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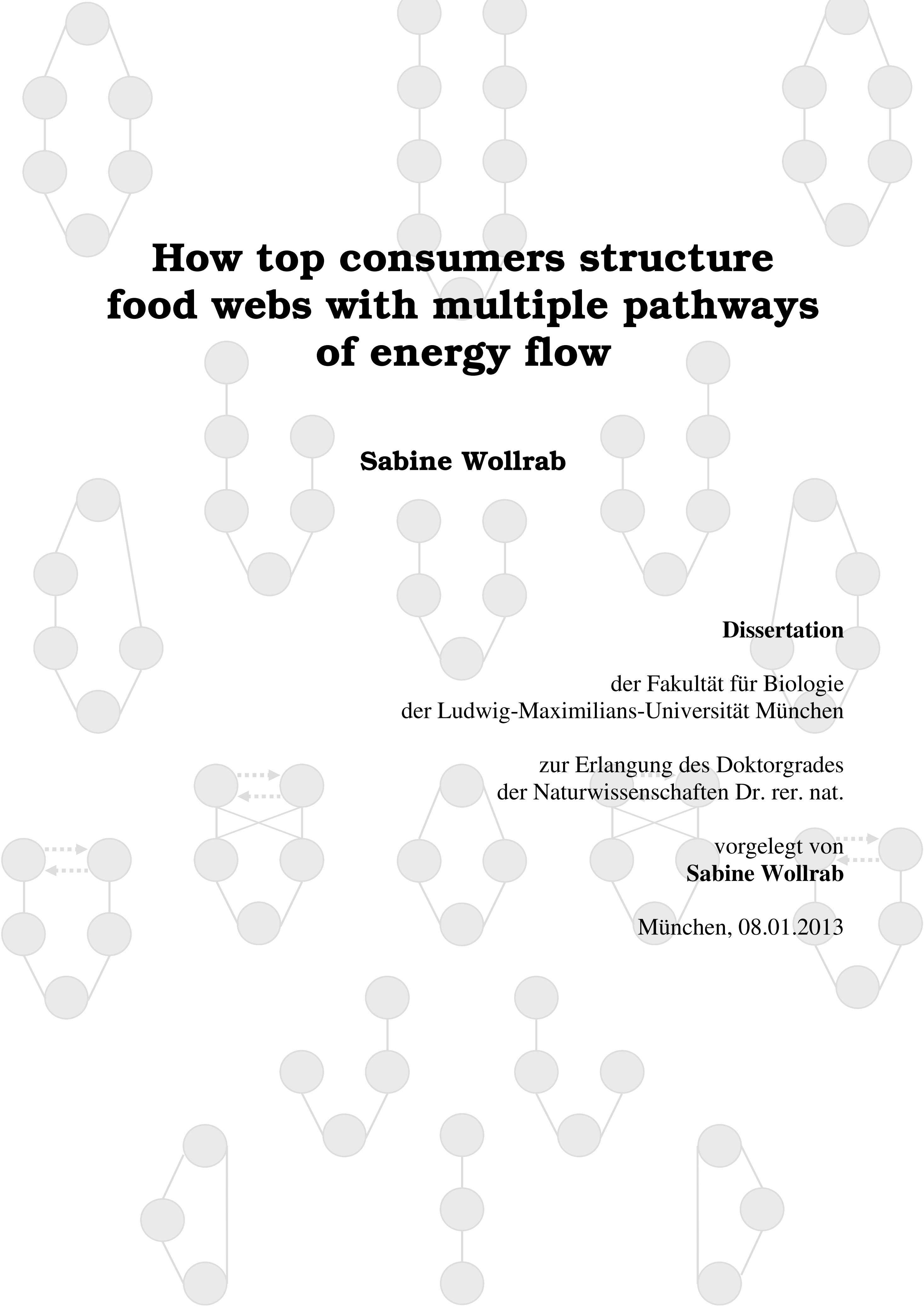

How top consumers structure food webs with multiple pathways of energy flow

Sabine Wollrab

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Sabine Wollrab

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To my family

Contents

Summary

Natural food webs are highly complex systems, however, this complexity arises from simple consumer-resource interactions. Feeding interactions not only determine food web structure but constitute the building blocks of the pathways of energy flow to higher trophic levels. Our understanding of how topological web properties determine these flows and the resulting community dynamics is still very fragmentary and limited to simple structures such as linear food chains and a few basic food web modules consisting of only 3-4 species. Nevertheless, forecasting community effects of external forcing through, for example, human induced stressors or climatic change, requires good knowledge of how bottom-up and top-down forcing will propagate through a given web. Empirical evidence suggests that apex predators take on a central role in this context.

In ***chapter 1*** of my thesis I take the approach of reducing the complexity of real food webs by assuming that its constituent species can be lumped into functional groups belonging to one of two alternative pathways of energy flow. The resulting webs consist of two food chains emerging from a shared limiting resource (e.g. a mineral nutrient) which may or may not be reconnected at the top through a generalist apex predator. Exploring dynamical models of a suite of 12 increasingly complex webs, I find that their equilibrium responses to nutrient enrichment and harvesting of apex predators are determined by only two easily measurable topological properties: the lengths of the component food chains (odd-odd, odd-even, or even-even) and presence vs. absence of a generalist apex consumer reconnecting the two pathways (yielding looped vs. branched webs). Many results generalize to other looped or branched web structures and the model can be easily adapted to include a detrital pathway. I therefore propose that models with alternative energy pathways may serve both ecosystem and community ecologists as a useful conceptual framework for the future.

The food web models explored in chapter 1 assume that a single variable per species - population number or biomass – is sufficient to fully describe species interactions in a food web. In ***chapter 2*** I relax this assumption and consider the common situation where individual consumers undergo substantial ontogenetic development, which often comes along with more or less pronounced ontogenetic diet shifts. Specifically, I theoretically explore the consequences of a diet shift from juvenile to adult predator stages for coexistence of two prey that compete for a single limiting resource. I find that stage structure in the predator population can create an ‘emergent’ competition-predation trade-off between prey, where food limitation in the predator stage feeding on the superior competitor creates a bottleneck in that stage, which enhances predation on the superior competitor and relaxes predation on the inferior competitor. Compared to a situation where juveniles and adults have identical diets, pronounced diet shifts therefore greatly enlarge the range of prey coexistence along a gradient of resource enrichment. With diet shifts, however, coexistence usually occurs as one of two alternative states and, once lost, may not be easily restored. Importantly, only a rather minor ontogenetic diet shift is necessary to produce the described patterns. My results are therefore an important generalization of existing theory on predator-mediated coexistence - which has so far ignored ontogenetic diet shifts.

The food web models explored in chapter 1 assume that the feeding rates of all consumers are either linear or saturating (= ‘type 2 response’) functions of food/resource density. Generalist top consumers feeding on prey from two food chains may, however, show more complex and flexible feeding behaviour. In particular, they may exhibit ‘switching’, i.e. feed disproportionally on the relatively more abundant prey (= ‘type 3 response’). In ***chapter 3*** I investigate the influence of such switching behaviour in a top consumer (a copepod) on the dynamics of the perhaps most widespread oceanic plankton community. In this food web two differently sized classes of primary producers (nano- and micro-phytoplankton) compete for a limiting nutrient and give rise to alternative energy pathways, one from nano-phytoplankton over ciliates to copepods, and the other from micro-phytoplankton directly to copepods. I numerically investigate system dynamics under various combinations of nutrient enrichment and top consumer (copepod) mortality under alternative assumptions on the copepod functional response (type 2 vs. type 3). I show that switching by the top consumer significantly enhances the area of stable coexistence compared to a type 2 response, but can also give rise to alternative community response patterns along the enrichment gradient and to bistability between alternative coexistence states. The results highlight the critical influence of the feeding behaviour of top consumers on system dynamics, which has important implications for marine plankton communities and the coupling between marine micro- and macrofauna.

General Introduction

Food web – a definition

The process of energy gain and loss is vital for all organisms. Energy is gained through consumption or resource acquisition (through primary production) and transformed into own biomass, and it is lost through respiration or by being consumed. Hence feeding interactions are the major structuring force in communities. A food web reflects this structure "*as a network of consumer–resource interactions among a group of organisms, populations or aggregate trophic units*" (Winemiller & Polis 1996). Food webs may differ in resolution by displaying feeding interactions for species, entire trophic levels, or in terms of functional groups (species that share the same resources and consumers).

While the structure of a food web is determined by the interactions among its constituent populations (May 1973, Rooney et al. 2008), population dynamics are in turn influenced by the structure of the food web (DeAngelis 1992). This implies that the community response cannot only be predicted by the properties of its constituent parts, but has to be investigated dynamically.

Conceptual background

The origins of food web theory date back to the beginning of the 20th century and is strongly based on insights from Elton (1927) and Lindeman (1942). Elton who introduced the community perspective to ecology, drew attention to the interrelation of abundance patterns between different trophic levels. The observation that high numbers of (small) prey are needed to sustain a single (larger) consumer is expressed in the 'Eltonian pyramid', where the total number of individuals decreases with increasing trophic level. Lindeman explained this observation on an energetic basis, i.e. in terms of biomass being a measure of energy content. Lindeman argued that, following the second law of thermodynamics, energy is lost at every transition to the next higher trophic level, which leads to a decrease in available energy towards higher trophic levels.

The energetic approach led to the prevalent view that communities are strongly bottom-up controlled, with the abundance of higher trophic levels being ultimately determined by available plant tissue and hence primary production. This view was contested by Hairston, Smith and Slobodkin (1960) in their seminal paper. These authors argued that, given the surplus of green plant biomass in natural communities, grazers seem not to be limited by food, but are rather under strong top-down control by their consumers, which releases plants from grazing pressure. While the so called ‘green world hypothesis’ was strongly debated in the following decades (Murdoch 1966, Polis & Strong 1996), it gave rise to a more conceptual thinking in terms of trophic dynamics and introduced the idea of trophic cascades.

Food chain theory

Based on the modelling approach by Lotka (1925) and Volterra (1926), who were the first to study population dynamics with the help of differential equations, Rosenzweig and MacArthur (1963) related the “green world hypothesis” to mathematical reasoning. Rosenzweig and MacArthur investigated general properties of predator-prey relationships and developed a theoretical basis for concepts such as predator control and primary productivity (Rosenzweig & MacArthur 1963, Rosenzweig 1971, reviewed in Fretwell 1987). It took another 15 years until Fretwell (1977) and Oksanen et al. (1981) developed a general framework for bottom-up and top-down control in food chains with more than three trophic levels.

Food chain theory predicts an alternating pattern of bottom-up versus top-down control from the top trophic level to the bottom (Fretwell 1977). Top consumers are assumed to be only limited by food supply and thereby control their prey (the sub-terminal species along the food chain), which in turn releases the prey of the sub-terminal species from predation pressure. This pattern then repeats itself alternatingly down the food chain. Concordantly, in each food chain the top trophic level and all levels in even distance from the top are bottom-up controlled (i.e. their equilibrium abundance/biomass increases with enrichment of the primary producers), whereas all trophic levels in odd distance to the top are top-down controlled (i.e. are kept at a constant level unaffected by enrichment) (Fig. 1). Furthermore, Oksanen et al. (1981) predicted a lengthening of the food chain with increasing enrichment, i.e. successful establishment of a next higher trophic level requires sufficient productivity at the base of the food chain (Fig. 1).

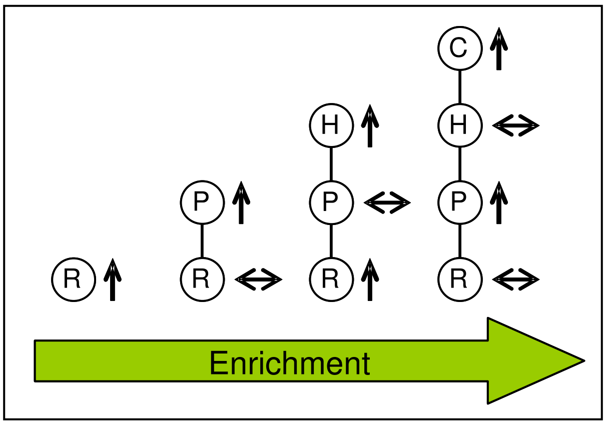

Fig. 1 Assembly sequence of successive trophic levels along an enrichment gradient with R-Resource, P-Primary producer, H-Herbivore, C-Carnivore. Arrows next to circles indicate the equilibrium response of the corresponding trophic level to enrichment, indicating either increase (upward arrows) or no change (horizontal arrows).

Food web theory

While food chain theory has given much insight into the consequences of trophic linkages, the study of many other central trophic interactions requires the incorporation of parallel pathways of energy flow. Food web modules consisting of only a few interacting species have been extensively used to explore the dynamical consequences of central ecological interactions (defined in Fig. 2) such as resource competition, shared ('apparent') predation, intraguild predation, and their interplay.

In the context of food webs with purely exploitative interactions, competition is always an indirect effect mediated through at least one intermediate compartment (sensu Abrams et al. 1996). Therefore, competition can be either mediated through a basal resource, referred to as 'exploitative competition' (Fig. 2a), or through a shared predator, referred to as 'apparent competition' (Fig. 2b).

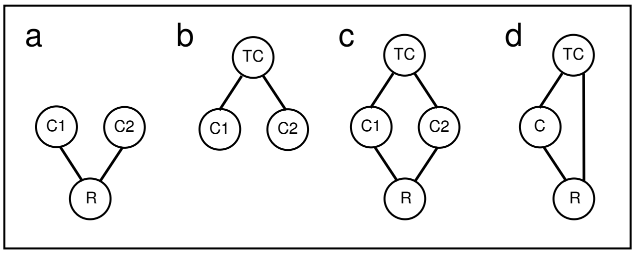

Fig. 2. Food web modules illustrating basic ecological relationships: a) exploitative competition, two consumer species (C1, C2) sharing a common resource (R), b) apparent competition, two consumer species sharing a common predator (TC) c) diamond module, a combination of modules a and b, d) intraguild-predation, a top consumer (TC) competing with its prey (C) for a shared resource (R).

With pure exploitative competition for a single limiting resource stable coexistence between competitors is not possible. The superior resource competitor, being able to persist at the lowest resource levels (R*), will always exclude the inferior one by suppressing resource levels below the minimum requirements of its competitor ('R*-rule', Tilman 1980). Similarly, with pure apparent competition the species, which can sustain the highest predator levels P*, and thus the highest predation pressure ('P*-rule', Holt et al. 1994), will exclude all more vulnerable prey (Holt et al. 1994). In contrast, if the resource and apparent competition modules are combined, two prey species sharing a common predator and a common limiting resource, the interaction of both processes can enable coexistence (Fig. 2c). Due to its shape, the corresponding food web module is referred to as 'diamond' web. A necessary condition for coexistence in the diamond web is that both competitors face an intrinsic competition-predation trade-off, i.e. the superior resource competitor is also more vulnerable to predation.

Through a gradual shift in competitive advantage from the superior resource competitor at low resource enrichment levels towards the less vulnerable competitor at high enrichment levels, coexistence becomes possible over a range of intermediate enrichment levels (Holt et al. 1994, Leibold 1996). Insights from the 'diamond' module have been very influential on both empirical and theoretical studies of predator mediated coexistence (reviewed in Chase et al. 2002).

Another important and ubiquitous trophic interaction is omnivory, i.e. the feeding on resources/prey from more than one trophic level (Polis & Strong 1996, McCann & Hastings 1997). Omnivory introduces links between non-adjacent trophic levels, resulting in a reticulate food web structure (Polis & Strong 1996). The smallest reticulate food web with omnivory is the intraguild predation module (IGP) consisting of an intraguild predator being involved in competition for a shared resource with its intraguild prey. A necessary condition for coexistence in the IGP module is that the intraguild prey is the superior resource competitor, which implies that it can persist with the resource alone at low levels of resource enrichment; stable coexistence of intraguild predator and prey may then be possible at intermediate levels of enrichment, whereas the intraguild prey is often excluded at high levels of enrichment (Holt & Polis 1997, Diehl & Feißel 2000). Within the range of stable coexistence the dominant interaction shifts from resource competition between intraguild prey and predator to apparent competition between resource and intraguild prey along an enrichment gradient. This shift is accompanied by a decrease in the intraguild prey and an increase in the intraguild predator, which leads to the exclusion of the intraguild prey at higher enrichment levels.

The intraguild predation web does not allow a clear comparison with trophic cascade theory, because the trophic level of the intraguild predator is at a non-integer trophic level above the trophic level of the intraguild prey. This holds true for omnivores in general and was one major criticism concerning the applicability of trophic cascade theory to real ecosystems (Polis & Strong 1996).

The above examples already highlight the potential for indirect effects mediated through multiple, parallel energy pathways to shape community dynamics and suggest a complex interplay with external forcing such as the availability of production limiting nutrients. Several extensions of the above food web modules including more trophic levels and more links between them, have been explored (e.g. Leibold 1996, Grover 1997, Abrams 1993, Hulot et al. 2000, Hulot & Loreau 2006). Still, a comprehensive framework for the prediction of bottom-up and top-down responses in food webs with alternative energy pathways, similar to the one established for simple, linear food chains (Fretwell 1977, Oksanen et al. 1981), is so far missing. Such a framework will be developed in chapter 1.

Ontogenetic diet shifts

Ontogenetic development is a fundamental life history process describing the development of an individual from birth to maturation. There are major differences between the pre- and post-maturation phase concerning energy allocation in individuals. While individuals will invest all their net biomass production into somatic growth before maturation, after maturity they will invest a large fraction of (and, in some species, all) net biomass production into new offspring. This implies that maturation as well as reproduction are food-dependent processes. Most species undergo a significant increase in body size from size at birth to size at maturation, which will often be accompanied by a shift in optimal prey size (Werner 1988, Hairston & Hairston 1993, Warren 1990, Warren & Lawton 1987, Rudolf & Lafferty 2011).

In the context of food webs ontogeny splits a population node into at least two stage-specific nodes (juveniles and adults), which are linked through maturation and reproduction. These stage-specific nodes may differ in their feeding links to both potential prey and potential predators. In spite of its prevalence in nature, ontogeny has been largely ignored by food web theory in general. Only recently the importance of ontogenetic development and corresponding feedbacks on community patterns have started to become increasingly recognized (see review by Miller & Rudolf 2011 and references therein).

Recent dynamical models of stage-structured populations with food dependent maturation and reproduction rates predict that population biomass accumulates in the most food-limited stage through unbalanced recruitment between the two stages (either high maturation and low reproduction rate or vice versa, dependent on which stage is more strongly food limited), forming a developmental bottleneck (De Roos et al. 2007). A population characterized by dominance of juveniles, and correspondingly high reproduction but low maturation rates, is called maturation-regulated (Fig. 3a), while in the opposite case it is reproduction-regulated (Fig. 3b) (De Roos et al. 2007). Irrespective of the type of regulation, the occurrence of a bottleneck stage may lead to counterintuitive responses like the increase of biomass in the alternative stage with increasing stage-specific or unspecific mortality. This overcompensation, i.e. an increase in biomass in response to increased mortality, results from relaxed resource competition within the bottleneck stage (De Roos et al. 2007). This feedback mechanism between stages has important implications for the interaction with other species like predators or competitors, where the interplay of internal (population) and external (community) feedbacks increases the range of possible indirect effects.

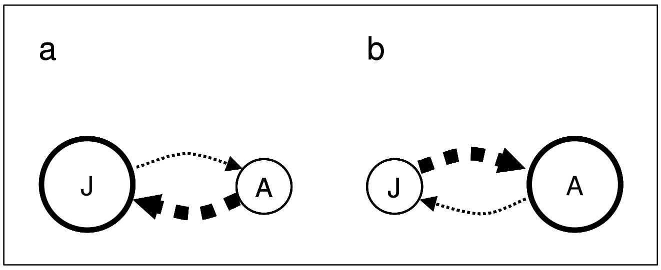

Fig. 3. Panel a and b show a stage structured population with a juvenile (J) and an adult (A) stage being either maturation-regulated with dominance of the juvenile stage (panel a), or reproduction regulated with dominance of the adult stage (panel b). Arrows from adults to juveniles represent reproduction, whereas arrows from juveniles to adults represent maturation, respectively. In panel a and b, the thickness of the arrows corresponds to the relative dominance of the corresponding rates.

For example, stage-specific predators may facilitate themselves by shifting the population structure of their prey towards a higher abundance of the stage they are feeding on. In doing so they take advantage of an overcompensatory response of their prey to increased mortality (i.e. harvesting by predators), which has been termed an emergent Allee effect (De Roos & Persson 2002). In contrast, if the stage-specific predator is absent, prey population structure may in fact inhibit its invasion, when strong density-dependent competition in the bottleneck stage of the prey strongly limits recruitment to the stage that is consumed by the predator (De Roos & Persson 2002).

Concerning exploitative competition for two limiting resources, stage-structure with food dependent maturation and reproduction has the potential to create niche partitioning between two otherwise identical consumer populations (Schellekens et al. 2010). This contrasts with predictions for unstructured populations, where coexistence of two species on two limiting resources needs a trade-off in resource use efficiency for the two resources (Tilman 1982).

Stage-structure also sheds new light on omnivory. Many species assigned to be omnivores at the population level are in fact life-history omnivores (Pimm & Rice 1987) that feed on different resources during different life stages. In the intraguild predation module this can be expressed by assuming a stage-structured predator where the juvenile stage is involved in resource competition with the prey of the adult stage (Fig. 4a). Investigations of this module showed that coexistence of the intraguild predator with the intraguild prey may be enhanced if one predator stage depends exclusively on the intraguild prey (Fig. 4a; Abrams 2011, Hin et al. 2011). In contrast, if the structured population can be sustained on the resource alone (Fig.

4b), coexistence may in fact be inhibited compared to the unstructured case (Van de Wolfshaar et al. 2006).

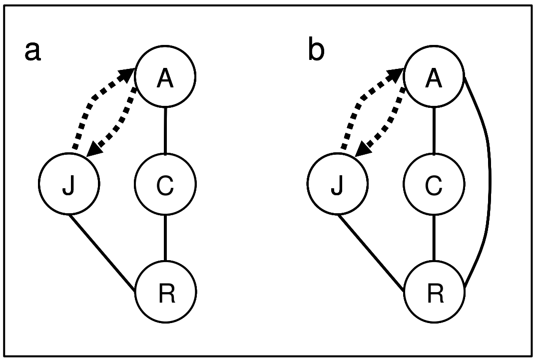

Fig. 4. Panel a and b show a life-history omnivore with juveniles competing with an unstructured consumer species (C) for a shared resource (R) and adults either feeding exclusively on C (panel a) or additionally on R (panel b). Bold dotted arrows indicate maturation and reproduction between juvenile and adult stages, respectively. Other connections represent feeding links.

Finally, while diet shifts may be beneficial to an individual consumer in a diverse community, it may also impose a higher risk of population extinction due to loss of stage-specific prey species compared to an unstructured generalist (Rudolf & Lafferty 2011).

Communities with stage-structured populations are notoriously prone to exhibiting alternative states, which are characterized by contrasting dominance patterns within the structured population (Schreiber & Rudolf 2008*,* Guill 2009). Once reached, these alternative states may be irreversible in the absence of severe disturbances due to positive feedbacks such as the one leading to the emergent Allee effect. A proposed, prominent real-world example for the relevance of the described feedback mechanisms is the lack of recovery of commercially overexploited cod populations after their collapses in the North West Atlantic and the Baltic Sea in spite of fishing moratoria (see references in Van Leeuwen et al. 2008). Theoretical investigations of this specific system propose that cod, if present, shifts the size-distribution of its prey in a favourable way, while the collapse of cod has led to a shift in the size-structure of its prey that inhibits cod recruitment (De Roos & Persson 2002, Van Leeuwen et al. 2008).

Due to the prevalence of ontogenetic diet shifts in nature, it is important to gain general insight into its potential effects on community dynamics and how they may arise through the interplay of stage-specific and community feedbacks. But the development of a synthetic theory of the influence of stage-structure on community dynamics is still in its infancy. For example, while predator-mediated coexistence of resource competitors is a conceptual cornerstone of ecology, the potential impact of stage-specific predation by an ontogenetic diet shifter on this phenomenon has not been investigated. Consequently, a variant of the diamond web with a stage-structured top consumer will be investigated in chapter 2.

Characterisation of feeding relationships – the functional response

While food web structure is determined by the shear abundance of feeding relationships, food web dynamics are strongly correlated to the dynamic properties of the corresponding feeding interactions. Consumption by a predator will most generally be dependent on prey density. The relationship between per capita consumption of a predator and prey density is described by the functional response. There are three main types of functional response curves: linear type 1, downward concave type 2 and sigmoid type 3 (Holling 1959, 65, Fig. 4a-c). In the following I focus on the characteristics of a type 2 versus type 3 functional response, since they are most relevant to a broad class of consumer species (Jeschke et al. 2004). Moreover, empirical data often do not allow for a clear distinction between these two types, because the shape of the functional response is often very sensitive to feeding rates at very low prey densities, where data are rarely collected.

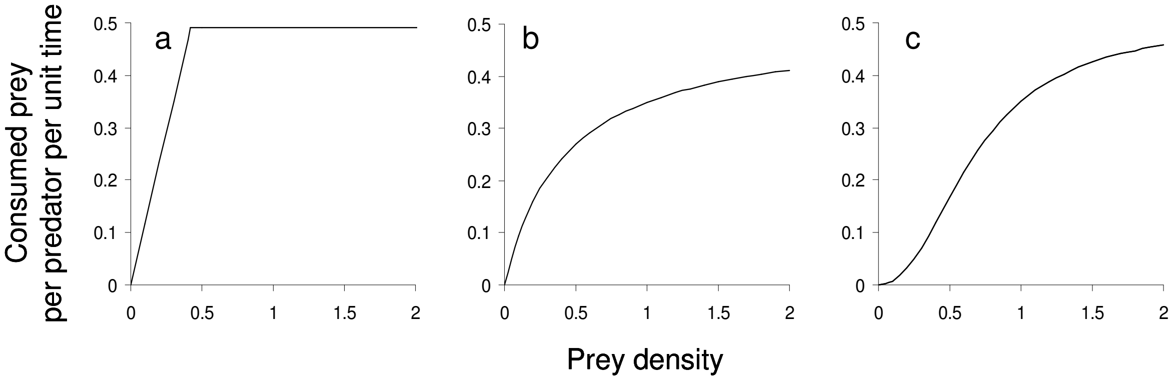

Fig. 4. Relationship between consumed prey by a single predator per unit time and prey density for (a) type 1, (b) type 2, (c) type 3 functional responses.

Both response types can be characterized by an attack rate/ searching efficiency (an area or volume that can be searched for and cleared of prey per unit time in the absence of handling) and a handling time (the time a predator needs to 'handle' its prey before searching for new prey) (Holling 1959, Murdoch & Oaten 1975). The handling time sets an upper limit to maximum ingestion rate at high prey densities. While a type 2 functional response assumes a constant attack rate, for a type 3 functional response the attack rate increases with prey density (Hassell et al. 1977, Real 1979). The latter is assumed to be typical for predators that are capable of some kind of learning process, which increases either their motivation to search and/or their searching efficiency/ attack rate through various behavioural mechanisms (Tinbergen 1960, Krebs 1974, Real 1977, Real 1979, Murdoch & Oaten 1975). This difference between both functional response types has important implications for the stability properties of consumer-resource dynamics.

A predator with a type 2 functional response has a strongly destabilizing influence on predator-prey dynamics, because per capita mortality of prey decreases with prey density, which allows prey to periodically escape predator control and favours the expression of transient or sustained predator-prey oscillations (Murdoch et al. 2003). In contrast, a type 3 functional response initially leads to a steep increase of per capita prey mortality with increasing prey density, which has a strong stabilizing influence (Oaten & Murdoch 1975). Furthermore, in the presence of multiple prey a predator with a type 2 functional response will feed on different prey species in proportion to their relative frequencies (Gentleman et al. 2003), whereas a predator with a type 3 functional response will feed disproportionately more on the more abundant prey, a response that has been termed switching (Murdoch 1969). A switching predator may therefore enhance coexistence by enabling prey to recover when rare, while exerting strong predation control on the more abundant prey (Van Baalen et al. 2010). The latter implies that the functional response type not only affects system dynamics, but also community patterns such as the relative and absolute abundances of alternative prey species.

However, the vast majority of theoretical research on the functional response has focussed on its consequences for system stability. This was very much triggered by theoretical studies of May (1973), based on randomly assembled food webs and stability analysis of corresponding linear interaction matrices, indicating that complexity tends to lower stability in complex food webs. Many subsequent studies were concerned with resolving the apparent mismatch between this theoretical result and the observation of abundant, seemingly stable but complex, natural communities, and attempted so by introducing more realistic food web properties concerning both network topology and the character of feeding relationships (McCann & Hastings 1997, Post et al. 2000, Fussmann & Heber 2002, Kondoh 2003, 2006, Williams & Martinez 2004, Brose et al. 2006, Kartascheff et al. 2009). Within this larger research agenda it was also shown that even simple 3-level food chains can exhibit complex dynamic behaviour including chaos (Hastings & Powell 1991), highlighting that not complexity itself counteracts stability but a critical interplay of structural and functional properties (Pahl-Wostl 1997, Fussmann & Heber 2002, Post et al. 2000).

Much less effort has been spent on the implications of the functional response for community composition and community response to environmental forcing. Knowledge on this issue is still very much restricted to simple predator-prey relationships (Murdoch & Oaten 1975) or basic ecological relationships like apparent competition (Abrams 1990, Krivan &

Sikder 1999, Abrams & Matsuda 2004, Krivan & Eisner 2006) and intraguild predation (Krivan 2000, Krivan & Diehl 2005). Theoretical studies of multiple interacting species rarely consider alternative assumptions about the shapes of functional responses. The few existing examples suggest, however, that community patterns may differ strikingly dependent on these assumptions (Gismervik & Andersen 1997, Anderson et al. 2010). This is of considerable concern given that data often do not allow a clear empirical distinction between type 2 and type 3 functional responses, and that a modeller's choice of functional response is therefore frequently arbitrary. Furthermore, the shape of the functional response may be critically altered by the presence of alternative prey (Murdoch & Oaten 1975, Abrams 1990), making the interpretation of empirical data more difficult (Smout et al. 2010). The interplay of structural web properties and the functional response type of a multispecies predator will therefore be investigated in chapter 3, using the lower oceanic food web as an example.

The Scope of this Thesis

The central scientific question of my thesis is how structural food web properties determine bottom-up and top-down response patterns. My studies are all based on analytical and numerical analysis of dynamic equation systems. As indicated in the previous sections, knowledge about how food web topology determines community patterns is merely based on food chains or simple ecological interactions in webs with up to 4 interacting species. In ***chapter 1*** of my thesis I therefore systematically study the bottom-up and top-down response patterns of a suite of 12 increasingly complex webs consisting of a shared resource (limiting nutrient) at the base of each web from which two alternative food chains emerge, which may or may not be reconnected on top by a shared consumer. The constituent chains can be of the same or different length and include up to five trophic levels (counted from the resource to the top species). I investigate the equilibrium response of each web to bottom-up forcing through an increase of nutrient availability and top-down forcing through increased top consumer mortality by analyzing the equilibrium solution of the corresponding differential equation system. For the simplest case with linear food uptake terms, I directly investigate the analytic equilibrium solution for its dependency on relevant system parameters, i.e. total amount of nutrients in the system and top-consumer mortality. For the case of saturating functional responses (= a type 2 functional response), investigations are based on a combination of analytical and numerical investigations.

In ***chapter 2*** I relax the assumption of homogenous populations and consider ontogenetic development at the top consumer level of the ‘diamond’ web (one consumer with two alternative prey species competing for a shared resource). I investigate the role of an ontogenetic diet shift between a juvenile and an adult consumer stage for coexistence between competing prey (*P1* and *P2*). The degree of diet shift is defined by the parameter q_C, assuming an ontogenetic trade-off in relative foraging efficiencies of juvenile vs. adult consumers for the two prey species. Dependent on q_C I can investigate the whole range from no diet shift in the absence of differences in resource use between both stages, to a complete diet shift where each consumer stage is specialized on a different prey. Numerical investigations are based on a stage-structured biomass model with food-dependent maturation and reproduction rates for juvenile and adult consumer stage, respectively. I investigate the influence of the degree of ontogenetic diet shift on equilibrium dynamics of the diamond web and possible community states by systematically varying the degree of diet shift for various levels of resource enrichment.

In ***chapter 3*** I investigate the consequences of flexible (= type 3 response, ‘switching’) vs. non-flexible (= type 2 response) feeding behaviour of a generalist top consumer for system dynamics of the lower oceanic plankton food web. The food web consists of two differently sized classes of primary producers (nano- and micro-phytoplankton), which compete for a limiting nutrient and give rise to alternative energy pathways through size-selective feeding by ciliates and copepods. One pathway originates from nano-phytoplankton over ciliates to copepods, and the other from micro-phytoplankton directly to copepods. I numerically investigate the equilibrium dynamics of the corresponding differential equation system under various combinations of nutrient enrichment and top consumer (copepod) mortality under alternative assumptions on the copepod functional response (type 2 vs. type 3).

