to consume detritus as well [20], they are generally selective grazers for fungi. Therefore, in the model they feed on fungi exclusively. We assume that the grazing rate on fungi depend on the density of fungi in the litter, and use a Holling type-II functional response to model the interaction between fungi and fungivores. The net production efficiency of fungivores is approximately 15% (calculated from Berg et al. [8], based on assimilation and gross production efficiencies). For simplicity, a constant loss term models predation, physical transport and natural death of all mesofauna.

Bacterivores. Flagellates, ciliates, amoeba and bacterivorous nematodes comprise the bacterivorous trophic group in the Wekerom soil ecosystem. We use a type-II response for bacterivorous consumption also. Moreover, we employ the same grazing rate and digestion time for bacterivores and fungivores for convenience. However, we assume that chitin sheaths of fungi are harder to metabolize than bacterial structures, and therefore, bacterivores have a higher assimilation efficiency (25%, calculated from Berg et al. [8]) than fungivores in the model.

Omnivores. The soil omnivores comprise omnivorous nematodes and enchytraeids, of which the latter are dominant in the Wekerom system. Therefore, we base the omnivores dynamics on the food acquisition method of enchytraeids, as described by Didden and Rombke [18, 19]. Enchytraeids feed by grazing the organic constituents of litter, and with the ingestion of litter, they automatically take up fungi and bacteria. Labile organic matter, as well as the bacteria and fungi, contain amino-acids and hydrocarbons, which can be used in combination for growth. In this case, again a complementary SU rules the merging process, where carbon is used at a potential 75% gross growth efficiency, which is the predicted theoretical maximum efficiency for heterotrophs [12], and nitrogen can be used at a maximum 100% gross growth efficiency. The labile carbon part is an important source for hydrocarbon assimilates; labile nitrogenous litter components contribute to the amino-acid pool. Fungi and bacteria donate both hydrocarbons and amino-acids. Therefore, litter composition, as well as the abundance of soil microbiota, is important for the dynamics of the enchytraeid population.

4.3 Modeling global change scenario's

We simulate three scenario's where aspects of global change affect litter quality, i.e. elevated CO_2 levels, enhanced UV-B irradiation and eutrophication with nitrogen. This section deals with the quantitative effects of these changes on litter quality, and the indirect effects on the accumulation of litter and the persistence of functional groups. Environmental changes are modeled by imposing changes in the composition of incoming litter. We aim to observe trends in the dynamic properties of the system, following upon changes in environmental conditions. Therefore, we employ modest perturbations from the default situation. Here, the relative difference in the composition of freshly fallen litter from the ambient conditions is called 'impact factor', and will never exceed 20%.

4.3.1 Elevated CO₂

Elevated levels of CO₂ increase the carbon and lignin content in plant materials [15, 16, 27, 57, 58]. This implies that the stable nitrogen content (θ_{S_N}), and the stable and labile carbon content (θ_{S_C} , θ_{L_C}) increase with increasing CO₂ levels, and consequently, the labile nitrogen content (θ_{L_N}) decreases simultaneously. We model the effect of elevated CO₂ by lowering θ_{L_N} and increasing fractions θ_{S_N} , θ_{S_C} and θ_{L_C} , while preserving the default relative proportions [7] of these three litter components for simplicity.

The CO₂ impact factor, which is on the horizontal axis of the diagrams (figures 4.2,4.3), increases with increasing atmospheric CO₂ concentrations. The factor refers to the percentual reduction of labile nitrogenous organic matter in the litter. The ambient percentage of this litter component is 5%, which corresponds to an impact factor of 1. An increment to 1.2 corresponds with a reduction of this percentage from 5% to $\frac{5}{1.2} \approx 4.17\%$.

None of the litter components are affected by CO_2 enhancement, although the quality of the litterfall is lower due to an inherent smaller fraction of labile nitrogenous compounds (figure 4.2, upper panel). Although fungal and bacterial densities in the litter seem unaffected, enhanced CO₂ impacts on the omnivore and fungivore populations (figure 4.2, lower panel). Omnivores suffer from reduced quality of the litter input, while the fungivore population becomes larger. Although their resource densities remain more or less constant, the model predicts pronounced effects of elevated CO_2 on the higher trophic groups. As there is no direct effect of litter quality on soil fauna, these changes in population size must be attributed to bottom-up effects. The model predicts that the change in fresh litter composition imposes an indirect shift in the competition ability of the omnivore enchytraeids. They suffer from a lower access to labile nitrogenous organics in the litter provided, which results in a lower population size and lower grazing pressure on fungi. Specialist fungivores benefit from this reduced competition with omnivores. Whether this model prediction holds when applied to natural systems remains to be tested.

The C:N-ratio increases as a consequence of CO_2 enhancement (figure 4.3), which is an indirect effect of the reduced population density of omnivores, which generally have a high nitrogen content. As can be observed from figure 4.2, upper panel, the mass and C:N of the abiotic litter pack itself are hardly affected by CO_2 elevation. In conclusion, the effects of CO_2 elevation-induced changes in fresh litter composition only become apparent in the highest trophic levels.



Figure 4.2: Masses of organic materials and biota in the top litter layer. The impact factor of CO_2 is on the horizontal axis. Here, a factor 1 refers to ambient conditions, while a factor 1.2 corresponds to a 1.2-fold less contribution of labile nitrogen to the fresh litter, caused by elevated CO_2 levels.



Figure 4.3: Characteristics of the top litter layer as a function of elevated CO_2 . The determination of the molar C:N-ratio considers both abiotic litter constituents and soil biota. The density of biota in the litter is defined as the lumped biotic biomasses in C-moles, divided by the lumped litter masses.

4.3.2 UV-B enhancement

Higher plants grown under elevated UV-B generally have higher phenolic content [40, 71, 72] and thicker cuticles [43, 77]. In modeling terms, this implies that UV-B enhancement results in higher fractions of recalcitrant litters (θ_{S_N} , θ_{S_C}) and lower fractions of labile litters (θ_{L_N} , θ_{L_C}). We implemented UV-B enhancement by taking a proportional increase in the fractions θ_{S_N} and θ_{S_C} and a simultaneous proportional decrease in fractions θ_{L_N} and θ_{L_C} .

On the horizontal axis of the diagrams (figures 4.4,4.5) is the UV-B impact factor. Here, a value of 1 corresponds to the ambient fresh litter composition as given in table 4.2. An increment in this factor corresponds to a proportional increment in the stable litter fractions (θ_{S_N} , θ_{S_C}) as compared to ambient conditions, so that an UV-B impact factor of 1.2 corresponds to a 120% increase in stable components in the fresh litter.

Contrary to the consequences of elevated CO_2 , UV-B enhancement has pronounced effects on the composition of the top litter layer (figure 4.4, upper panel). The model predicts that UV-B enhancement results in a thicker resident litter pack. This is mainly caused by the accumulation of refractory litter components, although labile nitrogenous litter also accumulates. The model predicts a decline in labile carbonous substances with increasing levels of UV-B.

The size of the microbial populations increases with increasing UV-B, however, their density in the litter remains approximately constant, as the litter mass increases in a proportional manner (figure 4.4). The graph to the right demonstrates that the mass and density of all soil mesofauna is suppressed under enhanced UV-B. As both fungi and bacteria utilize labile organic substances, this substrate type may be regarded as the system's primary resource. UV-B enhancement causes a decrease in labile carbonous substrates, which corresponds to an effective decline in energy availability to both bacteria and fungi. This limits their growth capacity, and reduces the potential for transforming organic nitrogen, which therefore accumulates. This result demonstrates that UV-B enhancement may shift the decomposition activity from nitrogen to energy limitation. The exploitation ecosystem hypothesis [59, 60] predicts a correlation between resource availability and herbivore density, and this might also be what happens in the model: a reduction in energy availability reduces the abundance of higher trophic niches in the litter, while leaving densities of the microflora intact.

Although UV-B imposes an evident shift in litter composition (cf. figure 4.4), the C:N ratio remains virtually constant over the range of UV-B impacts analyzed (figure 4.5). Here, the model shows that a summary statistic such as the litter C:N-ratio may not always be sufficient for the assessment of its nutritional quality to microbiota. This reasoning is in agreement with the results of Berg et al. [8], who calculated net N-immobilization by enchytraeids, which is impossible for heterotrophs, when food quality was expressed in terms of C:N.



