Population persistence in the face of size-dependent predation and competition interactions

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Population persistence in the face of size-dependent predation and competition interactions

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Chapter 1

Introduction and Summary

1.1 Population models

A population is defined as a group of individuals of one species within a defined area. Temporal variation in the number or biomass of the individuals in a population reflects the population dynamics. Individual-level processes that drive population dynamics are reproduction, growth and mortality. These processes, in turn, may be influenced by other species, such as predators or competitors. The development of theory on population dynamics and species interactions is aided by models. Often population models are used which lack information on the individual level and thus only provide a phenomenological description of reproduction and mortality at the population level. This leads to relatively simple mathematical equations, that are highly transparent. The models are often referred to as unstructured population models, as they do not account for structure in age or size within a population. With the use of these unstructured population models many interactions between populations and/or species have been studied, such as competition and predation (Oksanen et al. (1981)). Extensions to several populations connected by dispersal or more species, f.e. multi-trophic systems, have proven very useful in increasing the understanding of how intra- and/or inter-specific interactions influence populations.

Whereas the simplicity of the unstructured population models is an advantage, it is at the same time a limitation for modeling population dynamics. With a phenomenological approach all processes are described at the population level and the individual level is not taken into account. Moreover, all individuals within a population are assumed to be identical and invariant in individual properties such as size or foraging ability. In this modeling framework the modeler decides which assumptions, at the population level, are incorporated in the model, for example, density-dependent population growth.

Unstructured models thus ignore that individuals follow their own, unique life history from birth to death. Organisms grow during their life and it is likely that within a population individuals with different sizes will be present. If one wants to take differences between individuals into account, a physiological representation of individuals is needed to capture the individual-level processes. Acknowledging the individual level as the level of organization at which all processes take place implies that no assumptions are made on the population level. While describing physiological processes at the individual level, the population dynamics, *i.e.* the variation in time of the number or biomass of individuals, is the result of tracing all individuals over time. To model the individual physiology, and the emerging population dynamics, a theoretical framework and numerical tools termen physiologically structured population models (PSPMs) have been developed (de Roos et al. (1992)). Similar to the unstructured models described above, for these physiologically structured population models (PSPMs) also holds that reproduction, growth and mortality are the basic processes that determine the population dynamics. However, in a PSPM, these processes are a function of individual physiology, which allows for a mechanistic link between individual physiology and population dynamics, in contrast to the phenomenological approach of unstructured models. This fundamental difference in the level at which assumptions are made gives not only rise to population dynamics that emerge from individual-level assumptions, but also allows mechanisms that play an important role for population dynamics to manifest themselves. In contrast to the unstructured models these mechanisms arise from individual-level assumptions and not from a priori modeling decisions, as no assumptions are made at the population level.

1.2 Individual life history and environment

Increasing in size when developing from a juvenile into an adult is a common feature for most organisms, and the difference between adult size and juvenile size can be several orders of magnitude (Werner and Gilliam (1984); Werner (1988)). For many taxa, such as insects, amphibians or crustaceans, distinct stages can be recognized during development, while other species show more continuous growth during at least a large part of their life. The use of body size in most physiologically structured population models is justified by the significant influence of body size on the individual ecology.

The growth rate of an individual in general depends on its rate of energy intake, which is referred to as food-dependent development. The rate of food intake often depends on the size of the individual, f.e. because large individuals have higher searching capacities than small individuals. Of course food availability also plays an important role. Individuals that encounter high resource densities will grow faster than similar-sized individuals in a less profitable environment. The size of an individual has implications for many ecological interactions, such as competition or predation, and being of a certain size has both benefits and disadvantages (de Roos and Persson (2001)). For example, if small-sized individuals are more vulnerable to predation, fast growing individuals will be exposed for a shorter period of time to that mortality. Being small can also have benefits when prey hide in small cavities and cannot be reached by large predators. The size of an individual at a certain moment in time is a result of its life history, although of course bounded by its maximum growth rate. The life history of an individual is made up of all events that occur during its life. Hence, individuals that are born with similar sizes but that encounter a different environment will have different life histories, and may therefore reach different sizes.

A change in size has consequences for how an individual responds to its environment. The environment of an individual consists of abiotic elements, such as temperature, and biotic elements, such as (biotic) resource or other individuals. An example of a size-dependent response to the environment is the response of individuals to temperature. Small individuals have a metabolic advantage over larger ones in summer, because maintenance requirements scale faster with size than with food intake rate. It is therefore profitable to be small in summer, a metabolic advantage that declines when small individuals grow. On the other hand, winter mortality is most severe for small individuals because they have smaller fat reserves. In this case, growth during summer increases the survival chances of individuals during winter.

Besides its response to the environment, the size of an individual also determines the impact of the individual on its environment. Many organisms exhibit shifts in diet when they grow. These diet shifts are often, but not necessarily, accompanied by a shift in habitat, e.g. many insect species metamorphose from an aquatic juvenile stage into a terrestrial/aerial adult stage. Organisms that exhibit metamorphosis are a good example of how the impact of an individual on its environment can change with development. Also organisms that have a more gradual growth pattern may feed on different resources during different parts of their life cycle, a phenomenon referred to as life history omnivory (Polis and Strong (1996)). 'Omnivory' itself only accounts for foraging on more than one resource, which occurs simultaneously and throughout an individual's life, in contrast to life history omnivory, where a separation in time is taken into account. Predator species that exhibit life history omnivory often share as a juvenile a resource with their future prey, and while small 'predators' grow they change from competitor to predator. The role of the prey species hence changes with predator growth from being a competitor for a shared resource to being prey.

1.3 Population dynamics

Size determines the nature of many ecological interactions and most organisms grow in size during their life, hence size also influences population dynamics. As a consequence, predictions of population models that ignore size structure may differ significantly from those of models that take this into account. The PSPMs used in this thesis take not only differences in body size between individuals into account, but also growth of individuals. In the models the population consists of several cohorts (year classes), and each cohort consists of identical individuals, which were born at the same time. Individuals grow, reproduce and die and the population dynamics come about by keeping track of these individual events over time. In addition, the individuals have an impact on their biotic environment. When an individual consumes a food item, that item cannot be consumed again by other individuals. The total food intake summed over all individuals present in the population can have a major impact on resource density, which in turn affects individual food intake. Consequently, a feedback loop emerges between individuals and their biotic environment.

A good example of the population-level effect of a feedback loop between individuals and their resource, and a common outcome of physiologically structured population models, are the so called 'recruitment driven single cohort cycles'. This type of dynamics entirely results from the individual-level assumptions. The recruitment driven single cohort cycles are found in PSPMs if maintenance requirements scale faster with size than intake rates. As a consequence, small individuals have a metabolic advantage over large individuals at low resource densities. Adult individuals produce large numbers of offspring and these many small individuals suppress the resource density. As a result of their metabolic disadvantage the adults are outcompeted by their own offspring and die of starvation. The remaining juvenile cohort is now the only cohort in the population. The number of individuals in this dominant cohort decreases due to background mortality, which represents a chance to die from causes other than starvation, for example disease or predation. With the decline in the number of individuals the resource density increases again. This allows the surviving individuals to grow and reach large sizes. When the maturation size is reached the individuals can reproduce. However, once mature, this cohort is outcompeted by their own offspring, which gives rise to a new population cycle.

The cyclic population dynamics thus emerge from individual-level assumptions and the population feedback on resource density (Persson et al. (1998); Claessen et al. (2000)).

In each chapter of this thesis a physiologically structured population model is used to study the interactions between individuals and their environment. In these models individuals are characterized by their size, which determines individual properties such as fecundity and foraging capacity. All individuals exhibit food-dependent development. The dynamic feedback loop between individuals and their environment gives rise to patterns that are based on individual-level assumptions, but that govern populations dynamics and community structure. In Chapter 3 and 4 I study the impact of a changing abiotic environment on the feedback loop between consumers (perch, *Perca fluviatilis*) and their environment. In Chapter 5 and 6 the interactions between individuals of a consumer (roach, *Rutilus rutilus*) population and a predator (perch, *Perca fluviatilis*) population are studied, as well as the interaction between individuals within a population.

In all chapters feedbacks are crucial for the population dynamics. Moreover, the population feedback can act as a regulating factor for population persistence and extinction. When adult individuals are large, they produce large numbers of offspring. Although the young of the year (YOY) individuals are small, their large numbers cause resource competition to be high and thereby depressing the resource density. When these small individuals do not grow sufficiently during their first growth season, they will suffer from starvation mortality during their first winter. Recruitment failure, when recruitment of YOY to their second year fails, can hence occur as a result of a too high population fecundity (Chapter 3 and 4). Large individuals can thereby have a negative effect on their smaller conspecifics, not only by increasing the YOY intra-cohort competition for resource through fecundity, but also by increasing the interspecific resource competition. In Chapter 6, size-dependent predation of predators older than 1 year increases the population fecundity of the consumer population. Since YOY predators cannot yet forage on consumers, they compete for resource with consumer individuals. The latter, however, are the better competitors for this shared resource, hence an increase in consumer reproduction, decreases resource availability for the YOY predators and induces a juvenile bottleneck. As a result of the low per capita food intake the YOY predators exhibit retarded growth. Hence, by foraging on the consumer population large predators indirectly strengthen the inter-specific juvenile bottleneck imposed on their offspring. When predation on YOY consumers is sufficiently high and results in an increase of resource density due to the rapid decrease of their numbers, growth of YOY predators is again promoted. A larger body size at the age of 1, when small predators start predation on consumers, implies an increased predation attack rate on the latter. As a result, a positive feedback is present between one predator cohort to the next, which operates through predation on YOY consumers and the resulting release of resource density. Eventually, this population feedback results in recruitment failure and subsequently in extinction of the consumer population (Chapter 5).

1.4 Summary

In previously studied physiologically structured population models the winter period was assumed to be a period of complete stasis (Persson et al. (1998); Claessen et al. (2000)). Winter was therefore not modeled, and each growth season directly followed the previous growth season. Any temperature fluctuations, or seasonality, where discarded. However, for ectothermic organisms the level of activity depends on the ambient temperature. Temperature is known to affect small individuals in a negative manner (Post and Evans (1989)). In Chapter 3 the effect of seasonality on a consumer-resource system is studied. The model is parameterized for Eurasian perch (*Perca fluviatilis*) and its resource *Daphnia spp* (1.0 mm). Temperature affects both resource productivity (productivity is a measure of the rate of biomass production per unit area) and all physiological rates of consumers. When resource productivity and consumer physiological rates scale down with equal rates and to the same minimum level with decreasing temperature, the population dynamics resemble the results from models that assume winter to be a period of stasis. However, when the physiological rates of consumers, such as maintenance cost and food intake rate, scale down to a lesser extent with decreasing temperature than the resource productivity, consumers need reserves to cover maintenance requirements during the period of reduced temperatures. Including a winter season in a size-structured population model results in a size threshold that YOY individuals need to reach in order to have sufficient reserves to cover maintenance and survive winter. This size threshold will be reached if the per capita food intake of YOY allows for sufficient growth during the growth period. The per capita food intake and hence the growth of YOY can be compromised if the number of individuals is large. Whether due to a large reproduction pulse or a large number of individuals in general, recruitment failure occurs if resource availability for YOY is insufficient. As a result, the feedback from the population on resource density is shown to negatively affect population persistence. Small numbers of individuals can survive while a population cannot persist due to the feedback loop on resource density. The increase in number of individuals can hence result in an ecological suicide of the population.

A recent trend of increasing annual temperature has been documented, which is referred to as global warming. As is being discussed in Chapter 3, individuals respond to annual temperature changes as a function of their size. It is therefore to be expected that global warming will affect individuals differently depending on their size. When small individuals have a metabolic advantage in summer but suffer from starvation mortality in winter (Chapter 3), global warming can be expected to benefit small individuals. However, if small individuals suffer less starvation mortality in winter and survival rates are high, resource competition will increase. This has consequences for individual growth rates, which are likely to decrease because of the lower per capita resource intake. How global warming affects individuals and the population they are part of is studied in Chapter 4 using the same model as in Chapter 3. For freshwater ecosystems in maritime temperate regions, that are not covered with ice during winter, water and air temperatures are closely linked. Because the winter temperature increases more rapidly than summer temperature, global warming in such an environment primarily translates into an increase in the water temperature during winter (Easterling et al. (1997); Schindler (1997); Hughes (2000)). In boreal and continental temperate regions global warming will more likely lead to an increase in growth season duration due the decrease in the period of ice-cover (Magnuson et al. (2000)). These two global warming scenarios are studied: 1) an increase of summer duration, and 2) an increase of the minimum winter temperature. I find that small individuals cannot profit from global warming. In the first scenario the YOY suffer as a direct effect of summer prolongation via longer exposure to high mortality imposed by predators. However, due to this decrease in number during summer YOY do not suffer from starvation mortality during winter. In contrast, in the second scenario YOY do suffer from starvation mortality in winter due to high numbers of competitors that result from high population fecundity. In this scenario, the population feedback plays a more important role than the increase in minimum temperature. Large individuals, on the other hand, profit from global warming and can grow into even larger sizes in both scenarios. The individuals that survive a period with high mortality, either in summer or in winter, can benefit of the low resource competition and the high food intake, and hence profit from the population feedback mechanism. The size-dependent difference in response to global warming at the individual level may result in recruitment failure and extinction of the consumer population when population fecundity is increased.