Chapter 1

Simple rules describe bottom-up and top-down control in food webs with alternative energy pathways

Abstract

Many human influences on the world's ecosystems have their largest direct impacts at either the top or the bottom of the food web. To predict their ecosystem-wide consequences we must understand how these impacts propagate. A long-standing, but so far elusive, problem in this endeavour is how to reduce food web complexity to a mathematically tractable, but empirically relevant system. Simplification to main energy channels linking primary producers to top consumers has been recently advocated. Following this approach, I propose a general framework for the analysis of bottom-up and top-down forcing of ecosystems by reducing food webs to two energy pathways originating from a limiting resource shared by competing guilds of primary producers (e.g. edible vs. defended plants). Exploring dynamical models of such webs I find that their equilibrium responses to nutrient enrichment and top consumer harvesting are determined by only two easily measurable topological properties: the lengths of the component food chains (odd-odd, odd-even, or even-even) and presence vs. absence of a generalist top consumer reconnecting the two pathways (yielding looped vs. branched webs). Many results generalize to other looped or branched web structures and the model can be easily adapted to include a detrital pathway.

Introduction

Many human influences on the world’s ecosystems have their largest direct impacts at either the top or the bottom of the food web. For example, hunting, fishing, habitat loss, and bioaccumulation of toxicants typically most strongly affect larger-bodied carnivores and apex predators (Connell 1990, Laliberte & Ripple 2004, Schipper et al. 2008, Lotze & Worm 2009), whereas land use changes, fertilization, and climate change most immediately impact primary producers (Asner et al. 1997, Behrenfeldt et al. 2006, Haberl et al. 2007). These direct impacts frequently cascade up and down the food chain (Chavez et al. 2003, Baum & Worm 2009, Beschta & Ripple 2009), the community-wide consequences sometimes being so pervasive that they result in regime shifts (Cury & Shannon 2004, Estes et al. 2011). Clearly, to predict the ecosystem-wide consequences of human impacts we must understand how their direct effects propagate through entire food webs. Consequently, better conceptual integration of the interplay of bottom-up and top-down forces within ecosystems has been called for in several areas of applied ecology, e.g. in fisheries, oceanography, and climate impact research (Frank et al. 2007, Cury et al. 2008, Walther 2010).

While substantial progress has been made in the description and theoretical exploration of complex food webs (Pascual & Dunne 2006, Bascompte 2010), food web theory has historically focussed on network properties such as intervality, connectance, and interaction strength, but has made few tangible contributions to questions concerning human impacts on ecosystem function (e.g. standing stocks and fluxes of biomass) (Memmott 2009). A critical issue in the exploration of the effects of bottom-up and top-down forces on ecosystems is how to reduce food web complexity to a mathematically tractable, but empirically relevant system (Yodzis 1998, Cury et al. 2008). The most simplifying approach lumps species into trophic levels, resulting in a single food chain describing the whole ecosystem (Hairston et al. 1960, Oksanen et al. 1981). While food chain theory has had some success in describing empirical patterns (e.g. Persson et al. 1992, Crete 1999, Aunapuu et al. 2008), it has long been criticized for its oversimplification of trophic complexity (Polis and Strong 1996, Leibold et al. 1997).

A pervasive issue in the critique of community-wide food chain theory has been the recognition that primary producers differ vastly in size, defendedness and nutritional quality for herbivores (Murdoch 1966). These differences frequently lead to compensatory biomass responses within the primary producer level when productivity or herbivore pressure changes (Leibold 1989, Grover 1994, Hillebrand et al. 2007). Primary producers differing in size, defendedness and nutritional quality do, in turn, often have their own, distinct suites of consumers. In many systems a size relationship between herbivores and their food is observed, the body mass of herbivores typically increasing with increasing producer size and defendedness and with decreasing producer quality (Armstrong 1994, Hillebrand et al. 2009, Olff et al. 2009). The resulting food chains originating from different types of primary producers represent parallel pathways of energy flow through an ecosystem. These energy pathways may remain entirely separated, but are frequently connected by consumers at higher trophic levels (Rooney et al. 2006, Pringle & Fox-Dobbs 2008, Olff et al. 2009).

Simplification of food webs to main energy channels linking producers to top consumers is a recently advocated approach in the analysis of ecosystem dynamics which, in the marine realm, has been termed end-to-end models (Fulton 2010, Shin et al. 2010). Contrary to food chain theory this approach can describe differential responses to bottom-up and top-down forcing along alternative food chains (Stibor et al. 2004), but keeps ecosystem models much more tractable than complex, full-scale food web descriptions. While a number of food web modules with multiple food chains have been explored with dynamic models (Abrams 1993, Grover 1997, Hulot & Loreau 2006), a comprehensive theoretical treatment of the effects of bottom-up and top-down forcing on food webs with alternative energy pathways is lacking.

In this paper I propose a general theoretical framework for such an analysis by reducing food web structure to two main energy pathways originating from distinct types of primary producers (e.g. edible vs. defended plants or plants in two different microhabitats). The primary producers are assumed to compete for limiting resources and to support separate food chains of varying length (up to the secondary carnivore level), which may or may not include a generalist top consumer reconnecting the chains. To explore the effects of bottom-up and top-down forcing on these food webs I analyze their equilibrium responses to changes in supply with a limiting plant resource and in mortality of a top consumer. I find that the response patterns depend on only two structural properties: the number of trophic levels in each food chain and the presence vs. absence of a generalist top consumer. Within my modelling framework, food web responses to bottom-up and top-down forcing can therefore be described by a surprisingly small set of rules. Many of the results extend to food webs where multiple pathways originate and reconnect elsewhere than at the producer and top consumer levels, and the model can be easily modified to describe food webs including a detritus-based pathway of energy flow.

Model structure

I explored patterns of biomass and energy flow in model food webs consisting of two distinct chains that are linked at the bottom through a shared limiting nutrient. Webs where the two chains are additionally linked at the top through a shared (= generalist) top consumer are referred to as ‘looped’ webs, webs lacking a shared top consumer are termed ‘branched’ webs (Fig. 1). Within each web food chains are labeled chain 1 and chain 2, respectively. Each chain i can contain up to five trophic levels: the shared limiting nutrient (R), a primary producer (P_i), a herbivore (H_i), a primary carnivore (C_i), and a secondary carnivore (Fig. 1). The top consumer in a chain is labeled TC_i in branched webs and TC in looped webs, regardless of its trophic level.

Each food web is modeled with differential equations describing the rates of change of its constituent populations. The rate of change of the biomass density Y_i of each intermediate species (a species that is both a consumer and a prey/resource) in chain i is described by

$$\frac{dY_i}{dt} = Y_i\left(e_{X_iY_i}A_{X_iY_i}X_i - m_{Y_i} - A_{Y_iZ_i}Z_i\right) \tag{1a}$$

where X_i is the density of the prey/resource of species Y_i and Z_i is the density of the predator of Y_i. Depending on food web topology P_i, H_i, and C_i take on the roles of prey (X_i), intermediate consumer (Y_i) or predator (Z_i) in different equations, whereas R and secondary carnivores only take on the roles of resource (X_i) and predator (Z_i), respectively. The term $e_{X_iY_i}A_{X_iY_i}X_i$ describes the specific growth rate of species Y_i and $A_{Y_iZ_i}Z_i$ its specific loss rate due to consumption by Z_i. The rate of change of a top consumer is described by

$$\frac{dTC_i}{dt} = TC_i\left(e_{X_iTC_i}A_{X_iTC_i}X_i - m_{TC_i}\right) \tag{1b}$$

in the case of a specialist top consumer feeding on a single prey/resource in chain i, and by

$$\frac{dTC}{dt} = TC\left(e_{X_1TC}A_{X_1TC}X_1 + e_{X_2TC}A_{X_2TC}X_2 - m_{TC}\right) \tag{1c}$$

in the case of a generalist predator feeding on prey/resources from both chains.

In all equations above, A_{JK} describes a type 2 functional response of consumer K feeding on prey/resource J. When consumer K feeds on a single prey/resource, A_{JK} takes the form

$$A_{JK} = \frac{a_{JK}}{1 + a_{JK}h_{JK}J} \tag{2a}$$

where J is the biomass density of the prey/resource. When consumer K is a generalist top consumer feeding on prey/resources from both chains, A_{JK} takes the form

$$A_{J_iK} = \frac{a_{J_iK}}{1 + a_{J_1K}h_{J_1K}J_1 + a_{J_2K}h_{J_2K}J_2}\,, \tag{2b}$$

where J_i stands for the prey/resource in chain i. Note that intermediate species take on the respective roles of consumer ($Y_i = K$) and prey ($Y_i = J_i$) in the left-most and right-most terms in the parenthesis of equation 1a.

In equations 1a-c e_{JK} is the conversion efficiency of consumed prey/resources J into consumers K (biomass per biomass), and m is the density-independent specific mortality rate (per time). In equations 2a and 2b h_{JK} is handling time of consumer K for prey/resources J (time*consumer biomass/prey biomass), and a_{JK} is attack rate (area searched per biomass of consumer K per time). Note that functional responses are linear when handling times are zero.

The nutrient shared by the two chains in a web is assumed to limit primary production. For simplicity, the biomasses of all other food web components are expressed in units of the nutrient. I assume constant nutrient-to-carbon stoichiometries for all species. Consequently, nutrient and energy (= carbon) flows up a food chain are proportional. In the text I therefore describe the transfer of carbon and nutrients up a food chain in energetic terms rather than in terms of the nutrient currency used in the equations. For convenience I assume that the system is closed for nutrients. All results apply, however, equally to systems with chemostat-like dynamics (results not shown), and likely for many other open systems provided that inputs and outputs have approached a long term balance (i.e. $dR_{tot}/dt \rightarrow 0$; Grover 1997). The total amount of nutrients R_{tot} in the system remains constant over time and is a measure of nutrient enrichment. Nutrients not assimilated into living biomass are available for primary production (assuming instant recycling of excreted and dead biomass). The density of free mineral nutrients R can therefore be calculated from the mass balance equations 3a (for branched webs) and 3b (for looped webs):

$$R = R_{tot} - \sum_i Y_i - \sum_i TC_i \tag{3a}$$

$$R = R_{tot} - \sum_i Y_i - TC\ . \tag{3b}$$

Food web analyses

To investigate bottom-up and top-down influences I created branched and looped webs with up to five trophic levels and studied the signs of the equilibrium biomass changes of all web components in response to enrichment (increasing R_{tot}) and altered top consumer mortality (increasing m_{TC} or m_{TC_i}). For a given web topology, it is possible to gain analytical insights into the relationships among equilibrium biomasses of its components and their relationships to enrichment and top consumer mortality based on constraints to the equilibrium solution (see Appendix A1.1). These constraints fully determine the responses of all components in a web when functional responses are linear (see Appendix A1.2), but usually not when functional responses are saturating. I therefore explored the responses of webs with type 2 functional responses numerically and checked the outcomes for consistency with analytical constraints (see Appendix A1.1, A1.3). When functional responses are linear it is also possible to solve for the equilibria and to calculate the derivatives of all equilibrium densities with respect to R_{tot} and m_{TC} or m_{TC_i} (see Appendix A1.2). These calculations were done in Matlab [Mathworks Inc., Natick, MA, USA]. Numerical calculations assuming saturating functional responses were performed in Matcont 2.4 (Dhooge et al. 2003, as a package for Matlab).

When functional responses are saturating, equilibria are frequently unstable. It is well known that equilibrium and time-averaged population sizes may show opposite responses to enrichment when systems undergo sustained oscillations (Abrams & Roth 1994, Abrams & Fung 2010). Also, oscillating populations often go through long periods of very low population size with high risk of stochastic extinction. I therefore only present responses of stable equilibria. Moreover, the patterns obtained with saturating functional responses are very similar to, and more easily understood from, the patterns obtained with linear functional responses. I therefore present the patterns for linear functional responses first and subsequently highlight the similarities and differences arising from saturating functional responses.

I labeled each web with a two-number code (e.g. 4-3) for the lengths of its constituent food chains. Chain length was calculated as the number of nodes from the shared nutrient to the (shared or unshared) top consumer. I investigated plausible combinations of food chains of length 2 to 5 (Fig. 1) and distinguished three types of webs: (i) ‘odd-even webs’ consisting of one chain of odd and one of even length (3-2, 4-3, 5-4), (ii) ‘even-even webs’ consisting of two even chains (4-4), and (iii) ‘odd-odd webs’ consisting of two odd chains (3-3, 5-3, 5-5). Feasibility of an equilibrium and responses to enrichment and top consumer mortality differ systematically between these three types of webs. To facilitate understanding of how trophic structure arises and how it affects dynamics I have arranged all webs in a possible sequence of community assembly along a gradient of nutrient enrichment, starting from a simple 2-level food chain (Fig. 1). Some alternative assembly possibilities exist (e.g. web 1o instead of 1c may arise from 1b), but do not affect responses of a given web to enrichment.

I did not analyze webs with more than five nodes per chain, because it seems implausible that consumers linking the two chains would only occur at the top of such long food chains. I also did not analyze webs where the chains differ in length by more than two trophic levels (e.g. 5-2). For linear functional responses, the behavior of any food web with either longer chains or greater differences in length between its two chains can, however, be easily inferred from the general rules derived below. When functional responses are saturating, the same is true for branched webs, whereas some looped webs show parameter dependent response patterns.

Responses to nutrient enrichment: linear functional responses

The responses to nutrient enrichment in branched and looped food webs can be most easily understood if I first briefly review the well-known responses of single food chains. The top consumer in a model food chain is always strictly food limited and controls its prey/resource at a fixed equilibrium density where food consumption exactly meets the top consumer’s requirements to offset mortality. Consequently, the top consumer’s prey and all other populations at an odd distance below the top consumer remain at constant density, whereas the top consumer itself and all populations at an even distance from it increase with enrichment (Fig. 1 a, b, o). With sufficient nutrient enrichment the top consumer may reach an equilibrium density that permits the invasion of a higher level top consumer, adding one trophic level to the food chain and reversing the population responses to further enrichment (Oksanen et al. 1981). Alternatively, a second producer with a higher requirement for the basal nutrient may invade the resident food chain. The latter requires that enrichment has increased the nutrient to the density required by the invader, which is only possible if the resident food chain is of odd length (e.g. Fig. 1 b to c).

Adding a generalist consumer to a 2-level chain (Fig. 1i) or a second producer to a 3-level chain (Fig. 1c) produces the simplest possible looped and branched webs, respectively. Once there are two chains in a web, the response to nutrient enrichment depends on whether the web is branched or looped and on the type of web (i.e. odd-odd, odd-even or even-even).

Branched webs

Branched odd-even webs. In branched webs top consumers of both chains always control the populations at odd distance below themselves at constant biomass. For branched odd-even webs this implies that the shared nutrient is controlled by the top consumer of the even chain, whereas the producer in the odd chain is controlled by the top consumer of the odd chain. Because neither the nutrient nor the producer in the odd chain responds to enrichment, the odd chain as a whole cannot respond; in contrast, the chain of even length responds as it would in the absence of a second chain (Fig. 1c, e, g). In other words, in a branched odd-even web the even chain controls the odd chain. Consequently, biomass always increases with enrichment in the even chain but remains constant in the odd chain.

Branched even-even webs. Grover (1997) showed that a stable branched web of two even chains is not feasible. In the assembly scenario of Fig. 1 this would require a transition from an odd-even to an even-even web through invasion of a new top consumer into the odd chain. However, since the top species in the odd chain of an odd-even web stays constant with enrichment (Fig. 1c, e, g) its density cannot increase to the threshold required for invasion of a new top consumer preying on it, thus preventing the assembly of a branched even-even web. More generally, stable coexistence of two even chains depending on a single basal resource is impossible, because it requires that both food chains in isolation control the resource at the exact same equilibrium density R^*. Analogous to classical resource competition (where the species with the lower R^* excludes its competitor) two even chains with different R^* values cannot coexist, a phenomenon that Grover (1997) termed ‘cascade competition’.

Branched odd-odd webs. Invasion of the even chain in a branched odd-even web becomes possible once its top consumer has sufficiently increased after enrichment, giving rise to a branched odd-odd web (sequence Fig. 1 c to d, e to f, g to h). The two odd chains in such a web respond to enrichment in the same way as they would in isolation (Fig. 1 d, f, h).

Looped webs

We have just seen in branched webs that top-down control along one chain can suppress bottom-up responses along the other chain. Linking chains additionally through a generalist top consumer creates an opportunity for apparent competition, where bottom-up effects from one chain translate into top-down effects along the other chain. Looped webs therefore show more complex responses to enrichment than do branched webs.

Looped even-even webs. An even-even topology is possible when a food web is looped. In the assembly sequence looped even-even webs arise from branched odd-odd webs. Both top species in a branched odd-odd web increase with enrichment, eventually allowing a food limited generalist top consumer to invade (transition Fig. 1d to l). Once established, looped even-even webs respond to nutrient enrichment as would each of the constituent food chains in isolation (Fig. 1l).

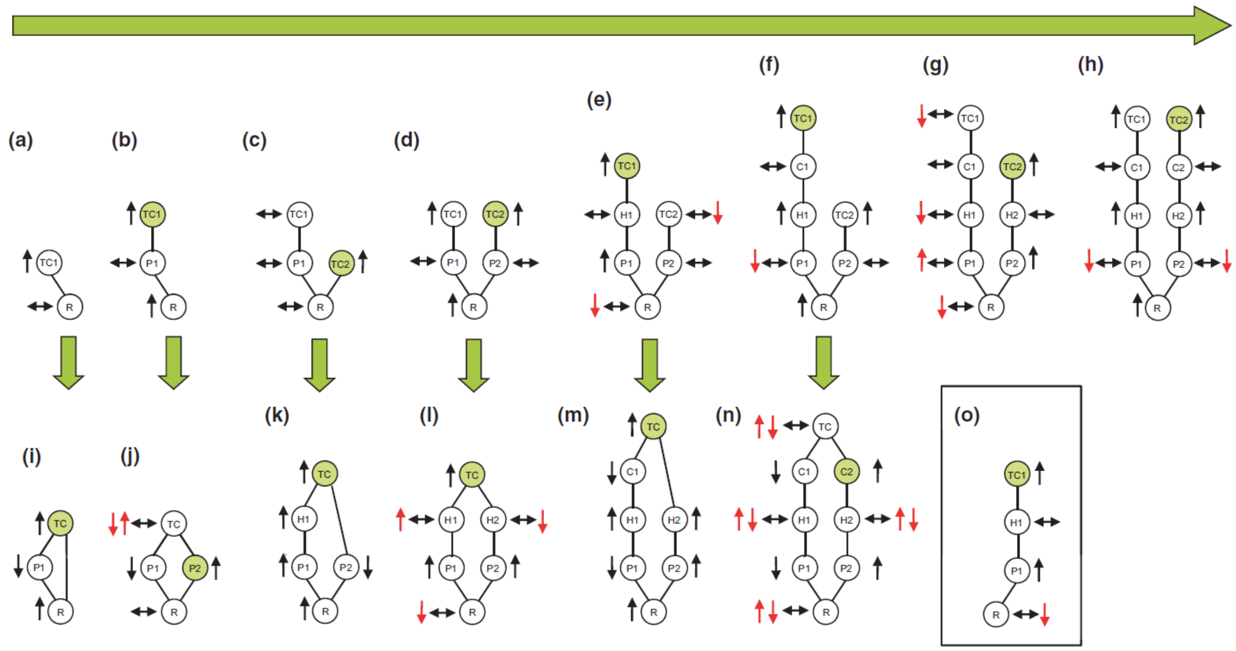

Fig. 1. Equilibrium responses to nutrient enrichment. Webs are arranged in possible assembly sequences along enrichment gradients (green arrows), the last invader being highlighted in green. Circles represent resource (R), producers (P_i), herbivores (H_i), and carnivores (C_i) in chain i (i = 1, 2) and specialist (TC_i) or generalist top consumers (TC). Black arrows next to circles indicate the direction of change in equilibrium biomass of the compartment in response to enrichment, with horizontal arrows indicating no change. Where saturating functional responses produce qualitatively different outcomes than linear functional responses, the former are shown with red arrows. Pairs of opposed arrows indicate that compartments either increase or decrease, the equilibrium responses of R^*, H_1^*, *and* H_2^* *in panel n being correlated. (a, b, o) 2-, 3-, 4-level food chains; (c-h) branched 3-2, 3-3, 4-3, 5-3, 5-4, 5-5 webs; (i-n) looped 3-2, 3-3, 4-3, 4-4, 5-4, 5-5 webs.*

Looped odd-odd webs. Because branched even-even webs are infeasible, looped odd-odd webs can only arise from branched odd-odd webs through invasion of a higher level consumer into one chain, which is immediately preyed upon by the resident top consumer of the other chain (Fig. 1b to j and f to n). In a looped odd-odd web the top consumer and all species at even distance below stay constant with enrichment, while species in odd distance from the top decrease along one chain and increase along the other (Fig. 1j, n). Total energy flow to the top remains thus constant with enrichment, while biomass accumulates in the chain with the lower transfer efficiency. The chain experiencing the biomass increase is always the one that was assembled last in the enrichment sequence (Fig. 1). With sufficient enrichment the decreasing prey of the top consumer will go extinct, the underlying mechanism being apparent competition. These patterns were first described for the simplest looped odd-odd web, the 3-3 web (Holt et al. 1994, Leibold 1996). Here I have shown that the patterns apply to looped odd-odd webs in general.

Looped odd-even webs. Looped odd-even webs show the least intuitive responses to enrichment: all species in the even chain increase; in contrast, in the odd chain species at even distance from the top also increase but species at odd distance decrease (Fig. 1i, k, m). In Appendix A1.2 I derive this pattern analytically. It can also be intuitively understood by comparing branched and looped webs of identical chain lengths. Enrichment of a branched web always increases energy flow up the even chain which, in turn, controls the resource and the odd chain at a constant level (Fig. 1c, e, g). Now, if the even chain's top consumer is also the top consumer of the odd chain, increased energy flow up the even chain increases predation pressure down the odd chain, reducing the biomass of species in odd distance from the top along the odd chain (compare Fig. 1c vs. i, e vs. k, and g vs. m by merging the top consumers of the branched chains into a single generalist top consumer). This will eventually lead to the extinction of the subterminal species in the odd chain, a theoretical result that is well established for the simplest looped odd-even web, an intraguild predation web (Fig. 1i; Diehl & Feissel 2000).

Responses to nutrient enrichment: type 2 functional responses

Again, I first consider single food chains. Food chains up to length three respond identically to enrichment whether functional responses are linear or saturating (Fig. 1a, b). Responses differ, however, for longer chains. Per capita mortality of a prey decreases with its own density when the functional response of its predator is saturating. This happens with enrichment to the third species from the top. In chains of length four or more, the third species from the top can therefore only be in equilibrium if the density of its food decreases with enrichment (Fig. 1o). While this has consequences for webs with longer chains, most enrichment responses of webs observed in the linear case are either conserved or accentuated when functional responses are saturating.

Branched webs

Branched even-even webs remain impossible with saturating functional responses because of 'cascade competition' between the two food chains (Grover 1997).

Branched odd-even webs. As in the linear case, enrichment increases biomass in the even chain but not in the odd chain, because the even chain controls the resource. In a 3-2 web enrichment responses are identical to the linear case (Fig. 1c, see Appendix A1.4). When the even chain is of length four, however, the resource decreases with enrichment. Consequently, the odd chain suffers from ‘de-richment’ and responds accordingly; i.e. the top consumer of the odd chain and all species at even distance from it decrease (Fig. 1e, g). In odd-even webs with one chain of length four, dominance of the even over the odd chain is therefore more pronounced than in the linear case; i.e. increased energy flow up the even chain is accompanied by decreased energy flow up the odd chain (Fig. 1e, g).

Branched odd-odd webs. As in the linear case both chains respond to enrichment as would the corresponding food chains in isolation (Fig. 1d, f, h). If one chain is of length five its producer decreases with enrichment; all other populations respond to enrichment as in the linear case (Fig. 1f, h).

Looped webs

Results for looped webs with saturating functional responses are based on numerical exploration backed up by analytical results (see Appendix A1.1, A1.3, A1.5, A1.6). Most response patterns from the linear case are conserved, but deviations occur in most compartments that remain constant in the linear case. For odd-even webs I only found examples where the response patterns of the linear system are fully conserved (Fig. 1i, k, m). Biomass constancy, observed for several members of linear webs, is, however, not a robust feature (Fig. 1j, l, n). With saturating functional responses I found constancy of a food web member only in the 3-3 web, where the basal resource remains constant (Fig. 1j, see Appendix A1.5). Generally, in odd-odd webs the top consumer may increase or decrease depending on parameter values, and so may all web members at even distance from the top in the looped 5-5 web (Fig. 1j, n). In the latter web the responses of the resource and the two herbivores are correlated (this follows from eqs. A1.1-3, A1.1-4 and A1.1-6, Appendix A1.1) and were also correlated with the top consumer in all my numerical runs with stable equilibria (Fig. 1 n).

Responses to top consumer mortality: linear functional responses

In any food chain with linear functional responses the top consumer always decreases with increasing own mortality (Fig. 2a, b, s). At equilibrium, this increase in the top consumer’s mortality must be balanced by an increase in the density of its prey, the effects of which cascade to the nutrient level. The nutrient therefore decreases with increasing top consumer mortality in an odd food chain (Fig. 2b), but increases in an even food chain (Fig. 2a, s). In webs consisting of two food chains, effects of increasing top consumer mortality then propagate through both chains, the exact responses depending on the type of web (branched or looped; odd-odd, odd-even, or even-even). In the case of branched odd-even webs I must also distinguish between cases where the top consumer of either the odd or the even chain experiences increased mortality. To more easily describe these responses I call a change in top consumer mortality a ‘manipulation’.

Common to all webs is that increasing top consumer mortality will eventually cause an extinction. Interestingly, however, it is not always the manipulated top consumer that dies out. Instead, the species going extinct is always the one that invaded last along the enrichment sequence (Fig. 2), owing to its more precarious energetic balance. This implies that the top consumer of an odd chain cannot go extinct in response to increasing own mortality, if the remaining community would form an ‘impossible’ branched even-even web. In such cases extinction always hits either the top consumer of the even chain (branched odd-even webs, Fig. 2c, f, j), or a subterminal consumer (looped odd-odd webs, Fig. 2n, r).

Branched webs

In a branched web, the (top-down) effects of top consumer mortality in one chain propagate via the shared nutrient up the other chain, with often counter-intuitive consequences. When the manipulated chain is even, increasing top consumer mortality translates into increased nutrient density and, thus, enriches the other chain. Total biomass therefore decreases in the manipulated chain and increases in the other chain, where the non-manipulated top consumer and every other population increases (Fig. 2d, g, k). In contrast, when the manipulated chain is odd, increasing its top consumer’s mortality translates into increased plant biomass in the manipulated chain. Plants in the manipulated odd chain then consume a larger fraction of the nutrient, thus ‘de-riching’ the other chain. Total biomass therefore decreases in the non-manipulated chain and increases in the manipulated chain (Fig. 2c, e, f, h, j, l). The manipulated top consumer of the odd chain itself decreases if both chains are of odd length. Seemingly paradoxically, however, the manipulated top consumer of the odd chain does not respond to its own mortality if the non-manipulated chain is even. In the latter case the non-manipulated even chain controls the nutrient - and all populations at even distance from the nutrient (including the manipulated top consumer) - at a constant level (Fig. 2c, f, j).

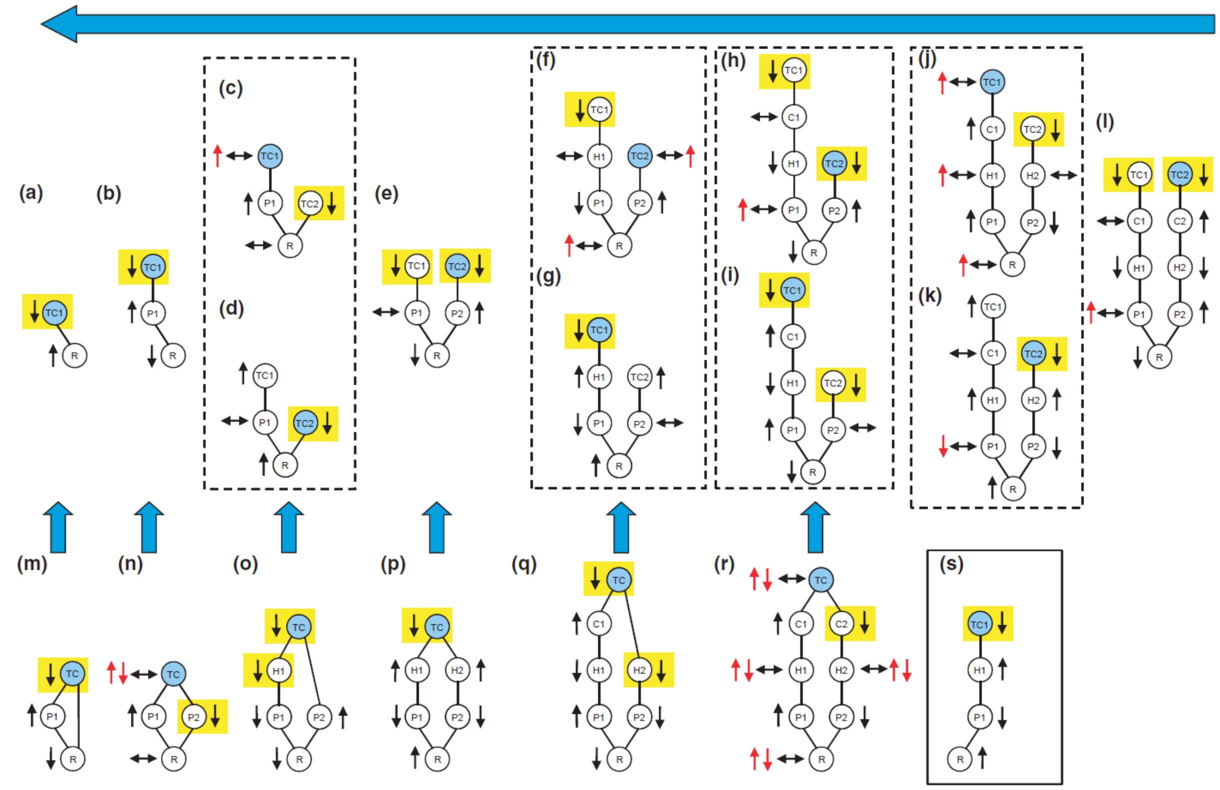

Fig. 2. Equilibrium responses to increased mortality of the top consumer highlighted in blue shading. Symbols and black and red arrows are defined as in fig. 1. The responses of R^*, H_1^*, *and* H_2^* *indicated by red arrows in panel r are correlated. Yellow background shading indicates species that may go extinct with sufficiently high top consumer mortality. Thick blue arrows point at webs resulting from such extinctions. When there are two possibilities for which species goes extinct, the outcome is shown that results in a reversal of the enrichment sequence of Fig. 1. This illustrates that, for a given community with fixed parameters, increasing its top consumer's mortality will reverse the enrichment assembly.*

Looped webs

In looped webs all populations that increase with enrichment decrease with increasing top consumer mortality and vice versa (Fig. 2 m-r). In looped odd-even webs the response pattern to increased top consumer mortality is therefore exactly opposite to the enrichment pattern (Fig. 2m, o, q). Populations that stay constant with enrichment remain, however, either constant (in looped odd-odd-webs, Fig. 2n, r) or increase (in looped even-even webs, Fig. 2p) with increasing top consumer mortality. These results were derived analytically (see Appendix A1.2), but can, for most food webs, be understood from three conditions: (i) with increasing top consumer mortality, at least one of its prey must increase to maintain top consumer mortality in balance with growth; (ii) at least one other population must decrease to maintain mass balance; (iii) populations at even distance from each other within a food chain must change in the same direction (otherwise the population between them is not in equilibrium).

Responses to top consumer mortality: type 2 functional responses

Again, most responses of webs observed in the linear case are preserved when functional responses are saturating. Deviations from the linear case occur largely in the same webs and links as the deviations in enrichment patterns and exclusively concern compartments that remain constant in the linear case (Fig. 2).

Branched webs

Identical to the linear case, increasing top consumer mortality in an even chain always enriches (increases nutrient flow into) the non-manipulated chain and hence decreases flow up the manipulated chain (Fig. 2d, g, k). Conversely, increasing top consumer mortality in an odd chain always 'de-riches' (decreases nutrient flow into) the non-manipulated chain and increases flow up the manipulated chain (Fig. 2c, e, f, h, j, l). Deviating from the linear case, in odd-even webs this increased flow causes an increase of *all* members of the manipulated odd chain including the nutrient and the top consumer; seemingly paradoxically, the top consumer of the odd chain thus increases in response to increased own mortality (Fig. 2c, f, j). While this increase with own mortality cannot go on indefinitely, in all numerical analyses the top consumer of the non-manipulated even chain went extinct before this threshold mortality was reached, reversing the enrichment assembly sequence and avoiding 'impossible' even-even webs (Fig. 2c, f, j). Also, with saturating functional responses, the fourth highest level in a non-manipulated chain responds non-intuitively to effects propagating from the other chain; i.e. it decreases with enrichment (Fig. 2k) and increases with 'de-richment' (Figs. 2f, h, l).