Figure 4.4: Masses of organic materials and biota in the top litter layer. The impact factor of UV-B is on the horizontal axis. Here, a factor 1 refers to ambient conditions, while a factor 1.2 corresponds to a 1.2-fold contribution of refractory constituents in the fresh litter, caused by UV-B enhancement.



Figure 4.5: Characteristics of the top litter layer as a function of enhanced UV-B. The determination of the molar C:N-ratio considers both abiotic litter constituents and soil biota. The density of biota in the litter is defined as the lumped biotic biomasses in C-moles, divided by the lumped litter masses.

4.3.3 Eutrophication with nitrogen

Enhanced nitrogen deposition elevates the nitrogen content of plants. Concentrations of both labile [3] and stable nitrogen-rich leaf components [63] become higher with increased nitrogen provisions. We model the effect of eutrophication on litterfall composition by assuming a proportional increase of nitrogenous litter fractions (θ_{S_N} , θ_{L_N}). Simultaneously, the fractions of nitrogen deficient litter fractions (θ_{S_C} , θ_{L_C}) are lowered.

The eutrophication factor is on the horizontal axis of the associated diagrams (figures 4.6, 4.7), and a value of 1 corresponds to ambient conditions. A factor of 1.2 raises the litterfall content of labile and refractory nitrogenous material to 120% of the ambient content (i.e. $\theta_{S_N} = 0.24$, $\theta_{L_N} = 0.06$).

The model predicts that eutrophication reduces the carbonous content of the litter, while both stable and labile forms of organic nitrogen increase. The model furthermore predicts that eutrophication has no pronounced effects on total litter accumulation. This results contrasts with the findings of Berg and Meentemeyer (2002). However, our model does not take into account potential toxicity [26] and retardation of ligninolytic enzymes under high nitrogen levels [41, 42, 69], both of which have been demonstrated in natural systems.

The microbial activity is not affected by the nitrogen enrichment (figure 4.6). Effects are most demonstrative at the highest trophic groups, which again suggest strong bottom-up relationships in the ecosystem. In the model, the fungivore population does not survive high nitrogen levels (factor ≥ 1.17). This finding contrasts with field observations. However, explanations may be found



Figure 4.6: Masses of organic materials and biota in the top litter layer. The eutrophication impact factor is on the horizontal axis. Here, a factor 1 refers to ambient conditions, while a factor 1.2 corresponds to a 1.2-fold contribution of nitrogenous constituents in the fresh litter, caused by eutrophication.



Figure 4.7: Characteristics of the top litter layer as a function of nitrogen enrichment. The determination of the molar C:N-ratio considers both abiotic litter constituents and soil biota. The density of biota in the litter is defined as the lumped biotic biomasses in C-moles, divided by the lumped litter masses.

in that the model takes into account neither changes in species composition within the functional group, nor changes in trophic structure due to changes in environmental conditions (for instance, collemboles may change their behavior and become omnivorous when fungal nutrition does not suffice). Still, the model predicts that among mesofauna, fungivores should be especially sensitive to nitrogen enrichment, a modeling result that may be tested empirically. Bacterivores are slightly hampered under nitrogen enrichment, but the omnivore population will grow larger. This may be caused by an improved quality of ingested litter by the omnivores. As the omnivore population grows larger with the improving nutritional quality of litterfall, it exerts a higher competitive pressure on the bacterivore and fungivore populations. This may cause the extinction of fungivores at high levels of nitrogen enrichment. Furthermore, this may explain why the incline in population size (figure 4.6, bottom right graph) halts at the point where fungivores are ousted. In the model, eutrophication reduces the C:N ratio of the top litter layer, which is known to happen in natural systems [62], and the biomass density becomes larger (figure 4.7). The latter can be attributed to the increased growth of the omnivore population. However, the fungivore population may vanish under severe eutrophication, so that eutrophication may cause the system to become structurally unstable, an effect that is not observed when effects of CO_2 enhancement and elevated UV-B irradiation are implemented.

4.4 Discussion and conclusions

4.4.1 Qualitative effects on food web characteristics

The model presented in this paper bases on field observations of litter mass and composition, biomass of functional groups, and food web architecture. It predicts biologically feasible steady state quantities of litter and biomasses for the particular food web components. In all simulations, stable fraction dominate the mass of the top litter layer, while the availability of labile compounds is much lower. The masses of microbiota and mesobiota are of the same order of magnitude, but enchytraeids generally constitute the larger part of biomass in the litter, which largely corresponds to field situations [64, 65]. However, a word of caution is required here. Model predictions of biomasses and densities are sensitive to changes in interaction parameters associated to the different trophic guilds. To our knowledge, there is no available data on these interactions parameters, so we conjectured them from existing ideas of soil dynamics (cf. model setup and assumptions).

The ecosystem modeled in this study is large as compared to most mechanistically oriented models [31, 46, 80]. The studies of May [44] and Pimm and Lawton [66] showed that complex systems tend to become more unstable as they become larger. However, recent investigations have shown that large systems may be stable, provided that the food web contains a number of weak interactions among trophic niches [45, 47, 67]. Our system qualifies as such a food web. Firstly, besides the strong competitive interactions between fungi and bacteria, there exists a weak link as fungi release labile compounds from refractory litters, and this also indirectly supplies bacteria with resources. A second weak interaction involves the enchytraeids, which are omnivores spreading their control over other trophic niches. Omnivory has been theoretically shown to be a stabilizing factor in food webs [37, 55].

With the parameter values tested, the model yields equilibrium dynamics in all of the scenario's; there are no oscillatory or chaotic dynamics, nor does the model exert multiple stable states in any part of the tested parameter space. This result suggests that the model's weak trophic interactions indeed stabilize the food web. However, the model consists of a large number of parameters, of which the interaction parameters have not been measured in the field. It is impractical, and beyond the scope of the study, to perform a full bifurcation analysis of the system, including the effects of changes in all parameter values on the dynamics of the system. Therefore, it is at this stage unknown whether complex dynamics can occur when interaction parameters, such as searching or maximum degradation rates, are varied.

We divided the food web into a limited number of functional groups. In the model, this number can easily be expanded by, for instance, making a distinction between fungivorous prostigmata, which feed exclusively on fungi, and fungivorous collembola, which may consume quantities of litter in addition to fungi. This expansion comes at the cost of extra model variables and parameters, and requires the mathematical implementation of differences in physiology between the splitted populations. The expansion also comes with the establishment of additional trophic links. If among them weak links are common, the resulting model should theoretically behave stable. In conclusion, the mechanistic modeling approach, advocated in our study demonstrates that, if weak interactions indeed stabilize ecosystem dynamics, ecological models of natural ecosystems should generally be stable.

4.4.2 Effects of global change on trophic groups

The model predicts that elevated CO_2 and eutrophication do not result in thicker litter packs, although eutrophication alters the chemical quality of litter. In the model, UV-B enhancement causes litter to become more persistent, resulting in an increased accumulation of litter. None of the scenario's, however, affect the density of microbiota in the soil. In contrast, the model predicts pronounced effects on the higher trophic niches. Trophic cascade theory predicts reciprocal effects on the abundance of adjacent trophic niches [61]. This suggests that decreasing grazer population densities should coincide with increasing microbial population sizes and lower litter masses. In correspondence to soil food web experiments of Mikola and Setälä [48], our model does not predict trophic cascade effects to occur. The absence of trophic cascades can be attributed to the omnivorous behavior of enchytraeids. This is a realistic feature of the model, as omnivorous activity has been empirically shown to reduce the potential for trophic cascades in soil food webs [49].

In the model omnivores and fungivores are most demonstratively affected by global change. Although the bacterivore population is predicted to decline with increasing UV-B irradiation, this trophic guild is hardly affected by other aspects of global change. Elevated CO_2 and UV-B enhancement affect omnivores and fungivores in an adverse manner. This suggests that the competition ability of higher trophic guilds is affected by the quality of litter. Omnivores tend to benefit when litters of higher nutritional quality, i. e. higher doses of labile litters, are provided to the system, while fungivores profit from larger contributions of refractory material. Whether this theoretical finding is valid in natural systems could serve as a hypothesis for an experimental test.