In contrast to Chapter 3 and 4, Chapter 5 and 6 deal with a changing biotic environment, and not a changing a-biotic environment. Two different species are studied, a consumer (roach, *Rutilus rutilus*) and a predator (perch, *Perca fluviatilis*), and for both species physiological structure is taken into account. The predator exhibits life history omnivory, and changes from foraging on the same resource as the consumer when small, to foraging on individuals of the consumer species when larger. This double interaction between two species, involving a competitive and a predator-prey interaction, is defined as intraguild predation (Holt and Polis (1997); Mylius et al. (2001)), and is common in many natural systems (Arim and Marquet (2004)). This type of interaction has not been studied before with the use of a PSPM. Previous modeling studies, that only accounted for 'omnivory', show that coexistence of predator and consumer is limited to intermediate levels of productivity (Holt and Polis (1997); Mylius et al. (2001)). In contrast to these model results, I show in Chapter 5 that accounting for life history omnivory reduces the occurrence of coexistence of predator and consumer along a productivity gradient. When juvenile predators, that are too small to predate on the consumer, do well on the shared resource, they grow to larger sizes and, hence, have a higher predation attack rate when they start predating on the consumer. Such a cohort of juvenile predators can do well on the shared resource if consumer densities are reduced through predation by older predator cohorts. This gives rise to a positive feedback loop between successive predator cohorts stemming from food-dependent development and size-dependent foraging abilities, which could not emerge from an unstructured model. In order to test whether higher performance as a predator due to an increased density of the shared resource and the resulting decrease in the occurrence of coexistence is more general and not limited to the size-structured model, we incorporated it into an unstructured model. The results of the unstructured model also show the negative effect of the positive feedback mechanism on coexistence. Moreover, results from a whole-lake experiment support the mechanism that I reveal by analyzing the model. In this experimental study recruitment of the consumer species is only successful when the number of small predators is very low (Persson unpublished). Using the PSPM I also study the effect of an exclusive resource for the predator on the community. When an exclusive resource for the predator is present, coexistence of predator and consumer is possible at a small range of intermediate productivity levels, resembling the results of previous modeling studies that did not incorporate physiological structure.

In Chapter 6 the same model is used as in Chapter 5, but in this study cannibalism for the predator is included. When predators cannibalize on their own offspring they actually reduce their own density. Cannibalism promotes coexistence between predator and consumer due to the decrease in the total number of predator individuals. When predator and consumer coexist we can study a more long-term interaction between the populations, in contrast to Chapter 5 where the dynamics concerning the consumer exclusion are discussed.

In this chapter I show that a feedback loop between predator and consumer arises, which results in increased consumer growth, but retarded predator growth. The latter is referred to as an interspecific juvenile bottleneck. When predators mainly feed on the small individuals in the consumer population, the surviving consumers experience an environment with high resource densities and little resource competition. The surviving consumers can hence grow into larger sizes and produce more offspring than without predation. Thus size-dependent predation on the consumer population leads to an increase in fecundity of adult consumers and hence to an increase in the number of YOY consumers, which are the main food for the predator. However, small predators cannot forage yet on consumers and compete with small consumers for the same resource. The high number of offspring of the consumer population suppresses the density of the shared resource to such a low level that the offspring of the predator experiences reduced growth rates. While large predators 'cultivate' their own food, they promote the juvenile bottleneck imposed on their own offspring (Chapter 6).

The models studied in this thesis take differences between individuals into account, and allow for growth and development to occur in a dynamic environment. Allowing for size-dependent interactions gives rise to a whole new scope of mechanisms that affect population dynamics. In Chapter 3 and Chapter 4 I show that the feedback of the population on resource density may cause recruitment failure and extinction of that population, even when conditions are such that a single individual can survive and reproduce. This implies that the establishment of a few individuals may not necessarily result in long-term population persistence. These two chapters are the first studies where explicitly the effect of an abiotic element of the environment is studied using a PSPM. The model used in Chapter 5 and Chapter 6 is the first physiologically structured population model in which for two species size-structure is incorporated. The feedback loop between predators, consumers and the shared resource results in a positive effect of predation by one predator cohort to the next predator cohort. This loop can cause extinction of the consumer species (Chapter 5). If a predator and a consumer population coexist the size-dependent interactions between individuals influence the dynamics of both populations. When coexisting, a juvenile bottleneck emerges for small predators, while small consumers grow more quickly (Chapter 6). All these mechanisms would not become apparent from unstructured models that use a phenomenological description at the population level. The mechanisms arising from physiologically structured population models are based on assumptions made at the individual level that have a strong link with empirical data. Physiologically structured models are therefore an asset to (theoretical) ecology, which, together with unstructured models and certainly empirical work, aid to our knowledge of the natural world.

Chapter 2

Introductie en Samenvatting

2.1 Populatie modellen

Een populatie wordt in het algemeen beschouwd als een groep individuen van een bepaalde soort die binnen een bepaald gebied voorkomt. De populatie dynamica wordt weer gegeven door de variatie in de tijd van aantallen of biomassa van de individuen in die populatie. Processen op het niveau van het individu die de dynamica beïnvloeden zijn reproductie, groei en sterfte. Deze processen, en daarmee de populatie dynamica, kunnen beïnvloed worden door andere soorten, bijvoorbeeld predatoren of concurrenten. Theorie over populatie dynamica en de interacties tussen soorten wordt ontwikkeld met behulp van modellen. Vaak worden er populatie modellen gebruikt waarbij informatie op het individu niveau ontbreekt en deze modellen geven daarom alleen een fenomenologische beschrijving van reproductie en sterfte op populatie niveau. Dit leidt tot relatief eenvoudig wiskundige vergelijkingen en een hoge mate van transparantie. Aan deze modellen wordt vaak gerefereerd als ongestructureerde populatie modellen omdat ze geen rekening houden met structuur, zoals leeftijd- of grootte-structuur, binnen een populatie. Met behulp van deze ongestructureerde populatie modellen zijn vele interacties tussen populaties en/of soorten bestudeerd, zoals competitie en predatie (Oksanen et al. (1981)). Uitbreiding naar meer populaties, bijvoorbeeld meta-populaties, of meer soorten, bijvoorbeeld multitrofische systemen, is erg nuttig gebleken om meer inzicht te krijgen in hoe intra- en/of inter-specifieke interacties populaties beïnvloeden.

Terwijl de eenvoud van de ongestructureerde modellen een voordeel is, is het tegelijkertijd ook een beperking. Met een fenomenologische aanpak worden alle processen op populatie niveau beschreven en het individu niveau wordt niet beschouwd. Bovendien wordt aangenomen dat alle individuen in de populatie identiek zijn en dat er geen variatie is in eigenschappen van individuen, zoals grootte of foerageer vermogen. In dit modelraamwerk is het de modelleur die de aannames doet, welke op populatie niveau in het model worden opgenomen, bijvoorbeeld dichtheidsafhankelijke populatie groei.

Ongestructureerde modellen negeren dus dat individuen hun eigen, unieke, levensgeschiedenis hebben van geboren worden tot sterven. Organismen groeien gedurende hun leven en het is waarschijnlijk dat binnen een populatie individuen van verschillende groottes aanwezig zullen zijn. Als men wil erkennen dat er verschillen zijn tussen individuen en daar ook daadwerkelijk rekening mee wil houden, dan is een fysiologische representatie van individuen nodig om de op individu niveau werkende processen vast te leggen. Het erkennen van het individu niveau als het organisatie niveau waarop alle processen plaatsvinden, houdt in dat er geen aannames op het populatie niveau worden gedaan. Terwijl de fysiologische processen op het individu niveau worden beschreven is de populatie dynamica, de variatie in de tijd van het aantal of de biomassa van individuen, het resultaat van het bijhouden van alle individuen in de tijd. Een theoretisch raamwerk en numerieke methoden zijn ontwikkeld om de fysiologie van individuen te kunnen modelleren, waarbij de populatie dynamica als het ware te voorschijn komt (de Roos et al. (1992)). Net zoals voor de hierboven beschreven ongestructureerde populatie modellen, geldt voor de fysiologisch gestructureerde populatie modellen (physiologically structured population model: PSPM) dat reproductie, groei en sterfte de basis processen zijn die de populatie dynamica bepalen. In een PSPM zijn deze processen echter een functie van de fysiologie van een individu, waardoor er een mechanistische link tussen fysiologie van individuen en de populatie dynamica ontstaat, in constrast met de fenomenologische aanpak van ongestructureerde modellen. Dit fundamentele verschil in het niveau waarop aannames worden gedaan, resulteert niet alleen in populatie dynamica die te voorschijn komt uit het bijhouden van alle individuen in de tijd, maar ook in mechanismen die zich als belangrijk voor de populatie dynamica manifesteren. In tegenstelling tot ongestructureerde modellen komen deze mechanismen voort uit aannames op het individu niveau en niet uit a priori model-beslissingen, aangezien er geen aannames op het populatie niveau worden gemaakt.

2.2 Individuele levensgeschiedenis en omgeving

Een toenemen in grootte bij de ontwikkeling van juveniel tot adult komt veelvuldig voor bij de meeste organismen. Het verschil in grootte tussen juveniel en adult kan meerdere orden van grootte zijn (Werner and Gilliam (1984); Werner (1988)). Voor veel taxa, zoals insekten, amfibieën of schaaldieren, kunnen aparte stadia herkend worden tijdens de ontwikkeling, maar er zijn ook soorten die meer continue groeien gedurende voor tenminste een groot deel van het leven. Het gegeven dat organismen groeien en verschillen in grootte maakt lichaamsgrootte een handig kenmerk om individuen van elkaar te onderscheiden. Maar nog belangrijker is de significante invloed van lichaamsgrootte op de individuele ecologie die het gebruik ervan rechtvaardigt in de meerderheid van de fysiologisch gestructureerde modellen.

De groei-snelheid van een individu hangt in het algemeen af van zijn snelheid van energie inname, wat voedsel afhankelijke ontwikkeling wordt genoemd. De snelheid van voedsel inname hangt vaak af van de grootte van het individu, grotere individuen bijvoorbeeld, hebben meer capaciteiten om voedsel te zoeken dan kleine individuen. Natuurlijk speelt de beschikbaarheid van voedsel ook een belangrijke rol. Individuen die een hoge voedseldichtheid aantreffen zullen sneller groeien dan individuen van vergelijkbare grootte in een minder voordelige omgeving. De grootte van een individu heeft implicaties voor veel ecologische interacties, zoals competitie en predatie, en het hebben van een bepaalde grootte heeft zowel voor- als nadelen (de Roos and Persson (2001)). Bijvoorbeeld, als kleine individuen kwetsbaarder zijn voor predatie, dan zullen snel groeiende individuen voor een kortere periode bloot staan aan deze mortaliteit. Klein zijn kan ook voordelen hebben, bijvoorbeeld als prooi zich in kleine holtes verschuilt en daardoor onbereikbaar is voor grote predatoren. De grootte van een individu op een bepaald moment in de tijd is het resultaat van zijn levensgeschiedenis, natuurlijk wel binnen de grenzen van zijn maximale groeisnelheid. De levensgeschiedenis van een individu bestaat uit alle gebeurtenissen die plaatsvinden gedurende zijn leven. Vandaar dat individuen die met vergelijkbare grootte worden geboren, maar die een verschillende omgeving treffen, een verschillende levensgeschiedenis zullen hebben en daarom verschillende groottes kunnen bereiken.

Een verandering in grootte heeft consequenties voor hoe een individu reageert op zijn omgeving. De omgeving van een individu bestaat uit abiotische elementen, bijvoorbeeld temperatuur, en biotische elementen, bijvoorbeeld voedsel of andere individuen. Een voorbeeld van een grootte-afhankelijke respons op de omgeving is de respons van individuen op temperatuur. Kleine individuen hebben een metabolische voordeel ten opzichte van grote individuen in de zomer omdat de kosten voor lichaamsonderhoud (maintenance requirements) sneller met grootte schalen dan de voedsel inname snelheid. Het is daarom een voordeel om klein te zijn in de zomer, dit metabolische voordeel neemt echter af wanneer kleine individuen groeien. Anderzijds is sterfte in de winter het hevigst onder kleine individuen omdat deze minder vet-reserves hebben. In dit geval vergroot groei in de zomer de overlevingskansen van een individu gedurende de winter.

Naast de respons van een individu op zijn omgeving, bepaald de grootte van een individu ook de impact van het individu op zijn omgeving. Veel organismen vertonen gedurende hun groei een verandering in hun dieet. Deze dieet-veranderingen gaan vaak, maar niet altijd, gepaard met een verandering van habitat, bijvoorbeeld veel insekt soorten veranderen van gedaante van een aquatisch juveniel stadium in een terrestrisch adult stadium. Organismen die van gedaante veranderen zijn een goed voorbeeld voor hoe de impact van een individu op zijn omgeving kan veranderen gedurende de ontwikkeling. Ook organismen met een meer geleidelijk groei patroon kunnen van verschillend voedsel eten tijdens verschillende perioden in de levenscyclus, een fenomeen dat 'levensgeschiedenis omnivorie' wordt genoemd (hier na life history omnivory genoemd) (Polis and Strong (1996)). 'Omnivorie' zelf houdt alleen eten van meer dan één voedselbron in, wat simultaan en tijdens het hele leven van een individu gebeurt. Dit in tegenstelling tot life history omnivory, waarbij met een scheiding in de tijd wordt rekening gehouden. Predator soorten die life history omnivory vertonen delen vaak als juveniel een voedselbron met hun toekomstige prooi. Terwijl kleine 'predatoren' groeien veranderen ze van concurrent in predator. De rol van de prooi soort verandert daarom met de groei van predatoren van concurrent voor een gedeelde voedselbron tot prooi.