Looped webs

Again, results for looped webs are based on numerical investigations backed up by analytical results. The response patterns of looped odd-even and looped even-even webs were always preserved under the assumption of saturating functional responses (Fig. 2 m, o-q). Odd-odd webs deviate in that compartments that stay constant in the linear case may either increase or decrease with top consumer mortality when functional responses are saturating (Fig. 2n, r). As with enrichment, constancy only holds for the resource in looped 3-3 webs, whereas in looped 5-5 webs all compartments at even distance to the top were positively correlated to the mortality response of the top consumer. The responses of these compartments to increased mortality need, however, not always be reversed to their enrichment responses (see Appendix A1.5).

Generalization to extended food web topologies

While my analysis has so far focussed on parallel energy pathways originating at the primary producer level, my results generalize to food webs where the branching occurs at higher trophic levels. I illustrate this with the looped 4-3 web (Fig. 3a-d), but the results apply to any branched or looped web with a single branching. When one or more linearly linked compartments are present below a branching node, enrichment at the base of this lower, linear structure will always propagate up to the branching node. Thus, the upper part of the web responds to enrichment at the base exactly as it would if the branching node was directly enriched (compare Figs. 3a-b to 1k). Similarly, links below a branching node do not influence how top-down effects propagate through the branched or looped upper parts of a web. Consequently, responses of that upper part of the web to top consumer mortality are also not altered (compare Figs. 3c-d to Fig. 2o).

It is also straightforward to see how my results extend to looped webs where the chains reconnect below the apex predator level. The response of the looped module to enrichment and top consumer mortality then depends on whether the chain beginning at (and including) the reconnecting node is of length two or three. I have only explored this for linear functional responses and illustrate the results again with the looped 4-3 module (Fig. 3e-h). Generally, a subterminal population is always held constant by a specialist top consumer in an enrichment situation, but must increase in response to increased top consumer mortality. For the reconnecting node this implies constant (Fig. 3f) vs. increasing (Fig. 3h) per capita mortality, respectively, when the top chain has length three. The responses of a looped module to enrichment and top consumer mortality are then the same as for the looped module in isolation (Fig. 3f vs. 1k; Fig. 3h vs. 2o). In contrast, when the subterminal population is the reconnecting node (top chain has length two), responses of the looped module to top consumer mortality are opposite to the responses of a looped web in isolation (Fig. 3g vs. 2o). Moreover, apparent competition between the two food chains cannot occur. Their members therefore respond to enrichment as would a branched web lacking the reconnecting species altogether (compare Fig. 3e with 1c).

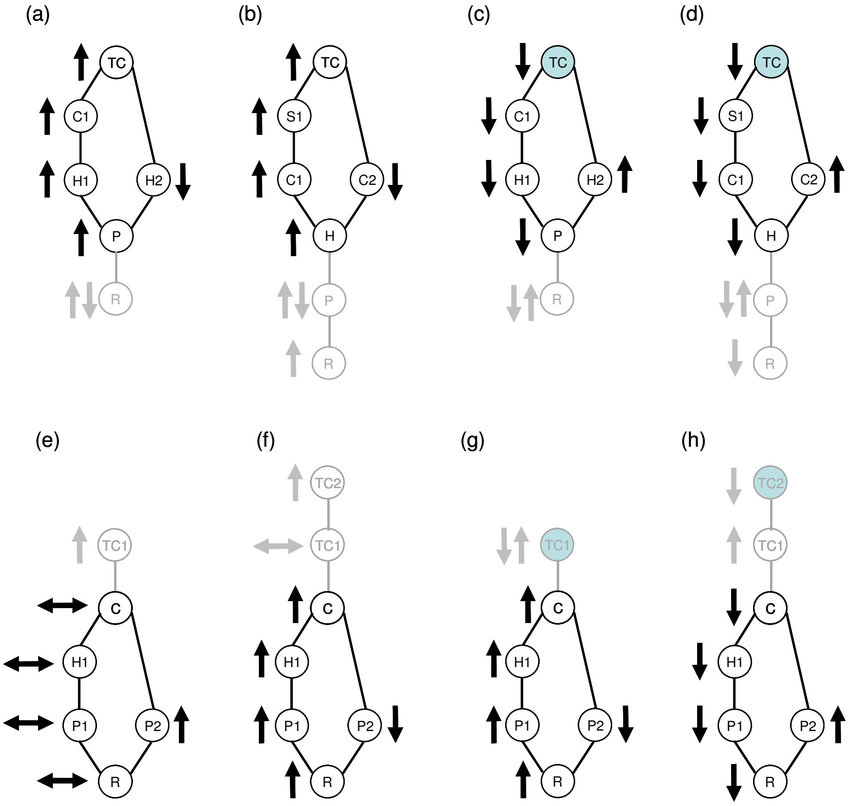

Fig. 3. Equilibrium responses to enrichment (a, b, e, f) and to increased top consumer mortality (c, d, g, h; top consumer highlighted in blue) of a looped 4-3 web module with one or two additional trophic levels below (a-d) or above (e-h). S_1 = secondary carnivore in chain 1; TC_1 = consumer one trophic level above the 4-3 module; TC_2 = consumer two trophic levels above the 4-3 module. Other symbols and arrows as in Fig. 1. Response patterns were derived analytically assuming linear functional responses. To focus on the looped 4-3 module other compartments are outlined in gray. Responses of some compartments outside the looped module are parameter dependent.

Discussion

I have theoretically explored bottom-up and top-down control in food webs with two alternative energy pathways. I propose that this relatively simple structure can serve as a useful, general abstraction of many real food webs, being representative of at least three common scenarios: (1) communities in which competing primary producers can be broadly lumped into edible and less edible categories which support different suites of herbivores (Armstrong 1994, Olff et al. 2009); (2) communities in which different types of primary producers occur in different (micro-)habitats that are sufficiently close in space for resource competition to occur among producers, e.g. benthic vs. pelagic lake habitats (Vadeboncoeur et al. 2002) or terrestrial canopy vs. understory habitats (Pringle & Fox-Dobbs 2008); (3) communities in which energy flow is dominated by a few species in alternative food chains, e.g. the ‘sardine’ vs. ‘anchovy’ pathways in coastal upwelling systems (Cury et al. 2008). My analyses can be easily extended to food webs where energy pathways branch at higher trophic levels or reconnect below the apex predator level. The modelling framework is therefore applicable to other food web topologies, including webs where parallel energy channels are based on living plants and on plant detritus, respectively (see below).

My analysis suggests that the presence of two alternative energy pathways affects food web responses to bottom-up and top-down forcing in easily predictable ways. Surprisingly few and simple rules govern the equilibrium responses of the investigated food webs, and only two pieces of information are needed to understand most of these responses: (i) Is the food web branched or looped? (ii) Are the component food chains (counted from the branching node) of odd or of even length? These two pieces of information fully determine the responses of all food web members when functional responses are linear, which is an appropriate approximation when small changes in equilibrium densities are investigated. When functional responses are saturating and equilibria are stable, the response patterns are very similar, with only a few deviations occurring in some populations that remain constant in the linear case (Fig. 1, 2). Note, however, that, when functional responses are far from saturation, predicted deviations from constancy would be weak and therefore difficult to distinguish from true constancy in empirical data. In summary, my analyses suggest that the equilibrium behaviour of food webs with two alternative energy pathways can be closely predicted from easily measured descriptors of food web topology.

Energy flow along odd versus even chains

A pervasive pattern emerging from my analysis is that energy flow along even chains has precedence over energy flow along odd chains. In branched odd-even webs top consumers of the odd chain remain constant or decrease with enrichment, while top consumers of the even chain always increase. This pattern is even more pronounced in looped odd-even webs, where all members of the even chain increase with enrichment, whereas at least one member of the odd chain decreases and eventually may go extinct. With respect to the simplest looped odd-even web, the intraguild predation web (Fig. 1i), a corollary of this finding is that the frequently predicted extinction of the intraguild prey with enrichment (Diehl & Feissel 2000, Mylius et al. 2001) is not the consequence of a direct, energetic shortcut to the top consumer (bypassing the longer 3-level chain). On the contrary, if the even chain in a looped odd-even web is longer than the odd chain (Fig. 1k), it is nevertheless a member of the (shorter) odd chain that may go extinct, highlighting the precedence of energy flow along even chains.

The primacy of energy flow along even chains appears to extend to food webs where energy pathways branch at higher trophic levels and/or reconnect below the apex predator level, as illustrated in Fig. 3. Importantly, odd vs. even chain length is defined starting from (and including) the branching node. This makes intuitive sense, because it is the branching node that transmits top-down effects between chains. Starting from the branching node, enrichment thus increases energy flow along pathways of length 4 (Fig. 3a, b, e) and 6 (Fig. 3f), respectively, whereas energy flow is constant (Fig. 3e) or decreases (Fig. 3a, b, f) along pathways of length 3 and 5.

Comparisons with food chain theory

The responses of food webs with alternative energy pathways to nutrient enrichment and top consumer mortality often deviate from predictions of classical food chain theory. The latter is particularly evident in looped odd-even webs, in which all trophic levels in the even chain increase with enrichment and decrease with increasing top consumer mortality. This is a remarkable phenomenon in models with purely prey-dependent functional responses. It suggests that, if dominant alternative pathways of energy flow in real food webs are frequently of odd vs. even length, one would not expect to observe community-wide trophic cascades (sensu Polis et al. 2000). More generally, it seems to be a rule that summed trophic level responses of food webs with one or more loops do not respond to enrichment in the way predicted for simple food chains (Fig. 1i-n; see also Abrams 1993, Hulot & Loreau 2006).

The propagation of effects through looped web structures may be relevant to a remarkable phenomenon described from many coastal upwelling areas, the regime shift between anchovy and sardine dominated food webs (Alheit & Niquen 2004, Barange et al. 2009). Available data suggest that the involved components can be described as a looped 5-5 web linking nutrients and top predators via a flagellate-small zooplankton-sardine chain and a diatom-large zooplankton-anchovy chain (van der Lingen et al. 2006). Scattered evidence indicates that periods of intensified upwelling (= nutrient enrichment) are accompanied by increased abundances of all members of the nutrient-diatom-large zooplankton-anchovy-top predator chain and by alternating changes along the other chain (flagellates decrease, small zooplankton increases, sardines decrease) (Verheye 2000, Taylor et al. 2008, Montecino & Lange 2009). While such an enrichment response is clearly compatible with a looped 5-5 web (Fig. 1n) other explanations have been proposed, including one involving mutual intraguild predation between anchovies and sardines (Irigoien & De Roos 2011). Importantly, both hypotheses assume a looped topology of competing food chains reconnected by consumers.

Also in branched webs deviations from food chain theory are commonplace. For example, the top consumer controlling the response of a branched web to enrichment need not be the top consumer of the longest food chain. If the odd chain in a branched odd-even web is longer than the even chain, the summed trophic level responses to enrichment will differ markedly from the predictions of food chain theory; i.e. the highest trophic level (and every second level below) will remain constant or even decrease rather than increase, and the second highest trophic level (and every second level below) will increase rather than remain constant (Fig. 1 c, g). These observations may lend rigor to the discussion of when a top trophic level should be considered 'functional' in the sense of exerting a regulating influence on a food web (Power 1992).

Indirect antagonisms and mutualisms

Vandermeer (1980) conjectured that herbivores in different food chains should be indirect mutualists and carnivores indirect antagonists, the interactions being mediated by resource competition between the respective food chains' primary producers. While apparent competition between chains precludes such regularities in looped webs, my study supports the conjecture for herbivores in branched webs, both of which usually respond to enrichment or top consumer mortality in the same direction (indicating mutualism). In contrast, however, carnivores in different chains of branched webs often respond in opposite or orthogonal directions, indicating antagonism or independence (Fig. 1d-h, 2e-l). A much clearer pattern in branched webs is instead that, independent of trophic level, top consumers of odd chains are indirect mutualists, and top consumers of even chains are indirect antagonists, of the other chain's top consumer. This frequently leads to counter-intuitive consequences of harvesting. For example, in branched webs harvested top consumers may increase while non-harvested top consumers in the other chain decrease, which cautions against harvesting as a straightforward management tool. In line with this Yodzis (1998) concluded from an analysis of the Benguela food web that harvesting of fish eating marine mammals may frequently reduce fisheries returns.

Empirical evidence of cascading effects, including counter-intuitive ones, from apex predators into other food chains is indeed accumulating (Kerfoot 1987, Ellis et al. 2011, Estes et al. 2011). For example, Anthony et al. (2008) reported that a sea otter decline on Aleutian islands was, unexpectedly, accompanied by increased bald eagle production. Sea otter declines are known to cascade to the dominant primary producers, kelp, via release of herbivorous sea urchins (Estes & Palmisan 1974). Anthony et al. therefore expected bald eagles to suffer from the sea otter decline, mediated through a decline in kelp forest habitat and associated prey fish production. However, the authors also observed a diet shift in bald eagles from fish to sea birds, suggesting an alternative scenario compatible with the response of a branched 3-2 web to increasing top consumer mortality in the even chain (Fig. 2d). Sea urchins are a food of several sea birds (Estes et al. 2009, Bustnes et al. 2010). Thus, the increase in sea urchins following the otter decline may have increased energy flow up the 3-linked urchin–sea bird-bald eagle chain.

Incorporation of detrital pathways

In many ecosystems a major fraction of primary production enters the food web as detritus rather than as living producer biomass (Hairston & Hairston 1993, Wetzel 1995, Cebrian 1999). A ‘green world’ view of trophic dynamics has therefore been criticized and it has been argued that prediction of bottom-up and top-down effects in real ecosystems requires consideration of detrital pathways (Polis & Strong 1996, Moore et al. 2004). I have deliberately studied a model of pure grazing chains, which makes the most general assumptions about interactions. Specifically, all interactions are reciprocal, i.e. energy flow between two compartments depends on the densities of both the resource and the consumer, whereas the link from plants to plant detritus is donor controlled. Topology, however, need not differ between grazing and detritus chains, and any food web including a grazing and a detritus chain (e.g. Fig. 4) has a ‘topological twin’ consisting of two grazing chains that branch off at the plant level (e.g. Fig. 3a). An obvious question is then whether the topological rules derived in this paper extend to food webs including a detrital pathway.

While a thorough exploration of this issue is beyond the scope of this paper, preliminary analyses suggest that responses of detrital food webs are also governed by simple, topological rules. For example, webs with a detritus pathway respond similarly to enrichment as do pure grazing webs when the plant-detritus link is in an odd chain (unpublished results, Fig. 4a), but can respond differently (though in predictable ways) when the plant-detritus link is in an even chain (Fig. 4b, c; chain length is counted from and includes the branching node in all cases). The important message is that conversion of a single link to donor control is all that is needed to apply my model to ecosystems with a detritus pathway, and that equilibrium responses of detritus webs are, again, related to topology. For the particular topology in Fig. 4b/c, numerical analyses of a more sophisticated model (including top predator switching and saturating functional responses) corroborate the existence of the depicted two alternative response patterns to nutrient enrichment (Attayde & Ripa 2008).

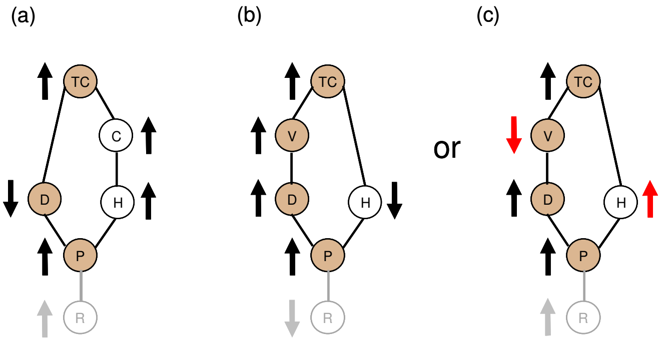

Fig. 4. Equilibrium responses to enrichment of 4-3 webs with one detritus based pathway. D = detritus; V = detritivore. Other symbols and arrows as in Fig. 1. To focus on the 4-3 module the nutrient is outlined in gray. The detritus chain is highlighted in brown. Response patterns were derived analytically assuming linear functional responses and donor-controlled input of dead plant material $m_P P$ *to the detritus compartment. (a) Detritus in 3-link chain: 4-3 module responds like a 4-3 web with two grazing chains (Figs. 1k, 3a). (b, c) Detritus in 4-link chain: responses of* V^* *and* H^* *depend on the top consumer's attack rates on detritivores (*a_{VTC}*) and herbivores (*a_{HTC}*) relative to the detritivores' and herbivores' mortality rates (*m_V *and* m_H*). (b) When* $\frac{a_{VTC}}{m_V} < \frac{a_{HTC}}{m_H}$*, the 4-3 module responds like a 4-3 web with two grazing chains. (c) When* $\frac{a_{VTC}}{m_V} > \frac{a_{HTC}}{m_H}$ *the response deviates as indicated by red arrows.*

Outlook

A challenge in the application of my approach to real ecosystems is the identification of major interaction pathways and their simplification to tractable branched or looped webs. This will require decisions on how to aggregate species into functional groups and which feeding links to neglect. From a conceptual perspective, it seems most meaningful to distinguish between 'fast' and 'slow' energy channels (consisting of strong vs. weak interactions, respectively). Coupling to slow channels buffers oscillatory tendencies in fast channels, and has been proposed to be the most critical, stabilizing structural component of real food webs (Rip et al. 2010, Rooney & McCann 2012). From an empirical perspective, quantitative approaches such as multivariate autogressive models (Ives et al. 2003, Hampton et al. 2006) and structural equation modelling (Wootton 1994, Gotelli & Ellison 2006) applied to observational and experimental data can guide food web simplification. Ideally, tests of model predictions will involve carefully designed new experiments, but existing ones could be re-analyzed based on a functional grouping into dominant interaction pathways. I caution, however, that many manipulative experiments with natural communities typically capture transients rather than the equilibrium states addressed by theory (Englund & Moen 2003). Long-term observational data of systems undergoing environmental changes may therefore be an important testing ground for my approach.

I conclude that the recently advocated reduction of food webs to major pathways of energy flow (Fulton 2010, Shin et al. 2010) holds promise. While there remain both practical and conceptual challenges when applying this approach to real food webs, I believe that my study assembles and organizes important theoretical insights into how topology affects food web dynamics, something food web theory has long been striving for. Given the productive impact of 'simple' food chain theory on ecology in the past, I propose that models with alternative energy pathways will serve both ecosystem and community ecologists as a useful conceptual framework for the future.

Appendix A1.1 General equilibrium conditions for looped and branched webs.

For a web of a given topology, it is possible to gain analytical insights into the relationships among equilibrium biomasses of different populations and their relationships to nutrient enrichment and top consumer mortality. These analytical relationships are necessary conditions for the existence of an interior equilibrium, but are usually not sufficient to completely determine the responses of all populations in the web when functional responses are saturating (Holling type 2). I have therefore explored the responses of webs with type 2 functional responses using numerical analyses and have checked the outcomes for consistency with the analytical conditions described below. In Appendix A1.3 I give detailed information on the numerical investigations and in Appendix A1.5 and A1.6 I give examples of how I used these analytical conditions.

First, the total amount of nutrient in the system is constrained by R_{tot}. Thus, at least one population in a web must increase with nutrient enrichment. Conversely, if a population increases with increasing top consumer mortality, at least one other population in the web must decrease to maintain mass balance.

Second, in the invasion sequence along an enrichment gradient (Fig. 1), a population that has managed to establish itself at a given enrichment threshold will, by continuity, initially continue to increase with further enrichment. Note, however, that some looped webs may exhibit alternative states. In such cases, invasion of a new species may be immediately followed by extinction of a resident species. I do not consider such cases in the equilibrium analysis, which is only meaningful for ecological scenarios in which all members of a given web coexist over some range of nutrient enrichment and top consumer mortality.

Third, the rates of change of all species in a web have to equal zero. This condition can sometimes be used to derive the direction of change of a population compared to another population or in response to a parameter change. Specifically, four types of general conditions can be derived:

(i) The equilibrium condition for a specialist top consumer TC_i in a branched web is

$$\frac{dTC_i}{dt} = TC_i\left(e_{X_iTC_i} \frac{a_{X_iTC_i}}{1 + a_{X_iTC_i} h_{X_iTC_i} X_i} X_i - m_{TC_i} \right) = 0 . \qquad \text{(A1.1-1)}$$

Eq. A1.1-1 can be solved for X_i, the prey species of the specialist top consumer in chain i, as

$$X_i^* = \frac{m_{TC_i}}{\left(e_{X_iTC_i} - m_{TC_i} h_{X_iTC_i}\right) a_{X_iTC_i}} \qquad \text{(A1.1-2)}$$

From eq. A1.1-2 follows that X_i is controlled by its specialist top consumer. It remains at a fixed value with enrichment or with a change in top consumer mortality in the other chain, but increases when the mortality rate of its own (top) consumer is increased.

(ii) The equilibrium condition for an intermediate species Y_i with a specialist consumer Z_i is

$$\frac{dY_i}{dt} = Y_i\left(e_{X_iY_i}\frac{a_{X_iY_i}X_i}{1+a_{X_iY_i}h_{X_iY_i}X_i} - m_{Y_i} - \frac{a_{Y_iZ_i}}{1+a_{Y_iZ_i}h_{Y_iZ_i}Y_i}Z_i \right) = 0\,. \qquad \text{(A1.1-3)}$$

It follows that, if Y_i and Z_i change in opposite directions with nutrient enrichment or with a change in top consumer mortality, X_i must change in the same direction as Z_i. The same is true if Y_i remains constant. If Z_i remains constant, X_i must change in opposite direction to Y_i.

(iii) The equilibrium condition of a generalist top consumer TC is

$$\frac{dTC}{dt} = TC\left(\frac{e_{X_1TC}a_{X_1TC}X_1 + e_{X_2TC}a_{X_2TC}X_2}{1+a_{X_1TC}h_{X_1TC}X_1 + a_{X_2TC}h_{X_2TC}X_2} - m_{TC} \right) = 0$$

which can be rearranged to

$$\left(e_{X_1TC} - m_{TC}h_{X_1TC}\right)a_{X_1TC}X_1^* = m_{TC} - \left(e_{X_2TC} - m_{TC}h_{X_2TC}\right)a_{X_2TC}X_2^*\,. \qquad \text{(A1.1-4)}$$

Since I assume that the generalist top consumer can persist on each prey species alone given sufficient prey density, both $\left(e_{X_1TC} - m_{TC}h_{X_1TC}\right)$ and $\left(e_{X_2TC} - m_{TC}h_{X_2TC}\right)$ must be positive. It therefore follows from eq. A1.1-4 that the two prey species of a generalist top consumer are always negatively correlated if their densities change in response to enrichment (increasing R_{tot}). In contrast, they may change in the same direction with a change in m_{TC} in some webs (Fig. 2p).

(iv) From the equilibrium condition for each prey species Y_i of a generalist top consumer TC

$$\frac{dY_i}{dt} = Y_i\left(e_{X_iY_i}\frac{a_{X_iY_i}X_i}{1+a_{X_iY_i}h_{X_iY_i}X_i} - m_{Y_i} - \frac{e_{Y_iTC}a_{Y_iTC}}{1+a_{Y_1TC}h_{Y_1TC}Y_1 + a_{Y_2TC}h_{Y_2TC}Y_2}TC \right) = 0$$

the following expression can be derived

$$\frac{\left(\dfrac{e_{X_iY_i}a_{X_iY_i}X_i^*}{1+a_{X_iY_i}h_{X_iY_i}X_i^*} - m_{Y_i} \right)}{e_{Y_iTC}a_{Y_iTC}} = \frac{TC^*}{1+a_{Y_1TC}h_{Y_1TC}Y_1^* + a_{Y_2TC}h_{Y_2TC}Y_2^*}\,. \qquad \text{(A1.1-5)}$$

The right hand side of eq. A1.1-5 is the same for both prey species (Y_1 and Y_2), which implies that

$$\frac{\left(\frac{e_{X_1Y_1}a_{X1Y1}X_1^*}{1+a_{X_1Y_1}h_{X_1Y_1}X_1^*}-m_{Y_1}\right)}{e_{Y_1TC}a_{Y_1TC_1}}=\frac{\left(\frac{e_{X_2Y_2}a_{X_2Y_2}X_2^*}{1+a_{X_2Y_2}h_{X_2Y_2}X_2^*}-m_{Y_2}\right)}{e_{Y_2TC}a_{Y_2TC}} \tag{A1.1-6}$$

From eq. A1.1-6 follows that the respective prey species of the subterminal species are positively correlated.

Appendix A1.2 Effects of nutrient enrichment and top consumer mortality on equilibrium population densities in webs with linear functional responses.

When functional responses are linear (i.e. handling times h_{JK} in eqs. 2a and 2b are zero) it is possible to analytically determine the direction of change of any population in any of the investigated webs in response to both nutrient enrichment and top consumer mortality. There are two alternative ways of doing this and I used both of them to double check my results. First, the signs of population changes can be derived from the equilibrium conditions, which are more stringent in the case of linear compared to saturating functional responses. I describe these more stringent conditions below and illustrate their use with an example. Second, for all populations in all investigated food webs it is possible to derive analytical equilibrium expressions. I analyzed the effects of nutrient enrichment and top consumer mortality on these equilibria by calculating their derivatives with respect to R_{tot} and m_{TC} or m_{TC_i} (i = 1,2). I illustrate this analysis in detail for the looped and branched 3-2 webs. For larger webs the equilibrium expressions become more complex, but their derivatives with respect to R_{tot} and m_{TC} or m_{TC_i} have always a unique sign (analyses not shown).

Constraints on equilibrium solutions

For the mass balance equations (3a,b) to be fulfilled, the sum of all equilibrium solutions of a specific web has to equal R_{tot}

$$R_{tot} = \sum N_i^* , \tag{A1.2-1a}$$

the sum of the derivatives of all state variables with respect to R_{tot} has to equal 1

$$1 = \sum \frac{\partial N_i^*}{\partial R_{tot}} , \tag{A1.2-1b}$$

and the sum of the derivatives of all state variables with respect to m_{TC} (looped webs) or m_{TCi} (branched webs) has to equal zero

$$0 = \sum \frac{\partial N_i^*}{\partial m_{TC}} ,\ 0 = \sum \frac{\partial N_i^*}{\partial m_{TC_i}} , \tag{A1.2-1c}$$

where $\sum N_i^*$ and $\sum \partial N_i^*$ are the sums of all state variables (including the mineral nutrient) and of their derivatives, respectively, at equilibrium. Furthermore, at equilibrium all dynamical equations describing the population rates of change (eqs. 1a-c) must balance to zero, which has the following implications: (i) the equilibrium densities of the resource/prey and the consumer of an intermediate species are linearly and positively related (eq. 1a); (ii) when the mortality of a top consumer increases, at least one of its prey must increase (eqs. 1b, c). In order to derive the signs of $\partial N_i^* / \partial m_{TC_i}$ in a branched web, one can therefore start from the top consumer's prey (knowing that it must increase) and use the remaining constraints listed above to derive the signs of the equilibrium changes of all other state variables. The derivation of the sign of $\partial N_i^* / \partial m_{TC}$ in a looped web is more complicated, because the second prey of the top consumer may increase or decrease with increasing top consumer mortality (eq. 1c). There is, however, always only one solution that satisfies all of the above constraints and it can be found by iteration (see example below).

Three final conditions are needed to derive the effects of nutrient enrichment. First, all members of a given web must coexist over the studied range of nutrient enrichment and top consumer mortality. Second, when one prey of the top consumer of a looped web increases, the other prey must decrease (eq. 1c). Third, it follows by continuity that the species that lastly invaded the web under study (when its threshold level of R_{tot} has been passed) continues to increase with further nutrient enrichment. Thus, the sign of $\partial N_i^* / \partial R_{tot}$ is known for that species (which is always highlighted in green shading in Fig. 1). Starting from that species, the remaining constraints listed above can be used to derive the sign of $\partial N_i^* / \partial R_{tot}$ for all other species (see example below).

Example 1: Effects of enrichment on equilibrium densities in looped odd-even webs derived from general constraints on equilibrium solutions

In this section I explain in general terms how nutrient enrichment influences equilibrium population densities in the odd and even chains of any looped odd-even web with linear functional responses. By continuity, a species that invades a food web once a critical threshold level of nutrient enrichment R_{tot} is reached will continue to increase with a further increase in R_{tot}. Consider the case of a looped odd-even web that arose from a branched odd-even web through invasion of the new top consumer (e.g. transitions from Fig. 1a to 1i, from Fig. 1c to 1k, and from Fig. 1e to 1m). It follows from the equilibrium condition of each subterminal population Y_i that a population X_i two trophic levels below the top consumer TC must also increase as TC increases with R_{tot}:

$$e_{X_iY_i} a_{X_iY_i} X_i - m_{Y_i} - a_{Y_iTC} TC = 0 \qquad \text{(A1.2-2a)}$$

This pattern repeats itself down both food chains, i.e. all populations at an even distance to the top consumer must increase with R_{tot}. Consequently, the free mineral nutrient R, which is at an even distance from the top consumer (counted along the odd chain), must also increase with R_{tot}. Starting from the mineral nutrient and applying the same reasoning in upward direction along the even chain, it follows that all species in even distance to R must increase with R_{tot}. Consequently, the subterminal species of the even chain also increases with R_{tot}. From the equilibrium condition of the top consumer TC

$$e_{X_1TC}a_{X_1TC}X_1 + e_{X_2TC}a_{X_2TC}X_2 - m_{TC} = 0 \tag{A1.2-2b}$$

follows that one of its prey populations X_i must decrease if the other one increases. Consequently, the subterminal population of the odd chain - and all populations in odd distance to the top consumer along the odd chain - must decrease with R_{tot}.

Similar reasoning applies to cases where a looped odd-even web arises through invasion of a branched odd-even web by a new top consumer of the even chain, which is immediately preyed upon by the resident top consumer of the odd chain (imagine, for example, that the branched 3-2 web depicted in Fig. 1c is invaded by a herbivore on species P_2 which itself is preyed upon by the resident H_1). The overall outcome for both invasion scenarios is that, once a looped odd-even web has established, all populations in the even chain increase with further nutrient enrichment, whereas populations in the odd chain show an alternating pattern of increase and decrease.

Example 2: Effects of enrichment on equilibrium densities in a looped 3-2 web derived from the partial derivatives of the analytical solution

In the equilibrium solutions and partial derivatives below the parameters R_{tot} and m_{TC} are highlighted in color (R_{tot} in red, m_{TC} in blue). All parameters have positive values.

Dynamical equations:

$$R = R_{tot}\text{-}P_1\text{-}TC \tag{A1.2-3a}$$

$$\frac{dP_1}{dt} = P_1\left(e_{RP_1}a_{RP_1}R\text{-}\ m_{P_1}\text{-}a_{P_1TC}TC\right) \tag{A1.2-3b}$$

$$\frac{dTC}{dt} = TC\left(e_{P_1TC}a_{P_1TC}P_1 + e_{RTC}a_{RTC}R\text{-}m_{TC}\right) \tag{A1.2-3c}$$

Equilibrium solution:

$$R^* = (\,e_{P_1TC}a_{P_1TC}\,R_{tot}\text{-}m_{TC} + e_{P_1TC}m_{P_1}\,)/\,Z \tag{A1.2-3d}$$

$$P_1{}^* = (\text{-}\,a_{P_1TC}e_{RTC}a_{RTC}\,R_{tot} + e_{RP_1}a_{RP_1}\,m_{TC} + a_{P_1TC}\,m_{TC}\,\text{-}\,e_{RTC}a_{RTC}\ m_{P_1}\,)/\,a_{P_1TC}/\,Z \tag{A1.2-3e}$$

$$TC^* = (\,e_{P_1TC}a_{P_1TC}e_{RP_1}a_{RP_1}\,R_{tot}\,\text{-}\,e_{RP_1}a_{RP_1}\,m_{TC} + e_{RTC}a_{RTC}\ m_{P_1}\text{-}\ e_{P_1TC}a_{P_1TC}\ m_{P_1}\,)/\,a_{P_1TC}/\,Z \tag{A1.2-3f}$$

where

$Z = e_{P_1TC}e_{RP_1}a_{RP_1} + e_{P_1TC}a_{P_1TC} \text{-} e_{RTC}a_{RTC} > 0$

The sign of Z is derived from the constraints on the equilibria as described in the previous section.

Derivatives with respect to R_{tot}:

$$\frac{\partial R^*}{\partial R_{tot}} = e_{P_1TC}a_{P_1TC}/Z > 0 \tag{A1.2-3g}$$

$$\frac{\partial P_1^*}{\partial R_{tot}} = \text{-}e_{RTC}a_{RTC}/Z < 0 \tag{A1.2-3h}$$

$$\frac{\partial TC^*}{\partial R_{tot}} = e_{P_1TC}e_{RP_1}a_{RP_1}/Z > 0 \tag{A1.2-3i}$$

Derivatives with respect to m_{TC}:

$$\frac{\partial R^*}{\partial m_{TC}} = \text{-}1/Z < 0 \tag{A1.2-3j}$$

$$\frac{\partial P_1^*}{\partial m_{TC}} = \left(e_{RP_1}a_{RP_1} + a_{P_1TC}\right)/a_{P_1TC}/Z > 0 \tag{A1.2-3k}$$

$$\frac{\partial TC^*}{\partial m_{TC}} = \text{-}e_{RP_1}a_{RP_1}/a_{P_1TC}/Z < 0 \tag{A1.2-3l}$$

<u>Example 3: Effects of enrichment on equilibrium densities in a branched 3-2 web derived from the partial derivatives of the analytical solution</u>

In the equilibrium solutions and partial derivatives below the parameters R_{tot} and m_{TC_i} are highlighted in color (R_{tot} in red, m_{TC_i} in blue). All parameters have positive values.