4.4.3 Formulating testable hypotheses using mechanistic models

Many traditional dynamic food web models focus on effects of trophic structures on stability properties of food webs. Although these models have been subject to debate due to their, sometimes extreme, simplifications of biological interactions, they have revealed some valuable patterns in ecosystem dynamics. Among these patterns are the 'paradox of enrichment', where it can be shown that food chains may become unstable due to nutrient enrichment [22, 70], and the potential for multiple stable states, where small perturbations in environmental circumstances can have dramatic irreversible effects on the structure and functioning of an ecosystem [38, 73, 74]. Unfortunately, traditional models usually lack the required detail to answer situation specific questions that experimental ecologists are faced with. Historically, this has made cooperations between empiricists and theoreticians rare. However, improved insight in the nature of ecological interactions, in combination with faster methods of solving the mathematical problems involved opens new ground for such collaborations.

The model presented in this study bases mainly on qualitative knowledge of decomposition in litter strata. It has to be noted that the model is simplistic in many respects. For instance, we used a number of parameters of which realistic values have, to our knowledge, hardly been established in laboratory experiments (e. g. searching rates and substrate affinities). In addition, we simplified aspects of biotic physiology. Metabolic maintenance or death were merely modeled implicitly in the litter loss rate *D*. We used a simple model as a starting point, while physiologically based models allowing for more biological detail and consistency are available (i. e. DEB theory [33, 34]). However, we need to make long-term predictions based on short-term experiments, and descriptive models cannot be used for that purpose. Our goal is to bring forward a modeling methodology that may be used for such long-term predictions.

The model yields a series of experimentally testable hypotheses. Examples are: fungivores are more sensitive to changes in environmental conditions than bacterivores, omnivores limit the potential for trophic cascades, and, natural ecosystems tend to equilibria due to the presence of weak trophic links. Furthermore, the model effectively uncloaks a number of largely unknown parameters in the study of decomposer food webs. We conclude that mechanistic models are helpful in directing experimental research, and this emphasizes that collaborations between empiricists and theoreticians are essential for understanding the structure and long-term functioning of ecosystems.

4.5 Acknowledgements

The authors are greatly indebted to Jaap Bloem who instilled this research with his expertise of microbial activity in forest litter layers. We thank Bas Kooijman for inspiring discussions.

4.6 Appendix I

The complementary synthesizing unit

We model production fluxes involved in biochemical transformations using a complementary SU, as described by Kooijman [32]. The general mathematical formulation is

$$j_{\text{product}} = \left(\frac{1}{j_{\text{max}}} + \frac{y_{j_1,\text{product}}}{j_1} + \frac{y_{j_2,\text{product}}}{j_2} - \frac{1}{\frac{j_1}{y_{j_1,\text{product}}} + \frac{j_2}{y_{j_2,\text{product}}}}\right)^{-1} (4.1)$$

Here, j_{product} is the product flux, j_1 and j_2 are the arrival fluxes of the two needed substrates and $y_{j_1,\text{product}}$ and $y_{j_2,\text{product}}$ are the particular amount of substrate units required for the synthesis of one unit of product, i. e. the stoichiometric couplers. Parameter j_{max} is the maximum production flux. In the model fluxes may be metabolites used for growth. However, an encounter rate between consumers and resources also qualifies as a flux.

Degradation of refractory litter

Fungal exogenic enzymes free labile materials from persistent litters. Their activity is described with the Michaelis-Menten equation (type-II functional response), so that production of labile materials amounts to

$$j_{L_N,D} = \left(\frac{1}{j_{L_N,Dm}} + \frac{7}{a_{S_N}^F m_{S_N}}\right)^{-1}$$
(4.2a)

$$j_{L_C,D} = \left(\frac{1}{j_{L_C,D_m}} + \frac{5}{a_{S_C}^F m_{S_C}}\right)^{-1} , \qquad (4.2b)$$

in which $j_{L_N,D}$ and $j_{L_C,D}$ are the biomass specific fluxes of released labile nitrogen and carbon, respectively, $j_{L_N,Dm}$ and $j_{L_C,Dm}$ are the associated maximum production rates and parameters $a_{S_N}^F$ and $a_{S_C}^F$ represent the enzymatic activities for the respective refractory litters. The numbers 7 and 5 are the stoichiometric coupling coefficients, corresponding to transformation 1 in Box 4.3. The variables m_{S_N} and m_{S_C} are the relative contributions of refractory nitrogen and carbon to the bulk litter mass. Densities m_X are defined as

$$m_X = \frac{X}{S_N + S_C + L_N + L_C},$$
 (4.3)

so that $m_{S_N}, m_{S_C}, m_{L_N}, m_{L_C}$ have a value between 0 and 1.

Fungal growth

In addition to direct uptake of available labile components, fungi may utilize labile material released from the persistent matrix. We employ the complementary SU from Equation 4.1. The biomass specific fungal production is

$$j_{F,G} = \left(\frac{1}{j_{F,Gm}} + \frac{26}{7 \, j_{L_C,I}^F} + \frac{2}{7 \, j_{L_N,I}^F} - \frac{1}{\frac{7}{26} j_{L_C,I}^F + \frac{7}{2} j_{L_N,I}^F}\right)^{-1}, \quad (4.4)$$

in which the arrival fluxes $j^F_{L_C,I}$ and $j^F_{L_N,I}$ are the combined direct and indirect uptake fluxes

$$j_{L_C,I}^F = a_{L_C}^F m_{L_C} + j_{L_C,D}$$
 (4.5a)

$$j_{L_N,I}^{F'} = a_{L_N}^{F'} m_{L_N} + j_{L_N,D} .$$
(4.5b)

The numbers 2, 7 and 26 in equation 4.4 are the stoichiometric couplers for the conversion of labile material into fungal biomass according to transformation 2 in Box 4.3.

Bacterial growth

Bacteria can only use the labile litter constituents L_N and L_C . These are merged by the bacterial complementary SU. The specific growth rate of bacteria is

$$j_{B,G} = \left(\frac{1}{j_{B,Gm}} + \frac{17}{7 a_{L_C}^B m_{L_C}} + \frac{4}{7 a_{L_N}^B m_{L_N}} - \frac{1}{\frac{7}{17} a_{L_C}^B m_{L_C} + \frac{7}{4} a_{L_N}^B m_{L_N}}\right)^{-1}$$
(4.6)

The stoichiometric coefficients are according to transformations 3 in Box 4.3.

Fungivores and bacterivores

Type-II functional responses model the specific growth rates of the fungivore and bacterivore populations. The specific growth rates are

$$j_{C_F,G} = \left(\frac{1}{j_{C_F,Gm}} + \frac{20}{3 a_F^{C_F} m_F}\right)^{-1}$$
 (4.7a)

$$j_{C_B,G} = \left(\frac{1}{j_{C_B,G_m}} + \frac{4}{a_B^{C_B} m_B}\right)^{-1},$$
 (4.7b)

in which the stoichiometric numbers correct for the yield of the grazers on their particular resources. These animals have to search for food and therefore, the parameters a should be interpreted as searching rates, rather than affinities.

Omnivores

Omnivores graze on litter and we use a type-II response for the modeling of litter ingestion, based on the density of labile carbon in the litter. Uptake of bacteria and fungi is taken proportional to their densities in the litter. Ingestion of material quantifies as

$$j_{L_C,I}^O = \left(\frac{1}{j_{L_C,Im}} + \frac{1}{a_{L_C}^O m_{L_C}}\right)^{-1}$$
 (4.8a)

$$j_{L_N,I}^O = \frac{L_N}{L_C} j_{L_C,I}^O$$
 (4.8b)

$$j_{F,I}^{O} = \frac{F}{L_{C}} j_{L_{C},I}^{O}$$
 (4.8c)

$$j_{B,I}^{O} = \frac{B}{L_{C}} j_{L_{C},I}^{O} ,$$
 (4.8d)

Ingested materials are processed and partly transformed in nitrogenous (P) and non-nitrogenous (H) precursor materials that can be used for growth (Box 4.3, transformations 6). Unassimilable materials are returned to their original litter pools. The quantities of H and P available for omnivore growth are

$$j_{H,A}^{O} = \frac{9}{50} j_{L_{C},I}^{O} + \frac{3}{7} j_{F,I}^{O} + \frac{9}{35} j_{B,I}^{O}$$
(4.9a)

$$j_{P,A}^{O} = \frac{7}{20} j_{L_{N},I}^{O} + \frac{6}{35} j_{F,I}^{O} + \frac{12}{35} j_{B,I}^{O} .$$
(4.9b)

Another complementary SU transforms the available precursors into omnivore biomass according to scheme 7 in Box 4.3. The biomass specific growth of omnivores amount to

$$j_{O,G} = \left(\frac{16}{21 \, j_{H,A}^O} + \frac{4}{7 \, j_{P,A}^O} - \frac{1}{\frac{21}{16} j_{H,A}^O + \frac{7}{4} j_{P,A}^O}\right)^{-1} \,. \tag{4.10}$$

Here, production is not a saturating function of precursor arrival, i. e. there is no maximum production flux $j_{O,Gm}$ in this equation. However, ingestion is a saturating function of labile litter density and this effectively bounds the omnivore population growth.