2.3 Populatie dynamica

Grootte bepaalt de aard van veel ecologische interacties en de meeste organismen groeien tijdens hun leven, vandaar dat grootte ook populatie dynamica beïnvloedt. Een consequentie hiervan is dat voorspellingen van populatie modellen die grootte-structuur negeren wezenlijk kunnen verschillen van de modellen die wel rekening houden met grootte-structuur. De PSPM's die gebruikt zijn in dit proefschrift houden niet alleen rekening met verschillen in lichaamsgrootte tussen individuen, maar nemen ook groei van individuen in beschouwing. De populatie in de modellen bestaat uit verscheidene cohorten (jaarklassen) en elk cohort bestaat uit identieke individuen die op het zelfde moment zijn geboren. Individuen groeien, reproduceren en sterven en de populatie dynamica komt tot stand door al deze individuele evenementen bij te houden in de tijd. Daar komt nog bij dat individuen een impact hebben op hun biotische omgeving. Als een individu een voedsel item heeft geconsumeerd dan kan dat voedsel item niet nog een keer gegeten worden door een ander individu. De totale voedsel inname, gesommeerd over alle individuen in de populatie, kan een grote invloed hebben op de voedseldichtheid, wat op zijn beurt weer effect heeft op de individuele voedsel inname. Zodoende onstaat er een terugkoppelingslus (hierna feedback loop genoemd) tussen individuen en hun biotische omgeving.

Een goed voorbeeld van het effect van een feedback loop tussen individuen en hun voedselbron op populatie niveau en een veel voorkomend resultaat van fysiologisch gestructureerde populatie modellen zijn de zo genaamde 'recruitement driven single cohort cycles' (door rekrutering gedreven cohort cycli waarbij maar één cohort voor het merendeel van de cyclus aanwezig is). De 'recruitement driven single cohort cycles' komen voor in PSPM's als de kosten voor lichaamsonderhoud sneller met grootte schalen dan de voedsel inname snelheid. Als gevolg hebben kleine individuen een metabolisch voordeel over grote individuen bij lage voedseldichtheden. Adulte individuen produceren grote hoeveelheden nakomelingen en deze vele kleine individuen onderdrukken de voedseldichtheid. Vanwege hun metabolische nadeel worden de adulten weggeconcurreerd door hun eigen nakomelingen en sterven van de honger. Het overgebleven juveniele cohort is nu het enige cohort in de populatie. Het aantal individuen in dit dominante cohort neemt af door achtergrond mortaliteit, wat een kans om dood te gaan aan oorzaken anders dan honger vertegenwoordigt, bijvoorbeeld ziekte of predatie. Met de afname van het aantal individuen neemt de voedseldichtheid weer toe. Hierdoor kunnen de nog aanwezige individuen groeien en een grote lichaamsgrootte bereiken. De individuen kunnen reproduceren als de maturatiegrootte is bereikt. Echter, dit nu adulte cohort wordt weggeconcurreerd door hun eigen nakomelingen, waarmee een nieuwe populatie cyclus begint. De cyclische populatie dynamica komt dus voort uit aannames op het individu niveau en de populatie feedback op voedseldichtheid (Persson et al. (1998); Claessen et al. (2000)).

In elk hoofdstuk van dit proefschrift is een fysiologisch gestructureerd populatie model gebruikt om de interacties tussen individuen en hun omgeving te bestuderen. In deze modellen worden individuen gekarakteriseerd door hun grootte, welke individuele kenmerken bepaald zoals fecunditeit en foerageer capaciteit. Alle individuen vertonen voedsel afhankelijke onwikkeling. De dynamische feedback loop tussen individuen en hun omgeving geeft aanleiding tot patronen die gebaseerd zijn op aannames op het individu niveau, maar die de populatie dynamica en structuur van de levensgemeenschap beheersen. In hoofdstuk 3 en 4 bestudeer ik de impact van een veranderende abiotische omgeving op de feedback loop tussen consumenten (baars, *Perca fluviatilis*) en hun omgeving. In hoofdstuk 5 en 6 worden de interacties tussen individuen van een consumenten populatie (roach, *Rutilus rutilus*) en een predator populatie (baars, *Perca fluviatilis*) bestudeerd, alsmede de interactie tussen individuen binnen een populatie.

In alle hoofdstukken zijn terugkoppelingen cruciaal voor de populatie dynamica. Bovendien, de populatie feedback kan als regulerende factor optreden voor populatie persistentie en extinctie. Als adulten groot zijn produceren ze een groot aantal nakomelingen.

Alhoewel de nul-jaar oude individuen (hierna YOY genoemd, afgeleid van 'young of the year') klein zijn, is vanwege hun grote aantallen de competitie voor voedsel hoog en onderdrukken ze de voedseldichtheid. Wanneer deze kleine individuen niet genoeg groeien in hun eerste groei-seizoen zullen ze in hun eerste winter blootstaan aan sterfte door honger. Het mislukken van rekrutering, wanneer YOY het volgende jaar niet halen, kan daarom een gevolg zijn van een te hoge populatie fecunditeit (hoofdstuk 3 en 4). Grote individuen kunnen daardoor een negatief effect hebben op hun kleinere soortgenoten; niet alleen door het verhogen van de competitie binnen het YOY-cohort door fecunditeit, maar ook door het verhogen van de competitie tussen soorten. In hoofdstuk 6 verhoogt grootte afhankelijke predatie van predatoren ouder dan 1 jaar de populatie fecunditeit van de consumenten populatie. Omdat YOY predatoren nog niet op consumenten kunnen foerageren, concurreren ze voor voedsel met de consumenten. Deze laatste echter, zijn de betere concurrent voor de gedeelde voedselbron. Daarom leidt een toename in reproductie van de consumenten tot een afname van voedselbeschikbaarheid voor YOY predatoren en wordt een juveniele bottleneck (knelpunt) geïnduceerd. Als gevolg van de lage per capita voedsel inname vertonen de YOY predatoren vertraagde groei. Daarom versterken grote predatoren indirect, door op de consumenten populatie te foerageren, de inter-specifieke juveniele bottleneck die hun nakomelingen wordt opgelegd door consumenten. Wanneer predatie op YOY consumenten voldoende hoog is en tot een toename van voedseldichtheid leidt door de snelle afname van hun aantal, wordt de groei van YOY predatoren weer bevorderd. Een grotere lichaamsgrootte als één jarige, wanneer kleine predatoren met predatie op consumenten beginnen, impliceert een hogere aanvalssnelheid op deze consumenten. Als resultaat onstaat er een positieve feedback van het ene predator cohort op het volgende, welke opereert door predatie op YOY consumenten en de resulterende toename in voedseldichtheid. Uiteindelijk resulteert deze populatie feedback in het mislukken van rekrutering en vervolgens de extinctie van de consumenten populatie (hoofdstuk 5).

2.4 Samenvatting

Temperatuur fluctuaties, of seizoensveranderingen, zijn nog niet eerder bestudeerd met een fysiologisch gestructureerd populatie model. Bij ectothermische organismen hangt het activiteitsniveau af van de temperatuur van de omgeving. In eerder bestudeerde fysiologisch gestructureerde populatie modellen werd daarom aangenomen dat winter een periode van volledige stasis is (Persson et al. (1998); Claessen et al. (2000)). Daarentegen is bekend dat temperatuur kleine individuen op een negatieve manier beïnvloedt (Post and Evans

(1989)). In hoofdstuk 3 wordt het effect van seizoensveranderingen op een consument-voedselbron systeem bestudeerd. De modelparameters zijn gebaseert op baars (*Perca fluviatilis*) en zijn voedsel watervlooien (*Daphnia spp* (1.0 mm)). Temperatuur beïnvloedt zowel de voedselproduktiviteit als de fysiologie van de consumenten (produktiviteit is een maat voor de snelheid van biomassa produktie per gebiedseenheid). Wanneer produktiviteit en de fysiologische snelheden van de consumenten naar beneden schalen tot het zelfde niveau met afnemende temperatuur (ze worden tot het zelfde niveau gereduceerd), dan lijkt de populatie dynamica op de resultaten van de modellen die aannemen dat winter een periode van stasis is. Echter, wanneer de fysiologie van consumenten in mindere mate naar beneden schaalt met afnemende temperatuur dan voedselproduktiviteit, dan hebben consumenten meer vetreserves nodig om de kosten voor lichaamsonderhoud te dekken gedurende de periode met lage temperaturen. Het opnemen van een winter-seizoen in een grootte-gestructureerd populatie model resulteert in een drempelwaarde voor lichaamsgrootte die YOY moeten halen om genoeg reserves te hebben voor lichaamsonderhoud en het overleven van de winter. Als de per capita voedsel inname van YOY voldoende is om genoeg te groeien in het eerste groeiseizoen zal de drempel voor lichaamsgrootte gehaald worden. De per capita voedsel inname en daarmee de groei van YOY, kan in gevaar komen als het aantal individuen groot is. Hetzij door een grote reproduktie puls of een groot aantal individuen in het algemeen, het mislukken van rekrutering tot het tweede levensjaar kan voorkomen als er niet genoeg voedsel beschikbaar is voor YOY. Het resultaat is dat de feedback tussen de populatie en de voedseldichtheid een negatief effect heeft op het voortbestaan van de populatie. Lage aantallen individuen kunnen overleven, terwijl een populatie niet kan bestaan vanwege de feedback op de voedseldichtheid. De toename van het aantal individuen kan resulteren in een 'ecologische zelfmoord' van de populatie.

De laatste jaren is er een trend van toenemende temperatuur gedocumenteerd, wat 'global warming' genoemd wordt, het opwarmen van de aarde. Zoals in hoofdstuk 3 wordt bediscussieerd, reageren individuen op temperatuur als functie van hun grootte. Het is daarom aannemelijk om te verwachten dat global warming individuen verschillen zal beïnvloeden, afhankelijk van hun grootte. Als kleine individuen een metabolisch voordeel hebben in de zomer maar hongerlijden en daar aan dood gaan in de winter (hoofdstuk 3), dan is het te verwachten dat global warming voordelig zal zijn voor kleine individuen. Echter, als er minder kleine individuen van de honger sterven in de winter en overlevingskansen groot zijn, zal competitie voor voedsel toenemen. Dit heeft consequenties voor individule groeisnelheden, die waarschijnlijk zullen afnemen door de lagere per capita voedsel inname. Welk effect global warming heeft op individuen en de populatie waar ze deel van uit maken wordt bestudeerd in hoofdstuk 4 met behulp van het zelfde model als in hoofdstuk 3. In zoetwater ecosystemen in maritiem gematigde regio's, die niet bedekt zijn met ijs in de winter, zijn water- en luchttemperatuur sterk gekoppeld. Omdat de winter temperatuur sterker stijgt dan de zomer temperatuur, global warming in zo'n soort omgeving zal zich hoofdzakelijk vertalen in een toename van de watertemperatuur in de winter (Easterling et al. (1997); Schindler (1997); Hughes (2000)). In meer noordelijk en continentaal gematigde streken is het aannemelijk dat gobal warming zal leiden tot een toename in de duur van het groeiseizoen vanwege de afname van de periode ijs (Magnuson et al. (2000)). Deze twee global warming scenarios worden bestudeerd: 1) een toename van de zomerduur, en 2) een toename van de minimum winter temperatuur. Ik vind als resultaat dat kleine individuen niet kunnen profiteren van global warming. In het eerste scenario de YOY lijden aan hoge mortaliteit door de langere blootstelling aan predatie als een direct gevolg van de verlenging van de zomer. Door deze afname in aantallen tijdens de zomer echter, sterven er geen YOY van honger in de winter. In tegenstelling tot dit scenario sterven er in het tweede scenario wel YOY van de honger in de winter door de grote aantallen concurrenten als gevolg van hoge populatie fecunditeit. In dit scenario speelt de populatie feedback een belangrijker rol dan de stijging van de minimum winter temperatuur. Grote individuen profiteren wel van global warming en kunnen groter groeien in beide scenarios. De individuen die een periode met hoge mortaliteit overleven, in zomer of winter, hebben voordeel van de lage voedsel-concurrentie na die periode en kunnen profiteren van het populatie feedback mechanisme. De grootte afhankelijke verschillen in respons op global warming op het individu niveau kan resulteren in het mislukken van rekrutering en extinctie van de populatie als populatie fecunditeit toeneemt.