Dynamical equations:

$$R = R_{tot}\text{-}P_1\text{-}TC_1\text{-}TC_2 \tag{A1.2-4a}$$

$$\frac{dP_1}{dt} = P_1\left(e_{RP_1}a_{RP_1}R\text{-}\ m_{P_1}\text{-}a_{P_1TC_1}TC_1\right) \tag{A1.2-4b}$$

$$\frac{dTC_1}{dt} = TC_1\left(e_{P_1TC_1}a_{P_1TC_1}P_1\text{-}m_{TC_1}\right) \tag{A1.2-4c}$$

$$\frac{dTC_2}{dt} = TC_2\left(e_{RTC_2}a_{RTC_2}R\text{-}m_{TC_2}\right) \tag{A1.2-4d}$$

Equilibrium solution:

$$R^* = m_{TC_2}/e_{RTC_2}/a_{RTC_2} \qquad \text{(A1.2-4e)}$$

$$P_1^* = m_{TC_1}/e_{P_1TC_1}/a_{P_1TC_1} \qquad \text{(A1.2-4f)}$$

$$TC_1^* = \left(e_{RP_1} a_{RP_1} m_{TC_2} - e_{RTC_2} a_{RTC_2} m_{P_1}\right)/e_{RTC_2}/a_{RTC_2}/a_{P_1TC_1} \qquad \text{(A1.2-4g)}$$

$$TC_2^* = \left(e_{RTC_2} a_{RTC_2} e_{P_1TC_1} a_{P_1TC_1} R_{tot} - e_{RP_1} a_{RP_1} e_{P_1TC_1} m_{TC_2} - e_{P_1TC_1} a_{P_1TC_1} m_{TC_2} - e_{RTC_2} a_{RTC_2} m_{TC_1} + e_{RTC_2} a_{RTC_2} m_{P_1} e_{P_1TC_1} \right)/e_{RTC_2}/a_{RTC_2}/e_{P_1TC_1}/a_{P_1TC_1} \qquad \text{(A1.2-4h)}$$

Derivatives with respect to R_{tot}:

$$\frac{\partial R^*}{\partial R_{tot}} = 0\,,\ \frac{\partial P_1^*}{\partial R_{tot}} = 0\,,\ \frac{\partial TC_1^*}{\partial R_{tot}} = 0\,,\ \frac{\partial TC_2^*}{\partial R_{tot}} = 1 \qquad \text{(A1.2-4i-l)}$$

Derivatives with respect to m_{TC_1}:

$$\frac{\partial R^*}{\partial m_{TC_1}} = 0\,,\ \frac{\partial P_1^*}{\partial m_{TC_1}} = 1/e_{P_1TC_1}/a_{P_1TC_1} > 0\,, \qquad \text{(A1.2-4m,n)}$$

$$\frac{\partial TC_1^*}{\partial m_{TC_1}} = 0\,,\ \frac{\partial TC_2^*}{\partial m_{TC_1}} = -1/e_{P_1TC_1}/a_{P_1TC_1} < 0 \qquad \text{(A1.2-4o,p)}$$

Derivatives with respect to m_{TC_2}:

$$\frac{\partial R^*}{\partial m_{TC_2}} = 1/\mathrm{e}_{\mathrm{RTC}_2}/\mathrm{a}_{\mathrm{RTC}_2} > 0\,,\ \frac{\partial P_1^*}{\partial m_{TC_2}} = 0 \qquad \text{(A1.2-4q,r)}$$

$$\frac{\partial TC_1^*}{\partial m_{TC_2}} = \left(e_{RP_1} a_{RP_1}\right)/e_{RTC_2}/a_{RTC_2}/a_{P_1TC_1} > 0 \qquad \text{(A1.2-4s)}$$

$$\frac{\partial TC_2^*}{\partial m_{TC_2}} = \left(-e_{RP_1} a_{RP_1} - a_{P_1TC_1}\right)/e_{RTC_2}/a_{RTC_2}/a_{P_1TC_1} < 0 \qquad \text{(A1.2-4t)}$$

Appendix A1.3 Illustration of the numerical analysis of equilibrium responses in a web with saturating functional responses.

The numerical investigation of response patterns for the case of type 2 functional responses were all done with Matcont 2.4 (Dhooge et al. 2003), a bifurcation analysis software that can be used as a package for Matlab [Mathworks Inc., Natick, MA, USA]. I exemplify the procedure with the looped 4-3 web. Matcont 2.4 (Dhooge et al. 2003) enables the continuation of equilibrium solutions in dependence on a chosen bifurcation parameter and the detection of certain bifurcation points. I implemented the differential equation system for the looped 4-3 web (A1.3-1-4) within matcont 2.4, substituting *R* with the right side of expression (A1.3-5).

$$\frac{dP_1}{dt} = P_1\left(\frac{e_{RP_1}a_{RP_1}R}{1+a_{RP_1}h_{RP_1}R} - m_{P_1} - \frac{a_{P_1H_1}H_1}{1+h_{P_1H_1}a_{P_1H_1}P_1}\right) = 0 \qquad \text{(A1.3-1)}$$

$$\frac{dH_1}{dt} = H_1\left(\frac{e_{P_1H_1}a_{P_1H_1}P_1}{1+h_{P_1H_1}a_{P_1H_1}P_1} - m_{H_1} - \frac{a_{H_1TC}TC}{1+h_{H_1TC}a_{H_1TC}H_1 + h_{P_2TC}a_{P_2TC}P_2}\right) = 0 \qquad \text{(A1.3-2)}$$

$$\frac{dP_2}{dt} = P_2\left(\frac{e_{RP_2}a_{RP_2}R}{1+a_{RP_2}h_{RP_2}R} - m_{P_2} - \frac{a_{P_2C}TC}{1+h_{H_1TC}a_{H_1TC}H_1 + h_{P_2TC}a_{P_2TC}P_2}\right) = 0 \qquad \text{(A1.3-3)}$$

$$\frac{dTC}{dt} = TC\left(\frac{e_{H_1TC}a_{H_1TC}H_1 + e_{P_2TC}a_{P_2TC}P_2}{1+h_{H_1TC}a_{H_1TC}H_1 + h_{P_2TC}a_{P_2TC}P_2} - m_{TC}\right) = 0 \qquad \text{(A1.3-4)}$$

$$R = R_{tot} - P_1 - P_2 - H_1 - TC \qquad \text{(A1.3-5)}$$

I arbitrarily selected a set of biologically reasonable parameter values (table A1.3-1) and tracked the equilibrium solution depending on the respective bifurcation parameter. In case of investigating the effects of enrichment, the bifurcation parameter was R_{tot} and in case of investigating the effects of top-consumer mortality it was m_{TC}. For bifurcations with regard to R_{tot}, I started with an initial value of 0.001 and no species present (all state variables except for free nutrients *R* being zero), and increased R_{tot} until reaching a bifurcation point at which one species can successfully invade the system. Then I continued the calculation from this threshold on, thus building up the web step by step as illustrated in figure 1. Within Matcont 2.4 each bifurcation run is stored including the equilibrium values of each state variable whose dynamics are defined through a differential equation (in this case P_1, H_1, P_2 and *TC*), the corresponding value of the bifurcation parameter and the corresponding eigenvalues. The equilibrium values of R were calculated using the mass balance constraint (A1.3-5). I repeated this procedure for several different combinations of parameter values (usually 2-4 times). An example of an equilibrium solution for the coexistence region of the looped 4-3 web is given in figure A1.3-1.

For bifurcations with regard to m_{TC}, starting values were chosen from the equilibrium solution derived from the R_{tot} -bifurcation within the coexistence range of the web, with R_{tot} being fixed at the respective value. Then m_{TC} was increased as well as decreased until reaching a bifurcation point in either direction, the bifurcation point coinciding with one state variable reaching a value of zero. I did this bifurcation analysis for at least two different starting values (different equilibrium points along the R_{tot} -axis). An example of a bifurcation run with respect to m_{TC} is shown in figure A1.3-2.

For the used parameter set (table A1.3-1), the equilibrium solution is stable over the whole range of enrichment levels where coexistence is possible. While stability over the entire coexistence range was not observed for most other parameter combinations, the depicted response patterns were always observed within the range of stable equilibria and also over the range of unstable equilibria of the looped 4-3 web (authors, unpublished data).

Table A1.3-1. Parameter values of the bifurcation analysis of the looped 4-3 web shown in Figs. A1.3-1 and A1.3-2.

Parameter	Value
e_{RP1}	1
a_{RP1}	1.4
h_{RP1}	0.9
e_{RP2}	1
a_{RP2}	1
h_{RP2}	1
e_{P1H1}	0.6
a_{P1H1}	1.4
h_{P1H1}	0.5
e_{P2TC}	0.5
a_{P2TC}	1
h_{P2TC}	2
e_{H1TC}	0.5
a_{H1TC}	1.4
h_{H1TC}	2
m_{P1}	0.05
m_{P2}	0.05
m_{H1}	0.1
m_{TC}	0.1

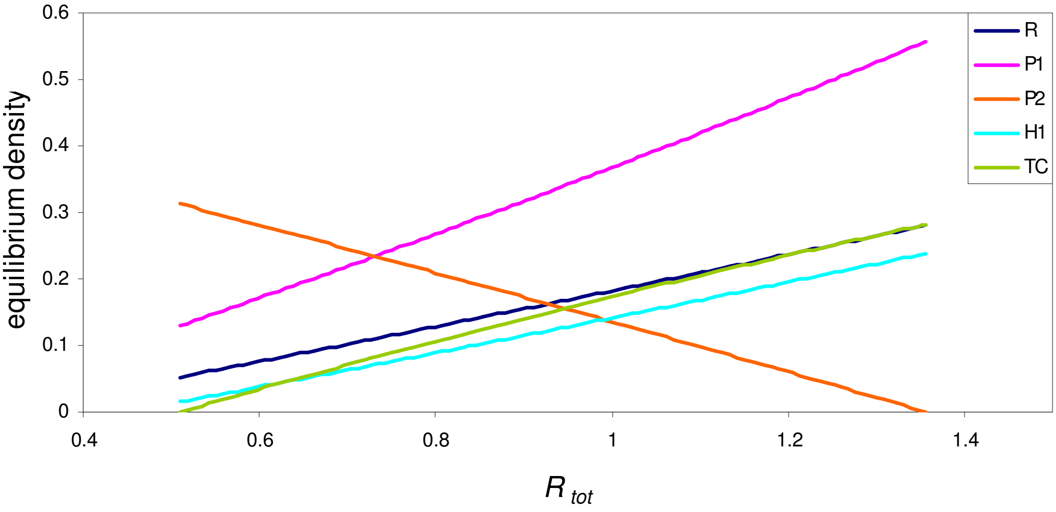

Fig. A1.3-1. Equilibrium solutions for all members of the looped 4-3 web as a function of R_{tot}*. All other parameters are listed in table A1.3-1. All equilibria are locally stable.*

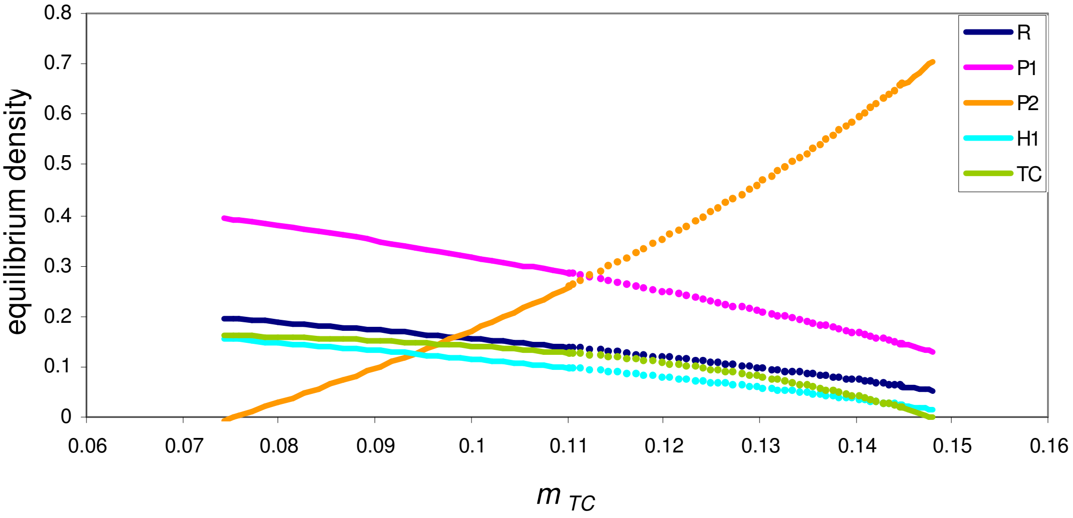

Fig. A1.3-2. Equilibrium solutions for all members of the looped 4-3 web as a function of m_{TC}*. Starting values for the bifurcation analysis were:* $m_{TC} = 0.1$, $R_{tot} = 0.9028$, $P_1 = 0.3185$, $P_2 = 0.1714$, $H_1 = 0.1156$, $TC = 0.1414$*. All other parameters are listed in table A1.3-1. Solid lines indicate stable and dotted lines indicate unstable equilibrium solutions.*

Appendix A1.4 Effects of enrichment and increased top consumer mortality on a branched 3-2 web with saturating functional responses.

The equilibrium condition for a branched 3-2 web with saturating functional responses is given by the following set of equations

$$\frac{dP_1}{dt} = P_1\left(\frac{e_{RP_1}a_{RP_1}R}{1+a_{RP_1}h_{RP_1}R} - m_{P1} - \frac{a_{P_1TC_1}TC_1}{1+h_{P_1TC_1}a_{P_1TC_1}P_1}\right) = 0 \qquad \text{(A1.4-1)}$$

$$\frac{dTC_2}{dt} = TC_2\left(\frac{e_{RTC_2}a_{RTC_2}R}{1+a_{RTC_2}h_{RTC_2}R} - m_{TC_2}\right) = 0 \qquad \text{(A1.4-2)}$$

$$\frac{dTC_1}{dt} = TC_1\left(\frac{e_{P_1TC_1}a_{P_1TC_1}P_1}{1+h_{P_1TC_1}a_{P_1TC_1}P_1} - m_{TC_1}\right) = 0 \qquad \text{(A1.4-3)}$$

$$R = R_{tot} - P_1 - TC_1 - TC_2 \qquad \text{(A1.4-4)}$$

Solving eq. A1.4-2 yields the resource equilibrium

$$R^* = \frac{m_{TC_2}}{a_{RTC_2}\left(e_{RTC_2} - m_{TC_2}h_{RTC_2}\right)}. \qquad \text{(A1.4-5)}$$

R^* is independent of R_{tot} and m_{TC_1} and increases with m_{TC_2}. Solving eq. A1.4-3 yields

$$P_1^* = \frac{m_{TC_1}}{a_{P_1TC_1}\left(e_{P_1TC_1} - m_{TC_1}h_{P_1TC_1}\right)}. \qquad \text{(A1.4-6)}$$

P_1^* is independent of R_{tot} and m_{TC_2} and increases with m_{TC_1}. Solving eq. A1.4-1 for TC_1^* yields

$$TC_1^* = \left(\frac{e_{RP_1}a_{RP_1}R^*}{1+a_{RP_1}h_{RP_1}R^*} - m_{P1}\right)\left(1+h_{P_1TC_1}a_{P_1TC_1}P_1^*\right)\frac{1}{a_{P_1TC_1}} \qquad \text{(A1.4-7)}$$

Substituting eqs. A1.4-5 and A1.4-6 into eq. A1.4-7 reveals that TC_1^* is independent of R_{tot} and increases with both m_{TC_1} and m_{TC_2}. The direction of change of TC_2^* can now be easily derived from mass balance considerations. Since all other populations remain constant, TC_2^* must increase with an increase in R_{tot}. Conversely, since all other populations either increase or remain constant, TC_2^* must decrease with an increase in both m_{TC_1} and m_{TC_2}.

Appendix A1.5 Effects of enrichment and increased top consumer mortality on a looped 3-3 web with saturating functional responses.

The equilibrium condition for a looped 3-3 web with saturating functional responses is given by the following set of differential equation.

$$\frac{dP_1}{dt} = P_1\left(\frac{e_{RP_1}a_{RP_1}R}{1+a_{RP_1}h_{RP_1}R} - m_{P_1} - \frac{a_{P_1TC}TC}{1+h_{P_1TC}a_{P_1TC}P_1 + h_{P_2TC}a_{P_2TC}P_2}\right) = 0 \qquad \text{(A1.5-1)}$$

$$\frac{dP_2}{dt} = P_2\left(\frac{e_{RP_2}a_{RP_2}R}{1+a_{RP_2}h_{RP_2}R} - m_{P_2} - \frac{a_{P_2TC}TC}{1+h_{P_1TC}a_{P_1TC}P_1 + h_{P_2TC}a_{P_2TC}P_2}\right) = 0 \qquad \text{(A1.5-2)}$$

$$\frac{dTC}{dt} = TC\left(\frac{e_{P_1TC}a_{P_1TC}P_1 + e_{P_2TC}a_{P_2TC}P_2}{1+h_{P_1TC}a_{P_1TC}P_1 + h_{P_2TC}a_{P_2TC}P_2} - m_{TC}\right) = 0 \qquad \text{(A1.5-3)}$$

$$R = R_{tot} - P_1 - P_2 - TC \qquad \text{(A1.5-4)}$$

Eqs. A1.5-1 and A1.5-2 can be rearranged to yield

$$\frac{1}{a_{P_1TC}}\left(\frac{e_{RP_1}a_{RP_1}R^*}{1+a_{RP_1}h_{RP_1}R^*} - m_{P_1}\right) = \frac{TC^*}{1+h_{P_1TC}a_{P_1TC}P_1^* + h_{P_2TC}a_{P_2TC}P_2^*} \qquad \text{(A1.5-5)}$$

$$\frac{1}{a_{P_2TC}}\left(\frac{e_{RP_2}a_{RP_2}R^*}{1+a_{RP_2}h_{RP_2}R^*} - m_{P_2}\right) = \frac{TC^*}{1+h_{P_1TC}a_{P_1TC}P_1^* + h_{P_2TC}a_{P_2TC}P_2^*} \qquad \text{(A1.5-6)}$$

Substitution of eq. A1.5-5 into eq. A1.5-6 yields an analytical expression for the equilibrium density of R^*. It is obvious that R^* is independent of both m_{TC} and R_{tot}. Consequently, the right hand sides of eqs. A1.5-5 and A1.5-6 must also be independent of m_{TC} and R_{tot}. From this follows that, if P_1^* changes with a change in m_{TC}, P_2^* must change in the opposite direction (if both P_1^* and P_2^* change in the same direction, TC^* would also have to change in the same direction to maintain constancy of the right hand sides of eqs. A1.5-5 and A1.5-6; with R^* being constant, this, however, violates mass balance, i.e. R_{tot} would not remain constant).

With a change in R_{tot} at least one component in the system has to change in the same direction as does R_{tot}. Independence of R^* from R_{tot} then implies that at least two of the populations on the right hand sides of eqs. A1.5-5 and A1.5-6 must change with changing R_{tot}. Thus, at least one of the two producer species must change. It can then be shown that P_1^* and P_2^* must change in opposite directions with a change in R_{tot}. Rearrangement of eq. A1.5-3 yields

$$\left(e_{P_1TC} - m_{TC}h_{P_1TC}\right)a_{P_1TC}P_1^* = m_{TC} - \left(e_{P_2TC} - m_{TC}h_{P_2TC}\right)a_{P_2TC}P_2^* \qquad \text{(A1.5-7)}$$

I assume that the top consumer can persist on each prey alone given a sufficient prey density. Therefore both $\left(e_{P_1TC} - m_{TC}h_{P_1TC}\right)$ and $\left(e_{P_2TC} - m_{TC}h_{P_2TC}\right)$ must be positive. If P_1^* changes with a change in R_{tot}, it then follows from eq. A1.5-7 that P_2^* must change in the opposite direction. In summary, I know that with both enrichment and increased top consumer mortality P_1^* and P_2^* must change in opposite directions, whereas R^* remains constant.

Eq. A1.5-7 can be solved for P_1^* as well as P_2^* respectively. Replacing P_1^* in eq. A1.5-5 and solving for TC^* yields

$$\left(\frac{e_{RP_1}a_{RP_1}R^*}{1+a_{RP_1}h_{RP_1}R^*} - m_{P_1}\right)\left(\frac{e_{P_1TC} + \left(h_{P_2TC}e_{P_1TC} - h_{P_1TC}e_{P_2TC}\right)a_{P_2TC}P_2^*}{\left(e_{P_1TC} - m_{TC}h_{P_1TC}\right)}\right)\frac{1}{a_{P_1TC}} = TC^*, \tag{A1.5-8}$$

replacing P_2^* in eq. A1.5-5 and solving for TC^* yields

$$\left(\frac{e_{RP_1}a_{RP_1}R^*}{1+a_{RP_1}h_{RP_1}R^*} - m_{P1}\right)\left(\frac{e_{P_2TC} - \left(h_{P_2TC}e_{P_1TC} - h_{P_1TC}e_{P_2TC}\right)a_{P_1TC}P_1^*}{\left(e_{P_2TC} - m_{TC}h_{P_2TC}\right)}\right)\frac{1}{a_{P_1TC}} = TC^*. \tag{A1.5-9}$$

As R^* remains constant with enrichment, the relation of TC^* to P_2^* in eq. A1.5-8, as well as to P_1^* in eq. A1.5-9, depends on the expression $\left(h_{P_2TC}e_{P_1TC} - h_{P_1TC}e_{P_2TC}\right)$ being positive or negative. E.g. if $\left(h_{P_2TC}e_{P_1TC} - h_{P_1TC}e_{P_2TC}\right) > 0$ then P_1^* is negatively and P_2^* is positively related to TC^*. If $\left(h_{P_2TC}e_{P_1TC} - h_{P_1TC}e_{P_2TC}\right) = 0$ TC^* will remain constant with enrichment, identical to the linear case, but increase with increasing mortality rate (m_{TC}). Generally, the response of TC^* to enrichment is thus not necessarily reversed to the response to increased mortality.

Appendix A1.6 Equilibrium relationships in a looped 4-3 web with saturating functional responses.

The equilibrium condition for a looped 4-3 web with saturating functional responses is given by the following set of equations.

$$\frac{dP_1}{dt}=P_1\left(\frac{e_{RP_1}a_{RP_1}R}{1+a_{RP_1}h_{RP_1}R}-m_{P_1}-\frac{a_{P_1H_1}H_1}{1+h_{P_1H_1}a_{P_1H_1}P_1}\right)=0 \qquad \text{(A1.6-1)}$$

$$\frac{dH_1}{dt}=H_1\left(\frac{e_{P_1H_1}a_{P_1H_1}P_1}{1+h_{P_1H_1}a_{P_1H_1}P_1}-m_{H_1}-\frac{a_{H_1TC}TC}{1+h_{H_1TC}a_{H_1TC}H_1+h_{P_2TC}a_{P_2TC}P_2}\right)=0 \qquad \text{(A1.6-2)}$$

$$\frac{dP_2}{dt}=P_2\left(\frac{e_{RP_2}a_{RP_2}R}{1+a_{RP_2}h_{RP_2}R}-m_{P_2}-\frac{a_{P_2C}TC}{1+h_{H_1TC}a_{H_1TC}H_1+h_{P_2TC}a_{P_2TC}P_2}\right)=0 \qquad \text{(A1.6-3)}$$

$$\frac{dTC}{dt}=TC\left(\frac{e_{H_1TC}a_{H_1TC}H_1+e_{P_2TC}a_{P_2TC}P_2}{1+h_{H_1TC}a_{H_1TC}H_1+h_{P_2TC}a_{P_2TC}P_2}-m_{TC}\right)=0 \qquad \text{(A1.6-4)}$$

$$R=R_{tot}-P_1-P_2-H_1-TC \qquad \text{(A1.6-5)}$$

Rearranging eqs. A1.6-2 and A1.6-3 leads to the following expressions

$$\frac{1}{a_{H_1TC}}\left(\frac{e_{P_1H_1}a_{P_1H_1}P_1^*}{1+h_{P_1H_1}a_{P_1H_1}P_1^*}-m_{H_1}\right)=\frac{TC^*}{1+h_{H_1TC}a_{H_1TC}H_1^*+h_{P_2TC}a_{P_2TC}P_2^*} \qquad \text{(A1.6-6)}$$

$$\frac{1}{a_{P_2TC}}\left(\frac{e_{RP_2}a_{RP_2}R^*}{1+a_{RP_2}h_{RP_2}R^*}-m_{P_2}\right)=\frac{TC^*}{1+h_{H_1TC}a_{H_1TC}H_1^*+h_{P_2TC}a_{P_2TC}P_2^*} \qquad \text{(A1.6-7)}$$

Substitution of eq. A1.6-6 into eq. A1.6-7 reveals that P_1^* and R^* are always positively related, irrespective of whether R_{tot} or m_{TC} is increased:

$$\frac{1}{a_{H_1TC}}\left(\frac{e_{P_1H_1}a_{P_1H_1}P_1^*}{1+h_{P_1H_1}a_{P_1H_1}P_1^*}-m_{H_1}\right)=\frac{1}{a_{P_2TC}}\left(\frac{e_{RP_2}a_{RP_2}R^*}{1+a_{RP_2}h_{RP_2}R^*}-m_{P_2}\right) \qquad \text{(A1.6-8)}$$

I already know from Appendix A1.1 that the two subterminal species in a looped web are always negatively correlated if one of them changes in response to R_{tot}. For the looped 4-3 web this can be derived by rearranging eq. A1.6-4:

$$H_1^*=\frac{m_{TC}}{a_{H_1TC}\left(e_{H_1TC}-m_{TC}h_{H_1TC}\right)}-\frac{a_{P_2TC}\left(e_{P_2TC}-m_{TC}h_{P_2TC}\right)}{a_{H_1C}\left(e_{H_1TC}-m_{TC}h_{H_1TC}\right)}P_2^* \qquad \text{(A1.6-9)}$$

where all terms in parentheses are positive. Finally, solving eq. A1.6-1 for H_1^* yields

$$H_1^*=\frac{1}{a_{P_1H_1}}\left(\frac{e_{RP_1}a_{RP_1}R^*}{1+a_{RP_1}h_{RP_1}R^*}-m_{P_1}\right)\left(1+h_{P_1H_1}a_{P_1H_1}P_1^*\right) \qquad \text{(A1.6-10)}$$

The left-most term in parentheses must be positive (eq. A1.6-1). It then follows from eqs. A1.6-8 and A1.6-10 that, with a change in R_{tot}, R^* and P_1^* are positively related to each other and to H_1^* and all are negatively related to P_2^*. I know furthermore from eq. A1.6-4 that either H_1^* or P_2^* or both must increase with an increase in m_{TC}. If both increase, it follows from eqs. A1.6-8 and A1.6-10 that also P_1^* and R^* increase. A correlated increase in H_1^*, P_2^* and R^* would, however, imply that TC^* also has to increase to fulfill the equilibrium condition of eq. A1.6-3. In this case *all* components of the web would increase in response to m_{TC}, which violates mass balance. Consequently, P_2^* has to change in opposite direction to H_1^* (and P_1^* and R^*) when m_{TC} is changed.

In summary, I know that with both enrichment and increased top consumer mortality R^*, P_1^* and H_1^* must always change in one and the same direction and P_2^* in the opposite direction. While I cannot constrain the sign changes further analytically, numerical runs always yielded the patterns depicted in Figs. 1k and 2o.

Chapter 2

Ontogenetic diet shifts promote predator-mediated coexistence

Abstract

It is widely believed that predation moderates interspecific competition and promotes prey diversity. Still, in models of two prey sharing a resource and a predator, predator-mediated coexistence occurs only over narrow ranges of resource productivity. These models have so far ignored the widespread feature of ontogenetic diet shifts in predators. Here, I theoretically explore the consequences of a diet shift from juvenile to adult predator stages for coexistence of two competing prey. I find that only very minor deviations from perfectly identical diets in juveniles and adults destroy the 'traditional' mechanism of predator-mediated coexistence, which requires an intrinsic trade-off between prey defendedness and competitive ability. Instead, predator population structure can create an ‘emergent’ competition-predation trade-off between prey, where a bottleneck in one predator stage enhances predation on the superior competitor and relaxes predation on the inferior competitor irrespective of the latter's intrinsic defendedness. Pronounced diet shifts therefore greatly enlarge the range of prey coexistence along a resource gradient. With diet shifts, however, coexistence usually occurs as one of two alternative states and, once lost, may not be easily restored.

Introduction

It is widely believed that the role of interspecific competition in structuring ecological communities decreases with the intensity of physical stress and mortality (Paine 1966, Grime 1973, Lubchenco 1978). This idea is deeply engrained in influential ecological concepts such as intermediate disturbance and predator-mediated coexistence (Levins & Culver 1971, Caswell 1978, Connell 1978). To promote long-term persistence of competitors all of these concepts require, however, additional niche opportunities such as trade-offs between competitive ability and the abilities to withstand or counter stress and mortality (Chesson & Huntly 1997). On physiological grounds, trade-offs between competitive ability and e.g. vulnerability to predators or pathogens are indeed expected to be common (e.g. Herms & Mattson 1992).

The empirical evidence for a prevalence of trade-offs between the abilities to compete and to withstand natural enemies is nevertheless rather mixed (Koricheva 2002, Viola et al. 2010). Moreover, such trade-offs alone are insufficient to promote substantial within-guild diversity (Chase et al. 2002, Chesson & Kuang 2008). For example, theoretical investigations of the smallest food web combining resource competition with shared predation, the ‘diamond web’ (consisting of two prey sharing a limiting resource and a predator) demonstrate that, unless one competitor is completely invulnerable, coexistence occurs only under fairly limited environmental conditions (Holt et al. 1994, Grover 1995, Leibold 1996). Typically, the superior resource competitor prevails at low resource productivity and the less vulnerable competitor at high productivity, while coexistence or priority effects may occur at intermediate productivity (Grover & Holt 1998). Stochastic extinctions during transient or unstable dynamics may further limit coexistence (Noonburg & Abrams 2005).

If intrinsic trade-offs between traits conferring competitive dominance vs. resistance to predation are neither universally found nor sufficient to explain widespread persistence of diverse guilds of competitors – which other mechanisms are then responsible for the frequent observation of positive impacts of predators on prey diversity (Paine 1966, Lubchenco 1978, Olff & Ritchie 1998, Worm et al. 2002)? Individual growth and development, ontogenetic diet shifts, and population size structure are ubiquitous properties of most species; consequently, many consumers exhibit pronounced shifts in resource use during ontogeny (Werner & Gilliam 1984, Werner 1988). In this chapter I explore whether these features provide a mechanism that can prevent competitive exclusion among their prey. I do so by introducing an ontogenetic diet shift between the juvenile and adult stages of the shared predator into a model of the diamond food web.

In most organisms individual growth and development are strongly food dependent. This food dependence generates, in turn, population dynamics that typically differ quite remarkably from the vast majority of models ignoring this perhaps most basic property of life (De Roos et al. 2003, 2008b). For example, feedbacks between stages can lead to counterintuitive population patterns such as biomass accumulating in the most food limited stage (De Roos et al. 2007). So far, theoretical studies of ontogenetic diet shifts in predators have only assumed non-interacting prey (Schreiber & Rudolf 2008, Schellekens et al. 2010). The question how individual development, ontogenetic diet shifts and population structure in shared predators affect the persistence of competing prey remains therefore unexplored.

In the absence of an ontogenetic diet shift my analyses retrieve the ‘classical’ result that coexistence is very limited in parameter space and requires an intrinsic competition-predation trade-off in the prey. For more pronounced diet shifts, however, I find that the predator stage specializing on the superior competitor overexploits this prey type. Independent of intrinsic defence traits, the resulting recruitment bottleneck to the predator stage specializing on the inferior competitor produces a dynamically ‘emergent’ competition-predation trade-off. The latter enables prey coexistence over an increasingly larger range of resource productivities the more pronounced the predator’s diet shift. My results therefore suggest that predator-mediated coexistence is a relatively uncommon outcome in the absence of predator stage structure, while ontogenetic diet shifts can promote the maintenance of prey diversity. The coexistence state with a diet shifter is, however, only one of two alternative states and, once lost, may not be easily restored.

Model structure

I explore the dynamics of the diamond web (Fig. 1) using a biomass-based model formulation that accounts for food dependence in both reproduction and individual growth/maturation of the top consumer (De Roos et al. 2008a). Model equations and parameter values are given in Table 2.1. Parameters were chosen for a planktonic nutrient-producer-herbivore system, with unicellular producers (phytoplankton) and a stage structured herbivore (a copepod), but numerical analyses indicate that the results are very robust to changes in parameters.

The resource at the base of the web (R) is assumed to be nitrogen. Biomass densities of all species are therefore measured in units of nutrient (mg N/L) and all rates are scaled accordingly. To keep the model directly applicable to systems where state variables are expressed in carbon biomass, I assume that losses from excretion, respiration and mortality are not recycled to the inorganic nutrient pool. Results do, however, not depend on this assumption (see discussion). Nutrients enter the system from outside with concentration R_{max} at rate l, are washed out at the same rate, and are consumed by primary producers P_1 and P_2, following linear functional responses with clearance rates a_{PiR}. Producers convert nutrients into biomass with efficiency e_{PiR}, and lose biomass through density independent mortality and respiration at rate m_{Pi} and through consumption by herbivores. Parameters were chosen such that $P1$ is the superior resource competitor ($a_{P1R} > a_{P2R}$, $e_{P1R} = e_{P2R}$, and $m_{P1} = m_{P2}$).