4.6.1 Model summary

The complete model can be constructed from the synthesis above. It resumes to

$$\frac{d}{dt}S_N = \theta_{S_N} \ J_{C_{in}} - 7 \ j_{L_N,D} \ F - D \ S_N$$
(4.11a)

$$\frac{d}{dt}S_C = \theta_{S_C} \ J_{C_{in}} - 5 \ j_{L_C,D} \ F - D \ S_C$$
(4.11b)

$$\frac{\mathrm{d}}{\mathrm{d}t}L_{N} = \theta_{L_{N}} J_{C_{\mathrm{in}}} + \left(j_{L_{N},D} - \frac{2}{7}j_{F,G}\right)F - \frac{4}{7}j_{B,G} B - \frac{1}{2}j_{L_{N},I}^{O} O - D L_{N}$$
(4.11c)

$$\frac{\mathrm{d}}{\mathrm{d}t}L_{C} = \theta_{L_{C}} J_{C_{\mathrm{in}}} + \left(j_{L_{C},D} - 3\frac{5}{7}j_{F,G}\right)F - 2\frac{3}{7}j_{B,G}B - \frac{1}{5}j_{L_{C},I}^{O}O - DL_{C}$$
(4.11d)

$$\frac{\mathrm{d}}{\mathrm{d}t}F = j_{F,G} \ F - \frac{20}{3} j_{C_F,G} \ C_F - j_{F,I}^O \ O - D \ F$$
(4.11e)

$$\frac{d}{dt}B = j_{B,G} B - 4 j_{C_B,G} C_B - j_{B,I}^O O - D B$$
(4.11f)

$$\frac{\mathrm{d}}{\mathrm{d}t}C_F = j_{C_F,G} C_F - D C_F \tag{4.11g}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}C_B = j_{C_B,G} C_B - D C_B \tag{4.11h}$$

$$\frac{d}{dt}O = j_{O,G} O - D O , \qquad (4.11i)$$

in which $J_{C_{\rm in}}$ is the daily litter input per square meter in C-moles, and $\theta_{S_N}, \theta_{S_C}, \theta_{L_N}, \theta_{L_C}$ are the respective fractions of stable, and labile nitrogenous and carbonous components in the litter. Parameter D models the simplified physical transport and abiotic decay of litters and death and predation by higher trophic levels of biota.

References

- [1] Adler E. (1977). Lignin chemistry past, present and future. *Wood Sci. Technol.* 11:169–218.
- [2] Bakker ES, Olff H, Boekhoff M, Gleichman JM, Berendse F. (2004). Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia* 138:91–101.
- [3] Baron JA, Rueth HM, Wolfe AM, Nydick KR, J. AE, Minear JT, B. M. (2000). Ecosystems responses to nitrogen deposition in the Colorado Front Range. *Ecosystems* 3:352–368.
- [4] Berg B. (2000). Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management* 133:13–22.
- [5] Berg B, Berg MP, Bottner P, Box E, Breymeyer A, Calvo de Anta R, Couteaux M, Escudero A, Gallardo A, Kratz W, Madeira M, Mälkönen E, McClaugherty C, Meentemeyer V, Muñoz F, Piussi P, Remacle J, Virzo de Santo A. (1993). Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. *Biogeochemistry* 20:127–159.
- [6] Berg B, Meentemeyer V. (2002). Litter quality in a north european transect versus carbon storage potential. *Plant and Soil* 242:83–92.
- [7] Berg MP. (1997). *Decomposition, nutrient flow and food web dynamics in a stratified pine forest soil.* PhD thesis, Vrije Universiteit Amsterdam.
- [8] Berg MP, De Ruiter P, Didden W, Janssen M, Schouten T, Verhoef H. (2001). Community food web, decomposition and nitrogen mineralisation in a stratified Scots pine forest soil. *Oikos* 94:130–142.
- [9] Berg MP, Kniese JP, Zoomer HR, Verhoef HA. (1997). Long-term decomposition of a nitrogen-saturated Scots pine forest soil. *Forest Ecology and Management* 107:159–172.
- [10] Berg MP, Verhoef HA. (1997). Ecological characteristics of a nitrogensaturated coniferous forest in The Netherlands. *Biology and Fertility of Soils* 26:258–267.
- [11] Bosatta A, Ågren GI. (1999). Soil organic matter quality interpreted thermodynamically. *Soil Biology and Biochemistry* 31:1889–1891.
- [12] Calow P. (1977). Conversion efficiencies in heterotrophic organisms. *Biol. Rev.* 52:385–409.
- [13] Copley J. (2000). Ecology goes underground. Nature 406:452–454.
- [14] Cotrufo MF, Ineson P. (1993). Effects of enhanced atmospheric CO_2 and nutrient supply on the quality and subsequent decomposition of fine roots of Betula pendula Roth and Picea sitchensis (Bong) Carr. *Plant and Soil* 170:267–277.

- [15] Cotrufo MF, Ineson P, Rowland AP. (1994). Decomposition of tree leaf litters grown under elevated CO₂ - Effect of litter quality. *Plant and Soil* 163:121–130.
- [16] Cotrufo MF, Ineson P, Scott A. (1998). Elevated CO₂ reduces the nitrogen concentration of plant tissues. *Global Change Biology* 4:43–54.
- [17] Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ. (2000). Accelaration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408:184–187.
- [18] Didden W, Rombke J. (2001). Enchytraeids as indicator organisms for chemical stress in terrestrial ecosystems. *Ecotoxicology and Environmental Safety* 50:25–43.
- [19] Didden WAM. (1993). Ecology of terrestrial enchytraeidae. *Pedobiologia* 37:2–29.
- [20] Filser J. (2002). The role of collembola in carbon and nitrogen cycling soil. *Pedobiologia* 46:234–245.
- [21] Fox CA. (2003). Characterizing soil biota in Canadian agroecosystems: state of knowledge in relation to soil organic matter. *Can. J. Soil Sci.* 83:245–257.
- [22] Fussmann GF, Ellner SP, Shertzer KW, Hairston Jr NG. (2000). Crossing the Hopf bifurcation in a live predator-prey system. *Science* 290:1358– 1360.
- [23] Gallardo A, Merino J. (1993). Leaf decomposition in 2 Mediterranean ecosystems of Southwest Spain - influence of substrate quality. *Ecology* 74:152–161.
- [24] Gillet NP, Zwiers FW, Weaver AJ, Scott PA. (2003). Detection of human influence on sea-level pressure. *Nature* 422:292–294.
- [25] Heinsdorf D. (1993). The role of nitrogen in declining Scots pine forests (Pinus sylvestris) in the lowland of East-Germany. *Water Air and Soil Pollution* 69:21–35.
- [26] Hogervorst RF, Dijkhuis MAJ, Van Der Schaar MA, Berg MP, Verhoef HA. (2003). Indications for the tracking of elevated nitrogen levels through the fungal route in a soil food web. *Environmental pollution* 126:257– 266.
- [27] King JA, Pregitzer KS, Zak DR, Kubiske ME, Holmes WE. (2001). Correlation and litter chemistry of sugar maple, Acer saccharum, as affected by elevated CO_2 and varying N availability, and effects on decomposition. *Oikos* 94:403–416.