In contrast met hoofdstuk 3 en 4 behandelen hoofdstuk 5 en 6 een veranderende biotische omgeving en niet een veranderende a-biotische omgeving. Twee verschillende soorten worden bestudeerd, een consument (blankvoorn, *Rutilus rutilus*) en een predator (baars, *Perca fluviatilis*)). Voor beide soorten wordt de grootte-structuur meegerekend. De predator vertoont life history omnivory (letterlijk: levensgeschiedenis omnivorie) en verandert van foerageren op de zelfde voedselbron als de consument, naar foerageren op individuen van de consumenten soort als de predator groter is. Deze dubbele interactie tussen twee soorten, waarbij zowel competitie als een predator-prooi interactie voorkomt, is gedefinieerd als intraguild predation (predatie binnen het eigen gilde)(Holt and Polis (1997); Mylius et al. (2001)). Intraguild predation komt veelvuldig voor in natuurlijke systemen (Arim and Marquet (2004)). Dit type interactie is nog niet eerder bestudeerd met een gestructureerd populatie model. Voorgaande modelstudies, die alleen met 'omnivorie' rekening houden, laten zien dat coëxistentie van predator en consument beperkt is tot gemiddelde produktiviteitsniveaus (Holt and Polis (1997); Mylius et al. (2001)). In tegenstelling tot deze model resultaten, laat ik in hoofdstuk 5 zien dat rekening houden met life history omnivory het voorkomen van coëxistentie van predator en consument langs een produktiviteitsgradient doet afnemen. Wanneer juveniele predatoren, die te klein zijn om op de consumenten te prederen, het goed doen op de voedselbron die ze delen met de consument kunnen ze groter groeien. Deze grotere individuen hebben een hogere aanvalssnelheid als ze beginnen met prederen op de consument. Zo'n cohort van juveniele predatoren kunnen het goed doen op de gedeelde voedselbron als de dichtheid van consumenten gereduceerd worden door predatie door oudere predator cohorten. Dit geeft aanleiding tot een positieve feedback loop tussen opeenvolgende predator cohorten, wat voortkomt uit de voedsel afhankelijke ontwikkeling en grootte afhankelijke foerageer mogelijkheden. Deze feedback loop kan daarom niet voortkomen uit een ongestructureerd model. Om te testen of een betere prestatie als predator als gevolg van een hogere dichtheid van de gedeelde voedselbron en de resulterende afname van het voorkomen van coëxistentie algemeen is en niet gelimiteerd tot het grootte-gestructureerde model, hebben we de feedback in een ongestructureerd model gestopt. De resultaten van het ongestructureerde model laten ook het negatieve effect zien van het positieve feedback mechanisme op coëxistentie. Daarbij komt nog dat resultaten van een studie over vissen in meren in Zweden het mechanisme wat hier met het model onthuld wordt bevestigen. In deze experimentele studie is rekrutering van de consument alleen succesvol als het aantal kleine predatoren heel laag is (Persson niet gepubliceerd). Het gestructureerde model is ook gebruikt om het effect van een exclusieve voedselbron voor de predator op de levensgemeenschap te bestuderen. Met een exclusieve voedselbron voor de predator is coëxistentie van predator en consument mogelijk voor een klein aantal gemiddelde waarden van produktiviteit, overeenkomend met de resultaten van de eerdere model studies zonder fysiologische structuur.

In hoofdstuk 6 is het zelfde model gebruikt als in hoofdstuk 5, maar in deze studie is kannibalisme voor de predator toegevoegd. Wanneer predatoren hun eigen nakomelingen opeten dan reduceren ze eigenlijk hun eigen dichtheid. Kannibalisme bevordert coëxistentie tussen predator en consument door de afname van het totale aantal predator individuen. Als predator en consument coëxisteren kunnen we een meer lange termijn interactie tussen de populaties bestuderen, in tegenstelling tot hoofdstuk 5 waar de dynamica van consument-exclusie worden besproken.

In dit hoofdstuk laat ik zien dat een feedback loop zich manifesteert tussen predator en consument, die resulteert in een toename in groei van consumenten, maar een achtergebleven groei van predatoren. Dit laatste wordt een interspecifieke juveniele bottleneck (lett. flessenhals) genoemd. Wanneer predatoren met name kleine individuen in de consument populatie eten, dan ervaren de consumenten die overleven een omgeving met een hoge voedseldichtheid en weinig concurrentie. Deze consumenten kunnen daarom een grotere lichaamsgrootte bereiken en produceren meer nakomelingen dan zonder predatie. Grootte afhankelijke predatie op de consumenten populatie leidt dus tot een toename in fecunditeit van adulte consumenten en daarmee tot een toename van het aantal YOY, die het belangrijkste voedsel vormen voor de predator. Kleine predatoren kunnen echter nog niet foerageren op consumenten en concurreren met kleine consumenten voor het zelfde voedsel. Het grote aantal nakomelingen van de consumenten populatie reduceert de dichtheid van de gedeelde voedselbron tot zo'n laag niveau dat de nakomelingen van de predator gereduceerde groei vertonen. Terwijl grote predatoren hun eigen voedsel 'kweken', promoten ze de juveniele bottleneck die wordt opgelegd op hun eigen nakomelingen (hoofdstuk 6).

De modellen die in dit proefschrift worden bestudeerd zijn gebaseerd op de erkenning van het feit dat verschillen tussen individuen bestaan en laten groei en ontwikkeling plaats vinden in een dynamische omgeving. Rekening houden met grootte afhankelijke interacties geeft aanleiding tot een geheel nieuw terrein van mechanismen die populatie dynamica beïnvloeden. In hoofdstuk 3 en hoofdstuk 4 laat ik zien dat de feedback van de populatie op de voedseldichtheid tot het mislukken van rekrutering en extinctie zou kunnen leiden, zelfs als een enkel individu wel kan bestaan. Dit impliceert dat de vestiging van een paar individuen niet noodzakelijkerwijs tot lange termijn persistentie van de populatie leidt. Deze twee hoofdstukken bespreken de eerste studies waar expliciet het effect van een a-biotisch element van de omgeving is bestudeerd met behulp van een fysiologisch gestructureerd model. Het model dat gebruikt is in hoofdstuk 5 en hoofdstuk 6 is het eerste fysiologisch gestructureerde populatie model waarin voor twee soorten fysiologische structuur is opgenomen. De feedback loop tussen predatoren, consumenten en de gedeelde voedselbron resulteert in een positief effect van predatie door het ene cohort op het volgende predator cohort. Deze feedback loop kan extinctie van de consument veroorzaken (hoofdstuk 5). De grootte afhankelijke interacties tussen individuen beïnvloeden de dynamica van beide populaties als predator en consument coëxisteren. Als er coëxistentie is dan manifesteert een juveniele bottleneck zich voor kleine predatoren, terwijl kleine consumenten sneller groeien (hoofdstuk 6). Al deze mechanismen zouden niet aan het licht zijn gekomen bij gebruik van een ongestructureerd model dat alleen een fenomenologische beschrijving van het populatie niveau gebruikt. De mechanismen die uit een fysiologisch gestructureerd populatie model voortkomen zijn gebaseerd op aannames op het individu niveau, welke een sterke link hebben met empirische data. Fysiologisch gestructureerde modellen zijn daarom een aanwinst voor (theoretische) ecologie, welke, samen met ongestructureerde modellen en met name empirisch werk, een bijdrage leveren aan onze kennis van de natuur.

Chapter 3

Temperature effects on size-structured populations; when mortality promotes persistence

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Unpublished manuscript

Abstract
In this paper we investigate the effect of seasonality on a physiologically structured population. Seasonality is modeled using a step function and a sine function in a size-structured consumer-resource model, with Eurasian perch (*Perca fluviatilis*) as consumer species. With the use of both functions a size-threshold becomes apparent that must be met by newborns in order to survive winter. An increase in mortality releases resource competition among young of the year, and promotes population persistence when consumers are less capable of adapting to reduced resource productivity. The population feedback on the environment and intraspecific interactions affect population persistence rather than the capacity of an individual to adapt its physiology to periods of low resource availability. Single individuals can survive when a population cannot persist due to the feedback loop on resource density, which can result in an ecological suicide if the number of individuals of an invading species increases over time.

3.1 Introduction

For most consumer species winter represents a period with reduced resource levels as low ambient temperatures limit the productivity of their food. To cope with this seasonal reduction in productivity a consumer must build up enough energy reserves during summer in order to survive the coming winter. Low winter temperatures also affect metabolic requirements. For homoiothermic species low temperatures increase metabolic requirements due to increased heat loss. Adaptations to conserve energy and heat loss vary between species and can come about through behavioral and physiological changes such as huddling in a community nest, increased fur thickness or torpor (Hales Jr. and Able (2001); Jackson et al. (2001); Humphries et al. (2003)). Poikilothermic species exhibit a passive and direct response to temperature, and become less active in winter. The reduction of physiological rates is beneficial for an individual because less energy is spent on maintenance or locomotion, but has a disadvantage since the energy gain through feeding is also reduced. As a consequence, maintenance requirements can exceed food intake during winter and energy reserves are needed to cover the energetic deficit.

Maintenance requirements and food intake depend, besides on the ambient temperature, also on individual body size. Maintenance requirements and food intake rate scale differently with body size, which allows smaller individuals to persist at lower resource levels without starving (Yodzis and Innes (1992); Persson et al. (1998)). The difference in the scaling of metabolic demand and attack rate with body size has been shown to be an important determinant of population dynamics. In a size-structured consumer population feeding on a shared resource, the competitive ability of small individuals over larger ones gives rise to population cycles driven by recruitment (Persson et al. (1998)). In the size-structured population models used to analyze these dynamics, reproduction is a pulsed event at the onset of summer, while winter is considered a period of complete stasis. After reproduction the high number of newborn individuals leads to suppression of the resource density. Because the newborns can sustain at lower resource densities than the adults, the latter are outcompeted and die of starvation imposed on them by their own offspring. As a consequence, the cohort of newborns is now the only cohort in the population, and is outcompeted by their own offspring. The cycle repeats it self resulting in stable recruitment driven single cohort cycles. These cohort cycles are commonly found in natural systems (Murdoch et al. (2002)) corroborating that small individuals can have an advantage over large ones at low resource densities (Persson et al. (1998)).

Potentially, the ability to survive at low resource densities may benefit small individuals when resource productivity decreases in winter. On the other hand, small individuals have less fat reserves than large individuals to prevent starvation. Large individuals have been shown to lose proportionally less weight and withstand starvation better than small ones during winter (Post and Evans (1989)). Several studies on winter mortality of fish, on both marine (Schwalme and Chouinard (1999); Beamish and Mahnken (2001); Hales Jr. and Able (2001)) and freshwater species (Olivier and Holeton (1979); Shuter et al. (1980); Post and Evans (1989); DeAngelis et al. (1991)), show that mortality during winter can be high for small individuals. Most commonly, overwinter survival and individual length follow an increasing sigmoid relationship, with no survival of individuals in small size-ranges (Shuter et al. (1980); Post et al. (1998)). Models focused on temperature effects and winter mortality of fish also predict that individuals have to reach a minimum size threshold in order to survive winter (Shuter et al. (1980); DeAngelis et al. (1991)).

Small individuals may thus have a competitive advantage over larger ones under growing conditions, but may be worse off when facing starvation. Hamrin and Persson (1986) studied a vendace population (*Coregonus albula*) which exhibited cyclic behavior with a periodicity of two years. During the summer period individual mortality was found to be positively correlated with body size, as a consequence of the competitive dominance of small individuals over larger ones. In winter, this relationship showed a negatively correlation, with small individuals experiencing a higher mortality rate than large ones (Hamrin and Persson (1986)).

These results show that the advantageousness of a certain body size changes over time, depending on food conditions and seasonal temperature fluctuations. It is, however, unclear how the size-dependent competition among conspecifics interacts with the seasonality in temperature in shaping the long term population dynamics. At an individual level results from experiments and models (e.g. Shuter et al. (1980); DeAngelis et al. (1991)) point out that the first growth season in an individual's life history plays an important role. However, these studies do not take any population feedback on the resource into account, which provides small individuals their competitive advantage over larger one's. Here we use a size-structured consumer-resource model to study the effect of seasonality on a consumer species and its resource, including the feedback of the consumers on the resource. This type of model allows us to model explicitly the size- and temperature-dependence of life history processes (feeding, growth, mortality, reproduction) at the individual level and describe population dynamics as a change in frequency distribution of differently sized individuals over time (Persson et al. (1998)). We will focus on how changes in consumer activity and resource productivity throughout the year influence the persistence of a size-structured consumer in a seasonally changing environment. The annual change in temperature is modeled either as a distinct growth and non-growth season, or as a sinusoidal change, including spring and autumn periods, while resource productivity and consumer activity track these changes in temperature.

3.2 Model

The consumer-resource system is modeled using a physiologically structured population model (PSPM), which describes the population dynamics in terms of physiological processes at the individual level. In a PSPM, an individual state or i-state is defined, which represents the physiological state of an individual. In addition, a population or p-state is recognized, which represents the frequency distribution over all i-states. Finally, the environment in which the consumers live is represented by an e-state, which in our model incorporates the ambient resource levels and temperature (Claessen et al. (2000); de Roos and Persson (2001)). In this model the assumption is made that the consumer population is size-structured and feeds on an unstructured resource, the latter follows semi-chemostat dynamics in absence of consumers (Persson et al. (1998)). Parameter values are listed in Table 3.1 and are valid for Eurasian perch (*Perca fluviatilis*) and its resource *Daphnia spp* (1.0 mm). The size-structured model was studied with the use of a numerical method for integration of physiologically structured models (de Roos et al. (1992)).

Consumer physiology, the i-state

Here we present only a brief outline of the individual life-history model, for a more detailed description we refer to Claessen et al. (2000); de Roos et al. (2002); Persson et al. (1998); de Roos and Persson (2001). The body mass of an individual is divided into irreversible (x) and reversible (y) mass. Irreversible mass consists of material which cannot be used to prevent starvation, such as bones and vital organs. Reversible mass is the mass that can be used to prevent starvation, such as fat, muscle tissue and gonad mass. The reversible/irreversible mass or fat ratio (y/x) is a measure of the condition of the individual. Ingestion, maturation and background mortality are assumed to be independent of the condition of an individual and hence depend on irreversible mass only. In contrast, the individual condition does influence maintenance, energy allocation to growth versus reproduction and starvation mortality, which hence depend on both reversible and irreversible mass.