Both consumer stages feed on primary producers following linear functional responses and convert this food into biomass with efficiency σ. Net-biomass production by juvenile and adult consumers, indicated as v_J and v_A, respectively, equals the difference between this biomass production and the maintenance rate T. Note that all rates are mass specific. Hence juveniles and adults do not differ in their mass specific rates, but do so on an individual basis dependent on body size (Schellekens et al. 2010).

Juveniles grow in body size at mass-specific rate v_J^+ only if their net-biomass production is positive (v_J^+ refers to the value of v_J if the latter is positive and equals 0 under starvation conditions when $v_J < 0$). Juveniles mature to the adult stage at mass-specific rate $y\left(v_J^+\right)$ (De Roos et al. 2008a), which equals 0 when net production is negative. Adults do not grow but invest positive net-biomass production v_A^+ entirely in reproduction, while stopping reproduction when starving ($v_A < 0$). Hence total biomass of juveniles increases through birth ($v_A^+ A$) and somatic growth ($v_J J$) and decreases through maturation to the adult stage ($y\left(v_J^+\right)J$) and mortality. Total biomass of adults increases through maturation of juveniles and decreases through mortality. The density independent mortality rate m_C is assumed to be equal for both stages. Juveniles and adults experience an increase in mortality rate of $-v_J$ and $-v_A$, respectively, under starvation conditions when their net production is negative (De Roos et al. 2008a).

The maturation rate $y\left(v_J^+\right)$ depends on juvenile net-production and mortality and on the ratio of newborn to adult body mass z. This function translates the maturation rate of an individual based, size-structured model at equilibrium into a food dependent, population-level maturation rate of a corresponding stage-structured model. The stage-structured model therefore has a rigorous individual basis and its dynamics fully capture the equilibrium behavior of the underlying size-structured model (De Roos et al. 2008a).

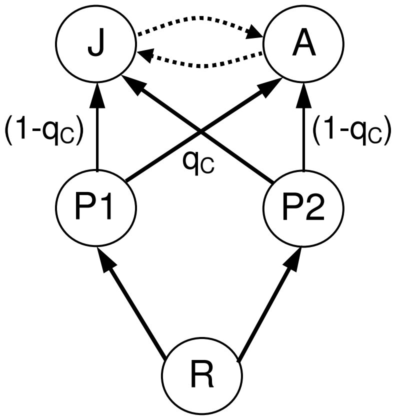

Fig. 1. Diamond food web with a stage structured consumer. Circles represent the biomasses of R = resource, P_i = primary producer i (i = 1, 2), J = juvenile and A = adult consumers, respectively. Solid arrows are feeding links and point from prey/resource to consumer. Dotted arrows are biomass flows between consumer stages related to maturation and reproduction. Relative foraging efficiency of each consumer stage on each prey species (in terms of q_C,) is indicated next to the corresponding feeding links, illustrating the symmetrical niche shift.

A predator's functional response equals the product of prey biomass density, a prey-specific clearance rate a_{CPi}, which may be negatively correlated with a_{PiR} to represent an intrinsic competition-predation trade-off, and a predator specific component (q_C or 1-q_C) that models an ontogenetic trade-off in the foraging efficiencies of juvenile *vs*. adult consumers. q_C takes on values between 0 and 1. I focus on a 'symmetrical niche' model, assuming a linear, symmetrical trade-off such that juveniles forage on *P1* and *P2* with efficiency (1-q_C) and q_C, respectively, whereas adults forage on *P1* and *P2* with the reversed efficiencies. Therefore q_C determines the degree of niche shift between the two stages. When $q_C = 0$ or 1 the niche shift is complete (juveniles and adults have exclusive resources), whereas there is no niche shift at all when $q_C = 0.5$. In the latter case the dynamics of total consumer biomass (obtained by summing the equations for juveniles and adults) are given by

$$\frac{d(J+A)}{dt} = (\sigma(0.5 \cdot a_{CP1}P_1 + 0.5 \cdot a_{CP2}P_2)\text{-}T)(J+A)\text{-}m_C(J+A) \qquad (1)$$

which retrieves the limiting case of an unstructured consumer population (i.e. the 'classical' diamond web). Parameters were chosen such that the inferior resource competitor *P2* is intrinsically less vulnerable to predation from a non-niche shifting consumer than *P1* ($a_{CP2} < a_{CP1}$).

Model analyses

I numerically investigated the influence of the degree of ontogenetic diet shift in the top consumer on equilibrium dynamics of the diamond web by systematically varying the parameter q_C for various levels of resource enrichment R_{max}. My model formulation with linear functional responses, stage-independent biomass specific rates, and a linear tradeoff between the prey specific foraging efficiencies of the two consumer stages enabled us to clearly separate effects of niche shifts and stage structure from potentially confounding effects of saturating functional responses and stage specific consumer traits.

I used Matcont 2.4 (Dhooge et al. 2003), a software package usable within Matlab [Mathworks Inc., Natick, MA, USA], to compute model equilibria and their stability and analyzed non-equilibrium dynamics using numerical simulations.

Results - overview

The system can attain five possible community states: the resource alone, or the resource with the superior competitor (*P1*), with *P1* and the consumer (*P1-C*), with both prey and the consumer (*coex*), and with *P2* and the consumer (*P2-C*). Fig. 2 summarizes for the symmetrical niche model how these community states depend on enrichment (R_{max}) and the degree of niche shift in the consumer (q_C). The figure is representative for any parameter choice that embodies an intrinsic competition-predation trade-off in the two prey species (Table 2.1).

Transitions between community states may occur at the threshold lines labelled I_{P1}, I_C, I_{P2}, *Co*, and E_{P1}, respectively (Fig. 2). I_{P1} is the minimum enrichment level needed for *P1* to invade a system with only the resource. I_C is the threshold at which the consumer can invade a *P1* equilibrium, and I_{P2} is the threshold for invasion of *P2* into a *P1*-consumer system (resulting in either 2 prey-consumer coexistence or replacing the *P1*-consumer by a *P2*-consumer equilibrium). *Co* labels the minimal enrichment level for which coexistence of both prey species and the consumer is possible, and E_{P1} labels the extinction-threshold of *P1* from a 2 prey-consumer system.

Compared to the unstructured case ($q_C = 0.5$), niche shifts in the consumer change the competition-predation balance for the prey species through shifts in food dependent recruitment between consumer stages. For a clearer understanding of how different system states and transitions between them depend on enrichment and the degree of niche shift between juvenile and adult consumers, I explore transects through the R_{max}-q_C plane (Fig. 2) along (i) the R_{max}-axis and (ii) the q_C-axis. Note the approximate symmetry of the state transition boundaries (Fig. 2). This symmetry arises, because the total effects of a niche shifting consumer (juveniles plus adults) on lower trophic levels depend primarily on the degree of niche shift (the deviation from $q_C = 0.5$ in either direction), whereas the absolute value of q_C primarily determines the population structure of the consumer. Lower trophic levels will therefore respond roughly similarly to consumers with a q_C of e.g. 0.2 and 0.8, while consumer population structure will show contrasting patterns. Although the symmetry is not perfect, it is therefore sufficient to illustrate enrichment effects in only one half of Fig. 2 ($0 \leq q_C \leq 0.5$).

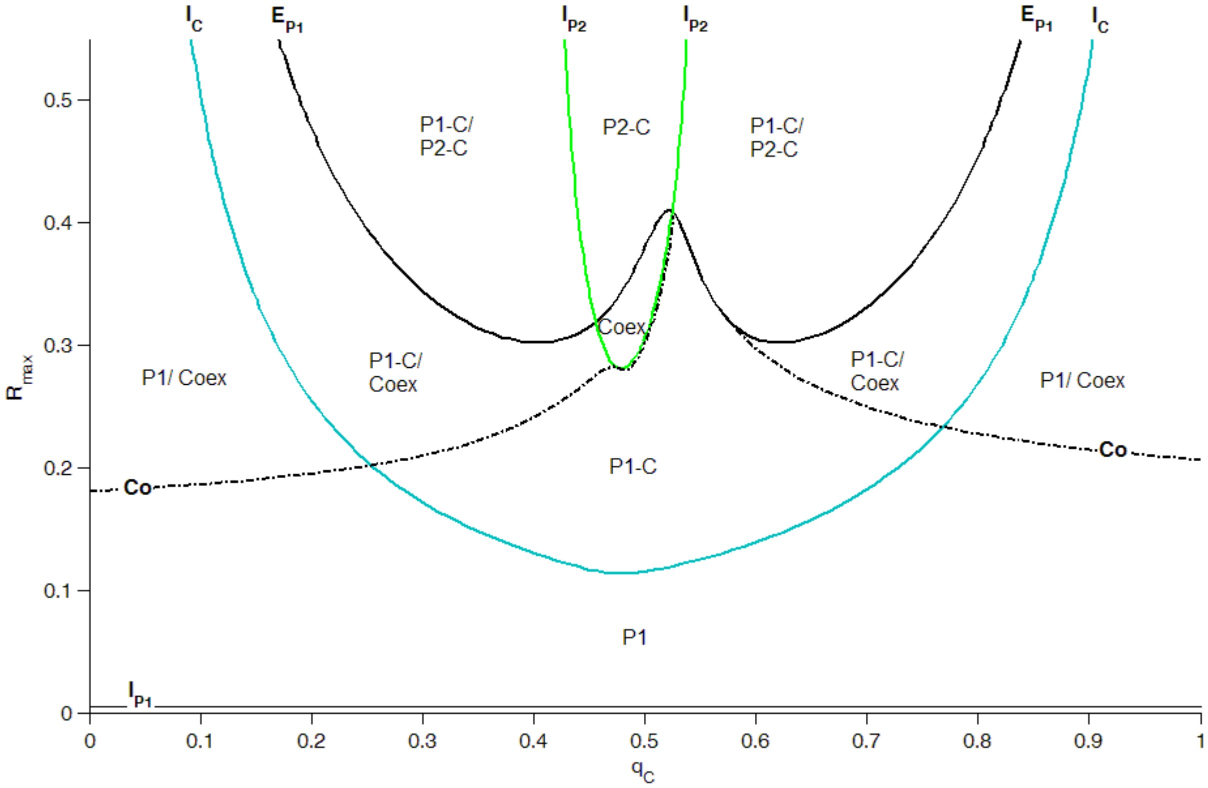

Fig. 2. Symmetrical niche model. Possible stable system states as a function of enrichment (R_{max}) and the degree of niche shift in the consumer (q_C). Labelling indicates the following states: P1 alone (P1), P1 and consumer (P1-C), P2 and consumer (P2-C), and coexistence (coex). In areas of bistability possible states are separated by a slash. Lines separate regions with unique combinations of single or alternative states and indicate invasion thresholds for P1 into an empty system (I_{P1}, thin black, solid), the consumer into a P1 state (I_C, blue), P2 into a P1-C state (I_{P2}, green), the extinction threshold for P1 from a coexistence equilibrium (E_{P1}, thick black, solid), and the minimum enrichment level needed for coexistence (Co, black dash-dotted). Parameters as in Table 2.1.

Enrichment patterns for different degrees of niche shift q_C

I first review the well-known case of a non-niche shifting consumer ($q_C = 0.5$, Fig. 3a), which recovers the classical diamond food web (Holt et al. 1994, Leibold 1996). At the lowest enrichment levels no species can persist in the system and (unused) resource concentrations are equal to R_{max}. At I_{P1} resource levels become high enough for the superior competitor *P1* to establish. As the consumer is absent, this threshold is independent of q_C (Fig. 2). With further enrichment *P1* increases (and controls the resource at a constant level) until it reaches a sufficient level for the consumer to invade. This occurs at I_C, where the *P1*-state is replaced by a *P1*-consumer state. Now *P1* is controlled by the consumer and only the consumer and the resource increase with further enrichment. When the resource has increased sufficiently, the inferior but less vulnerable competitor *P2* can invade and the *P1*-consumer state is replaced by the coexistence state. The corresponding threshold is labelled I_{P2}/*Co*, as the threshold for invasion of *P2* (I_{P2}) coincides with the threshold for coexistence (*Co*) at $q_C = 0.5$ (but not for most other values of q_C, see below). Within the coexistence state resource and consumer biomasses remain constant with further enrichment, while the superior competitor *P1* decreases and the less vulnerable competitor *P2* increases. With sufficient enrichment (threshold E_{P1}) *P1* goes extinct and coexistence is replaced by a *P2*-consumer state. Hence, for $q_C = 0.5$ there is a continuous sequence of unique stable states along an enrichment gradient (*P1* → *P1-C* → *coexistence* → *P2-C*). This continuous sequence remains qualitatively the same only within a very narrow range around $q_C = 0.5$ where the *Co* and I_{P2} lines coincide (Fig. 2).

With only a minor degree of niche shift in the consumer this pattern breaks down and alternative states become possible in increasingly larger regions of parameter space. For $q_C = 0.45$ the same five community states occur as in the unstructured case, but not in a continuous sequence. Instead, at intermediate enrichment levels I find bistability between the *P1*-consumer state and either the coexistence state (between *Co* and E_{P1}) or the *P2*-consumer state (between E_{P1} and I_{P2}) (Fig. 3b). The coexistence threshold (*Co*) and the minimum threshold for successful invasion of *P2* (I_{P2}) no longer coincide, and both the coexistence threshold (*Co*) and the threshold for extinction of *P1* from a coexistence state (E_{P1}) now occur at lower enrichment levels than I_{P2}. Bistability is accompanied by the appearance of an unstable (saddle) equilibrium (dashed line in Fig. 3b) between alternative stable states. Similar to the unstructured case *P1* will outcompete *P2* at low enrichment levels (below *Co*), whereas *P2* will outcompete *P1* at high enrichment levels (above I_{P2}). Over intermediate ranges of enrichment smooth transitions are, however, only possible between stable states with *P2* present, but not between stable states with *P2* present in one and absent in the other state. Alternative states are, in turn, stabilized by contrasting consumer population structure, with *P1* dominated states being associated with high biomass of the stage preferentially feeding on *P2* (adults in Fig. 3b), and *P2* dominated states with high biomass of the stage preferentially feeding on *P1* (juveniles in Fig. 3b). As a consequence, a competition-predation trade-off and hence coexistence only occurs when *P2* is dominant over *P1*, which also explains why a smooth transition between a state without *P2* to a coexistence state with (low biomass of) *P2* is impossible.

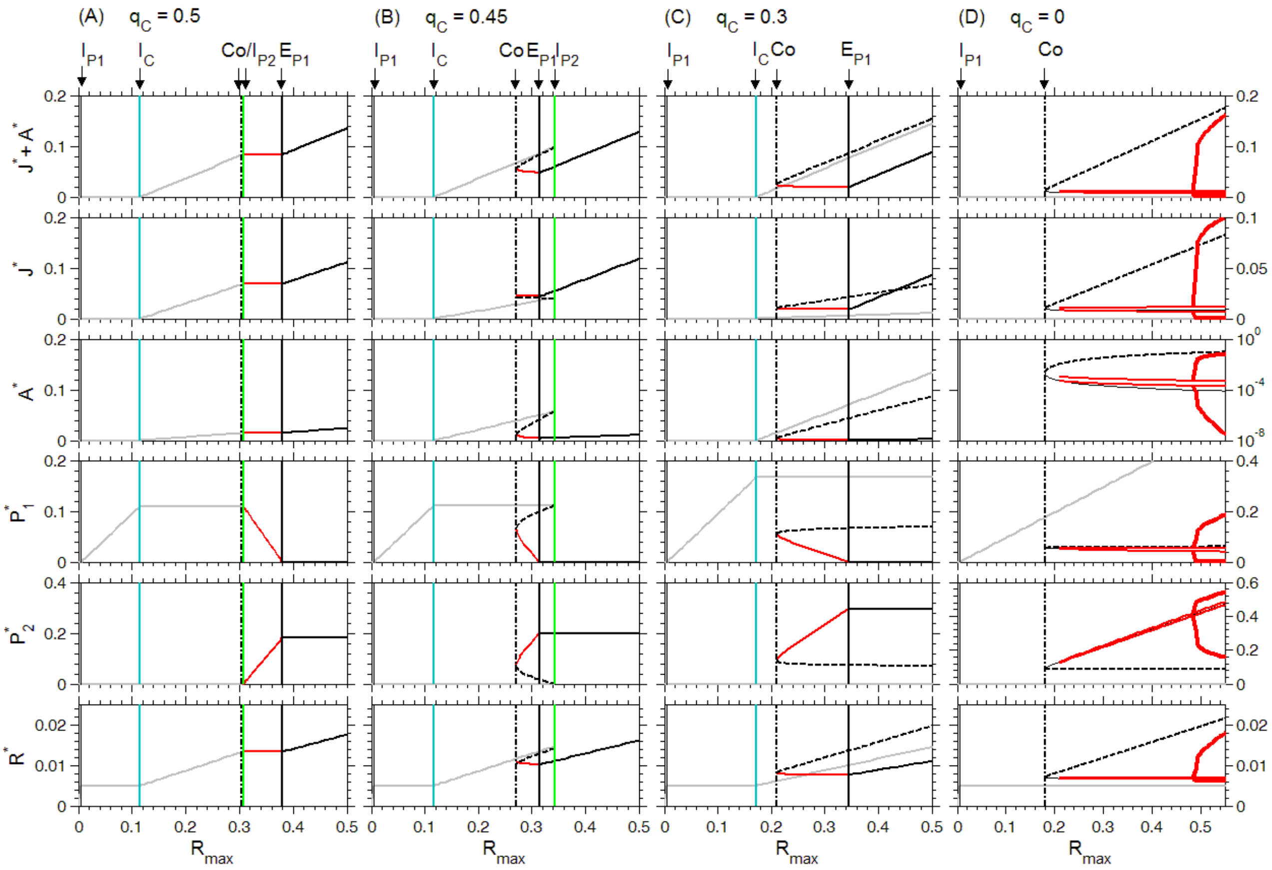

Fig. 3. Symmetrical niche model. Equilibrium biomasses (mgN L^{-1}) as a function of enrichment (R_{max}) for values of the niche shift parameter q_C of (A) 0.5, (B) 0.45, (C) 0.3, and (D) 0.0. Rows display equilibrium biomasses of total consumers ($C^* = J^* + A^*$), juveniles (J^*), adults (A^*), primary producers ($P1^*$, $P2^*$), and resource (R^*). Vertical lines indicate invasion and extinction thresholds, labelled as in Fig. 2. Different community states are colour coded: grey = P2 absent, red = coexistence, black = P1 absent. Dashed lines indicate unstable (saddle) equilibria separating two alternative states. For q_C = 0 thin and thick red lines indicate minima and maxima of a small and a large amplitude cycle, respectively. Note that the scales of most y-axes in panel D differ from panels A-C (A^* being shown on a logarithmic scale). Parameters as in Table 2.1.

With stronger niche shifts in the consumer (e.g. $q_C = 0.3$) all of the patterns described for $q_C = 0.45$ become more accentuated. In particular, the enrichment threshold I_{P2} for invasion of *P2* into a *P1*-consumer system shifts to infinity (Fig. 2). Thus *P2* cannot invade a *P1*-consumer equilibrium from low density at any enrichment level (Fig. 3c). Instead, a *P1*-consumer equilibrium exists as an alternative stable state to either a *P2*-consumer equilibrium (at high enrichment) or a coexistence state (at intermediate enrichment; Fig. 3c). This coexistence region is considerably larger than the coexistence region in the unstructured case and becomes even larger with further diet specialization of the consumer stages (Fig. 2). Note that for most enrichment levels total consumer biomass is higher in the *P1*-consumer state than in both the coexistence and the *P2*-consumer states (Fig. 3c), suggesting that communities dominated by the inferior competitor *P2* channel energy less efficiently to the consumer than do communities with abundant *P1*.

For $q_C = 0$ juvenile and adult diets do not overlap at all. The consumer then cannot persist in a system with only one prey (E_{P1} and I_C shift to infinity; Fig. 2). Hence the only possible states are a *P1*-only and a coexistence state, the latter again being dominated by *P2* (Fig. 3d). In coexistence all populations cycle with very small amplitude. At higher enrichment levels a second large amplitude cycle emerges around the first one. Importantly, compared to the unstructured case, the range of enrichment permitting coexistence is substantially enlarged, extending to infinite enrichment (Fig. 2). Losing an arbitrary community member from a coexistence state makes subsequent extinctions of other species inevitable, leaving a system with only one primary producer from which it is difficult to return to the coexistence state.

Shifting mechanisms of predator-mediated coexistence with shifting diet specialization

For very weak niche shifts (q_C near 0.5 in the symmetrical niche model), predator mediated coexistence is governed by the same mechanism as in the unstructured case; i.e. the inferior resource competitor balances its competitive disadvantage by being intrinsically better defended against both stages of the consumer. For most parameterizations this balance is only met over a narrow range of enrichment. Because the superior resource competitor *P1* always has a higher per capita growth rate than *P2*, a competition-predation trade-off must also be responsible for coexistence at intermediate to complete niche shifts. This trade-off is, however, not defined a priori but emerges from changes in the consumer population structure. With the baseline parameterization, for example, the inferior competitor *P2* suffers from higher predation by adults than does *P1* for all $q_C < 0.375$, whereas *P1* remains more vulnerable to juvenile consumers. Conversely, at $q_C > 0.625$ *P2* suffers from higher predation by juveniles than does *P1*. Thus, an ‘emergent’ competition-predation trade-off arises for $q_C < 0.375$ if adult biomass is not too high relative to juvenile biomass, and for $q_C > 0.625$ if juvenile biomass is not too high. Accordingly, the coexistence state is always characterized by high juvenile and low adult consumer biomass at low q_C and by the opposite consumer population structure at high q_C (Fig. 4).

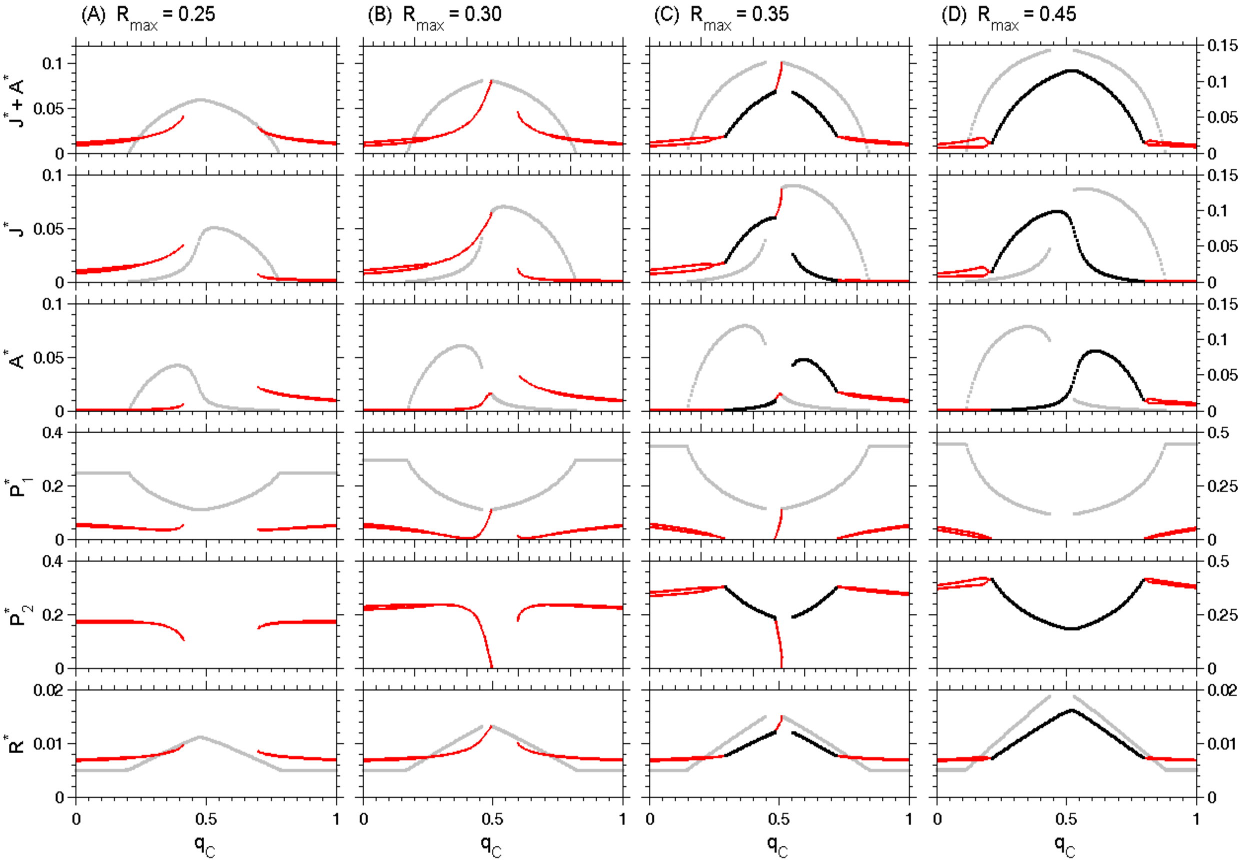

Fig. 4. Symmetrical niche model. Equilibrium biomasses (mgN L^{-1}) as a function of the niche shift parameter q_C for values of R_{max} of (A) 0.25, (B) 0.30, (C) 0.35, and (D) 0.45. Rows display equilibrium biomasses of total consumers ($C^* = J^* + A^*$), juveniles (J^*), adults (A^*), primary producers $P1^*$ and $P2^*$, and resource (R^*). Different community states are colour coded as in Fig. 3: grey = P2 absent, red = coexistence, and black = P1 absent. For better visibility invasion and extinction thresholds from Fig. 2 are not displayed. Note that the scales of the y-axes in panel D differ from panels A-C. Parameters as in Table 2.1.

In the same vein, emergence of a consumer population structure that weakens the intrinsic competition-predation trade-off explains why an alternative *P1-C* state cannot be invaded by *P2* from low density. *P1-C* states are always dominated by the consumer stage (adults at $q_C < 0.5$, juveniles at $q_C > 0.5$) that has a relatively higher feeding rate on the inferior competitor *P2* and a relatively lower feeding rate on the superior competitor *P1*. Consequently, the intrinsic competition-predation trade-off is weakened (and disappears completely at values of $q_C < 0.375$ and $q_C > 0.625$, respectively), making the *P1-C* state non-invasible for *P2*.

Contrasting patterns of consumer population structure also characterize situations where *P1-C* and *P2-C* are the respective alternative states (at higher R_{max}, see Fig. 4c, d). Typically, in systems with non-interacting prey species, a niche shifting consumer population tends to settle to one of two alternative coexistence states, which are dominated by either juvenile or adult biomass (De Roos et al. 2007, Schreiber & Rudolf 2008, Guill 2009, Schellekens et al. 2010). Because prey species compete, only one of these two coexistence states is possible in the diamond food web. This coexistence state is always characterized by strong predation pressure on the superior competitor *P1* and dominance of the inferior competitor *P2* over *P1*. Therefore, the consumer stage relying more on *P1* is strongly food limited, and biomass transfer (through maturation or reproduction) from this stage to the next is low, whereas biomass transfer from the stage relying more on *P2* to the limited stage is high. Hence consumer biomass accumulates in the food limited bottleneck stage feeding on *P1*. This feedback between the two stages relaxes predation pressure on *P2*, but enhances predation pressure on the superior competitor *P1*, thus enabling coexistence.

The degree of niche shift not only influences consumer population structure but, as indicated above, feeds also back on the absolute biomasses of consumers, prey, and the resource. Generally, within a given equilibrium state total consumer biomass and the resource increase with decreasing niche shift (moving from extreme values of q_C towards $q_C = 0.5$), while total prey biomass (*P1* + *P2*) decreases (Fig. 4). For most values of q_C total consumer biomass is higher in the *P1-C* state than in the alternative coexistence or *P2-C* states. Prey biomass is always dominated by *P2* in coexistence states, and *P1* is always greatly reduced in a coexistence state compared to an alternative *P1-C* state (Fig. 4). The potential of a niche shift to enhance coexistence becomes most obvious at the lowest and highest levels of enrichment (Fig. 4a and d), where coexistence is possible for extreme to intermediate degrees of niche shift, but impossible near $q_C = 0.5$ (unstructured case). Thus, the predator facilitates itself by enabling prey coexistence in regions of the R_{max}-q_C space (near $q_C = 0$ and 1) where it cannot establish in a one-prey system (Figs. 2, 4).

Coexistence in absence of an intrinsic competition-predation trade-off

The role of consumer niche shifts and the operation of the emergent competition-predation trade-off in mediating the coexistence of resource competitors is nicely illustrated with a different model parameterization. When clearance rates for both prey species are assumed to be identical ($a_{CP1} = a_{CP2}$), the formerly assumed intrinsic competition-predation trade-off disappears. Coexistence is then impossible in the absence of a consumer niche shift ($q_C = 0.5$, i.e. the ‘classical’ unstructured diamond web) but is still fully feasible (as one of two alternative states) over increasingly larger ranges of enrichment towards more pronounced niche shifts (Fig. 5). Bistability between a *P1*-consumer and a *P2*-consumer state is also possible with moderately niche shifting consumers, but the absence of an emergent competition-predation trade-off makes it impossible for *P2* to persist at weaker niche shifts, regardless of the level of enrichment (Fig. 5).

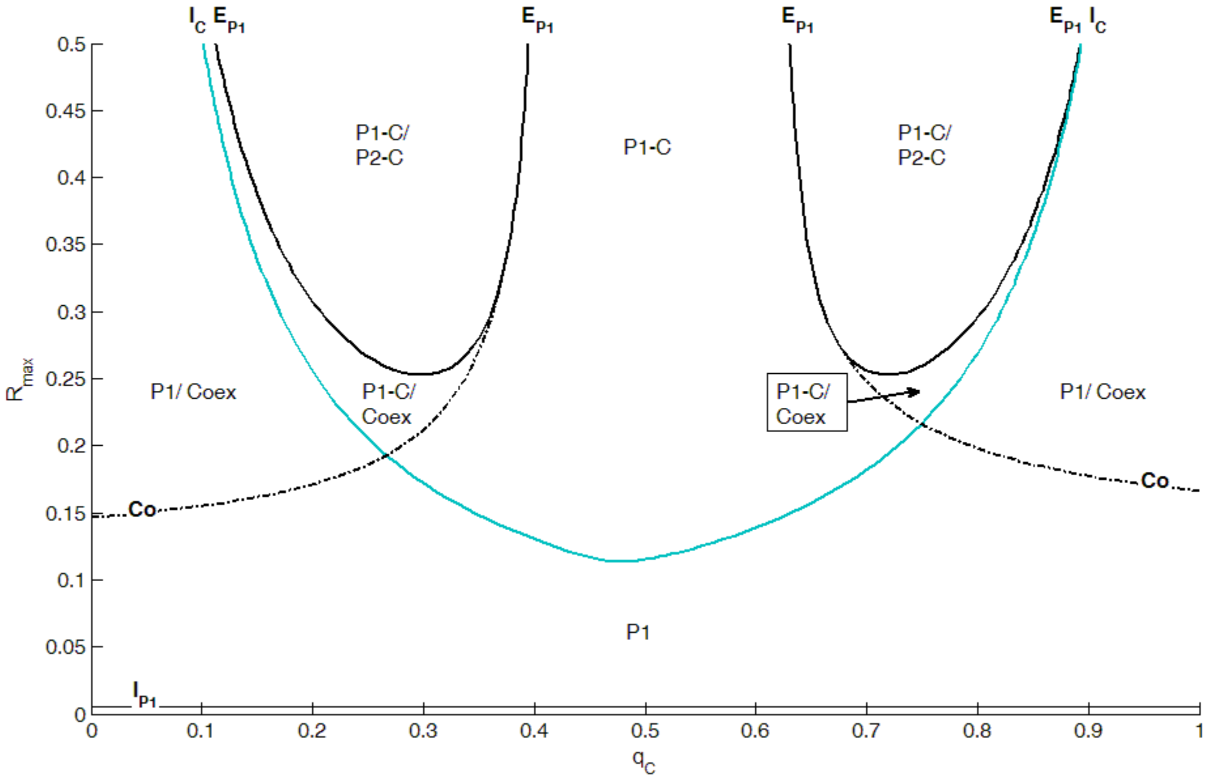

Fig. 5. Symmetrical niche model. Possible stable system states as a function of enrichment (R_{max}) and the degree of niche shift in the consumer (q_C). Parameters as in Table 2.1, except that clearance rates of the consumer for both prey species are identical ($a_{CP1} = a_{CP2} = 4$). Labelling of system states and definitions of lines as in Fig. 2.

Discussion

I have shown that an ontogenetic diet shift in a shared consumer can strongly promote coexistence of competing prey, the effect being the stronger the more pronounced the consumer's diet shift. The underlying mechanism involves the development of a bottleneck stage in the consumer population, which increases predation pressure on the superior resource competitor while simultaneously relaxing predation pressure on the inferior resource competitor. Thus, while coexistence in the 'classical' diamond food web requires an intrinsic competition-predation trade-off in the prey (Holt et al. 1994, Leibold 1996), this condition is not required when the consumer undergoes an ontogenetic diet shift. Instead, such a trade-off can emerge dynamically as a consequence of consumer population structure regardless of the traits of the prey species. Note, however, that the (realistic!) assumption of food dependence of both reproduction and individual growth and maturation (De Roos et al. 2007) is crucial for this feedback mechanism to become expressed.