- [28] Kinnunen H, Huttunen S, Laakso K. (2001). UV-B absorbing compounds and waxes of Scots pinen needles during a third growing season of supplemental UV-B. *Environmental Pollution* 112:215–220.
- [29] Kirk TK, Farrell RL. (1987). Enzymatic 'combustion': the microbial degradation of lignin. Ann. Rev. Microbiology 4:465–505.
- [30] Kirk TK, Fenn P. (1982). Formation and action of the ligninolytic system in basidiomycetes. In: Frankland JC, Hedger JN, Swift MJ, editors. *Decomposer basidiomycetes: their biology and ecology*, chapter 4. Cambridge University Press.
- [31] Kooi BW, Kuijper LDJ, Kooijman SALM. (2004). Consequences of symbiosis for food web dynamics. *J. Math. Biol.* In press.
- [32] Kooijman SALM. (1998). The synthesizing unit as a model for the stoichiometric fusion and branching of metabolic fluxes. *Biophysical Chemistry* 73:179–188.
- [33] Kooijman SALM. (2000). Dynamic energy and mass budgets in biological systems. Cambridge University Press.
- [34] Kooijman SALM. (2001). Quantitative aspects of metabolic organization; a discussion of concepts. *Phil. Trans. R. Soc. B.* 356:331–349.
- [35] Kuijper LDJ, Anderson TR, Kooijman SALM. (2004). C and N gross growth efficiencies of copepod egg production studied using a dynamic energy budget model. *Journal of Plankton Research* 26:1–15.
- [36] Kuijper LDJ, Kooi BW, Anderson TR, Kooijman SALM. (2004). Stoichiometry and food chain dynamics. *Theoretical Population Biology* Submitted.
- [37] Kuijper LDJ, Kooi BW, Zonneveld C, Kooijman SALM. (2003). Omnivory and food web dynamics. *Ecol. Modell*. 163:19–32.
- [38] Kuznetsov YA. (1995). *Elements of applied bifurcation theory*. Springer Verlag.
- [39] Laakso K, Sullivan JH, Huttunen S. (2000). The effects of UV-B radiation on epidermal anatomy in loblolly pine (Pinus taeda L.) and Scots pine (Pinus sylvestris L.). *Plant Cell and Environment* 23:461–472.
- [40] Lavola A, Aphalo PJ, Lahti M, Julkunen-Tiitto R. (2003). Nutrient availability and the effect of increasing UV-B radiation on secondary plant compounds in Scots pine. *Environmental and Experimental Botany* 49:49– 60.
- [41] Leatham GF, Kirk TK. (1983). Regulation of lignolytic activity by nutrient nitrogen in white-rot Basidiomycetes. *FEMS Microbiology letters* 16:65– 67.

- [42] Lodge DJ. (2001). Implications for nitrogen additions from air pollutants on litter decay fungi and ecosystem processes. *Mycological Research* 105:898–899.
- [43] Manetas Y, Petropoulou Y, Stamatakis K, Nikolopoulos D, Levizou E, Psaras G, Karabourniotis G. (1977). Beneficial effects of enhanced UV-B radiation under field conditions: Improvement of needle water relations and survival capacity of Pinus Pinea L. seedlings during the dry Mediterranean summer. *Plant Ecology* 128:100–108.
- [44] May RM. (1972). Will a large complex system be stable? *Nature (Lond.)* 238:413–414.
- [45] McCann KS. (2000). The diversity-stability debate. *Nature (Lond.)* 405:228–233.
- [46] McCann KS, Hastings A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proc. R. Soc. Lond. B Biol. Sci.* 264:1249–1254.
- [47] McCann KS, Hastings A, Huxel GR. (1998). Weak trophic interactions and the balance of nature. *Nature (Lond.)* 395:794–798.
- [48] Mikola J, Setälä. (1998). No evidence of trophic cascades in an experimental microbial-based soil food web. *Ecology* 79:153–164.
- [49] Mikola J, Setälä. (1999). Interplay of omnivory, energy channels and C availability in a microbial based soil food web. *Biol. Fert. Soils* 28:212–218.
- [50] Mindermann G. (1968). Addition, decomposition and accumulation of organic matter in forests. *J. Ecol.* 56:355–362.
- [51] Moore JC, McCann K, Setälä H, De Ruiter PC. (2003). Top down is bottom-up: does predation in the rhizosphere regulate aboveground dynamics? *Ecology* 84:846–857.
- [52] Moore JC, Walter DE, Hunt H. (1988). Arthropod regulation of microand mesobiota in below-ground detrital food webs. *Ann. Rev. Entomol.* 33:419–439.
- [53] Moore TR, Trofimow JA, Taylor B, Prescott C, Camire C, Duchene L, Fyles J, Kozak L, Kranabetter M, Morrison I, Siltanen M, Smith S, Titus B, Visser S, Wein R, Zoltai S. (1999). Litter decomposition rates in Canadian forests. *Global Change Biology* 5:75–82.
- [54] Muller EB, Nisbet RM, Kooijman SALM, Elser JJ, McCauley E. (2001). Stoichiometric food quality and herbivore dynamics. *Ecology Lett.* 4:519–529.
- [55] Mylius SD, Klumpers K, De Roos AM, Persson L. (2001). Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *Am. Nat.* 158:259–276.

- [56] Nannipieri P, Ascher J, Ceccherini MT, Landi L, Pietramellara G, Renella G. (2003). Microbial diversity and soil functions. *European Journal of Soil Science* 54:655–670.
- [57] Norby RJ, Cotrufo MF. (1998). Global change A question of litter quality. *Nature* 396:17–18.
- [58] Norby RJ, Cotrufo MF, Ineson P, O'neill EG, Canadell JG. (2001). Elevated CO₂, litter chemistry and decomposition: a synthesis. *Oecologia* 127:153– 165.
- [59] Oksanen L, Fretwell SD, Arruda A, Niemela P. (1981). Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118:240.
- [60] Oksanen L, Oksanen T. (2000). The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist* 155:703–723.
- [61] Pace ML, Cole JJ, Carpenter SR, Kitchell JF. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14:483–488.
- [62] Parker JL, Fernandez IJ, Rustad LE, Norton SA. (2001). Effects of nitrogen enrichment, wildfire and harvesting on forest-soil carbon and nitrogen. *Soil Science Society of America Journal* 65:1248–1255.
- [63] Penuelas J, Filella I. (2001). Herbaria century record of increasing eutrophication in Spanish terrestrial ecosystems. *Global Change Biology* 7:427–433.
- [64] Persson T, U. L. (1977). Energetical significance of the annalids and arthropods in a Swedish grassland soil. *Ecological Bulletin* 23:1–211.
- [65] Petersen H, Luxton M. (1982). A comparative analysis of soil fauna population and their role in decomposition processes. *Oikos* 39:287–388.
- [66] Pimm SL, Lawton JH. (1978). On feeding on more than one trophic level. *Nature (Lond.)* 275:542–544.
- [67] Polis GA. (1998). Stability is woven by complex webs. *Nature (Lond.)* 395:744–745.
- [68] Prietzel J, Kolb E, Rehfuss KE. (1997). Long-term study of formerly litterraked Scots pine ecosystems in NE Bavaria: recent changes in soil chemical properties and stand nutrition. *Forstwissenschaftliches Centralblatt* 116:269–290.
- [69] Reid ID. (1991). Nutritional regulation of synthetic lignin (DHP) degradation by *Phlebia (Merulius) tremellosa*: effects of nitrogen. *Can. J. Botany* 69:156–160.
- [70] Rosenzweig ML. (1971). Paradox of enrichment: the destabilization of exploitation ecosystems in ecological time. *Science (New York)* 171:385– 387.

- [71] Rozema J. (1999). UV-B radiation and terrestrial ecosystems: processes, structure and feedback loops. In: Rozema J, editor. *Stratospheric ozone depletion: the effects of enhanced UV-B radiation on terrestrial ecosystems*, chapter 6. Backhuys Publishers, Leiden, The Netherlands.
- [72] Rozema J. (2000). Effects of solar UV-B radiation on terrestrial biota. In: Hester RE, Harrison RM, editors. *Issues in environmental science and technology: 14. Causes and environmental implications of UV-B radiation*, pp. 85–105.
- [73] Scheffer M, Carpenter SR. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution* 18:648–655.
- [74] Scheffer M, Carpenter SR, Foley JA, Folke C, Walker B. (2001). Catastrophic shifts in ecosystems. *Nature (Lond.)* 413:591–596.
- [75] Schröter D, Wolters V, De Ruiter PC. (2003). C and N mineralisation in the decomposer food webs of a European forest transect. *Oikos* 192:294– 308.
- [76] Smith VC, Bradford MA. (2003). Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. *Applied Soil Ecology* 24:197–203.
- [77] Solovchenko A, Merzlyak M. (2003). Optical properties and contribution of cuticle to UV protection in plants: experiments with apple fruit. *Photochemical and Photobiological Sciences* 2:861–866.
- [78] Stouffer RJ, Manabe S, Vinnikov KY. (1994). Model assessment of the role of natural variability in recent global warming. *Nature* 367:6334–6336.
- [79] Vollenweider RA. (1985). Elemental and biochemical composition of plankton biomass; some comments and explorations. *Arch. Hydrobiol*. 105:11–29.
- [80] Vos M, Kooi BW, Mooij WM, De Angelis DL. (2004). Inducible defenses and the paradox of enrichment. *Oikos* In press.
- [81] Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F. (2002). Ecological responses to recent climate change. *Nature* 416:389–395.
- [82] Wollecke J, Munzenberger B, Huttl RF. (1999). Some effects of N on ectomycorrhizal diversity of Scots pine (Pinus sylvestris L.) in northeastern Germany. *Water Air and Soil Pollution* 116:135–140.