Individual consumers forage on the unstructured resource following a Holling type II functional response. Foraging is assumed to be size-dependent, with attack rate and handling time as functions of individual size (Persson et al. (1998)). The attack rate

Table 3.1: Model Parameters for perch and its resource (Claessen et al. (2000); Persson et al. (2003, 2004)).

Symbol	**Value**	**Unit**	**Interpretation**
i-state			
x_m	4.6	g	Irreversible mass at maturation
w_b	0.0018	g	Weight of a neonate
k_r	0.5	-	Gonad egg conversion
x_{opt}	4.7	g	Optimal consumption weight
μ_0	0.01	d^{-1}	Background mortality rate
μ_j	varied	d^{-1}	Added juvenile mortality rate
s	0.2	d^{-1}	Starvation coefficient
A	3.0E+4	L/d	Attack rate constant
α	0.5	L/d	Attack rate exponent
ξ_1	3.2	$\mathrm{d/g}^{(1+\xi_2)}$	Digestion time constant
ξ_2	-0.8	-	Digestion time exponent
ρ_1	0.033	$\mathrm{g}^{(1-\rho_2)}/\mathrm{d}$	Maintenance allometric constant
ρ_2	0.77	-	Maintenance allometric exponent
k_e	0.61	-	Food conversion efficiency
q_j	0.74	-	Juvenile reversible/irreversible mass ratio
q_a	1.37	-	Adult reversible/irreversible mass ratio
q_s	0.2	-	Starvation condition
e-state			
r	0.1	d^{-1}	Resource growth rate
K	3.0E-3	g/L	Resource carrying capacity
V	1.0E+9	L	Total lake volume
S	90	d	Step function summer duration
S	160	d	Sine function summer duration
Y	365	d	Year length
T_{max}	20	^{o}C	Maximum summer temperature
T_{min}	4	^{o}C	Minimum winter temperature
Θ	0.2	-	Steepness seasonality shift
γ_c	varied	-	Consumer winter rate reduction
χ_r	varied	-	Resource winter rate reduction

Table 3.2: Model equations describing the individual-level model of perch with irreversible mass x and reversible mass y, and the dynamics of the unstructured resource population. The index i refers to perch cohorts and each cohort consists of N_i individuals.

Subject	**Equation**
Attack rate	$a(x) = A(\frac{x}{x_{opt}} exp(1 - x/x_{opt}))^{\alpha}$
Handling time	$h(x) = \xi_1 x^{\xi_2}$
Maintenance	$E_m(x, y, \tau) = \gamma(\tau)\rho_1(x + y)^{\rho_2}$
Ingestion	$I(x, \tau) = \gamma(\tau)a(x)R/(1 + a(x)h(x)R)$
Net energy	$E_n(x, y, \tau) = k_e I(x, \tau) - E_m(x, y, \tau)$
Energy allocation to irreversible mass	$\kappa(x, y) = \begin{cases} \frac{1}{(1+q_j)q_j}\frac{y}{x} & \text{if } x \leq x_m \\ \frac{1}{(1+q_a)q_a}\frac{y}{x} & \text{if } x > x_m \end{cases}$
Fecundity	$f = \begin{cases} \frac{k_r(y - q_j x)}{w_b} & \text{if } x > x_m \text{ and } y > q_j x \\ 0 & \text{otherwise} \end{cases}$
Starvation mortality	$\mu_s = \begin{cases} s(x/y - 1) & \text{if } y < q_s x \\ 0 & \text{otherwise} \end{cases}$
Background mortality	$\mu_b = \begin{cases} \gamma(\tau)(\mu_0 + \mu_j) & \text{if } x < x_m \\ \gamma(\tau)\mu_0 & \text{otherwise} \end{cases}$
Resource dynamics	$\frac{dR}{dt} = r(\chi_t K - R) - \frac{1}{V}\sum_i I(x)N_i$

is modeled using a hump-shaped function (see Table 3.2). This shape is based on the assumption that with increasing size locomotion and visual abilities increase. The decrease in the attack rate function is related to a decrease of rod density, which affects the ability to discern small prey (Persson et al. (1998); Claessen et al. (2000)). The handling time decreases with size due to increasing gape and gut size (Persson et al. (1998); Claessen et al. (2000); de Roos et al. (2002)).

Consumed food is converted into energy with a constant conversion efficiency, after which maintenance costs are subtracted. When the ingested energy exceeds maintenance costs, the net energy is invested into growth of irreversible and reversible mass according to an allocation function (see Table 3.2), which targets for a constant ratio between reversible and irreversible mass equal to q_j or q_a, for juveniles and adults respectively. Consumer energetics hence follow the net production model (Lika and Nisbet (2000)).

We assume that individuals mature when a certain size threshold x_m is reached (Claessen et al. (2000)). When an individual reaches maturity it starts to invest more energy into reversible mass, which is modeled by using a larger maximum fat ratio q_a for adults than the fat ratio q_j for juveniles ($q_a > q_j$)(Table 3.2). The amount of reversible mass exceeding $y = q_j x$ is considered gonad mass, which is accumulated during the growth period. At the start of the non-growth period gonad mass is fixed for egg production and stored until reproduction the following spring. Only if starvation is imminent, egg mass is reabsorbed to cover maintenance. In our model egg mass is hence the last of the reversible mass to be used during a period of starvation, this is in contrast with previous size-structured models where it was used first (Persson et al. (1998); Claessen et al. (2000); de Roos et al. (2002)). This priority of using reversible mass before gonad mass is supported by data on Atlantic cod (*Gadus morhua*) that show that gonad mass actually increased during winter while carcass and liver dry weight decreased. The latter are suggested to be used to satisfy maintenance requirements and prevent starvation (Schwalme and Chouinard (1999)). Reproduction occurs at the beginning of a growth period in a pulsed event. If a mature individual survives the winter period, it will reproduce using the amount of egg mass that was set at the start of winter or all of it that is left over in case gonad mass has actually been used to cover maintenance costs. Any reversible mass that is left after egg production is considered somatic reserve. Together the newborn, young of the year (YOY) individuals form a new cohort. Their number equals the summed per capita fecundity of all adults.

When the energy intake does not suffice to cover the maintenance requirements, reversible mass is used as an energy source to cover maintenance demands. The fat-ratio reversible/irreversible mass (y/x) is a measure of the condition of the individual, and if the fat-ratio y/x drops below a threshold value q_s, the individual starts to suffer from starvation mortality with a rate μ_s. The rate of starvation increases with decreasing reversible mass and is modeled such, that death is imminent when there is no reversible mass left (Table 3.2). Besides the possibility of starvation mortality, all individuals suffer from background mortality. This background mortality, μ_0, represents a chance to die due to other causes than starvation. Juveniles ($x < x_m$) suffer an extra mortality on top of the background mortality, μ_j. Because of their small size, juveniles are more vulnerable to predation, f.e. by insect larvae. The total per capita mortality rate is the sum of starvation, background and juvenile mortality (Persson et al. (1998); Claessen et al. (2000)).

Consumer environment, the *e*-state

The resource follows semi-chemostat dynamics,with turn-over rate r and maximum abundance K, in absence of consumption. Hence, maximum resource productivity equals rK (in g/L · day). Semi-chemostat resource growth has been argued to describe more realistically the growth of a prey population with invulnerable, but mature, size classes (Persson et al. (1998); Claessen et al. (2000)). Both the resource and the consumer experience the same annual temperature regime. We model and compare two different representations of the annual temperature fluctuation. In the first representation temperature is assumed to change in a stepwise manner from a minimum of 4°C in winter to a maximum of 20°C in summer. If τ $(0 \leq \tau < 365$ days) indicates the time since the beginning of the year and $T(\tau)$ represents the temperature at a particular time of the year, this representation is hence described by the following step function:

$$T(\tau) = \begin{cases} 20.0 & \text{if } 0 \leq \tau < S \\ 4.0 & \text{if } S \leq \tau < Y \end{cases} \tag{3.1}$$

Here, S represents the duration of the summer period, which is assumed to last 90 days, in accordance with a growth period in temperate regions (Persson et al. (1998); Claessen et al. (2000)). The parameter Y represents the year length ($Y = 365$ days). Notice that the time point $\tau = 0$ is chosen equal to the start of the growth period. We study this step-function representation of the annual temperature fluctuations, because it allows for a more detailed mathematical analysis of the individual-level response to varying temperature and for comparisons with earlier studies of size-structured consumer-resource interactions, which considered the winter period to be a period of complete stasis (Persson et al. (1998); Claessen et al. (2000)).

The second representation used to model annual temperature fluctuations is a sinusoidal function, which we adapted from Turchin and Hanski (1997):

$$T(\tau) = \begin{cases} T_{min} + \dfrac{T_{max} - T_{min}}{2}\left(1 + \left(\sin \frac{\pi\tau}{S}\right)^{\Theta}\right) & \text{if } 0 \leq \tau < S \\ T_{min} + \dfrac{T_{max} - T_{min}}{2}\left(1 - \left(\sin \frac{\pi(\tau - S)}{(Y-S)}\right)^{\Theta}\right) & \text{if } S \leq \tau < Y \end{cases} \tag{3.2}$$

As before, $T(\tau)$ represents the temperature at day τ during the year, and fluctuates between $T_{min} = 4$°C in winter and $T_{max} = 20$°C in summer. To represent summer and winter periods of unequal length the sinusoidal function (3.2) is a composition of two parts, each incorporating a sine function on the interval $[0; \pi]$ raised to the power Θ. The two sine functions have different periods S and $Y - S$, respectively, representing the parts of

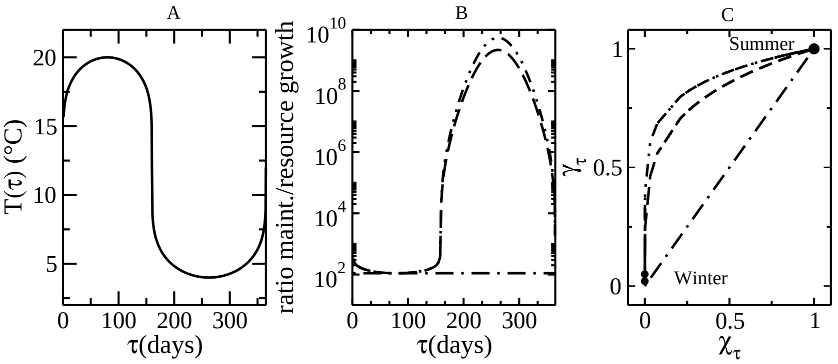

Figure 3.1: A: Annual changes in temperature in case of the sinusoidal regime described by Equation 3.2. B: Changes in the ratio between maintenance requirements of a 1 gram consumer and the resource productivity during the year in case of the sinusoidal temperature regime for $\gamma_c = 1 \cdot 10^{-9}$ (dashed-dotted line), $\gamma_c = 0.02$ (dashed line) and $\gamma_c = 0.05$ (dashed-double dotted line). In all cases $\chi_r = 1 \cdot 10^{-9}$. C: Changes in the reduction of consumer physiological rates, $\gamma(\tau)$, and the reduction in resource productivity, $\chi(\tau)$, due to changing temperature within a year. The dashed-dotted line delineates $\gamma(\tau) = \chi(\tau)$. The dashed line and the dashed-double dotted line represent the trajectory of $\gamma(\tau)$ and $\chi(\tau)$ in case of the sinusoidal temperature regime with $\gamma_c = 0.02$ and 0.05, respectively ($\chi_r = 1 \cdot 10^{-9}$). The black circles represent summer and winter values of $\gamma(\tau)$ and $\chi(\tau)$ in case of the stepwise temperature regime with $\chi_r = 1 \cdot 10^{-9}$ and $\gamma_c = 0.02$ and $\gamma_c = 0.05$.

the year during which temperature is above (for $0 < \tau < S$) and below (for $S < \tau < Y$, $Y = 365$ days) the midpoint temperature $T_{min} + (T_{max} - T_{min})/2$. The shape of the sinusoidal function can be manipulated with Θ (Turchin and Hanski (1997)). When Θ equals 1 the two parts of the temperature regime are pure sine functions. With decreasing Θ the slope at the transition point where $T(\tau)$ crosses the midpoint $(T_{min}+(T_{max}-T_{min})/2)$ becomes more steep, resembling a step function near $\Theta = 0$. Here $\Theta = 0.2$ is used (Turchin and Hanski (1997)). We have used $S = 160$ days for the duration of the summer period. This choice results in a roughly 90 day period of temperatures above 19°C, which is close to the summer period of the stepwise temperature regime. The sinusoidal temperature regime is illustrated in Figure 3.1(A), and shows that this regime explicitly represents periods of increasing and decreasing temperature that reflect spring and autumn, respectively.