Highlighting the generality of this mechanism, the results are robust against different parameter settings (Fig. 5 and unpublished results) and against different model assumptions. In addition to the ‘symmetrical niche’ model I also investigated an ‘inclusive niche’ model, in which the two consumer stages are always fully specialized on opposite prey types and attack the alternative prey with efficiency q_C. Hence, this case is identical to the symmetrical niche model at $q_C = 0$ (complete niche shift), whereas equality with the unstructured case (no niche shift) is reached at $q_C = 1$. Overall, this alternative model yields qualitatively similar results (see Appendix A2.1). The same results are also obtained under the assumption of a closed system in which losses from excretion, respiration and mortality are immediately recycled to the inorganic nutrient pool (see Appendix A2.2). Given the prevalence of ontogenetic shifts in resource use among many consumer species (Werner & Gilliam 1984, Werner 1988) the reported phenomena should therefore be of high relevance to real food webs.

My results suggest furthermore that the predictions derived for the case of an unstructured consumer may be applicable to only a limited set of natural systems. Just a slight ontogenetic niche shift in the consumer is required to introduce bistability and produce qualitatively different predictions. The resulting alternative stable states are a very general property of webs with stage structured consumer populations, provided that both stages can potentially control their respective food source (Guill 2009, Nakazawa 2011), and are typically characterized by contrasting dominance patterns within the structured population (De Roos et al. 2007, Schreiber & Rudolf 2008, Guill 2009, Hin et al. 2011).

Independently of whether prey species compete or not, coexistence states are always governed by the same mechanism, i.e. high biomass of prey for one consumer stage leads to fast recruitment to and hence dominance by the other consumer stage (Schreiber & Rudolf 2008). The major difference between systems with and without an additional competitive link between prey species is that at most one of the alternative states allows for prey coexistence if the prey compete. A competition-predation trade-off emerges dynamically only if the consumer stage that preys most efficiently on the superior resource competitor is dominant. If the consumer stage preying most efficiently on the inferior resource competitor dominates the latter is excluded. At extreme values of niche shift, however, exclusion of one prey also leads to the exclusion of the consumer itself. Hence the alternative state to coexistence is a depauperate community with only the superior resource competitor.

My results share some commonalities with another simple food web that integrates competition and predation, i.e. the intraguild predation (IGP) web. Here the intraguild predator simultaneously feeds on the intraguild prey and competes with it for the shared resource. Coexistence in an unstructured IGP web requires that the intraguild prey is the superior resource competitor, but coexistence is typically predicted over only a narrow range of intermediate enrichment levels (Holt & Polis 1997, Diehl & Feißel 2000, Diehl 2003). The assumption that the IGpredator performs an ontogenetic diet shift between its two alternative prey yields similar results as in the diamond web. Specifically, the region of coexistence becomes enlarged with more pronounced diet shifts and extends towards infinite enrichment at extreme diet shifts (Hin et al. 2011).

Despite the potentially positive effect of pronounced ontogenetic diet shifts on prey coexistence my results also suggest that, once such a coexistence state is lost, it may not be easily restored. The sensitivity of highly specialized life stages to resource loss and its consequences for food web stability and resilience have recently been highlighted by Rudolf & Lafferty (2011), who cautioned that stage structure can reverse a positive complexity-stability relationship into a negative one. Ecologists have become increasingly aware of the potential for alternative stable states in many real ecosystems (Scheffer & Carpenter 2003, Folke et al. 2004), including freshwater (Carpenter et al. 1999), marine (Hare & Mantua 2000), and terrestrial systems (Staver et al. 2011). The potential role of stage structure in the occurrence of regime shifts and the stabilization of alternative states has, however, so far received relatively little attention (De Roos & Persson 2002, Persson & De Roos 2003, Rudolf 2007, Schreiber & Rudolf 2008, Van Leeuwen et al. 2008, Schröder et al. 2012). Particularly in the context of overexploited fish stocks there is strong evidence that feedbacks between different life stages may be responsible for the lack of recovery in spite of fishing moratoria (De Roos & Persson 2002, Huss et al. 2012).

My results strengthen the importance of recognizing population structure with food-dependent transitions between size classes or stages as a critical dynamical component of natural communities. While feedbacks between predator stages and their prey species potentially enhance diversity, they also introduce the possibility of alternative states, and disturbances can lead to sudden shifts to depauperate communities. Future research should therefore investigate how diverse alternative community states can be maintained and restored. Two candidate mechanisms have recently been explored in the unstructured diamond food web. Seasonality of the environment can create temporal invasion windows (Klausmeier & Litchman 2012), while source-sink dynamics can locally maintain threatened populations in larger meta-communities (Amarasekare 2008). This calls for future investigations of the potential influence of these processes on local and regional persistence of stage structured consumers and the communities they depend on.

Table 2.1. Dynamical equations, state variables and parameters of the standard (= ‘symmetrical niche’) model.

Dynamical equations	Description
(T1.1) $\frac{dR}{dt} = l(R_{\max} - R) - a_{P1R}RP_1 - a_{P2R}RP_2$	Dynamics of resource
(T1.2) $\frac{dP_1}{dt} = ea_{P1R}RP_1 - (1 - q_C)a_{CP1}P_1J - q_Ca_{CP1}P_1A - m_{P1}P_1$	Dynamics of superior resource competitor (*P1*)
(T1.3) $\frac{dP_2}{dt} = ea_{P2R}RP_2 - q_Ca_{CP2}P_2J - (1 - q_C)a_{CP2}P_2A - m_{P2}P_2$	Dynamics of inferior resource competitor (*P2*)
(T1.4) $\frac{dJ}{dt} = v_A^+(P_1, P_2)A + v_J(P_1, P_2)J - y(v_J^+(P_1, P_2))J - m_CJ$	Dynamics of juvenile consumers
(T1.5) $\frac{dA}{dt} = y(v_J^+(P_1, P_2))J + v_A(P_1, P_2)A - v_A^+(P_1, P_2)A - m_CA$	Dynamics of adult consumers

Functions	Description
(T1.6) $v_J(P_1, P_2) = \sigma((1 - q_C)a_{CP1}P_1 + q_Ca_{CP2}P_2) - T$	Net biomass production of juveniles
(T1.7) $v_A(P_1, P_2) = \sigma(q_Ca_{CP1}P_1 + (1 - q_C)a_{CP2}P_2) - T$	Net biomass production of adults
(T1.8) $y(v_J^+(P_1, P_2)) = \begin{cases} \frac{v_J(P_1, P_2) - m_C}{1 - z^{(1 - m_J/v_J(P_1, P_2))}} & \text{if } v_J > 0 \\ 0 & \text{if } v_J \le 0 \end{cases}$	Maturation rate of juvenile into adult biomass
(T1.9) $v_A^{\prime +}(P_1, P_2) = \begin{cases} v_A & \text{if } v_A \ge 0 \\ 0 & \text{if } v_A < 0 \end{cases}$	Production rate of biomass of newborns by adults

Variables	Unit	Definitions
J	mgN L^{-1}	Biomass density of juvenile consumers
A	mgN L^{-1}	Biomass density of adult consumers
P_1	mgN L^{-1}	Biomass density of producer 1 (superior resource competitor)
P_2	mgN L^{-1}	Biomass density of producer 2 (inferior resource competitor)
R	mgN L^{-1}	Density of shared resource (assumed to be nitrogen)

Table 2.1 continued.

Parameters	**Values**	**Units**	**Definitions**
R_{max}	0-0.6	mgN L^{-1}	Maximum resource density
T	0.1	day^{-1}	Maintenance rate of juvenile and adult consumers
L	0.1	day^{-1}	Nutrient renewal rate
z	0.01	$mgN(mgN)^{-1}$	Ratio of newborn to adult body mass
m_C	0.01	day^{-1}	Mortality rate of consumer
q_C	0-1	dimensionless	Relative foraging efficiency of adults on *P1* and of juveniles on *P2*
σ	0.5	$mgN(mgN)^{-1}$	Conversion efficiency of producer into consumer biomass
a_{CP1}	4	$L(mgN*day)^{-1}$	Clearance rate of consumer for *P1*
a_{CP2}	2.4	$L(mgN*day)^{-1}$	Clearance rate of consumer for *P2*
e_{CP1}	1	$mgN(mgN)^{-1}$	Conversion efficiency of *P1* for *R*
e_{CP2}	1	$mgN(mgN)^{-1}$	Conversion efficiency of *P2* for *R*
a_{P1R}	20	$L(mgN*day)^{-1}$	Clearance rate of *P1* for *R*
a_{P2R}	15	$L(mgN*day)^{-1}$	Clearance rate of *P2* for *R*
m_{P1}	0.1	day^{-1}	Mortality plus maintenance rate of *P1*
m_{P2}	0.1	day^{-1}	Mortality plus maintenance rate of *P2*

Appendix A2.1 The inclusive niche model

In addition to the ‘symmetrical niche’ model I also investigated an ‘inclusive niche’ model, in which the two consumer stages are always fully specialized on opposite prey types (implemented by replacing 1-q_C with 1 in eqs. T1.6 and T1.7) and attack the alternative prey with efficiency q_C. Hence at $q_C = 0$ the two models are identical and foraging effort on the alternative prey increases with q_C until both stages spend equal foraging effort on both prey species at $q_C = 1$. As in the symmetrical niche model at $q_C = 0.5$, at $q_C = 1$ the inclusive niche model retrieves the unstructured case without a niche shift, but with a doubled feeding rate (compare eq. A2.1-1 to eq. 1):

$$\frac{d(J+A)}{dt} = (\sigma(a_{CP1}P_1 + a_{CP2}P_2)\text{-}T)(J+A)\text{-}m_C(J+A) \qquad \text{(A2.1-1)}$$

Consequently, the graph of possible system states in R_{max}-q_C space (Fig. A2.1.1; $0 \leq q_C \leq 1$) looks very similar to the left half of the corresponding graph for the symmetrical niche model (Fig. 2; $0 \leq q_C \leq 0.5$), with similar relative positioning of the state transition boundaries. Importantly, an alternative coexistence state arises again over increasingly larger ranges of enrichment towards increasing niche shift in the consumer, supporting that the described emergent competition-predation trade-off is a generic feature of the diamond food web with a stage structured, niche shifting top consumer.

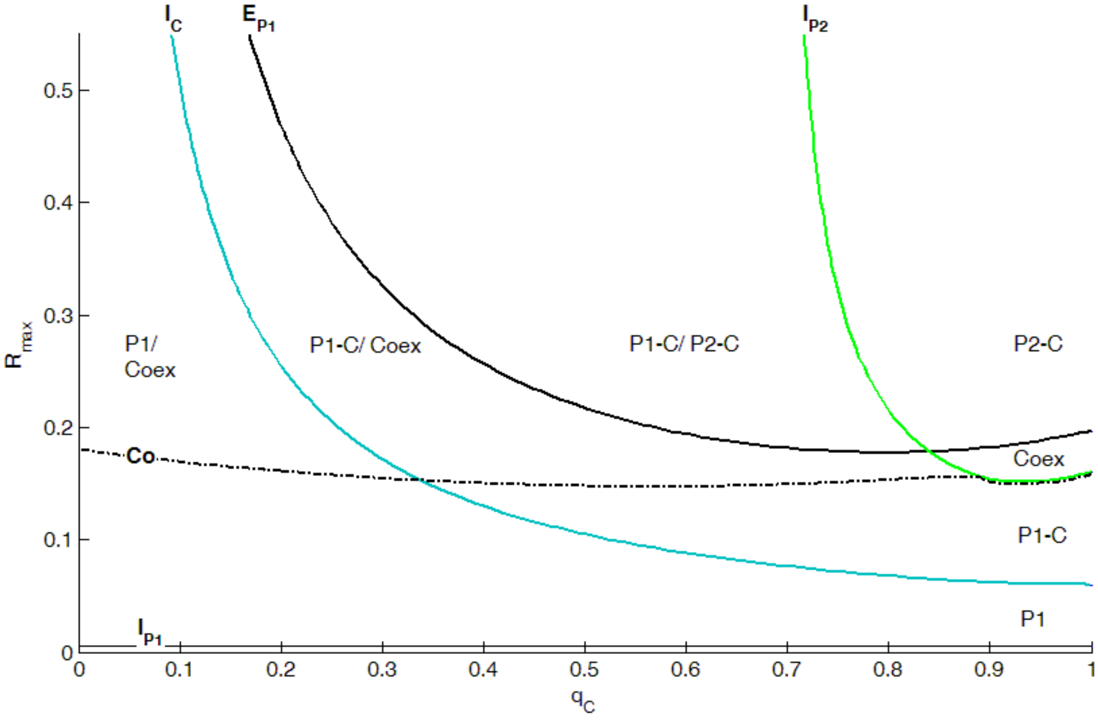

Figure A2.1.1. Inclusive niche model. Possible stable system states as a function of enrichment (R_{max}) and the degree of niche shift in the consumer (q_C). Parameters as in Table 2.1, except that the parameter (1- q_C) is set equal to 1. Labelling of system states and definitions of lines as in Fig. 2.

Appendix A2.2 The symmetrical niche model under the assumption of nutrient recycling

In the original model formulation the system is assumed to be open with respect to nutrients. Mineral nutrients enter the system at constant rate l and concentration R_{max} and leave the system at the same rate. Furthermore it is assumed that losses from excretion, respiration and mortality are not recycled to the inorganic nutrient pool. To ascertain how these assumptions influence the qualitative outcome of the system, I additionally investigated the dynamics of the stage-structured diamond food web under the assumption of a closed system. In a closed system all state variables (which are measured in terms of nutrient content, mg N/L, see Table 2.1) sum up to the total amount of nutrients in the system R_{tot}, which is assumed to be constant in time. To calculate the concentration of mineral nutrients I therefore replaced the equation for resource dynamics in the original model (T1.1) by a mass balance constraint (A2.2-1), keeping all other equations and parameter values the same:

$$R = R_{tot} - P1 - P2 - J - A \qquad \text{(A2.2-1)}$$

With this model formulation all nutrients not assimilated into living biomass are available for primary production, i.e. it is assumed that nutrients from dead biomass and non-assimilated food are immediately recycled.

Calculation of the invasion boundaries for $P1$, the top consumer and $P2$ as a function of q_C and productivity level (now given by R_{tot}) reveal that the shapes and positions of the boundaries in the resulting q_C-R_{tot} plot (Fig. A2.2.1) are nearly identical to the original q_C-R_{max} plot (Fig. 2). Notably, the result that more pronounced niche shifts greatly enhance the coexistence range along the productivity axis still holds.

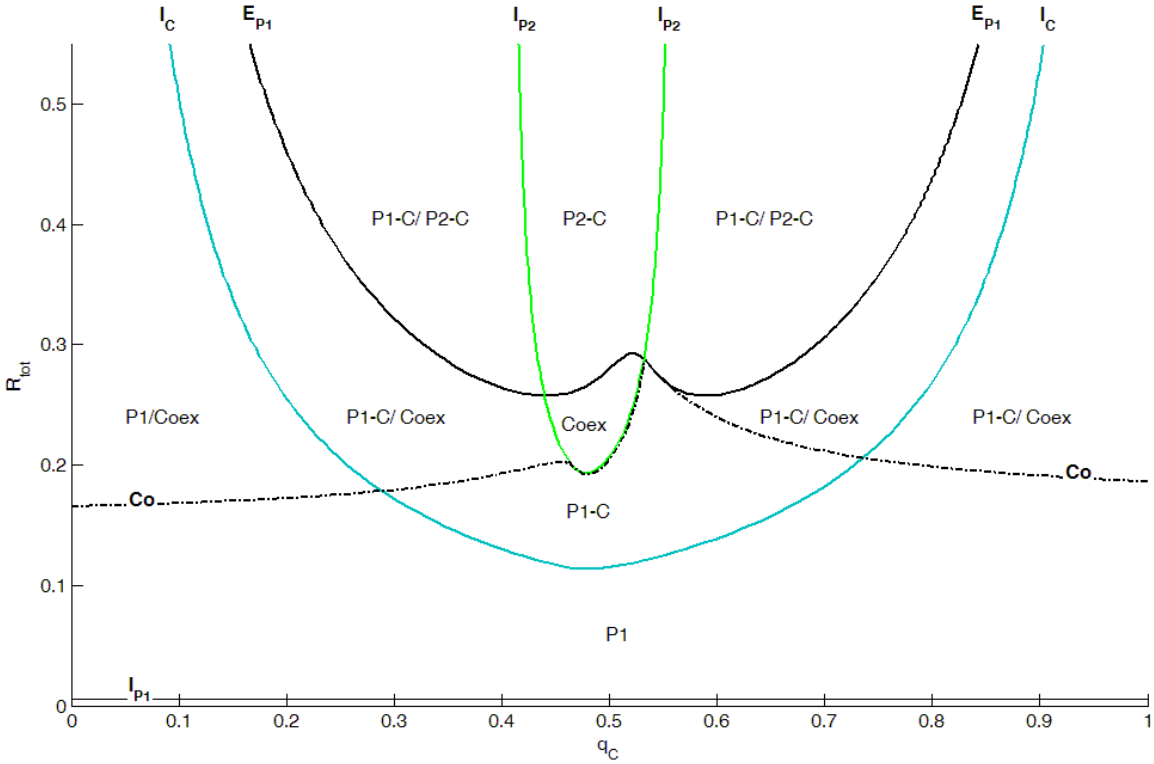

Fig. A2.2.1. Symmetrical niche model under the assumption of a closed system with instant nutrient recycling. Possible stable system states as a function of total amount of nutrients in the system (R_{tot}) and the degree of niche shift in the consumer (q_C). Parameters specifying the dynamics of P1, P2, and C as in Table 2.1. Labelling of system states and definitions of lines as in Fig. 2.

Chapter 3

Consumer functional response type mediates bottom-up responses of the ‘pentagon module’ in the lower oceanic food web

Abstract

It is well established that the dynamics of pairwise consumer-resource interactions depend on the shape of the functional response, which describes consumption rate as a function of food abundance. It has been much less explored how the shape of the functional response affects the dynamics of entire communities, especially when consumers feed on resources that are dynamically linked through multiple pathways. Here I theoretically investigate the influence of the functional response (type 2 vs. type 3) of the top consumer on the dynamics of a looped food web with five compartments (‘pentagon web’), exemplified by the lower oceanic web consisting of a shared limiting nutrient, two groups of primary producers (small nano- and large microphytoplankton), ciliates feeding on nanophytoplankton, and copepod top consumers feeding on ciliates and microphytoplankton. Numerical analyses reveal that the top consumer’s functional response can have dramatic consequences for community responses to bottom-up (nutrient enrichment) and top-down (copepod mortality) forcing. Specifically, when top consumers have a type 3 response (as demonstrated for several copepod species) the pentagon web is strongly stabilized, but may show non-monotonic responses to enrichment and multiple coexistence states. The underlying mechanisms involve an interplay between feeding behavior (switching towards the more abundant prey) and structural properties of the pentagon web (yielding negative covariance between alternative prey). My results have important implications for the interplay of bottom-up and top-down forcing in the lower oceanic food web and demonstrate that switching effects inherent to the type 3 functional response can be amplified by food web topology to produce complex community responses to environmental forcing.

Introduction

The functional response, which describes the relationship between a consumer's per capita consumption rate and resource abundance, quantitatively links the dynamics of consumers and their resources and therefore is a crucial determinant of community and ecosystem dynamics (Holling 1973, Murdoch & Oaten 1975, Hassell et al. 1977, Nunney 1980, Yodzis & Innes 1992, Fussmann & Blasius 2005). Based on empirical data it is, however, often difficult to unambiguously determine the shape of a functional response. For example, the fundamental distinction between a destabilizing, downward concave type 2 functional response and a stabilizing, sigmoid type 3 functional response depends critically on the availability of high quality data at very low prey densities, which are rarely collected (Sarnelle & Wilson 2008). Thus, while existing empirical data suggest a prevalence of type 2 functional responses among species (reviewed in Jeschke et al. 2004), other studies caution that the type 3 might be more common than generally assumed (Hassell et al. 1977, Chow-Fraser & Sprules 1992, Sarnelle & Wilson 2008).

In simple one predator-one prey systems a type 3 functional response is stabilizing when the equilibrium density of the prey is in a region where per capita mortality of the prey increases with prey density (Oaten & Murdoch 1975). The resulting negative feedback tends to move prey density back to equilibrium after a temporary disturbance (Murdoch et al. 2003). In contrast, a type 2 functional response is always destabilizing since per capita prey mortality decreases over the entire range of prey densities, thus creating positive feedback between prey density and prey population growth (Oaten and Murdoch 1975). Being relatively well understood in the setting of simple one predator-one prey systems (Murdoch et al. 2003, Fussmann & Blasius 2005), it is much less clear how the functional response type affects system behavior and stability in food webs with multiple interacting species and where predators may feed on more than one prey. For a predator with multiple prey and a type 2 functional response, the relative feeding effort for different prey types is proportional to their relative abundances in the environment. In contrast, with a functional response type 3 the predator feeds disproportionately more on the more abundant prey, releasing the alternative prey from predation pressure. The latter behaviour has been termed switching (sensu Murdoch 1969). It is conceivable that switching effects could be either damped or amplified when consumers feed on resources that are dynamically linked through multiple trophic pathways in a food web. To my knowledge this possibility has not yet been explored.

One of the few studies investigating the influence of alternative functional response types on the dynamics of multispecies food webs was performed by Gismervik & Andersen (1997).

They theoretically studied the dynamics of a marine, planktonic intraguild predation system in which copepods act as top consumers preying simultaneously on ciliates (intraguild prey) and a shared algal resource with either a type 2 or a type 3 functional response. Copepods, like many other zooplankton taxa, have been traditionally assumed to exhibit a type 2 functional response (Mullin et al. 1975, Kleppel 1993), but there is good evidence that several ecologically important copepod species have a type 3 functional response (Frost 1975, Chow-Fraser & Sprules 1992, Gismervik & Andersen 1997). Copepods are, in turn, a crucial link between the marine micro- and macrofauna, serving as an important food source for most planktivorous fishes in the global ocean (Nunn et al. 2012). The factors controlling energy transfer through the lower oceanic food web to zooplankton is therefore the focus of much recent research, as is the impact of zooplankton grazing on phytoplankton diversity and productivity (Sommer & Stibor 2002, Stibor et al. 2004, Shin et al. 2010). Theoretical studies suggest that the functional response type of copepods has a crucial impact on these processes (Prowe et al. 2012).

While the theoretical study of Gismervik & Andersen (1997) reveals strong potential effects of the copepod functional response type on overall system dynamics (a type 3 response being strongly stabilizing and greatly enhancing the parameter space allowing for coexistence of ciliates with copepods), their representation of the planktonic food web simplifies the (often distinct) feeding niches of ciliates and copepods. Typically, many copepods feed preferentially on larger (micro-)phytoplankton taxa (e.g. diatoms), while most ciliates feed preferentially on smaller (nano-)phytoplankton (Sommer & Stibor 2002, Sommer et al. 2005). The two size classes of algae therefore give rise to two distinct food chains, one from small phytoplankton over ciliates to copepods and an alternative chain from large phytoplankton directly to copepods. Short-term field experiments have shown that the existence of these alternative food chains can bring about contrasting responses of the two phytoplankton size fractions to bottom-up and top-down forcing, with copepods acting as a switch between these food chains and the summed, total phytoplankton response being dependent on the initial size structure of the phytoplankton community (Stibor et al. 2004).

In the present study I expand on these experimental results and theoretically investigate the influence of the functional response type of copepod top consumers on the dynamics of a (still simplified) representation of the lower oceanic food web that differentiates two size groups of primary producers (nano- and microphytoplankton), ciliates, copepods, and a growth limiting nutrient (Fig. 1). For ease of description I term this food web the ‘pentagon module’, acknowledging that a similar term has been used by Grover (2002) to describe a differently structured web with five compartments. Because human impacts on this part of the oceanic food web act primarily at the bottom (e.g. through eutrophication) and at the top (e.g. through fishing induced alterations of copepod mortality), I explore the dynamical consequences of different copepod functional responses (linear, type 2, type 3) along gradients of nutrient enrichment and for different levels of copepod mortality.

Model description

The 'pentagon module' of the lower oceanic food web consists of five compartments, a limiting nutrient at the base of the web which is assumed to be nitrogen (*R*), two competing groups of primary producers differing in size, i.e. small (nanophytoplankton, P_S) and large (microphytoplankton, P_L) primary producers, ciliates (*C*) feeding on P_S, and copepod top consumers (*TC*) feeding on P_L as well as on *C* (Fig. 1e). Dynamics of the pentagon module are described by a dynamic equation system. I assume a closed, well-mixed system with the total amount of nitrogen given by R_{tot}. Parameter values and the forms of the functional responses were chosen from the literature (see Table 3.1). All biomass densities are measured in units of nitrogen, assuming constant carbon to nitrogen ratios for all species. Because the system is closed all state variables obey a mass balance constraint which implicitly determines the concentration of free nutrient *R* (dissolved mineral nitrogen) (Eq. 1). The dynamics of all other state variables are described by differential equations 2-5:

$$R = R_{tot} - P_S - P_L - C - TC \qquad (1)$$

$$\frac{dP_L}{dt} = P_L\left(\frac{e_{RP_L} a_{RP_L} R}{1 + a_{RP_L} h_{RP_L} R} - m_{PL}\right) - \frac{a_{P_L TC} P_L^n}{1 + a_{P_L TC} h_{P_L TC} P_L^n + a_{CTC} h_{CTC} C^n} TC \qquad (2)$$

$$\frac{dP_S}{dt} = P_S\left(\frac{e_{RP_S} a_{RP_S} R}{1 + a_{RP_S} h_{RP_S} R} - m_{PS} - \frac{a_{P_S C} C}{1 + a_{P_S C} h_{P_S C} P_S}\right) \qquad (3)$$

$$\frac{dC}{dt} = C\left(\frac{e_{P_S C} a_{P_S C} P_S}{1 + a_{P_S C} h_{P_S C} P_S} - m_C\right) - \frac{a_{CTC} C^n}{1 + a_{P_L TC} h_{P_L TC} P_L^n + a_{CTC} h_{CTC} C^n} TC \qquad (4)$$

$$\frac{dTC}{dt} = TC\left(\frac{e_{P_L TC} a_{P_L TC} P_L^n + e_{CTC} a_{CTC} C^n}{1 + a_{P_L TC} h_{P_L TC} P_L^n + a_{CTC} h_{CTC} C^n} - m_{TC}\right) \qquad (5)$$

The biomasses of all intermediate species (P_L, P_S, and *C*) increase in proportion to the uptake of their respective prey/resources (*R* or P_S) (left hand terms in Eqs. 2-4). For both ciliates and primary producers the uptake terms are described by a functional response type 2 (Holling 1959, 1965) with attack rate a_{IJ} and handling time h_{IJ} of consumer *J* for prey/resource *I* (note that the Holling type 2 notation is fully equivalent to the Monod notation more commonly used for nutrient dependent growth of microalgae). Consumed prey/resources are converted into consumer biomass with conversion efficiency e_{IJ}. All intermediate species decrease at density independent mortality rate m_J and through consumption by predators (right hand terms in Eqs. 2-4). Top consumers TC increase in proportion to their consumption of ciliates and large primary producers and decrease at density independent mortality rate m_{TC} (Eq. 5). Food ingestion by the top consumer is described by a multispecies functional response (Murdoch & Oaten, 1975) where uptake of one prey is dependent on the abundance of the alternative prey (both prey densities appear in the denominator). In the presence of only one prey the multispecies functional response reduces to the corresponding functional response of a specialist consumer. The parameter n determines the shape of the top consumer's functional response, with $n = 1$ yielding a type 2 response and $n = 2$ yielding a type 3 response.

Analyses

To investigate the dynamics of the pentagon food web in dependence on the functional response type of its top consumer (copepods), I performed a bifurcation analysis of the differential equation system (Eq. 1-5) for $n = 1$ (type 2 response) and $n = 2$ (type 3 response), respectively. For both functional response types I investigated system dynamics as a function of nutrient enrichment (R_{tot}) and top-consumer mortality (m_{TC}), All numerical analyses were performed in Matcont 2.4 (Dhooge et al. 2003), a software package usable within Matlab [Mathworks Inc., Natick, MA, USA]. For the analysis of non-equilibrium dynamics numerical simulations were used. I also briefly review earlier, analytical results obtained for the assumption of linear functional responses in all food web components.

Results

Community assembly

Much insight into the behaviour of the pentagon module can be gained from its assembly along a nutrient enrichment gradient, starting from an empty system at the lowest enrichment levels. Independent of functional response type there are two possible invasion sequences that can be followed to build up the pentagon module, one starting with large algae (P_L), the other with small algae (P_S). With the chosen parameterization large algae are the better resource competitor, which is a reasonable assumption for e.g. diatoms under silicon-rich conditions (Banse 1991). Hence, large algae are able to establish first along an enrichment gradient. Still, under different environmental conditions small algae could be superior, and I present both invasion sequences (Fig. 1).

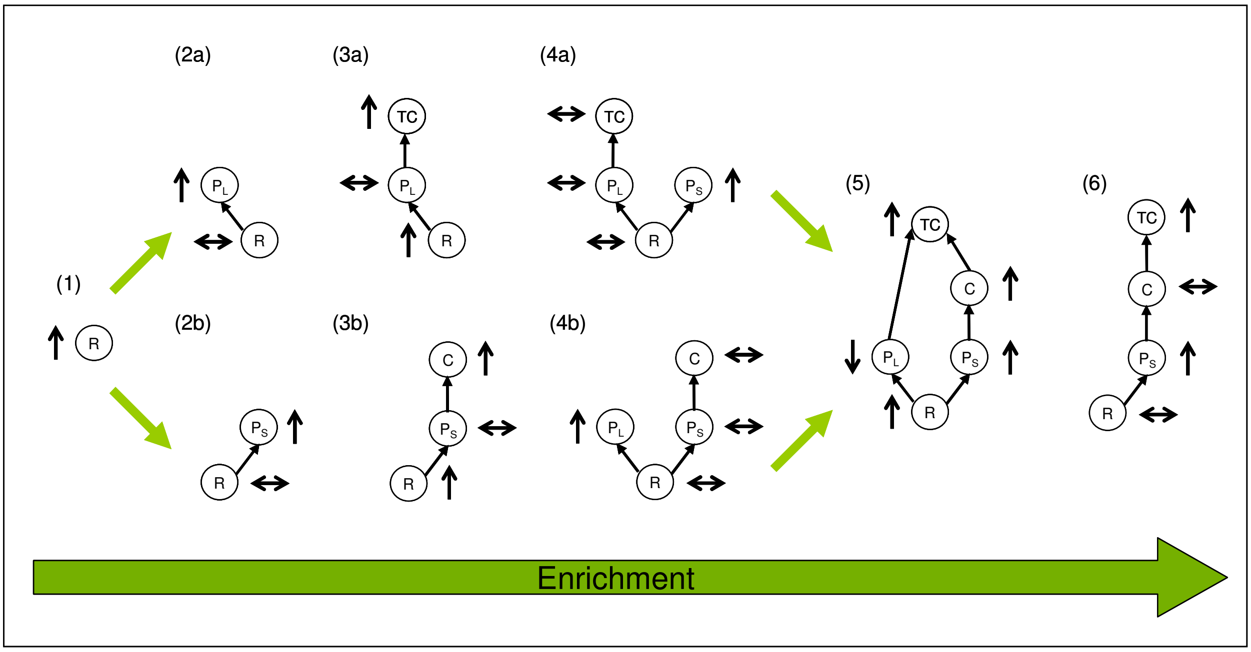

Fig. 1. Possible community assembly sequences in a gradient of nutrient enrichment (increasing R_{tot} *). Also shown are, for each community, the equilibrium responses to enrichment of its constituent species and of free mineral nutrients under the assumption of linear functional responses in all interactions. Circles represent the different compartments of the pentagon module and are labelled correspondingly: R - resource,* P_L *- large phytoplankton, TC - top consumer,* P_S *- small phytoplankton, C - ciliates. Arrows between circles represent feeding links pointing from prey to consumer. Arrows next to circles give the equilibrium response of the corresponding compartment to further enrichment: upward and downward arrows indicate increase and decrease, respectively, and horizontal double arrows indicate no change. Starting from an empty system without producers (1), there are two possible assembly sequences leading to the full pentagon module (5), depending on whether large or small algae are superior nutrient competitors and invade first. System states along the respective invasion sequences are (2a) R-*P_L*, (3a) R-*P_L*-TC, (4a) R-*P_L*-TC-*P_S *and (2b) R-*P_S*, (3b) R-*P_S*-C, (4b) R-*P_S*-C-*P_L*. Since* P_L *decreases with enrichment in the full pentagon module, it eventually goes extinct, leaving the 4-level food chain (6) R-*P_S*-C-TC.*

The superior nutrient competitor will establish first along the enrichment gradient (Fig. 1, transition from (1) to (2a) and (2b), respectively), followed by the invasion of its respective direct consumer (Fig. 1, transition from (2a) to (3a) or from (3a) to (3b)), resulting in a 3-level food chain (including the resource at the base of the web). Now with further enrichment both the respective top consumer of the 3-level chain and free nutrients increase, enabling the successful invasion of the inferior nutrient competitor at higher enrichment levels. This results in a branched web consisting of a 3-level chain plus a 2-level chain with the inferior resource competitor on top (Fig. 1, (4a) and (4b)). With further enrichment only the primary producer along the 2-level chain increases, controlling the resource and therefore the entire 3-level chain (Wollrab et al. 2012). When the inferior nutrient competitor in the 2-level chain has increased sufficiently, invasion of its direct consumer becomes possible at higher enrichment, and the full pentagon module becomes established (Fig. 1, transition from (4a) or (4b) to (5)). There are thus two possible invasion sequences: P_L-TC-P_S-C for the default parameterization (large algae are superior resource competitors), and P_S-C-TC-P_S if small algae are superior resource competitors. Once the pentagon module is established the invasion sequence has, however, no further influence on the qualitative patterns observed with further enrichment or with increasing top consumer mortality. I therefore subsequently only present the results for the default parameterization (but see Appendix A3.1 for an example of the alternative assumption of P_S being the better resource competitor).