Summary

The role of trophic structures on the dynamics of food webs

This thesis expands on the realistic characterization of trophic links in food webs. Recent studies have led to the notion that the presence of weak links promote the persistence and stability of food webs. Here, weak links are defined as trophic interactions with low interaction strengths. For instance, the link between an omnivore and an edible plant is weak when the omnivore is generally carnivorous. In contrast, a specialist predator and its prey are typically strongly linked. Theoretical studies, aiming to assess the effect of interaction strengths in food webs usually consider interactions among species populations, while interactions between species and non-living resources are modeled in a simplistic manner. However, variability in the quality of their resources influences the nutritional quality of the lower trophic guilds to higher ones, and this is bound to affect the dynamics of a food web. Nutritional status and food web structure cannot be considered separately; they figure together in the dynamics of food webs. This thesis provides a mechanistic modeling methodology to treat these concurring aspects of food web dynamics.

Basic to modeling the influence of food quality in ecosystems is the notion that all organisms need multiple elements in their nutrition, and not always are those present in the right proportions. The element composition of an organism may differ substantially from the element composition of its food. Stoichiometry deals with this matter, however, the traditional use of stoichiometry in food webs is simplistic. Firstly, in traditional stoichiometry, multi-substrate transformations are modeled according to Liebig's law of the minimum, where a minimum-operator effectuates a switch between different metabolic modes, depending on which element limits biomass production. This switch makes the mathematical tractability of such models cumbersome. Secondly, classic stoichiometry generally bases itself on element limitation, whereas the elements considered are available in many forms. For instance, nitrogen may be present as a mineral, an amino-acid, or in refractory phenolic matrices. As amino-acids can be used at much higher efficiency than lignin from which amino acids can only be excised after high energy investments, the classic approach does not always do justice to the thermodynamics involved in biochemical transformations. As an alternative to the classic approach, this thesis explores the use of DEB, including synthesizing units (SUs) for the uptake and use of potentially limiting substrates. It is demonstrated that this approach is able to grasp macro-biochemical processes, such as growth and maintenance, on a physiologically sound basis.

The four chapters in this thesis treat a series of models with different levels of ecological detail concerning trophic transfer. These models all consist of a set of non-linear ordinary differential equations, and they are analyzed using bifurcation analysis, to study their long term behavior.

Chapter 1 considers a classic chemostat tri-trophic food chain model with a single explicitly modeled basal resource. As a deviation from the classic food chain, the top-predator is replaced with an omnivore, which predates on both a predator and a producer species. The focus of this chapter is on the effect of omnivory in the context of nutrient enrichment. While modest omnivory, figuring as a weak trophic link in the model, is expected to stabilize the food chain, nutrient enrichment is deemed to cause adverse effects. The model shows that omnivory may indeed stabilize nutrient enriched food chains. Low interaction strengths between the omnivore and the producer species promote this stabilizing effect. The model also predicts the existence of multiple stable states and thereby accentuates the potential for omnivory induced hysteresis loops.

Chapter 2 concentrates on the use of SUs in a physiologically based model of a copepod species. This chapter demonstrates that, unlike models in traditional stoichiometry, SUs are able to effectively capture multiple element limitation in zooplankton. The model developed here is a Dynamic Energy Budget model, in which copepods ingest algae of varying nutritional quality. The model divides assimilates among nitrogenous and non-nitrogenous reserve pools. Reserves are mobilized and used to meet costs for maintenance and reproduction of the copepod. This chapter points out the need to use physiologically based models to understand the effects of food quality.

Chapter 3 incorporates the model developed in chapter 2 into a DEB-based food web model of a simple basic structure. The web consists of a diatom population, feeding on mineral nitrogen and carbon and using light for photosynthesis, and grazed upon by copepods. Dead organic detritus is decomposed into minerals and excreted minerals are recycled. Both diatoms and copepods consist of three biomass components, namely structural biomass, nitrogenous reserves and a non-nitrogenous reserves. The mass-balance formulation requires keeping track of all carbon and nitrogen in the model, and this results in a relatively large number of model state variables for a bi-trophic food chain (ten in piece). The nutritional quality of diatoms to copepods depends on the mineral resource composition. The focus of the study is the effect of different mineral provisions on long-term dynamics of this food web. Similar to classic theory, the addition of mineral nitrogen can destabilize the food chain. In contrast, carbon depletion may have a similar effect, which shows that resource depletion may also destabilize food webs. The conclusion therefore holds that the nutritional balance may be important for the stability of food webs. In the model, carbon appears to be non-limiting to the diatom species, but although carbon enrichment is unable to stimulate growth of the diatom population, it does fuel the copepod population indirectly, through changes in diatom composition. Thus, the concept of nutrient limitation may apply well to any particular trophic group, it need not work at the ecosystem level.

In chapter 4, the step from small hypothetical food webs towards larger realistic ecosystems is made. The model studied in this chapter considers a top litter layer of a pine forest soil in Wekerom, The Netherlands. This ecosystem has been empirically studied in detail, so that its trophic structure is known well. The emphasis of this work is on the potential use of mechanistically based models in field ecology. The structure of the Wekerom system is as follows. Two routes of litter decomposition can be distinguished. Bacteria are generally responsible for the decomposition of labile litter fragments, while fungi break down stable litter components, such as lignin and hemi-cellulose. The model splits up litter into four components. These are nitrogenous and nonnitrogenous components, each of which both a stable and a labile organic form exists. In addition to the resources (i.e. the 4 litter types) and microbiota, the food web model describes the dynamics of fungivores and bacterivores, as well as soil omnivores, capable of breaking down litter and grazing on both bacteria and fungi. The associated model thus captures both elements of multiple resource availability and trophic structure. To maintain a manageable number of state variable and parameters, the model used is a Monod-type model. The focus is on the effect of changes in fresh litter composition on the dynamics of the food web. These changes relate directly to effects of eutrophication, elevated atmospheric CO₂ and UV-B enhancement on the composition of litter. The ecosystem is in stable equilibrium in all of the scenario's tested. However, the persistence of higher trophic groups may be threatened by changes in environmental circumstances. The activity of lower trophic levels is hardly affected by litter composition. The modeling results should, however, been interpreted with caution. A number of model parameters have not been measured in field experiments. On the bright side is that the model therefore gives direction to experimental research finding proper parameter values. The conclusion of this study is that the use of mechanistic models is inevitable for the understanding of the long-term dynamics of natural ecosystems, but the knowledge upon which the models base is still limited. This points out that collaborations between theoreticians and experimentalists should be stimulated.

The work presented in this dissertation yields a number of general ideas on the dynamics of ecosystems, as dependent on food web structure and resource availability. Here, omnivory stands model for weak trophic interactions. This thesis firstly treats a traditional food chain model with omnivory, and then explores a series of models each diverting in a different direction from the traditional modeling philosophy. In the traditional food chain model, with low biological detail, omnivory may act as a stabilizing factor in the food chain.