Temperature responses of consumer and resources

All parameter values for the individual-level physiological processes of the consumer and the productivity of the resource presented in Table 3.1 represent estimates for summer conditions, i.e. for when $T = 19 - 20$°C. We assume that with decreasing water temperature in winter the physiological rates of the consumer as well as resource productivity slow down and we describe the species specific reduction of physiological rates using the Arrhenius equation (Kooijman (2000a)). At a temperature of $T(\tau)$ the physiological rates of the consumer are hence scaled by the following multiplication factor:

$$\gamma(\tau) = \gamma_c^{\left(\frac{1.0-\frac{T_{max}}{T(\tau)}}{1.0-\frac{T_{max}}{T_{min}}}\right)} \tag{3.3}$$

The parameter γ_c denotes the reduction in physiological rates that the consumer can realize at $T(\tau) = T_{min}$, while $\gamma(\tau)$ evaluates to 1 for $T(\tau) = T_{max}$. A lower value of γ_c implies that consumers are more able to reduce their physiological rates. With the stepwise temperature regime $\gamma(\tau)$ equals 1 in summer and γ_c in winter. With the sinusoidal temperature regime the value of $\gamma(\tau)$ varies continuously with the variation in temperature $T(\tau)$, described by Eq. 3.2. We assume that at lower temperatures consumer mortality, maintenance and ingestion rate (attack rate and handling time) decrease and hence scale the rates of these processes with the factor $\gamma(\tau)$ (see Table 3.2).

We assume that decreasing temperature also reduces resource productivity and describe its temperature dependence with a similar relationship:

$$\chi(\tau) = \chi_r^{\left(\frac{1.0-\frac{T_{max}}{T(\tau)}}{1.0-\frac{T_{max}}{T_{min}}}\right)} \tag{3.4}$$

Resource productivity during the year is described by the product $rK\chi(\tau)$, in which $\chi(\tau)$ varies from χ_r in winter when $T(\tau) = T_{min}$ to $\chi(\tau) = 1$ in summer when $T(\tau) = T_{max}$. As for $\gamma(\tau)$, $\chi(\tau)$ changes in a discrete manner between 1 in summer and χ_r in winter in case of the stepwise temperature regime, while it varies continuously with the sinusoidal temperature regime.

3.3 Results

Our main focus is to study the dynamics of the size-structured model as a function of γ_c and χ_r. The ratio between $\gamma(\tau)$ and $\chi(\tau)$ is a measure of the extent to which consumers adapt their physiology to the changing resource availability in winter. This ratio can be interpreted as a measure of winter severity, (*i.e.* a bigger difference between the two values implies a more severe winter (Figure 3.1B). If γ_c and χ_r are equal (Figure 3.1B, dashed-dotted line), the ratio between consumer rates and resource productivity does not change throughout the year. The decreasing temperatures during winter in this case only imply a slowing down of dynamics, which is identical for consumers and resource. Temperature variation hence represents a scaling of time. This scaling is such that population changes during that winter period with slow dynamics are identical to the changes that would occur in a shorter period at faster rates. Therefore, independent of whether a stepwise or sinusoidal temperature regime is assumed, for $\gamma_c = \chi_r$ incorporating a winter period in the size-structured model has the same effect as choosing a slightly longer interval between consumer reproduction pulses in the size-structured models that consider winter to be a period of complete stasis (Persson et al. (1998)).

When γ_c is larger than χ_r the ratio between $\gamma(\tau)$ and $\chi(\tau)$ changes within one year. Figure 3.1C illustrates how γ_c and χ_r relate to each other during the year for $\chi_r = 1 \cdot 10^{-9}$ and various values of γ_c. For the sinusoidal temperature regime with $\gamma_c > \chi_r$ the values of $\gamma(\tau)$ and $\chi(\tau)$ follow a trajectory over time that differs from the diagonal line $\gamma(\tau) = \chi(\tau)$ (Figure 3.1C). With a divergence from the diagonal line $\gamma(\tau) = \chi(\tau)$, an unequal scaling of consumer physiology and productivity occurs, which turns out to be disadvantageous for the consumer. Consider the net energy production of a consumer individual of size x:

$$E_n(x,y) = \gamma(\tau)(k_e(a(x)R/(1+a(x)h(x)R)) - \rho_1(x+y)^{\rho_2}) \tag{3.5}$$

With decreasing temperature $\gamma(\tau)$ decreases, which scales down both maximum ingestion capacity as well as the metabolic energy demands of the consumer. Simultaneously, however, the resource density R will decline as the decreasing temperature also reduces resource productivity by the factor $\chi(\tau)$. When $\gamma_c > \chi_r$ the decline in resource productivity will be more rapid than the decrease in maximum ingestion capacity and metabolic demands of the consumer. As a consequence, the consumer will experience periods of food limitation, while its energy demands are still relatively high. These periods with low food availability and high demands, *i.e.* with a large discrepancy between the actual values of $\gamma(\tau)$ and $\chi(\tau)$, specifically occur during spring and autumn. During autumn resource productivity drops quickly, but consumer rates are still relatively high, while in spring consumer rates jump ahead of resource productivity when temperature rises (Figure 3.1C). A consumer individual will therefore have a more negative net energy during autumn, and will more rapidly deplete its reversible mass.

Individual-level starvation dynamics

Individuals with a reversible mass above the threshold value $q_s x$ do not suffer from starvation mortality. On the other hand, the starvation mortality function (Table 3.2) is such that an individual will die with certainty if it fully depletes all its reversible mass, *i.e.* $y = 0$. Hence, an individual will have a decreasing probability to survive the winter period the more its fat ratio y/x drops below q_s. Assuming that the food intake during winter equals zero, the reversible mass of an individual decreases during winter, as it is used to cover maintenance requirements. For the stepwise temperature regime these dynamics can be described using the following function:

$$\frac{dy}{dt} = -\,\gamma_c \rho_1 (x + y)^{\rho_2} \tag{3.6}$$

The factor γ_c reduces the maintenance requirements during winter and affects the rate at which reversible mass is depleted. Hence, with a lower value of γ_c individuals can endure longer periods before suffering from starvation mortality. Note that irreversible mass x is assumed not to change during this period.

Equation 3.6 can be solved explicitly, which leads to the following expression for the time τ_s it takes for an individual with irreversible mass x to deplete all fat reserves $y(0)$ at the start of the starvation period down to the starvation threshold, where $y(\tau) = q_s x$.

$$\tau_s = \frac{(x + y(0))^{(1-\rho_2)} - (x + q_s x)^{(1-\rho_2)}}{\gamma_c \, \rho_1 \, (1 - \rho_2)}$$

Under the assumption that an individual has the optimal amount of reversible mass $y = q_j x$ at the beginning of the winter, and taking τ_s equal to the duration of the winter (W), this equation can be solved for x. The resulting value x_s denotes the minimum irreversible mass that a growing juvenile consumer should have in order to survive the winter without experiencing any starvation mortality at all:

$$x_s = \left(\frac{\gamma_c \rho_1 \, (1 - \rho_2) \, W}{\left(1 + q_j\right)^{1-\rho_2} - (1 + q_s)^{1-\rho_2}} \right)^{(1-\rho_2)^{-1}} \tag{3.7}$$

An analogous derivation leads to an expression for the minimum irreversible mass x_0 that an individual should have in order to have any chance at all to survive the winter:

$$x_0 = \left(\frac{\gamma_c \rho_1 \, (1 - \rho_2) \, W}{(1 + q_j)^{1-\rho_2} - 1} \right)^{\frac{1}{1-\rho_2}} \tag{3.8}$$

For values below x_0 the consumer will deplete its fat reserves $y = q_j x$ with which it enters the winter period down to 0 before the end of winter, and will hence die with certainty. For successful recruitment to the second year a young of the year (YOY) consumer hence has to reach at least this lower size threshold x_0 during its first growth period.

For individuals with an irreversible mass $x_0 < x < x_s$ at the onset of winter the probability to survive starvation, P_s, ranges between 0 and 1, and is larger for larger values of x. P_s can be computed by numerical integration of differential equation 3.6 together with the differential equation describing the dynamics of P_s:

$$\frac{dP_x}{dt} = -\mu_s(x, y)P_s \tag{3.9}$$

Note that this equation only considers dying from starvation (see Table 3.2), and hence assumes that P_s equals 1 at the start of winter. Figure 3.2A shows the survival probability P_s as a function of the irreversible mass x for individuals that have an optimal fat ratio at the start of winter ($y(0) = q_j x$). P_s is a sigmoidal function of individual size, rising rapidly from 0 at $x = x_0$ to 1 at $x = x_s$ with increasing body size. Both x_0 and x_s increase with increasing duration of the starvation period and the maintenance scaling coefficient in winter, $\gamma_c \rho_1$ (see Figure 3.2B). In addition, x_s is larger for larger values of q_s. The starvation mortality coefficient s determines the steepness of the curve of P_s as a function of x between the two size thresholds x_0 and x_s.

Stepwise temperature regime

In absence of the additional juvenile mortality the consumer-resource model shows a recruitment driven single cohort cycle with a period of 8 year, if it is assumed that the growth period lasts 90 days and winter is a period of complete stasis (Persson et al. (1998); Claessen et al. (2000)). The recruitment driven cycles begin with a strong reproductive pulse of a newly matured age class. The numerical dominance of YOY causes a strong reduction of the resource level immediately after the reproductive pulse. Since the maintenance requirements scale faster with body size than intake rates, the low resource values will cause adults to die from starvation but not the YOY. This YOY cohort is now the only cohort in the population. The YOY grow and become mature at an age of somewhat more than 7 years. After maturation they produce a large number of offspring, and like their parents they are subsequently outcompeted by their offspring, which starts the cycle anew (Figure 3.3 top panel)(Persson et al. (1998)).

Figure 3.4 presents the bifurcation diagram of the population dynamics as a function

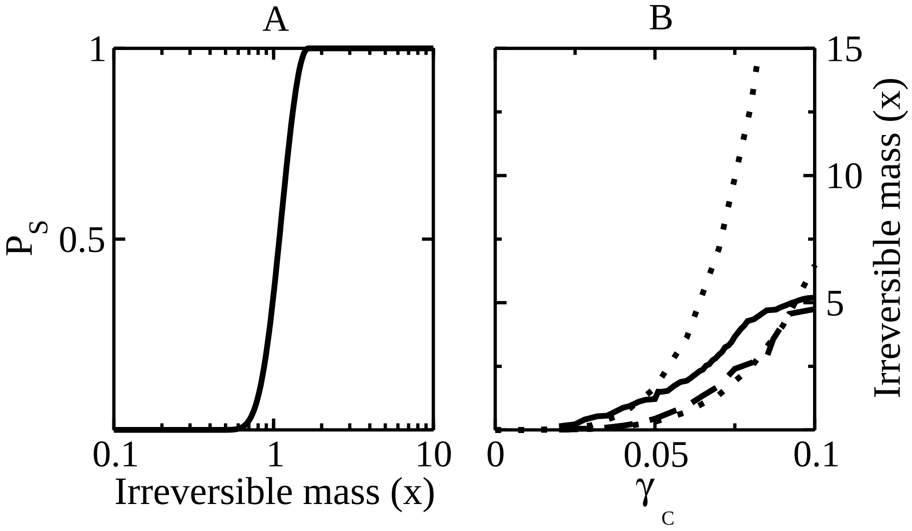

Figure 3.2: A: Survival probability (P_s) of consumers during a period without any food intake as a function of their irreversible mass x. P_s only considers surviving starvation mortality, background mortality is not included. At the start of the starvation period individuals have the optimal fat ratio $y = q_j x$. The curve relates to a starvation period of 275 days with $\gamma_c = 0.05$. B: Minimum irreversible mass as a function of γ_c that is needed for a non-zero chance to survive a starvation period of 275 days (x_0, lower dotted line) and to survive this period without suffering any starvation mortality at all (x_s, upper dotted line). At the start of the starvation period individuals have the optimal fat ratio $y = q_j x$. Also shown is the minimum individual size of YOY consumers that survive the winter in case of the stepwise temperature regime (dashed line) and the sinusoidal temperature regime (solid line). These latter two lines are obtained from the bifurcation analysis of the model with varying juveniles mortality and pertain to the lowest value of juvenile mortality for which the consumer population can persist.

of juvenile mortality μ_j. The figure shows the number of YOY and juveniles consumers, recorded at the end of the year, and the size that YOY have reached at the end of their first growth season. The three columns of panels in the figure show these relationships for different values of the consumer winter rate reduction γ_c, the factor by which consumers can reduce their physiological rates in winter, while $\chi_r = 1 \cdot 10^{-9}$. For $\gamma_c = 1.0 \cdot 10^{-9}$ (left panels), *i.e.* the winter period is virtually a period of complete stasis. For low juvenile mortality the population exhibits an 8 year single cohort cycle as described above (Persson et al. (1998)). When juvenile mortality increases, juveniles die more rapidly, which relaxes resource competition. As a consequence, resource density increases, individuals grow quicker, and reach the size of maturity more quickly. The period of the cycles shortens if individuals manage to grow so quickly that they can advance their first reproduction

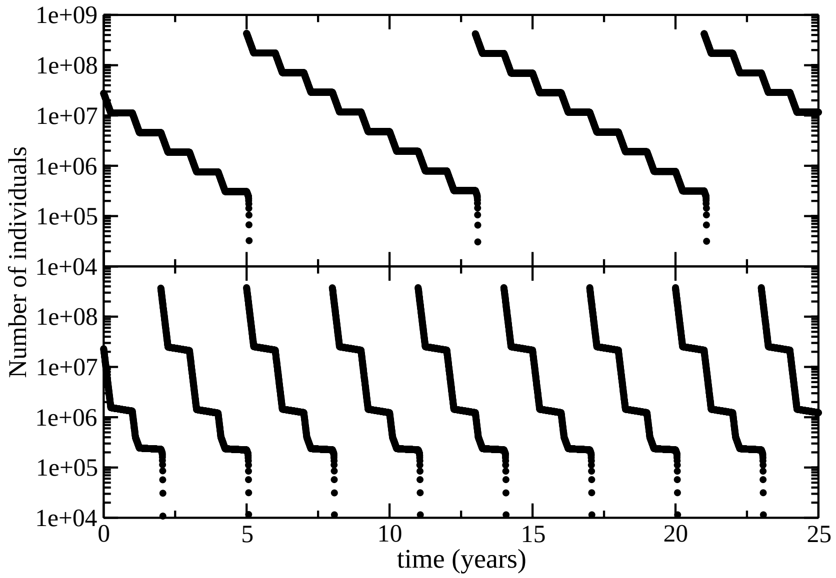

Figure 3.3: Model dynamics for two different values of μ_j and γ_c in case of the stepwise temperature regime. The top panel shows a regular eight year single cohort cycle in the number of consumer individuals for $\mu_j = 0.0$ and $\gamma_c = 0.0$. The low panel shows a three year single cohort cycle that occurs for $\mu_j = 0.02$ and $\gamma_c = 0.02$ (See also Fig.3.4).

event 1 full year. With increasing juvenile mortality the duration of the single-cohort cycle therefore reduces in a stepwise manner.