Analytical insights from a system with linear functional responses

The looped architecture of the pentagon module, with a chain of odd (R-P_L-TC) and a chain of even length (R-P_S-C-TC) being connected both at the bottom and at the top, has important consequences for its responses to bottom-up and top-down forcing. When all consumers have linear functional responses, Wollrab et al. (2012) have analytically shown for webs consisting of one odd and one even chain that, with enrichment, energy flow and equilibrium densities increase in all compartments of the even chain, but decrease in every other compartment of the odd chain. Thus, in the pentagon module, all trophic levels in the even chain increase in density, while the intermediate species of the odd chain (P_L) decreases with enrichment (Fig. 1, (5)). This implies that coexistence in the pentagon module is limited to an intermediate range of enrichment levels with P_L going extinct at higher enrichment levels (Fig. 1, (6)). The response of the pentagon module to increased top consumer mortality is exactly opposite to its response to enrichment, i.e. all species along the even chain decrease and P_L increases with increasing top consumer mortality (Wollrab et al. 2012). Numerical analyses suggest that the above response patterns are valid at stable equilibrium conditions also when all species have type 2 functional responses (Wollrab et al. 2012). In the following sections I discuss in detail the responses of the pentagon module to nutrient enrichment and top consumer mortality in the model described by eq.s 1-5 under the alternative assumptions of either a type 2 or a type 3 functional response in the top consumer (copepods).

System dynamics when top consumers have a type 2 functional response

The combined influences of nutrient enrichment (R_{tot}) and top consumer mortality (m_{TC}) on the pentagon module under the assumption of a type 2 functional response in the top consumer are summarized in Fig. 2. The sequence of invasion threshold lines with increasing enrichment reflects the default parameterization. The invasion threshold of large algae at very low enrichment is independent of m_{TC} and therefore a straight line parallel to the y-axis. In contrast, the invasion threshold of TC is downward concave with an upper boundary at m_{TC} = 0.4, because higher mortality rates exceed the maximum growth rate of copepods at saturating food densities (Appendix A3.2). All following invasions (P_S and C) depend on the presence of TC and therefore follow the shape of the TC invasion threshold. When passing the invasion threshold for C, the pentagon module becomes fully established.

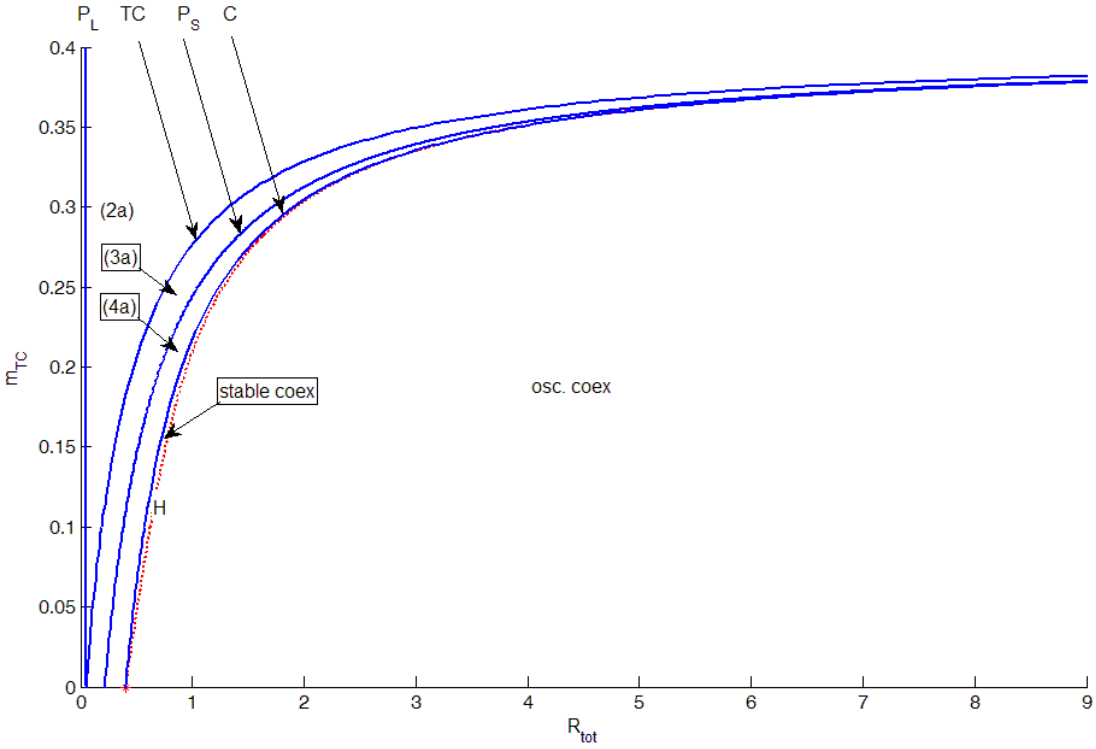

Fig. 2. Bifurcation plot of the pentagon module and its sub-communities as a function of enrichment (R_{tot}) and top consumer mortality (m_{TC}) when the top consumer has a type 2 functional response. Other parameters are listed in Table 3.1. Labels indicate the following states: (2a) R-P_L, (3a) R-P_L-TC, (4a) R-P_L-TC-C, (stable coex) stable equilibrium states of the full pentagon module, (osc. coex) oscillatory coexistence of the full pentagon module. Lines separate different system states. Blue solid lines are invasion thresholds labelled by the name of the invading species. To the right of the red-dotted line H the stable coexistence state is replaced by an oscillatory coexistence state.

The most striking feature of the full pentagon module is the strongly destabilizing impact of a type 2 functional response of its top consumer on food web dynamics. There is only a very narrow range of stable point equilibria and very slight enrichment (red, dotted line in Fig. 2) is sufficient to move the system onto an oscillatory attractor with steeply increasing cycle amplitudes. Fig. 3 illustrates this for a transect along the R_{tot}-axis at the default copepod mortality $m_{TC} = 0.1$. Interestingly, this oscillatory attractor enables coexistence at enrichment levels for which large algae are predicted to go extinct in a stable equilibrium (similar to the linear functional response case, Fig. 1(6), Wollrab et al. 2012). Still, the huge cycle amplitudes, with cycle minima of all species getting close to zero soon after passing the stability boundary (Fig. 3), suggest that species extinctions become very likely in the unstable parameter space.

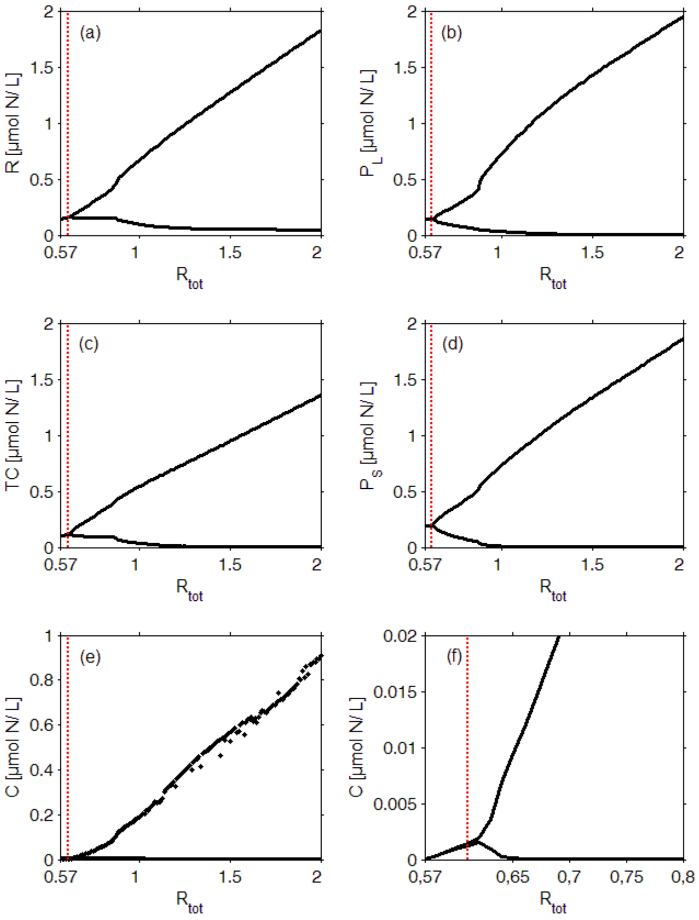

Fig. 3. Densities of free nutrients R (a), large algae P_L (b), copepods TC (c), small algae P_S (d), and ciliates C (e, f) in the coexistence region of the pentagon module as a function of enrichment (R_{tot}) for $m_{TC} = 0.1$ when the top consumer has a type 2 functional response. Other parameters are listed in Table 3.1. At $R_{tot} = 0.61$ (red dotted line, see threshold H in Fig. 2) a stable equilibrium is replaced by an oscillatory coexistence state. Equilibrium densities are shown to the left of the stability boundary, while minima and maxima of the cycle amplitudes are displayed to the right. Panel f is a magnified section of panel e near the stability boundary. Note that in all panels the x-axis starts at the invasion threshold for C ($R_{tot} = 0.57$).

System dynamics when top consumers have a type 3 functional response

When top consumers have a type 3 functional response, the sequence of community assembly in R_{tot}- m_{TC} space remains identical to the previous cases (Fig. 1, 2), but several important differences arise (Fig. 4). First, while the invasion thresholds of P_L and TC show a similar dependence on R_{tot} and m_{TC} as in the case of a type 2 response, the invasion thresholds for P_S and C now tend towards infinity also at the low end of top consumer mortality rates. This is a consequence of the type 3 functional response leading to high top consumer biomass (and thus high amounts of nutrient locked up in top consumers) when top consumer mortality rates are very low. Thus higher total nutrient levels R_{tot} are required to reach the threshold concentration of free nutrients required for invasion of the inferior nutrient competitor (see more details in Appendix A3.2).

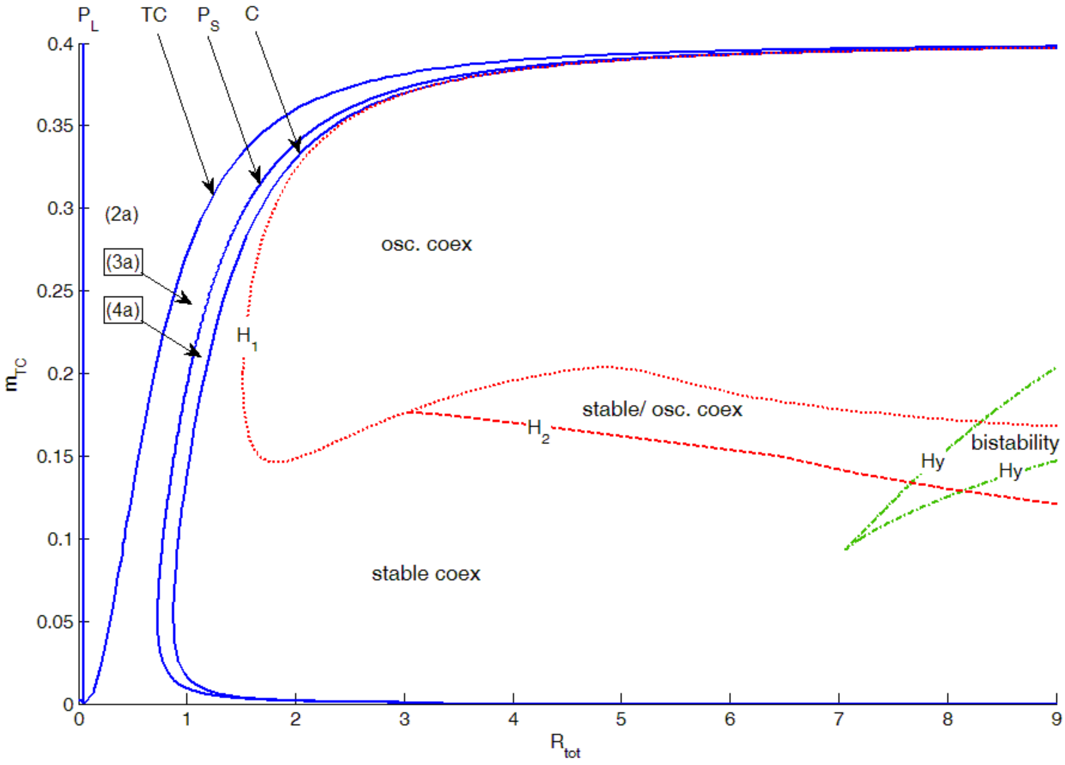

Fig. 4. Bifurcation plot of the pentagon module and its sub-communities as a function of enrichment (R_{tot}) and top consumer mortality (m_{TC}) when the top consumer has a type 3 functional response. Other parameters are listed in Table 3.1. For labelling of invasion thresholds and system states see Fig. 2. The stable coexistence state is replaced by an oscillatory coexistence state when passing the threshold H_1 (red dotted line). In the area enclosed by H_2 (red broken line) and H_1 stable and oscillatory coexistence occur as alternative states. The green dash-dotted lines (Hy) indicate a hysteresis area (bistability) with bistability between two alternative stable coexistence states for values of top consumer mortality below H_1 and bistability between a cyclic and a stable equilibrium above H_1.

Second, a type 3 response in the top consumer strongly stabilizes the pentagon module. When top consumer mortality is low to intermediate the system has a stable equilibrium over the entire investigated enrichment space (Fig. 4). The destabilizing influence of higher top consumer mortality, moving the system onto an oscillatory attractor, can likely be explained as follows. Similar to one predator-one prey systems, a multispecies functional response is stabilizing over the range of (low) prey densities for which per capita prey mortality increases with prey density. Such low prey densities can only be stable when top consumer mortality is low (and, consequently, the equilibrium prey density required to balance top consumer losses is low). At sufficiently high top consumer mortality prey densities will eventually exceed the stabilizing range of the type 3 functional response and the system must go unstable. In a narrow region of intermediate top consumer mortality this oscillatory state exists as an alternative state to a stable equilibrium, and becomes the only possible state at higher top consumer mortality.

Finally, when the top consumer has a type 3 response the pentagon module may show enrichment responses (e.g. alternative states and non-monotonous responses to enrichment) that differ qualitatively from what is possible with linear and type 2 responses. Specifically, within the region of stable dynamics two qualitatively different response patterns to enrichment occur in different regions of enrichment (Fig. 5). At low to moderate enrichment the response resembles the familiar patterns from the linear and stable type 2 response cases (Fig. 1, 3), i.e. all compartments of the even chain increase and large algae decrease. At higher enrichment levels, however, the biomasses of copepods, ciliates and large algae approach asymptotes, whereas small algae show a sharply accelerated biomass increase and free nutrients shift from an increase to a decrease. The transition between these two qualitatively different enrichment responses is smooth at low copepod mortalities (Fig. 5a), but is a discrete jump at higher top consumer mortalities, giving rise to an increasingly larger region of alternative stable states (Fig. 4, 5b,c).

Four ingredients synergistically give rise to this qualitative shift in the community response at higher enrichment levels. First, as is the case with linear and type 2 functional responses, the specific community feedbacks in the pentagon module produce a gradual shift in the relative densities of ciliates (increasing) and large algae (decreasing) with enrichment. Second, because a type 3 response implies switching, these relative density shifts of the copepods' alternative prey lead to a fairly abrupt, disproportional increase in the per capita feeding rate of copepods on ciliates when ciliate biomass starts to exceed large algae biomass. Third, to keep ciliates in balance this sharply increasing ciliate mortality must be counterbalanced by increased food (= small algae) intake. Consequently, small algae must also sharply increase. Finally, the steepness of the small algae's' response to enrichment depends critically on the ciliates' type 2 functional response, which causes per capita mortality of small algae to decrease with their own density and thus enables small algae to escape from control by ciliates. High densities of small algae saturate, in turn, the feeding and growth rates of ciliates. Consequently, the enrichment response of copepods, which is strongly determined by its main food source ciliates, must also level off.

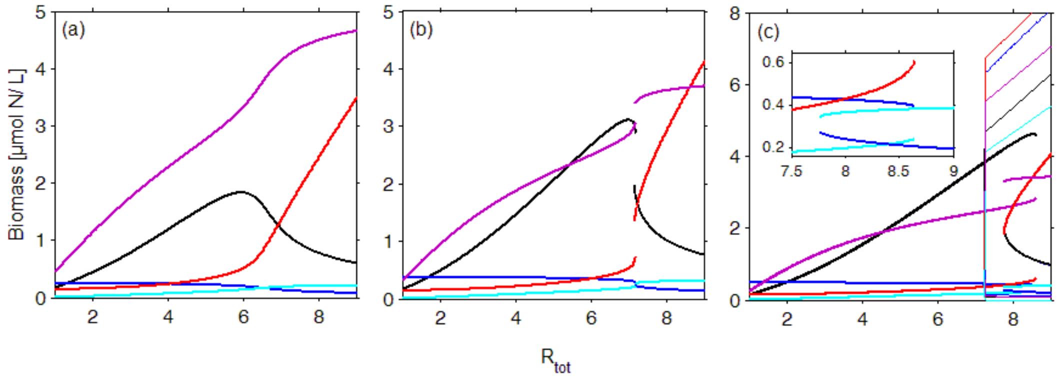

Fig. 5. Stable equilibrium densities and cycle amplitudes of the full pentagon module as a function of enrichment at m_{TC} *= 0.05 (a), 0.1 (b), and 0.14 (c), respectively, when the top consumer has a type 3 functional response. State variables are indicated by different colours: R black,* P_L *blue, TC violet,* P_S *red, and C turquoise. Thick lines refer to stable equilibria. In panel c, a large amplitude cycle surrounds the stable equilibria at high enrichment levels. Minima and maxima of the cycle amplitudes are indicated by thin lines. The inset in panel c shows a magnified section of the bistability region at high enrichment and low biomass levels. Note that in all panels the x-axis starts at an* R_{tot} *value of 1.*

In summary, effects of a switching type 3 functional response at the copepod level cascade down to small algae and subsequently feed back on ciliates and copepods, thus causing the described qualitative shift in the community response at high enrichment. Importantly, all of the four listed ingredients are needed to produce the pattern. The validity of this mechanism can be demonstrated by changing the functional response of ciliates from saturating to linear. If ciliates have a linear functional response, all else being equal (i.e. copepods having a type 3 response and all other species having type 2 responses), per capita mortality of P_S increases with enrichment, because the specific feeding rate of ciliates on P_S remains constant while ciliates increase with enrichment. In this case P_S cannot escape the control by its predator and the alternative response pattern with all densities but P_S levelling off cannot arise (see Appendix A3.3).

Discussion

My investigations clearly demonstrate that the form of the functional response of the top consumer in a food web with two alternative pathways of energy flow can have dramatic consequences for system dynamics. First, in line with results from simple predator-prey models (Oaten & Murdoch 1975, Fussmann & Blasius 2005), a top consumer with a type 3 response strongly stabilizes the dynamics of the pentagon module, enabling stable coexistence within a very large region of parameter space. Second, the potential for switching in a top consumer with a type 3 response plays out particularly strongly in the context of the pentagon module, where feedbacks between the linked food chains produce a negative correlation between the top consumer's alternative prey. Top consumer switching towards the more abundant prey can therefore prevent the less abundant prey from going extinct and/or the system from going unstable. It also gives rise to an alternative enrichment response pattern and the possibility of bi- and multi-stability between alternative coexistence states. Hence, the responses to environmental change of a pentagon shaped food web with a switching top consumer are more multi-layered and add qualitatively new dynamics (especially towards higher enrichment levels) compared to scenarios of exclusively linear or type 2 functional responses.

Gismervik & Andersen (1997) investigated the oceanic plankton food web in the simplified setting of an intraguild predation (IGP) web, with copepods as intraguild (top) consumers and ciliates as intraguild prey competing for a single, shared phytoplankton compartment. While Gismervik & Andersen (1997) come to similar results concerning the stabilizing effect of a type 3 functional response in the top consumer, their predictions differ in several aspects from the pentagon module. First, although the IGP web also has a potential for bistability (Garay et al. 2012), which in turn is due to the negative correlation between intraguild prey and shared resource (Diehl & Feißel 2000, Wollrab et al. 2012), alternative enrichment responses were not reported by Gismervik & Andersen (1997). More importantly, because of structural differences the IGP and pentagon webs make several deviating predictions concerning bottom-up responses. Specifically, ciliates are predicted to decrease with enrichment in the IGP web (Gismervik & Andersen, Diehl & Feißel 2000) but to increase in the pentagon web. Additionally, the IGP web cannot resolve contrasting responses within the phytoplankton compartment and related feedback mechanisms with higher trophic levels. Given the empirical evidence for differences between the food size spectra of copepods and ciliates (Sommer & Stibor 2002, Sommer et al. 2005) and their importance for the propagation of bottom-up and top-down forces through the lower oceanic food web

(Stibor et al. 2004), the chosen resolution of the pentagon module seems to more appropriately capture important features of the marine plankton community, where feeding relations are strongly size dependent (Armstrong 1994, Thingstad 1998, Lundvall et al. 1999).

A key prediction of the pentagon module is that phytoplankton in the smaller size range consumed by ciliates should increase while larger phytoplankton should decrease with enrichment. This prediction is very robust (i.e. independent of the copepods' functional response), but seems to contrast with the observation that very small algae dominate in the most oligotrophic environments, whereas larger algae get increasingly dominant towards more eutrophic environments (Chisholm 1992, Kiørboe 1993, Philippart et al. 2000, Arin et al. 2002, Iriarte & González 2004, Irwin et al. 2006, Cermeño & Figueiras 2008). Within the phytoplankton community there are typically three size classes distinguished: pico-, nano- and microphytoplankton with cell sizes below 2 μm, between 2 and 20 μm and above 20 μm respectively (Kiørboe 2008). Frequently the link between picophytoplankton (which is not considered in the pentagon module) and microzooplankton (e.g. ciliates) is described as being mediated through heterotrophic nanoflagellates (Sommer & Sommer 2006, Kiørboe 2008), but ciliates may also directly feed on picophytoplankton (Christaki et al. 1998, Sommer & Sommer 2006). An empirical relationship between nutrient supply and abundance is most evident for pico- and microphytoplankton (P_L in the pentagon module), with a clear dominance of picophytoplankton in oligotrophic systems and increasing dominance of microphytoplankton towards more enriched marine environments (Chisholm 1992, Kiørboe 1993). Nanophytoplankton (P_S in the pentagon module) shows more ambiguous responses to enrichment, either correlating with pico- (Arin et al. 2002, Iriarte & Gonzalez 2004, Cermeño & Figueiras 2008) or microphytoplankton (Marañón et al. 2001, Irigoien et al. 2005, Mahaffey et al. 2012). Many nutrient rich upwelling and coastal areas are clearly dominated by diatoms (Arin et al. 2002, Huete-Ortega et al. 2009, Fehling et al. 2012).

Speculations about the dynamical consequences of the inclusion of picophytoplankton (and its consumers) into a model of the lower oceanic food web are beyond the scope of this paper. It seems, however, at least equally relevant to explore the dynamics of the pentagon module in the context of the upper oceanic food web. A more holistic explanation of the empirical patterns of nano- and microphytoplankton may have to involve top-down feedbacks from higher trophic levels (Pauly et al. 1998, Cloern 2001, Irigoien et al. 2005). To my knowledge, the dynamics of the pentagon module in presence of higher trophic levels have so far only been explored under the assumption of linear functional responses in all interactions (Thingstad & Sakshaug 1990, Wollrab et al. 2012). These results suggest that the presence of higher trophic levels can modulate the response of the pentagon module to enrichment in ways that are compatible with empirical patterns. Specifically, the introduction of one additional trophic level above TC, e.g. planktivorous fishes or jellyfish feeding on copepods, shifts the dynamics of the pentagon module such that microphytoplankton (P_L) increases with enrichment, whereas nanophytoplankton (P_S) is controlled at a constant level (Thingstad & Sakshaug 1990, Wollrab et al. 2012). This qualitative change in the phytoplankton response arises because, when planktivores control copepods at a constant level, apparent competition between the two chains of the pentagon module is prevented. Consequently, the compartments below the copepod level behave qualitatively as they would in the complete absence of copepods, with large algae in the 2-level chain (R-P_L) increasing with enrichment and thus controlling the shared resource, and all trophic levels in the 3-level chain (R-P_S-C, which includes nanophytoplankton) at constant levels (Thingstad & Sakshaug 1990, Wollrab et al. 2012). Conversely, adding yet another trophic level (e.g. piscivores controlling planktivores) would release copepods from predator control and therefore revert the response of the pentagon module back to the pattern observed in absence of higher trophic levels (Wollrab et al. 2012).

Worldwide, marine piscivores were heavily overfished during the last century and many fish stocks have collapsed (Pauly et al. 1998, Baum & Worm 2009, Steneck 2012). This collapse was typically followed by a strong increase in planktivorous fishes and a corresponding decrease in copepod abundances (Micheli 1999, Cury & Pauly 2000, Daskalov 2002, Daskalov et al. 2007, Baum & Worm 2009). Hence, trophic downgrading of the marine food web could indeed lead to a situation where copepods are strongly controlled by planktivorous fish, which, in turn, should lead to the proliferation of large algae with enrichment. This pattern would only be reinforced if planktivores, due to continued overfishing down the food chain, would be replaced by heavily planktivorous jellyfish, a phenomenon that has been reported from several marine regions (Shiganova 2000, Daskalov 2002, Daskalov 2003, Kamburska & Fonda-Umani 2006, Lynam et al. 2006, Watermeyer et al. 2008, Lynam et al. 2011). Phrased differently, the frequent observation of a dominance of large algae in many nutrient rich areas may already be a consequence of heavy depletion of upper trophic levels (Daskalov 2002, 2003, Pauly et al. 1998). Additionally, increased grazing intensity on copepods through planktivorous fishes or jellyfish could shift the system from a stable attractor to an oscillatory one, where trends in the marine community would be less predictable, impeding the development of sustainable management strategies (Watermeyer et al. 2008).

It remains to be investigated how the dynamics of the pentagon module in the presence of planktivores (and piscivores) are affected by more realistic (i.e. type 2 and type 3) functional responses. It remains also to be shown to what extend the dynamics of the pentagon module are preserved if embedded in a more complex representation of the marine food web (but see (Vasas et al. 2007) for promising results from a structural network analysis). Instead of focussing the discussion on the relative importance of bottom-up versus top-down control of marine communities (see for example Frank et al. 2005 versus Greene & Pershing 2007, Frank et al. 2007), more effort should be spent on the investigation of the interplay of bottom-up and top-down forces (see Cloern 2001, Daskalov 2002, Cury et al. 2003, Watermeyer et al. 2008). For the understanding and prediction of combined effects of biotic and abiotic drivers of marine community dynamics, which are imperative to sustainable management strategies, a more holistic approach is needed not only in theoretical, but also empirical studies, accounting for alternative energy pathways, size related feeding links across all trophic levels, and relevant descriptions of feeding behaviour such as the functional response.

Table 3.1. Default values and units of model parameters.

Parameter	Value	Unit	Source
attack rates			
a_{RPS}	0.3711	L /µmol N /day	calculation based on data from Canellas 1997
a_{RPL}	1.1079	L /µmol N /day	calculation based on data from Canellas 1997
a_{PSC}	5.875	L /µmol N /day	calculation based on data from Gismervik & Andersen 1997 and Gismervik 2005
a_{CTC}	1.5323	L /µmol N /day	calculation based on data from Gismervik & Andersen 1997
a_{PLTC}	1.1751	L /µmol N /day	calculation based on data from Gismervik & Andersen 1997
handling times			
h_{RPS}	1	day	calculation based on data from Canellas 1997
h_{RPL}	0.9091	day	calculation based on data from Canellas 1997
h_{PSC}	0.4	day	calculation based on data from Gismervik 2005 and Gismervik & Andersen 1997
h_{CTC}	2	day	calculation based on data from Gismervik & Andersen 1997
h_{PLTC}	2	day	calculation based on data from Gismervik & Andersen 1997
conversion efficiencies			
e_{RPS}	1	dimensionless	
e_{RPL}	1	dimensionless	
e_{PSC}	0.8	dimensionless	Gismervik & Andersen 1997
e_{CTC}	0.8	dimensionless	Kiørboe et al. 1985
e_{PLTC}	0.8	dimensionless	Kiørboe et al. 1985
mortality rates			
m_{PS}	0.05	day^{-1}	Vézina 1989
m_{PL}	0.05	day^{-1}	Vézina 1989
m_{C}	0.5	day^{-1}	Gismervik & Andersen 1997
m_{TC}	0.1	day^{-1}	Carlotti & Nival 1992

Appendix A3.1 Dynamics of the pentagon module when small algae (P_S) are the better resource competitor

To investigate the influence of assuming P_S to be the superior resource competitor on overall system dynamics, I exchanged the attack rates and the handling times of P_L and P_S in the parameter set (Table 3.1), all else being equal to the default case. As for the default case, I investigated system dynamics dependent on enrichment and top consumer mortality when top consumers exhibit a type 2 as well as a type 3 functional response. The results are summarized in Fig. A3.1.1 and A3.1.2 respectively. For P_S being the superior resource competitor, the assembly sequence is P_S-C-P_L-TC, corresponding to sequence b in Fig. 1. Since in this scenario TC invades the system last, the first three invasion lines are independent of top consumer mortality rate and hence straight lines along the m_{TC}-axis, located at the minimum enrichment level needed for successful invasion of the respective species. The invasion line of TC is downward concave with an upper boundary of top consumer mortality for which the invasion threshold tends towards infinity. Following the invasion of TC, the patterns in Fig. A3.1.1 and A3.1.2 show the same general trends as the default case, although the range of each section differs quantitatively. Especially, a type 3 functional response still highly stabilizes system dynamics compared to a type 2 functional response.

The only difference emerges at the lowest m_{TC} values when top consumers are assigned a type 2 functional response. The lower the mortality rate, the lower the prey density needed for successful invasion. In the R-P_S-C system the resource as well as ciliates increases with enrichment. This leads to a situation where at the lowest top consumer mortality rates, ciliates reach the threshold density for successful invasion of TC before R has reached high enough levels for successful invasion of P_L. After invasion of TC, the resource in the resulting four-level food chain is top-down controlled, thus preventing the subsequent invasion of P_L. Hence at the lowest top consumer mortality rates, only the food chain along R-P_S-C-TC can establish along the enrichment gradient (*stable fc*) and is replaced by an oscillatory attractor (*osc. fc*) when passing the red-dotted line (*H*). For slightly higher mortality rates, where P_L invades before TC along the enrichment gradient, the coexistence equilibrium is stable throughout its range, until P_L, which is decreasing along the enrichment gradient in a stable equilibrium (corresponding to Fig. 1 (5)), goes extinct when passing the extinction threshold E_{PL} (black dash-dotted line) replacing the stable coexistence state by a stable state of the remaining food chain (R-P_S-C-TC). For even higher mortality rates the coexistence equilibrium gets unstable before a possible extinction of P_L and the system settles to an oscillatory coexistence state which extends towards the highest investigated enrichment levels.