The next question is whether inclusion of biological detail alone may stabilize food chains. A methodology for including physiological detail in population models is brought forward. It appeared that the stability properties of the physiologically based food chain model are similar to those of traditional food chain models. The inclusion of physiological detail does not promote stability in the associated model. To the contrary, recycling, an important feature in natural systems, potentially destabilizes the food chain. The implementation of organismal physiology comes with an increased model complexity. On the other hand, it facilitates the quantitative use in ecosystem studies and makes the models more suitable for experimental backup. Adding physiological detail in larger food webs with a higher connectance reduces the potential for oscillatory behavior. It is, for the time being, impossible to attribute the ubiquity of stable steady states in this model to weak trophic links. However, the combined results presented in this thesis suggest that the reticulate trophic interactions imposed on this model are responsible for food web stability. This suggestion could serve as a working hypothesis for food web studies in the years to come. Again, the inclusion of physiological realism makes the model suitable for experimental backup. In addition, the model exposes gaps in ecological knowledge. The expectation spoken out here is that only the collaboration between experimental ecologists and theoreticians will result in fundamental advance in ecology. While experimentalists need a mechanistic framework to design the proper experiments, modelers need empirical data to validate their results.

Samenvatting

De rol van trofische structuren in de dynamiek van ecosystemen

Het wordt wereldwijd steeds warmer, we worden steeds meer blootgesteld aan UV-straling, de concentraties broeikasgassen zijn in de afgelopen eeuw flink gestegen en de menselijke populatie wordt steeds groter, waardoor we een steeds groter beroep doen op natuurlijke bronnen. Het klimaat op de wereld is aan het veranderen, zoveel staat vast. Hoe al deze veranderingen de stabiliteit van ecosystemen beïnvloeden is daarentegen helemaal niet zo bekend. Hoe zou de vlag erbij hangen als we over pakweg 100 jaar uit het raam kijken? Zal de natuur wel bestand blijken tegen klimaatsverandering? De wetenschap heeft hier wel ideeën over, maar de meningen lopen uiteen, omdat we nog niet goed begrijpen hoe ecosystemen eigenlijk werken. Toch is die kennis nodig om meer inzicht te verkrijgen in de effecten van klimaatverandering op ecosystemen. Alleen zo kunnen we hun gedrag voorspellen en verstandige besluiten maken om hun voortbestaan te garanderen.

Ecosystemen zijn in het algemeen dusdanig gecompliceerd dat het absoluut onmogelijk is om ze tot in detail te begrijpen en nauwkeurige voorspellingen, van bijvoorbeeld de populatiegrootte van een belangwekkende soort, op de lange termijn te doen. Wel kunnen we wiskundige modellen maken van ecosystemen, waarbij we ons concentreren op eigenschappen die naar onze huidige inzichten het meest sturend zijn in het dynamische gedrag ervan. Daarbij worden interacties tussen soorten onderling, en tussen soorten en hun milieu nagebootst. Hierbij worden details, waarvan men aanneemt dat ze niet of nauwelijks van invloed zijn, weggelaten. Vervolgens is het mogelijk om te bezien hoe zo'n model, dat nu een verregaande versimpeling van een echt ecosysteem is, zou reageren op veranderingen in het milieu. De volgende stap is dat men teruggaat naar de natuur om vast te stellen of de modelvoorspellingen naar redelijkheid kloppen met waarnemingen in het veld. Wanneer dat niet het geval is, dan luidt de conclusie dat er iets mis met de aannames achter het gebruikte model. Door gemiste details die blijkbaar toch van belang waren op te sporen verkrijgt men meer begrip in de sturende factoren achter ecosystemen.

Bij het maken van een ecosysteem-model moeten natuurlijke systemen

enorm worden versimpeld, en het valt niet licht daarin de juiste keuzes te maken. Omdat ecologie de kennis is van interacties tussen organismen en hun milieu, ligt het voor de hand om een goede wiskundige beschrijving van deze interacties centraal te stellen bij het maken van ecosysteem-modellen. Eén van de meest in het oog springende interacties tussen een soort en zijn milieu is het vinden van voedsel in dat milieu. Modellen uit de populatie-dynamica concentreren zich dan ook veelal op het voedingsgedrag van soorten. Daarin zijn verschillende gedragingen mogelijk. Zo kunnen planten groeien van mineralen en licht, eten herbivoren planten en eten carnivoren weer herbivoren, en misschien ook wel andere carnivoren. Maar al die soorten scheiden ook weer stoffen uit, of gaan dood waarna ze worden afgebroken. Zo komen weer voedingsstoffen in het milieu, die dan weer door planten kunnen worden gebruikt en daarmee is het voedselweb rond. In het bovenstaande voorbeeld worden alle planten gemakshalve op één hoop gegooid, evenals herbivoren en carnivoren. Deze indeling in zogenaamde trofische groepen is erop gebaseerd dat de soorten binnen zo'n groep onderling min of meer op dezelfde wijze met voedsel omgaan. Het voorbeeld hierboven klinkt misschien wel simpel, maar toch blijkt het analyseren van een wiskundig model waarin het is uitgewerkt al buitengewoon ingewikkeld.

De eerste modellen van voedselwebben waren van nog eenvoudiger structuur dan het hierboven beschreven voedselweb. Meestal betrof het een eenvoudige voedselketen, bestaande uit een populatie van producenten, consumenten die leven van deze producenten, en predatoren die weer jagen op consumenten. Toch bleken deze modellen soms in staat realistische voorspellingen te doen van het gedrag van natuurlijke ecosystemen. Een voorbeeld van zo'n modelvoorspelling is de verwachting dat ecosystemen die blootgesteld worden aan een overmaat van nutriënten instabiel kunnen worden. In de praktijk blijkt overbemesting, een vorm van nutriëntenverrijking, inderdaad een oorzaak van veel problemen in zoetwater-ecosystemen. Een andere voorspelling van dergelijke modellen is dat ecosystemen zich chaotisch kunnen gedragen. In dat geval is het fundamenteel onmogelijk om hun lange termijn gedrag te voorspellen. Of chaos ook in natuurlijke ecosystemen voorkomt, daarover lopen de meningen uiteen.

In een voedselketen staat elke populatie slechts in directe verbinding met haar voedingsbron en haar predatoren, zodat het aantal verbindingen per trofische groep niet groter is dan 2. Een recent naar voren gekomen idee is echter dat ecosystemen stabieler zullen zijn naarmate er het aantal verbindingen tussen de verschillende trofische groepen toeneemt. Een voorbeeld van een extra verbinding zou kunnen zijn de toevoeging van een omnivoor, die zowel predatoren als consumenten eet. Door de aanwezigheid van de omnivoor staat de consument nu niet alleen meer in directe verbinding met zijn voedsel en de predator populatie, maar ook met de populatie omnivoren. Een andere mogelijkheid tot uitbreiding van het aantal verbindingen is het toekennen van meerdere voedselbronnen aan het model. Veel soorten organismen zijn in de natuur ook afhankelijk van meerdere voedselbronnen, zodat langs deze weg ook een groter ecologisch realisme in het model tot stand komt. Dit proefschrift gaat over de effecten van dit soort verbindingen op de dynamiek van wiskundige voedselweb modellen. Daarbij wordt gebruik gemaakt van de Dynamische Energie Budget (DEB) theorie. Dat is een biologische theorie die op consistente wijze regels voorschrijft voor de opname en het gebruik van energie en nutriënten door organismen. De DEB-theorie baseert zich op behoudswetten en natuurkundige principes, en kan vanwege deze systematische aanpak worden toegepast op alle levende organismen.

In hoofdstuk 1 wordt een omnivoor toegevoegd aan een voedselketen, waarin de producent een voedselbron gebruikt en wordt bejaagd door predatoren en omnivoren, die naast consumenten ook predatoren bejagen. In dit hoofdstuk wordt afgeleid dat omnivorie stabiliserend kan werken op het gedrag van ecosystemen, onder de voorwaarde dat omnivoren, in vergelijking tot predatoren, minder goed zijn in het bejagen van consumenten. Ook wordt daar aangetoond dat de aanwezigheid van omnivorie kan voorkomen dat een voedselweb zich chaotisch gedraagt. Tot slot voorspelt het model dat omnivorie kan leiden tot het bestaan van meerdere stabiele ecologische evenwichten. Dat betekent dat, onder invloed van een veranderend milieu, de omvang van de deelnemende populaties plotseling naar een ander stabiel niveau kan omslaan. Door het naast elkaar bestaan van stabiele situaties zal, wanneer de verstoring wordt opgeheven, het ecosysteem niet terugkeren naar de oorspronkelijke situatie, maar in de nieuw ontstane samenstelling blijven voortbestaan.