For $0.03 < \mu_j < 0.08$ individuals start reproducing at an age of 2 and the population at the beginning of the growth season is either made up of newborns and adults of 2 years old or 1 year old juvenile individuals. For larger values of μ_j the population exhibits fixed-point dynamics, in which the state of the population at the beginning of each growth period is the same. The YOY reach maturity within their first growth season and the population at the beginning of the growth season consists of newborns and adult individuals only. The size that YOY attain at the end of their first growth period increases with increasing juvenile mortality, as the latter leads to reduced resource competition. The surviving individuals have a higher per capita food intake and attain larger sizes. The maximum size a YOY can reach at the end of its first growth season is bounded by the length of this period (90 days in case of the stepwise temperature regime) and by its maximum rate of resource ingestion.

The middle and right panels of Figure 3.4 show the bifurcation diagram for $\gamma_c = 0.02$ and $\gamma_c = 0.05$, respectively. For $\gamma_c = 0.02$ (*i.e.* all physiological rates, including mortality, of the consumer proceed in winter at a rate equal to 2% of its summer equivalent), persistence of the population is not possible for values of μ_j below 0.0027 (Fig. 3.4, middle panels). For $0.0027 < \mu_j < 0.015$ irregular dynamics are observed, where regular single-cohort cycles occurred with a very low value of $\gamma_c = 1 \cdot 10^{-9}$. Although irregular, these dynamics do consist of recruitment-driven single cohort cycles (results not shown). For both $\gamma_c = 0.02$ and $\gamma_c = 1 \cdot 10^{-9}$ regular single-cohort cycles with a period of two or three years as well as fixed-point dynamics occur for comparable values of the juvenile mortality if $\mu_j > 0.0015$. Figure 3.3 (lower panel) shows the three year single cohort cycle to illustrate the reduction in cycle length with increasing values of μ_j. Note that for $\mu_j = 0.02$ and $\gamma_c = 0.02$ the number of individuals decreases quickly during summer and slowly during winter (lower panel), while for $\mu_j = 0.0$ and $\gamma_c = 0.0$ the number of individuals decreases during summer but does not change during winter (top panel). With an increase of γ_c winter is no longer a period of complete stasis and physiological rates (including mortality) are reduced to a lesser extent. The difference in the capacity of an individual consumer to reduce its physiological rates, hence leads to (1) a lack of persistence for very low values of juvenile mortality and (2) a perturbation of the regular single-cohort cycles leading to irregular dynamics for intermediate values of juvenile mortality. The lack of consumer persistence is very pronounced for larger values of the winter rate reduction, $\gamma_c = 0.05$ (*i.e.* all physiological rates, including mortality, of the consumer proceed in winter at a rate equal to 5% of its summer equivalent), as persistence is only possible for $\mu_j > 0.045$ (Fig. 3.4, right panels). Irregular dynamics are observed as well, but only over a small range of values of juvenile mortality.

From the bifurcation diagrams (Figure 3.4) we can infer for a given value of γ_c both the lowest and the highest value of μ_j, for which the consumer population can persist. The highest of these two values of μ_j we will refer to as the 'invasion threshold', as it indicates the level of juvenile mortality below which a low number of consumers is able to increase in numbers and build up a population. The lowest of μ_j values will be referred to as the 'persistence threshold', as below this level of juvenile mortality the population will go extinct. We repeated the bifurcation studies for a large range of different values of γ_c and thus constructed the invasion and persistence boundary, respectively, that bound the parameter combinations of γ_c and μ_j for which the population can persist. The left panel of Figure 3.5 shows the parameter diagram of γ_c and μ_j with the two boundaries for the stepwise temperature regime. The invasion threshold (solid line) occurs at lower μ_j values when γ_c increases. With higher values of γ_c consumers reduce their maintenance requirements during winter to a lesser extend and hence their fat ratio y/x is more likely to drop below the threshold q_s. They are therefore more likely to experience bouts of starvation, such that lower levels of juvenile mortality are already sufficient to

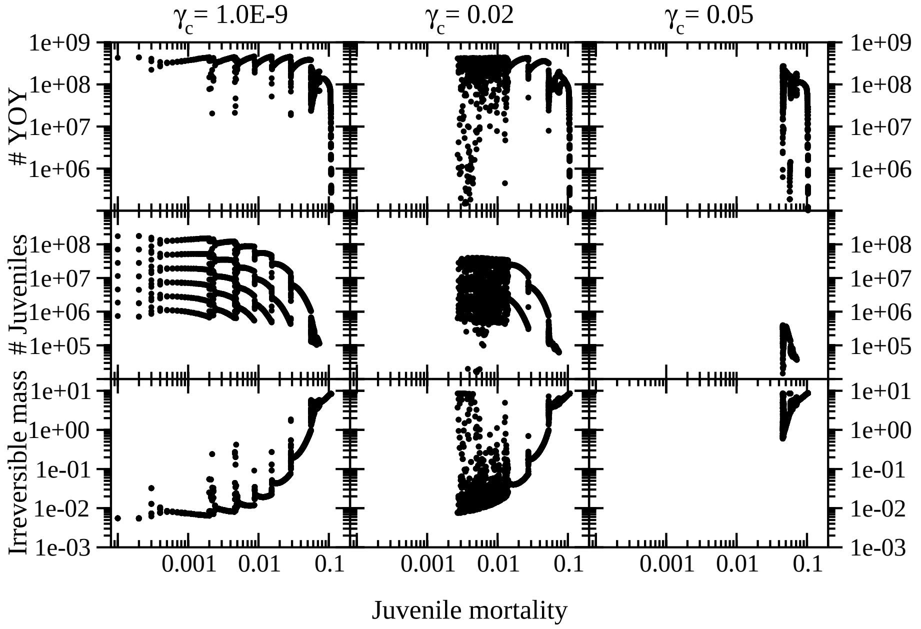

Figure 3.4: Bifurcation diagram of the consumer population with μ_j as the bifurcation parameter in case of the stepwise temperature regime for different values of γ_c, the factor by which consumer can reduce their physiological rates in winter ($\chi_r = 1 \cdot 10^{-9}$). Top and middle panels show the number of YOY and juveniles, respectively, at the beginning of each year (day 0). The bottom panels show the size of YOY after their first growth period, *i.e.* the sized they reach at the age of 1 year.

drive the consumer population extinct. The persistence boundary (dashed line) follows a non-monotonic relationship between γ_c and μ_j. For $\gamma_c < 0.1$ an increase of γ_c implies that the persistence boundary shifts to higher values of μ_j, as was already clear from Figure 3.4. With higher values of γ_c the YOY have to attain large sizes at the end of their first growth period to have a chance at surviving the winter period (Figure 3.2B). These large sizes can only be achieved when competition for resources among the YOY is reduced, *i.e.* at higher levels of juvenile mortality when their numbers decrease more rapidly. For $\gamma_c > 0.1$, however, the persistence boundary bends back to lower values of μ_j with increasing values of γ_c. Here, an increase in γ_c leads to that individuals start to suffer from their decreased ability to adjust maintenance requirements and hence deplete their energy reserves to a larger extend during winter. As a result the total population fecundity declines and fewer YOY are produced. Resource competition among YOY is hence reduced and YOY grow more quickly, such that with lower juvenile mortality they manage to reach sufficiently large body sizes at the end of the growth period to survive winter.

The range of mortality conditions for which persistence is possible hence narrows sub-

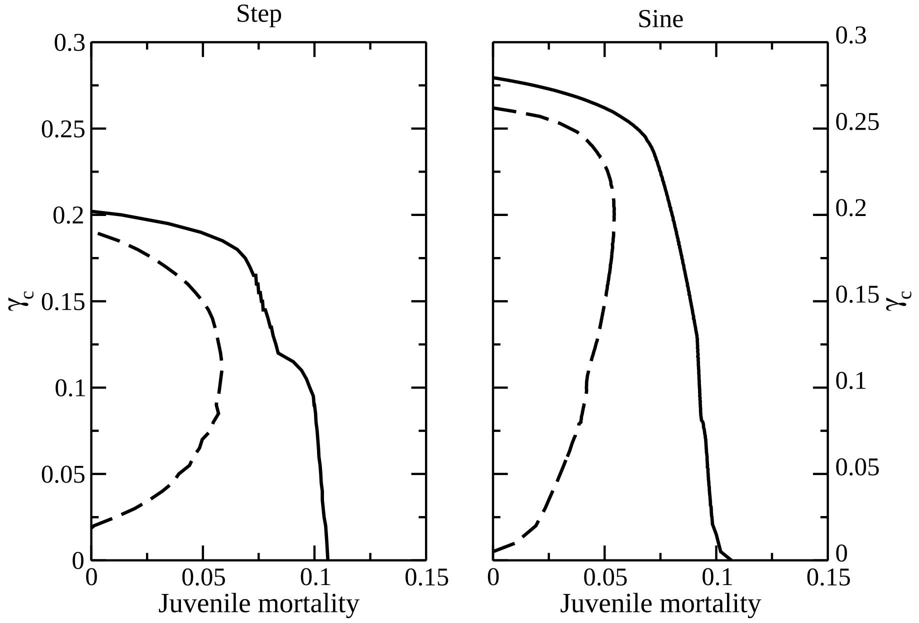

Figure 3.5: Invasion (solid line) and persistence boundary (dashed line) of the consumer population as a function of μ_j and γ_c in case of the stepwise (left panel) and the sinusoidal (right panel) temperature regime ($\chi_r = \cdot 10^{-9}$). All parameter combinations to the left and below the invasion boundary allow for consumer invasion into a system with only resource. Of those parameter sets the combinations of μ_j and γ_c to the left and below the persistence boundary lead to consumer extinction after invasion. Consumer persistence hence occurs for those parameter values between the invasion and the persistence boundary.

stantially with increasing values of consumer reduction factor γ_c. In addition, consumer invasion is possible for a large range of parameter values, but the population will nonetheless go eventually extinct (to the left and below the persistence boundary Figure 3.5). In this parameter region low densities of consumers do well and built up a population, but eventually the feedback of high population densities on the resource leads to reduced growth rates of YOY and their starvation during winter. Figure 3.2B compares the minimum irreversible mass x of YOY reached at the end of their first growth period (dashed line), which we observed at the minimum value of μ_j that allows for persistence, with the analytically derived thresholds x_0 and x_s (Eq. 3.8 and 3.7, dotted lines). The figure shows that the size of YOY at the end of the growth period, which we derived from the bifurcation studies, are close to the analytically derived minimum size threshold x_0 that allows for any survival during winter at all. Hence, consumer persistence is possible as long as a small fraction of YOY manage to survive the winter period.