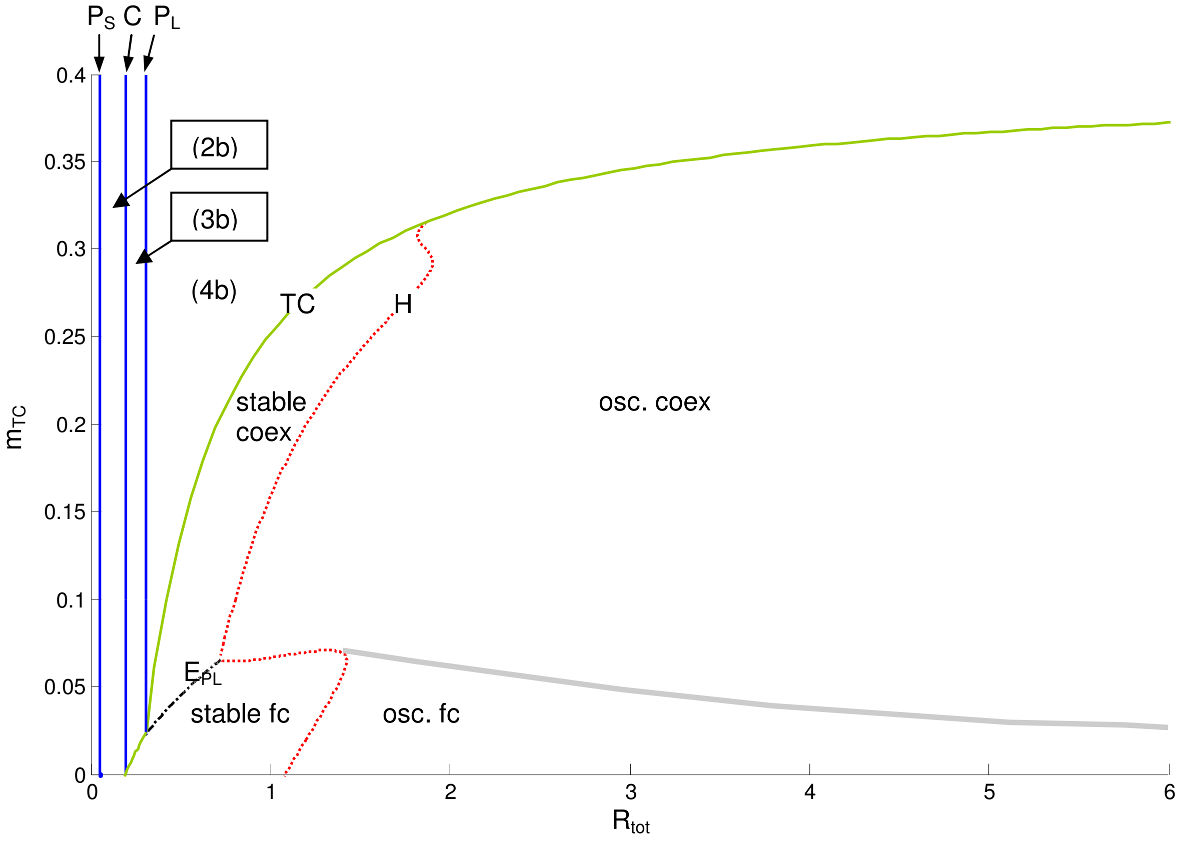

Fig. A3.1.1. Bifurcation plot of the pentagon module and its sub-communities, for the case of P_S *being the superior resource competitor and top consumers are assigned a type 2 functional response, as a function of enrichment (*R_{tot}*) and top consumer mortality (*m_{TC}*). Labels indicate the following states: (2b) R-*P_S*, (3b) R-*P_S*-C, (4b) R-*P_S*-C-*P_L*, (stable coex) stable equilibrium states of the full pentagon module, (osc. coex) oscillatory coexistence of the full pentagon module, (stable fc) stable equilibrium and (osc. fc) oscillatory state of the food chain (R-*P_S*-C-TC) with* P_L *absent. Lines separate different system states. Blue solid lines are invasion thresholds labelled by the name of the invading species. The green line indicates the invasion threshold for TC. To the right of the black dash-dotted line* E_{PL} *(extinction threshold for* P_L*), the stable coexistence state is replaced by a stable state of the remaining food chain (R-*P_S*-C-TC). To the right of the red-dotted line H the stable states are replaced by a corresponding oscillatory state. The grey line separates the region of oscillatory coexistence from the region of the oscillatory food chain, but is only an approximation.*

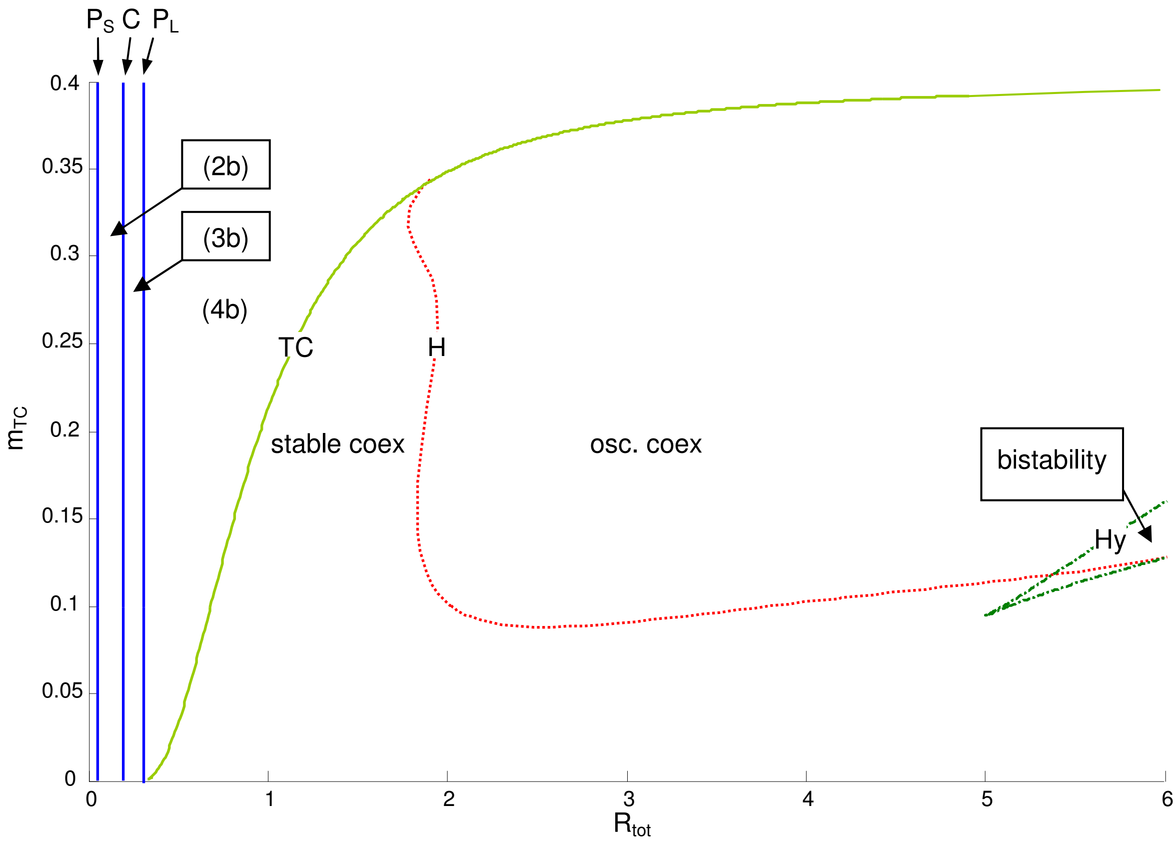

Fig. A3.1.2. Bifurcation plot of the pentagon module and its sub-communities, for the case of PS being the superior resource competitor and top consumers are assigned a type 3 functional response, as a function of enrichment (R_{tot}) and top consumer mortality (m_{TC}). For labelling of invasion thresholds and system states see Fig. A1.1. The stable coexistence state is replaced by an oscillatory coexistence state when passing the threshold H_1 (red dotted line). The green dash-dotted lines (Hy) indicate a hysteresis area (bistability) with bistability between two alternative stable coexistence states for values of top consumer mortality below H_1 and bistability between a cyclic and a stable equilibrium above H_1.

Appendix A3.2 Analytical derivation of invasion thresholds during community assembly

Generally a species can successfully invade a system, if the density of its prey/resource is high enough to allow for positive growth. The prey/resource density at which negative growth turns positive is the invasion threshold. It can be analytically derived by setting the differential equation of the invader to zero and solving it for prey/resource density. In the following I will successively derive all invasion thresholds along the assembly sequence of the pentagon web in the scenario with P_L being the superior resource competitor (R-P_L-TC-P_S-C, Fig. 1, sequence a).

Threshold for the invasion of P_L into an empty system (R)

The minimum resource density R^*_{PL} for successful invasion of P_L into the empty system (no species present, Fig. 1 panel 1), is derived from Eq. 2 (the density of TC being zero). R^*_{PL} (A3.2-1) is independent of m_{TC}. In an empty system R equals R_{tot}, hence R^*_{PL} is identical to the minimum enrichment level R_{totPL} for successful invasion of P_L.

$$R_{totPL} = R^*_{PL} = \frac{m_{PL}}{a_{RP_L}\left(e_{RP_L} - m_{PL}h_{RP_L}\right)} \tag{A3.2-1}$$

Threshold for the invasion of TC into an R-P_L system

The minimum density P^*_{LTC} for successful invasion of TC into an R-P_L system is derived from Eq. 5 (with C equalling zero).

$$P^*_{LTC} = \left(\frac{m_{TC}}{a_{P_LTC}\left(e_{P_LTC} - m_{TC}h_{P_LTC}\right)}\right)^{\frac{1}{n}} \tag{A3.2-2}$$

Because P_L in an R-P_L system equals $R_{tot} - R^*_{PL}$, the invasion threshold for TC in terms of R_{tot} becomes

$$R_{totTC} = \left(\frac{m_{TC}}{a_{P_LTC}\left(e_{P_LTC} - m_{TC}h_{P_LTC}\right)}\right)^{\frac{1}{n}} + R^*_{PL} \tag{A3.2-3}$$

The invasion threshold (A3.2-3) depends on the functional response type (n) and on top consumer mortality m_{TC}. To balance higher top consumer mortality rates, the minimum prey density P^*_{LTC} (and thus R_{totTC}) has to increase with m_{TC}. But the top consumer's saturating functional response limits the range of its mortality rates which can be balanced by increasing prey density. This is reflected in the threshold tending towards infinity for values near $m_{TC} = \frac{e_{P_L TC}}{h_{P_L TC}}$, for which the denominator of expression A3.2-3 approaches zero. Derivation of R_{totTC} with respect to m_{TC} reveals, that for both functional response types R_{totTC} increases monotonously with m_{TC} (Eq. A3.2-4a and b, in both cases the denominator has to be positive for positive values of P_{LTC}^*).

type 2 (n = 1): $$\frac{dR_{totTC}}{dm_{TC}} = \frac{e_{PLTC} a_{PLTC}}{\left(e_{PLTC} a_{PLTC} - m_{TC} a_{PLTC} h_{PLTC}\right)^2} > 0 \qquad \text{(A3.2-4a)}$$

type 3 (n = 2): $$\frac{dR_{totTC}}{dm_{TC}} = 0.5 \frac{e_{PLTC} a_{PLTC}}{\sqrt{m_{TC}\left(e_{PLTC} a_{PLTC} - m_{TC} a_{PLTC} h_{PLTC}\right)^3}} > 0 \qquad \text{(A3.2-4b)}$$

<u>Invasion of P_S into the R-P_L-TC system</u>

The minimum resource density R_{PS}^* for successful invasion of P_S into the R-P_L-TC system is derived from Eq. 3 (C equals zero).

$$R_{PS}^* = \frac{m_{PS}}{a_{RPS}\left(e_{RPS} - h_{RPS} m_{PS}\right)} \qquad \text{(A3.2-5)}$$

The threshold value R_{totPS} at which R reaches R_{PS}^* is defined by the equilibrium resource density R_{TC}^* in the R-P_L-TC system. In the following I derive the invasion threshold for small algae as a function of R_{tot} and m_{TC} first for the case of a type 2 and then for the case of a type 3 functional response of top consumers.

When top consumers have a type 2 functional response, the equilibrium solution for the R-P_L-TC system is given by Eqs. A3.2-6 to 8.

$$R_{tot} = R^* + P_L^* + TC^* \qquad \text{(A3.2-6)}$$

$$P_L^* = \frac{m_{TC}}{a_{PLTC}\left(e_{PLTC} - m_{TC} h_{PLTC}\right)} \qquad \text{(A3.2-7)}$$

$$TC^* = \left[\frac{e_{RPL} a_{RPL} R^*}{1 + a_{RPL} h_{RPL} R^*} - m_{PL}\right]\left(\frac{1}{a_{PLTC}} + h_{PLTC} P_L^*\right). \qquad \text{(A3.2-8)}$$

The value R_{totPS} at which R reaches the threshold R_{PS}^* for successful invasion of P_S into the R-P_L-TC system is derived by substituting TC^* from Eq. A3.2-8 into Eq. A3.2-6 and replacing R^* by R_{PS}^* (eq. A3.2-5).

$$R_{totPS} = R_{PS}^{*} + P_{L}^{*} + \left[\frac{e_{RPL} a_{RPL} R_{PS}^{*}}{1 + a_{RPL} h_{RPL} R_{PS}^{*}} - m_{PL} \right] h_{PLTC} P_{L}^{*} + \left[\frac{e_{RPL} a_{RPL} R_{PS}^{*}}{1 + a_{RPL} h_{RPL} R_{PS}^{*}} - m_{PL} \right] \frac{1}{a_{PLTC}} \text{ . (A3.2-9)}$$

Since R_{PS}^{*} is independent of m_{TC}, the dependence of R_{totPS} on m_{TC} is mediated by P_{L}^{*}. Since P_{L}^{*} increases monotonously with m_{TC} (eq. A3.2-2), the dependence of the invasion threshold R_{totPS} on m_{TC} can be derived from the derivative of Eq. A3.2-9 with respect to P_{L}^{*}.

$$\frac{dR_{totPS}}{dP_{L}^{*}} = 1 + \left[\frac{e_{RPL} a_{RPL} R_{PS}^{*}}{1 + a_{RPL} h_{RPL} R_{PS}^{*}} - m_{PL} \right] h_{PLTC} > 0 \qquad \text{(A3.2-10)}$$

dR_{totPS} / dP_{L}^{*} is positive (the term in brackets must be positive because it is the specific growth rate of P_{L} minus its mortality rate excluding the mortality caused by *TC* (Eq. 3 and A3.2-8)). Hence the total nutrient concentration R_{totPS} at which small algae can invade an R-P_L-TC system also increases monotonously with m_{TC}.

When top consumers have a type 3 functional response, the equilibrium solution for the R-P_L-TC system is given by Eqs. A3.2-11-A3.2-13.

$$R^{*} = R_{tot} - P_{L}^{*} - TC^{*} \qquad \text{(A3.2-11)}$$

$$P_{L}^{*} = \sqrt{\frac{m_{TC}}{\left(e_{PLTC} a_{PLTC} - m_{TC} a_{PLTC} h_{PLTC}\right)}} \qquad \text{(A3.2-12)}$$

$$TC^{*} = \left[\frac{e_{RPL} a_{RPL} R^{*}}{1 + a_{RPL} h_{RPL} R^{*}} - m_{PL} \right] \left(\frac{1}{a_{PLTC} P_{L}^{*}} + h_{PLTC} P_{L}^{*} \right) \qquad \text{(A3.2-13)}$$

Again, substituting expressions A3.2-13 and A3.2-5 into Eq. A3.2-11 yields:

$$R_{totPS} = R_{PS}^{*} + P_{L}^{*} + \left[\frac{e_{RPL} a_{RPL} R_{PS}^{*}}{1 + a_{RPL} h_{RPL} R_{PS}^{*}} - m_{PL} \right] h_{PLTC} P_{L}^{*} + \left[\frac{e_{RPL} a_{RPL} R_{PS}^{*}}{1 + a_{RPL} h_{RPL} R_{PS}^{*}} - m_{PL} \right] \frac{1}{a_{PLTC} P_{L}^{*}}$$

(A3.2-14)

The derivative of R_{totPS} with respect to P_{L}^{*} is inversely related to the square of P_{L}^{*}

$$\frac{dR_{totPS}}{dP_{L}^{*}} = 1 + \left[\frac{e_{RPL} a_{RPL} R_{PS}^{*}}{1 + a_{RPL} h_{RPL} R_{PS}^{*}} - m_{PL} \right] \left(h_{PLTC} - \frac{1}{a_{PLTC} P_{L}^{*2}} \right) \qquad \text{(A3.2-15)}$$

The term in square brackets is the specific growth rate of P_{L} minus its mortality rate excluding the mortality caused by *TC* and has to be positive (Eq. 3 and A3.2-13). It is therefore obvious that dR_{totPS} / dP_{L}^{*} switches sign from negative to positive when P_{L}^{*} increases from very small to large values. Note that P_{L}^{*} is a monotonously increasing function of m_{TC}

(Eq. A3.2-2) and can indeed take on very small values when m_{TC} is very small (*TC* requires low food density at low own mortality). Thus, there is a value of P_L^* where dR_{totPS}/dP_L^* (and thus dR_{totPS}/dm_{TC}) has a minimum, i.e. $dR_{totPS}/dP_L^* = 0$ (A3.2-16) and $d^2R_{totPS}/dP_L^{*2} > 0$ (Eq. A3.2-17). Solving $dR_{totPS}/dP_L^* = 0$ for P_L^* derives expression A3.2-16. It has two roots of which only the positive one ($P_L^* > 0$) is relevant.

$$P_L^{*2} = \frac{\left[\frac{e_{RPL}a_{RPL}R_{PS}^*}{1+a_{RPL}h_{RPL}R_{PS}^*} - m_{PL}\right]}{\left(1+\left[\frac{e_{RPL}a_{RPL}R_{PS}^*}{1+a_{RPL}h_{RPL}R_{PS}^*} - m_{PL}\right]h_{PLTC}\right)a_{PLTC}} \qquad \text{(A3.2-16)}$$

$$\frac{d^2R_{tot}}{dP_L^{*2}} = 2\left[\frac{e_{RPL}a_{RPL}R_{PS}^*}{1+a_{RPL}h_{RPL}R_{PS}^*} - m_{PL}\right]\frac{1}{a_{PLTC}P_L^{*3}} > 0 \text{ for positive } P_L^* \qquad \text{(A3.2-17)}$$

Substituting Eq. A3.2-12 into Eq. A3.2-16 yields the value of m_{TC} at which the invasion threshold of P_S has its minimum in R_{tot} (Eq. A3.2-18):

$$m_{TC} = \frac{e_{PLTC}\left[\frac{e_{RPL}a_{RPL}R_{PS}^*}{1+a_{RPL}h_{RPL}R_{PS}^*} - m_{PL}\right]}{1+2h_{PLTC}\left[\frac{e_{RPL}a_{RPL}R_{PS}^*}{1+a_{RPL}h_{RPL}R_{PS}^*} - m_{PL}\right]} \qquad \text{(A3.2-18)}$$

which yields a value of 0.0512 with the default parameterization (Fig. 4).

Invasion of *C* into the *R-P$_L$-TC-P$_S$* system

The minimum density P_{SC}^* for successful invasion of *C* into the *R-P$_L$-TC-P$_S$* system is derived from Eq. 4.

$$P_{SC}^* = \frac{Z}{\left(e_{P_SC}a_{P_SC} - a_{P_SC}h_{P_SC}Z\right)} \qquad \text{(A3.2-19)}$$

$$Z := \left[m_C + \frac{a_{CTC}C^{*(n-1)}TC^*}{1+a_{P_LTC}h_{P_LTC}P_L^{*n} + a_{CTC}h_{CTC}C^{*n}}\right] \qquad \text{(A3.2-20)}$$

In order to invade an *R-P$_L$-TC-P$_S$* system *C* has to balance both density independent mortality m_C and losses from predation by *TC* (expressed by the ratio in expression A3.2-20). In an *R-P$_L$-TC-P$_S$* system at equilibrium (Eqs. A3.2-21 to 24), *TC* as well as *R* and P_L are, however, constant and only P_S increases with R_{tot}.

$$R^{*} = \frac{m_{PS}}{\left(e_{RP_S} a_{RP_S} - m_{PS} a_{RP_S} h_{RP_S}\right)} \tag{A3.2-21}$$

$$P_L^{*} = \left(\frac{m_{TC}}{e_{P_L TC} a_{P_L TC} - m_{TC} a_{P_L TC} h_{P_L TC}}\right)^{\left(\frac{1}{n}\right)} \tag{A3.2-22}$$

$$TC^{*} = \left[\frac{e_{RP_L} a_{RP_L} R^{*}}{1 + a_{RP_L} h_{RP_L} R^{*}} - m_{PL}\right]\left(\frac{1}{a_{P_L TC} P_L^{*(n-1)}} + h_{P_L TC} P_L^{*}\right) \tag{A3.2-23}$$

$$P_S^{*} = R_{tot} - R^{*} - P_L^{*} - TC^{*} \tag{A3.2-24}$$

Hence with P_L^{*} and TC^{*} being constant and only P_S increasing with increasing R_{tot} in the R-P_L-TC-P_S system, the invasion threshold R_{totC} of C closely follows the shape of the invasion threshold of P_S at $R_{totC} = R_{totPS} + P_{SC}^{*}$ (Fig. 4).

Appendix A3.3. Response pattern of the pentagon module to enrichment under the assumption of a type 3 functional response for top consumers and a linear functional response for ciliates.

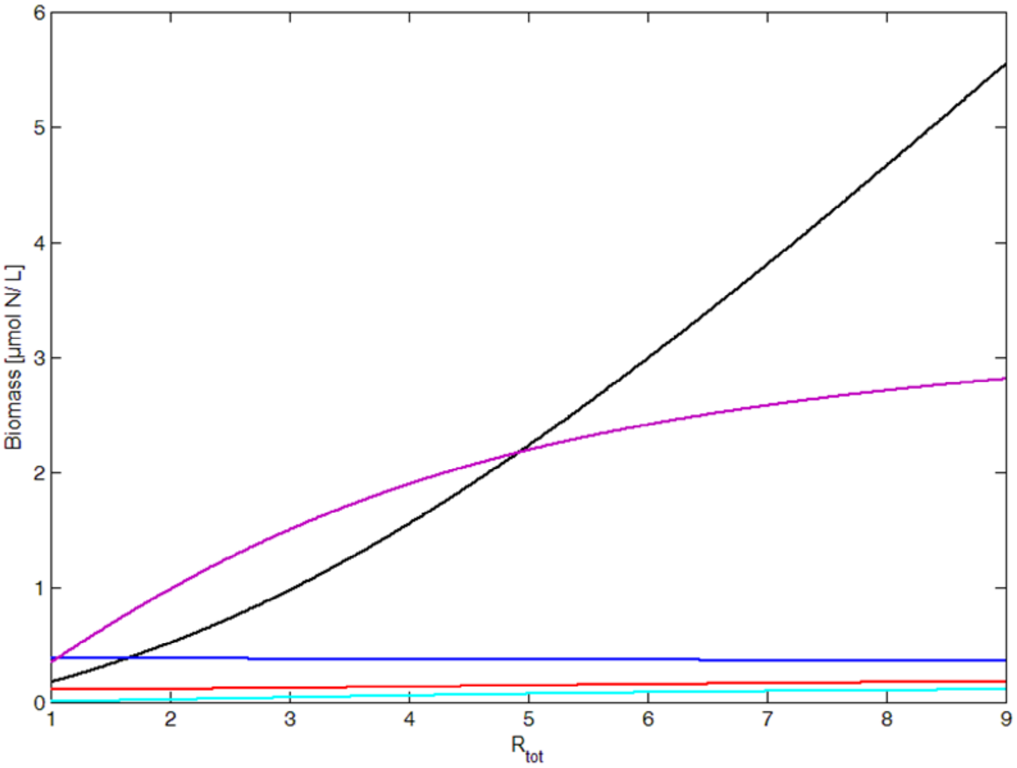

Fig. A3.3.1. Stable equilibrium densities (µmol N/L) of the full pentagon module along an enrichment gradient (R_{tot}) with a switching top consumer (type 3 functional response) when ciliates are assigned a linear functional response (h_{PSC} = 0). Other parameters are listed in Table 3.1. State variables are indicated by different colours: R black, P_L blue, TC violet, P_S red, and C turquoise. Note that the x-axis starts at an R_{tot} value of 1. For further explanations see main text.

General Discussion and Research Outlook

"The general ecologist needs a raft from which to cast his sampling plankton net. The plankton may be patchy and the work of collection and synthesis very laborious, but if he has some clear principles by which to sort out the material, great advances are possible."
[Elton 1949, p.1-2]

The aim of my thesis was to gain general insight into structural properties of webs consisting of two alternative energy pathways with specialist versus generalist top consumers. I found that equilibrium response patterns to bottom-up and top-down forcing can be broadly categorized on the basis of only two easily measurable descriptors of food web topology, namely chain length (odd-odd, odd-even, even-even) and presence or absence of a generalist predator (looped versus branched). The most prominent response pattern is the precedence of the even chain with respect to bottom-up forcing and of the odd chain with respect to top-down forcing when combined in a single web. The general patterns give important insight into the interplay of food web dynamics and nutrient flow and may therefore serve as a new baseline for community as well as ecosystem ecology (DeAngelis 1992, Loreau 2010).

While for each web the bottom-up and top-down response is strongly predictable along each of the constituent chains, the summed trophic level response will frequently deviate from food chain theory. The strength of the presented framework is therefore not only that it provides predictions about community responses along alternative chains, but that it explains deviations from food chain theory based on otherwise identical assumptions about density-dependence in pair wise consumer-resource interactions. In fact, the response patterns can be deduced by reasoning from food chain theory about alternating control patterns in chains of odd versus even length and its implications for the control of the shared basal level.

The developed framework can also be viewed as an extension to investigations on basic ecological relationships, with exploitative and apparent competition between chains instead of single populations. My investigations therefore not only extend food chain theory to two alternative pathways, but also add some generalities to theory about exploitative and apparent competition (see also Grover 1997).

Integration of more than two pathways

In chapter 1 it was stated that the patterns are still valid if branching occurs higher up in a food chain instead of the basal resource. Similarly, it is likely that some of the patterns can be extended to webs with more than two parallel pathways, which would relax the restrictive assumption of only two major pathways. Imagine, for example, a branched web with three chains emerging from different-sized primary producers, all involved in competition for a shared nutrient pool, but each with a specialist top consumer (Armstrong 1994). With only odd chains present, all top trophic levels will respond positively to enrichment, but in the presence of a single chain of even length, this chain will control nutrients at the base of the web and limit nutrient flow up all odd chains (see some hints in that direction in Armstrong 1994). Similar reasoning may hold true for certain connections of looped webs with more than two chains. For example, the derived pattern for looped even-even webs suggests that a generalist predator could possibly connect multiple chains of even length without violating the general pattern, i.e. all chains responding as if in isolation. However, the number of parallel chains, as well as chain length itself, will be restricted by nutrient availability (Armstrong 1994, Thingstad 1998).

Top-down shapes bottom-up

There is a prevalent discussion among ecologists about the relative importance of bottom-up versus top-down control in natural webs (reviewed in Power 1992, but see more recent examples Frederiksen et al. 2006, Kos et al. 2011, Rzanny et al. 2012). The results from my thesis support the view that the bottom-up response of a given web is strongly determined by top-down control (Hairston et al. 1960, Paine 1980, empirical evidence Carpenter et al. 1985, Reid 2000, Schmitz et al. 2000, Baum & Worm 2009, Faithfull et al. 2011, Estes et al. 2011, Marczak et al. 2011, Levi & Wilmers 2012). However, in the presence of alternative energy pathways, community responses to top-down manipulations will frequently deviate from predictions of models that aggregate the community to a single food chain.

Given these results it is not surprising that there are many empirical examples where clear trophic cascades at the level of the entire community could not be found and that, conversely, communities exhibiting clear trophic cascades are often characterized by strong interactions between only a few, dominant species that are engaged in chain-like interactions (see Shurin et al. 2002, Shurin et al. 2006, Sommer & Sommer 2006). Still, my results caution that the loss of a top-predator will normally lead to a shift in control-patterns between and within chains and may even cause secondary extinctions of species, if the web resulting from top-predator removal would form a non-feasible branched even-even web (Grover 1997).

With regard to the interplay of top-down and bottom-up forcing, my results show that bottom-up and top-down responses are generally opposite to each other, meaning that the net-response to combined forcing cannot be stated a priori. Results from chapter 3 suggest, however, that simultaneous bottom-up and top-down forcing is destabilizing and may shift environmental conditions to regions with a high potential for alternative states and abrupt regime shifts. The disruption of upper trophic levels by humans combined with anthropogenic eutrophication therefore synergistically act to destabilize natural communities (Sala 2006, Estes et al. 2011). This theoretical observation seems to be supported by accumulating evidence of regime shifts in marine (Hare & Mantua 2000), freshwater (Carpenter et al. 1999) and terrestrial ecosystems (Staver et al. 2011).

Re-introduction of apex predators has therefore been proposed as a measure for the restoration of a sustained ecosystem functioning, taking advantage of the regulating influences of apex predators (Sala 2006, Levi & Wilmers 2012). However, especially in the marine realm it has been shown that re-establishment of apex predators may be prevented by altered community structure, especially if stage-dependent feedback mechanisms are involved (De Roos & Persson 2002, Van Leeuwen et al. 2008, Steneck 2012).

The influence of ontogenetic diet-shifts on basic ecological interactions

A comparison of the results from chapter 2 with other recent studies point at some generalities in the influence of consumer stage structure and ontogenetic diet shifts on the basic ecological interactions that constitute the building blocks of more complex food webs, i.e. resource competition (Schellekens et al. 2010), shared resource competition and predation (chapter 2), and intraguild predation (Hin et al. 2011). In the absence of differences between consumer stages, coexistence of competitors in these three interaction modules requires intrinsic trade-offs between the abilities to exploit alternative resources (resource competition module), between the abilities to compete for resources and to withstand predation (diamond module), or between the abilities to compete for resources and to feed on a competitor (intraguild predation module). However, ontogenetic diet shifts in combination with food-dependent maturation and reproduction rates can easily create such trade-offs as emergent phenomena. Stage-structure thus does not eliminate the necessity of such trade-offs for coexistence, but offers a new mechanism for the creation of trade-offs through differential feeding responses on alternative prey/resources expressed through dominance patterns between stages. Note however that the same mechanisms are responsible for the emergence of alternative states and may thus also hinder coexistence or invasibility.

In light of these results and the prevalence of ontogenetic diet shifts in nature, in order to gain a better understanding of community responses to environmental forcing, it seems advisable to more generally consider differences in resource use and stage-specific feedback-mechanisms in both monitoring and manipulative studies (De Roos et al. 2003, Persson & De Roos 2006, Ohlberger et al. 2011, Schröder et al. 2012).

More complexity at the top consumer level – current results and future perspectives

In chapter 2 and 3 of this thesis it has been shown that under more complex, nevertheless realistic, assumptions on population structure and feeding interactions the bottom-up response may deviate from predictions based on homogenous populations and linear or type 2 functional responses. However, community level consequences of more complex assumptions at the population level still depend on structural web properties and the position in the corresponding web. For example, in the context of spatially structured webs (two food chains originating from distinct resources, connected by a structured population, each stage being specialized on a prey from a different chain) it has been shown that the potential for alternative states critically depends on the position of the two stages along each chain (if at least one stage is under top down control along its respective food chain, alternative states cannot arise) (Nakazawa 2011).

Negative co-variance of alternative prey of a generalist top consumer is a general feature of looped odd-odd and looped odd-even webs. In chapter 3 it has been shown that switching plays out especially strong in the context of negatively correlated prey species along a gradient of nutrient enrichment. This feature of looped odd-odd and looped odd-even webs is preserved in the presence of ontogenetic diet shifts or switching functional responses at the top consumer level. This can be deduced from the fact that, in equilibrium, the fixed mortality rate of a generalist consumer (note that also structured populations experience a fixed mortality rate at the population level) has to be balanced by feeding on both prey. Hence if one prey decreases along an environmental gradient this has to be balanced by an increase of the alternative prey and vice versa.

Knowledge about structural web properties is therefore also necessary to forecast community level consequences of external forcing under more complex assumptions on the population level. In light of the results from this thesis, there is a need for more general insight into the role of ontogenetic diet shifts and flexible foraging for community dynamics in the context of multiple interacting species. Given the prevalence of ontogenetic diet shifts in nature, a sensible extension of the current framework would therefore be a more general investigation of the interplay between structural web properties and ontogenetic diet shifts. Looped webs seem to be especially suited for this purpose since they allow for diet shifts between alternative energy pathways. Systematic investigations of stage structure and ontogenetic diet shifts in looped odd-odd, odd-even and even-even webs may enable more general insight on community level consequences of differences in resource use during life-history. Similar reasoning holds true for a systematic study of flexible feeding responses.

The approach taken on in this thesis to broadly categorize webs due to their structural properties, allows for most general predictions on community dynamics under external forcing. The main categories - odd-odd, odd-even, even-even, branched and looped webs - are furthermore an ideal baseline for systematic investigations of food web dynamics under various possible extensions of the current framework, some of which were indicated in the previous sections, e.g. inclusion of a donor-controlled detritus pathway, of more than two parallel pathways or more complex assumptions at the population level.

Recent findings that the trophic role of species (defined by its direct feeding links towards resources and consumers and its position in corresponding food web ‘motifs’) is highly preserved across different communities (Stouffer et al. 2012), highlight the strength of a more structural based approach for investigations on community dynamics. In light of the results from this thesis, a combination of knowledge on community structure and a species trophic role may enable to predict community level consequences of species gain or loss on the basis of its impact on community structure. This also adds a new perspective to investigations on invasions of non-native species (Strayer 2012).

In light of multiple anthropogenic stressors and their severe impact on natural communities worldwide, insight from this thesis that food web structure is a strong determinant of community response to external forcing is very promising with regard to the development of sustainable management strategies to preserve ecosystem functioning.

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Erklärung

Diese Promotion wurde im Sinne §12 der Promotionsordnung von Prof. Dr. Sebastian Diehl betreut. Ich erkläre hiermit, dass die Dissertation keiner anderen Prüfungskommission vorgelegt worden ist und dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

Eidesstattliche Erklärung

Ich versichere hiermit an Eides statt, dass die vorgelegte Dissertation von mir selbständig und ohne unerlaubte Hilfe angefertigt ist.

München, den 08.01.2013 ___________________________

(Sabine Wollrab)