Hoofdstuk 2 concentreert zich op de invloed van meerdere benodigde voedselbronnen op de dynamica van een roeipootkreeft, genaamd *Acartia tonsa*. Roeipootkreeftjes zijn zeer algemeen voorkomende zeer kleine kreeftachtigen, voorkomend in water. In dit hoofdstuk wordt voor het eerst gebruik gemaakt van de DEB-theorie. Hier tonen we aan dat, voor een realistische beschrijving van de eierproduktie van dit dier, een realistischer model dan dat tot voor kort meestal werd gebruikt nodig is voor het omgaan met meer dan één voedselbron. We concluderen dat de DEB-theorie hierin een belangrijke bijdrage kan leveren.

Het roeipootkreeftjes-model uit het tweede hoofdstuk dient als model-onderdeel in hoofdstuk 3. Hierin wordt een voedselketen waarin meerdere voedselbronnen een rol spelen geanalyseerd. De structuur van dit model is als volgt: een populatie van diatomeeën (een soort algen) groeit op licht, koolstof en stikstof en wordt begraasd door de roeipootkreeftjes uit hoofdstuk 2. Stoffen die worden uitgescheiden door deze twee soorten worden weer afgebroken, zodat ze weer kunnen dienen als voedingsstof voor de diatomeeën. Ook dit wiskundige model is opgezet volgens de DEB-theorie. Het model voorspelt onder meer dat een hoge mate van stikstoftoevoeging leidt tot destabilisatie van het voedselweb. Dat is een conclusie die strookt met de traditionele voedselketen-modellen. De belangrijkste conclusie is echter dat het model goed gebruikt kan worden om effecten van het voedselaanbod aan de producenten (de diatomeeën) op de dynamiek van de predator-populatie (de roeipootkreeftjes) te bestuderen, waar dat met de klassieke modellen niet goed mogelijk was. De gebruikte modelaanpak is daarmee beter geschikt om de invloed van voedselwebstructuren op het gedrag van ecosystemen te bestuderen.

Hoofdstuk 4 behandelt een model van biologische afbraak van dood organisch materiaal in een bosbodem-ecosysteem. Dit model is gebaseerd op een bestaand naaldbos-ecosysteem nabij Wekerom, in de buurt van Wageningen. In dit hoofdstuk wordt geprobeerd een brug te slaan tussen theoretische modellen en veldonderzoek, om zo met gebundelde kennis tot een beter begrip van de werking van ecosystemen te komen. Hier komen begrippen als omnivorie en verscheidenheid in voedselbronnen samen voor in een model dat bestaat uit een wat groter aantal deelnemers. Het betreft hier schimmels en bacteriën die verantwoordelijk zijn voor de afbraak van naalden, maar ook schimmel- en bacterie-eters, en daarnaast nog omnivoren die leven van zowel dood naaldmateriaal als schimmels en bacteriën. Het hoofddoel van deze studie is om aan te tonen dat de eerder in dit proefschrift gepropageerde methoden om ecosystemen te modelleren ook kunnen worden toegepast op bestaande, wat ingewikkelder, ecosystemen. Het blijkt echter dat de in experimenten opgedane kennis veelal ontoereikend is bij het ontwikkelen van dergelijke modellen. Het positieve hiervan is de observatie dat het model effectief gaten in benodigde kennis blootlegt. De conclusie is dan ook dat de voorgestelde modelleer-aanpak sturend kan werken bij het ontwikkelen van veld-experimenten en dat een goede samenwerking tussen modelmakers en experimentatoren een voorwaarde is in de vooruitgang van ecologisch onderzoek.

Dankwoord

Een dankwoord, dat schrijft men met verdeelde gevoelens. De ontvanger opent immers het proefschrift bij het het dankwoord. Dat gelezen hebbende (fijn! ik sta erin!) wordt het boekje in de kast gezet bij de andere dissertaties, terwijl een enkeling het onder zijn hoofdkussen legt (je schijnt er beter op te slapen). De boodschap van vier jaar werk ontgaat de typerende dankwoordlezer dan ook volkomen. En dat contrasteert in hevige mate met des schrijvers vurige wens van erkenning van de inhoudelijke kant. Wie geen dankwoord schrijft noopt zijn lezers op zijn minst tot het lezen van de Nederlandse samenvatting, waarmee die missie is volbracht.

Maar laten we reëel zijn. De impact, maar vooral de waardering van een proefschrift houdt min of meer op bij het dankwoord, dus kan dat stuk maar beter van uitstekende kwaliteit zijn. En aangezien er heel wat te bedanken valt, zal ik maar eens van leer trekken.

In de eerste plaats wil ik Bas bedanken. Jij krijgt het als geen ander voor elkaar om een stimulerende werkomgeving te bieden. Een open atmosfeer zonder geheimen en altijd ruimte voor discussie. Ooit noemde je jezelf schertsend een verlicht despoot, maar daarmee zit je niet ver van de waarheid.

Voorts mijn dank voor mijn 'partner in crime', wanneer het gaat over bifurcatie-analyse. Het gaat hier natuurlijk over Bob, die zich altijd met ongebreideld enthousiasme stort op alle wiskundige en biologische probleempjes die je je maar kunt voorstellen. Ik spreek voor velen als ik zeg dat het met niemand zo prettig samenwerken is als met Bob.

I would also like to thank Tom, who has been very enthusiastic from the beginning, when I wrote him a humble e-mail, suggesting a potential co-operation. I hope there will be more fruitful collaborations between the two of us. And may the Saints be the next premiership champions!

Ook wil ik Tineke in het bijzonder bedanken, als ex-kamergenoot. Het was altijd erg gezellig en, gestuurd door het feit dat flauwe grappen in de buurt van onze ingenieur verboden zijn, het ging ook altijd ergens over. Maak er wat moois van in het Zwitserse!

Daarnaast dank aan mijn stage-student Elly. Af en toe denk ik dat je jezelf onvoldoende realiseert hoe vruchtbaar het werk is dat jij hier hebt gedaan. Veel succes, maar vooral ook plezier in Finland!

De andere leden van de vakgroep hebben ook allemaal zo hun bijdrage

geleverd. Matthijs als trouwe ondersteuning als ik weer eens stom zat te doen met een TeX-document. Op naar de lvl 99! Paul Doucet was altijd erg gezellig om even mee bij te kletsen als je een muisarm pauzetje neemt. Je wordt gemist. Cor, met wie het erg goed kletsen is over communicatie-overdracht. Daar wordt menig artikel een stuk beter leesbaar van. Tjalling, altijd erg gezellig en betrokken. José, naast collega ook gewoon een goede vriend. Jacques, inmiddels werkzaam op een middelbare school, ik hoop toch niet dat je weg bent gegaan vanwege onze wat mindere bridgeprestatie op de OC&W-sportdagen? Inge, veel succes met je avonturen op het eiland. Bernd, altijd in de markt voor een goed gesprek en een biertje in de stelling. Stelling? Hoor ik daar stelling? Uiteraard, mijn dank gaat ook uit naar de actieve leden van Gyrinus, die dit fijne etablissement nog steeds goed draaiende weten te houden. Jorn, Anne-Willem, en George van TL (vroeger TB), laten we elkaar er nog vaak ontmoeten. Daan, succes met het afronden van je studie.

Dan de mensen van dieroecologie. Het was altijd heel leuk om op maandagmorgen contact te houden met waar het voor mij allemaal begon: de ecologie. Vooral een Matty maakt je duidelijk dat ecologie toch wel erg leuk is. Herman, pas op dat je je Senseo-apparaat niet kwijtraakt, die dingen zijn duur hoor! Afdelingsuitjes, kerstdiners, ik ben er bij geweest en het zulks vergeet men niet licht. Errug gezellug, zeggen we dan maar, bedankt voor de gastvrijheid en de leuke samenwerking!

Verder wil ik het talent-scouting bureau RoCa nog bedanken voor de door hen geleverde paranimfen Ronnie en Stevie. Dat wordt vast een goed feessie.

Verder wil ik al mijn vrienden en kennisen bedanken, die het leven naast de universiteit een stuk prettiger maken. Zeilweekendjes, bridgekroegentochten, de Ardennen, eetclubjes, Jazz-avondjes, port & whisky en de wekelijkse smulpaperij te Uilenstede 70B. Het leven is zo onaangenaam niet!

Tot slot wil ik nog extra dank betuigen aan mijn ouders, zusje en zwager. Met zo'n familie achter me kon dit avontuur nooit mislukken! Iedereen, hou je taai!

Lothar