As pointed out before, the ratio between γ_c and χ_r is a measure of winter severity. With

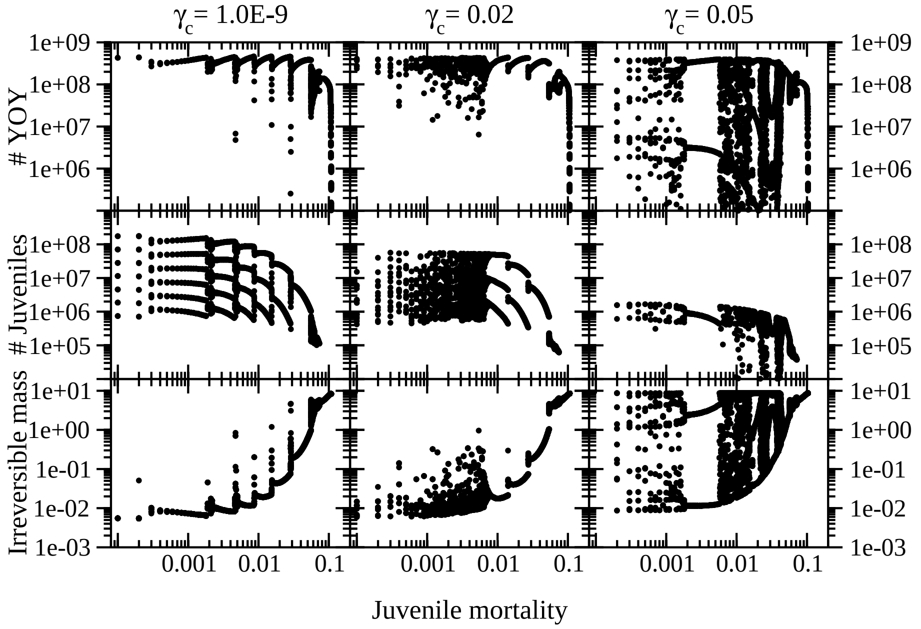

Figure 3.6: Bifurcation diagram of the consumer-resource model with μ_j as the bifurcation parameter in case of the stepwise temperature regime for different values of γ_c the factor by which consumer can reduce their physiological rates in winter ($\chi_r = 1 \cdot 10^{-3}$). Top and middle panels show the number of YOY and juveniles, respectively, at the beginning of each year (day 0). The bottom panels show the size of YOY after their first growth period, *i.e.* the sized they reach at the age of 1 year.

higher values of χ_r resource productivity is reduced to a lesser extent during winter and some resource may still be available for consumer to forage on during winter. Figure 3.6 presents the same bifurcation diagrams as a function of μ_j as Figure 3.4, but now for a value of $\chi_r = 1 \cdot 10^{-4}$ instead of $\chi_r = 1 \cdot 10^{-9}$. For $\gamma_c = 1 \cdot 10^{-9}$ the bifurcation patterns for the two χ_r values are comparable (left panels Figure 3.4 and Figure 3.6), starting with an eight year single cohort cycle, while cycle length decreases in a stepwise manner with increasing μ_j. When $\chi_r = 1 \cdot 10^{-4}$ and γ_c equals 0.02 and 0.05 the population can persist at significantly lower values of μ_j than when $\chi_r = 1 \cdot 10^{-9}$. Due to the higher resource productivity in winter resource availability is no longer limiting consumer food intake. Instead, food intake during winter is limited by the slowing down of the consumer's physiological rates, *i.e.* by the low value of γ_c. A lack of population persistence for low values of μ_j (cf. Figure 3.4) will occur again when resource availability limits consumer food intake, *i.e.* at higher values of γ_c (results not shown).

Sinusoidal temperature regime

Figure 3.7 shows the bifurcation diagrams of the size-structured model as a function of juvenile mortality rate μ_j for the sinusoidal temperature regime. This figure is comparable to Figure 3.4 for the stepwise temperature regime, showing the changes in number of YOY and juveniles and the size of YOY reached at the end of the growth period as a function of juvenile mortality rate μ_j, for three different values γ_c and with $\chi_r = 1 \cdot 10^{-9}$. Overall, the results in Figure 3.4 and 3.7 are very similar, especially for $\gamma_c = 1 \cdot 10^{-9}$. For $\gamma_c = 0.02$ the persistence threshold occurs at higher values of μ_j with the sinusoidal temperature regime compared to the stepwise temperature regime. As another difference, the number of YOY are lower, while their sizes at the end of the growth period are larger, using the sinusoidal temperature regime with both $\gamma_c = 0.02$ and $\gamma_c = 0.05$. The sinusoidal temperature regime results in an autumn and a spring, when the consumer rates are relatively high compared to resource productivity (Figure 3.1C). These periods result in a larger size threshold that YOY need to reach at the end of the growth period in order to survive winter. In addition, these periods also affect the amount of energy adults can accumulate for reproduction, leading to reduced offspring production.

The sinusoidal temperature regime leads to qualitatively the same invasion and persistence thresholds for the consumer population as the stepwise temperature regime (compare the left and right panel in Figure 3.5). The two temperature regimes differ, however, quantitatively in the range of parameter values for which the population can exist. Surprisingly, the spring and autumn periods, with high physiological rates for the consumer relative to the resource productivity, do allow the consumers to persist even if its capacity to adapt to winter conditions is limited (compare the persistence up to $\gamma_c = 0.20$ and $\gamma_c = 0.28$ for the stepwise and the sinusoidal temperature regime, respectively). Despite these periods with a relatively high energy demand, resource productivity measured over an entire year is higher with the sinusoidal temperature regime than with the stepwise temperature regime. Most importantly, also with the sinusoidal temperature regime a large region of parameter values exists where consumers can invade but where a population eventually will go extinct (Figure 3.5, left and below of the persistence boundary).

Figure 3.2B (solid line) shows the irreversible mass of YOY at the end of their first growth period as a function of the consumer reduction factor γ_c. These values of YOY irreversible mass represent the observations for the lowest juvenile mortality rate for which population persistence is possible. Similar to the stepwise temperature regime, the irreversible mass of a YOY individual increases when γ_c increases. However, with the sinusoidal temperature regime the amount of irreversible mass that must be reached at the end

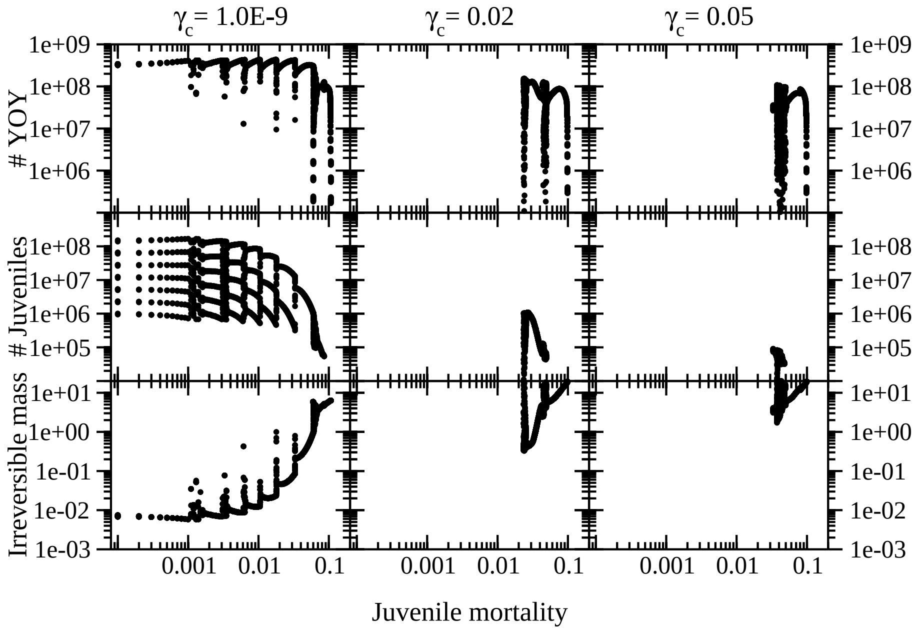

Figure 3.7: Bifurcation diagram of the consumer-resource model with μ_j as the bifurcation parameter in case of the sinusoidal temperature regime for different values of γ_c the factor by which consumer can reduce their physiological rates in winter ($\chi_r = 1 \cdot 10^{-9}$). Top and middle panels show the number of YOY and juveniles, respectively, at the beginning of each year (day 0). The bottom panels show the size of YOY after their first growth period, *i.e.* the sized they reach at the age of 1 year.

of the growth period is higher than with the stepwise temperature regime, because a larger amount of reversible mass is needed to cover the relatively high maintenance requirements during autumn and spring.

3.4 Discussion

In agreement with earlier studies (DeAngelis et al. (1991); Post et al. (1998)) our results indicate the importance of reaching a minimum body size at the start of winter for individuals to survive the ensuing period of starvation. Because growth is food-dependent and hence influenced by intraspecific competition, this minimum size threshold may lead to population extinction as a consequence of population feedback on resources. For substantial ranges of low juvenile mortality, small numbers of consumers may do well and increase in abundance, whereas starvation of newborn individuals during winter will drive the population extinct when reaching high densities. Since low mortality rates are beneficial for individual fitness, extinctions under these circumstances represent a conflict of interest between a single individual and the population as a whole. Population persistence may thus be more related to interactions among individuals and their environment than individual-level performance it self. The maximum resource density, determined by the (abiotic) environment, and the individual capacity to reduce physiological rates are not prohibiting population persistence, as at low densities individuals are able to invade. Instead, the resource density is not sufficient for population persistence as soon as it gets depressed by large numbers of individuals.

We have shown that spring and autumn may influence population persistence if the rapid changes in resource productivity with temperature are out of sync with changes in consumer physiology. On the one hand, the spring and autumn negatively affect population persistence as the minimum body size that individual consumers should reach to survive winter increases. On the other hand, the spring and autumn period lead to lower reproduction pulses and thereby decrease resource competition among newborns. The latter hence grow faster and can reach larger sizes before winter sets in. The effect of spring and autumn on consumers depends on the assumption that temperature determines both resource productivity as well as consumer physiology. It has been shown that zooplankton populations respond more to changing light intensity than changing temperature at the end of the winter period (Beaugrand et al. (2003)). The positive effect of spring and autumn on consumer persistence that we found may change if different environmental cues, such as light, determine the annual changes in productivity and consumer activity.

Even though at an individual level growth in body size is the crucial process, at a population level persistence is largely determined by individual mortality and intraspecific competition. Intense competition among newborns and high survival at low levels of juvenile mortality may lead to recruitment failure, such that YOY stand little chance to survive their first winter. In our model, the consumer population exhibits single cohort cycles, in which adults are being outcompeted by their own offspring and YOY form the only cohort in the population. In addition, the model is deterministic in the sense that all individuals that are born in a particular year remain identical in size throughout their life. In this setting recruitment failure in a single year obviously leads to immediate extinction. When relaxing these conditions, that is in case of dynamics other than single cohort cycles and with more variability in life history of similarly aged individuals, the effect of recruitment failure will be less extreme. Nonetheless, even then we expect that the combination of large densities of offspring and low mortality will result in a low recruitment success and therefore pose an increased risk of extinction.

If a certain size is needed to overcome a (yearly) environmental event such as winter, the presence of predators can facilitate persistence by reducing intra-specific competition.

In a variety of natural systems this beneficial role of predation on population persistence has been revealed. For example, tadpoles in temporary ponds have to reach a certain size to metamorphose before the pond dries out. Data show an increased number of metamorphs when, in a pond with high tadpoles density, predators are present (Wilbur (1988)). Without the predators most tadpoles were too small to metamorph and survive due to the high competition pressure. Byström et al. (1998) showed for YOY perch that high resource competition during summer resulted in smaller individuals with a lower condition in autumn. These smaller individuals suffered from higher winter mortality compared to the larger individuals from the control experiment with low competition. In a field experiment with isopods and amphipods, amphipod size increased with predator presence (Sparrevik and Leonardsson (1999)). In this respect cannibalistic populations are of special interest, as adult cannibals may impose the necessary mortality on their own offspring for the latter to grow fast enough to survive the winter. Cannibalism does not only reduce the density of competing individuals but also provides an energy gain for the cannibal, thereby relaxing competition between cannibals and their victims in two separate ways. Cannibalistic populations can hence be hypothesized to have a higher chance to persist under more severe winter conditions and when individuals have to survive on energy reserves for a longer time. In agreement with this Post et al. (1998) note that the average length of individuals entering winter was indirectly affected by cannibalism through reduced competition. In addition, for Arctic charr (*Salvelinus alpinus*) it has been shown that the frequency of cannibalism increases with latitude (Griffiths (1994)). Size-structured interactions between predator and prey can affect individual prey growth in more indirect manners, such as predator induced morphological changes in body size (Brönmark and Miner (1992)), or behavioral changes of the prey that might interfere with foraging behavior (Byström et al. (2003)). Only if predation leads to accelerated growth of prey individuals, population persistence is promoted.

The dynamics of reindeer (*Rangifer tarandus*), introduced to St. Matthew Island in 1944, may provide an example of a small population of consumers that can expand, but which eventually go extinct due to winter starvation when reaching high population densities (Klein (1968)). Reindeer were introduced to the island in 1944 and increased in abundance from 29 animals to 6,000 in 1963. In 1957 the weight of the reindeer were significantly higher than the individual weight in domestic herds of reindeer, but body weight declined with roughly 40% over the following years as a consequence of high populaiton densities. In the winter of 1963/64 the entire population of 6,000 reindeer died of starvation due to extreme snow conditions. This pattern of reindeer population growth and die-off on St. Matthew Island was claimed to reflect similar dynamics on other island situations with introduced animals. It was believed to be a product of the limited development of ecosystems as well as the deficiency of potential population-regulation factors, such as predation (Klein (1968)). Like our modeling results, these data highlight the important role that population feedback might play in the persistence of populations. For invading species one has to consider the possibility that successful establishment of a few individuals does not necessarily mean successful persistence of an entire population. With increasing population abundance also the impact on the environment grows, which may eventually lead to unsustainable environmental conditions and to ecological suicide of the total population.

3.5 Acknowledgements

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Chapter 4

Size-dependent responses to global warming: indulging adults and dying juveniles

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Unpublished manuscript

Abstract

For freshwater ecosystems in more maritime temperate regions, an increase in temperature is likely to result in an increase in winter temperatures rather than an increase in growth season duration, which will be more likely in more boreal and continental temperate regions due the decrease in the period of ice-cover. The effects of these two global warming scenarios on a consumer-resource system are studied using a size-structured population model, which allows us to make assumptions about the effects of temperature changes on the individual level. In contrast to other models dealing with the effects of global warming, the population dynamics are an outcome of keeping track of all individuals over time. We find that, for both scenarios, large individuals benefit due to high mortality rates early in life. The state of their condition is represented by high population fecundity. When growth season duration is prolonged small individuals suffer as a direct effect of summer prolongation via longer exposure to high mortality. However, when the minimum

winter temperature is increased small individuals suffer from high resource competition and high winter mortality, due to high number of offspring produced by prospering adults. In this scenario, the population feedback plays a more important role than the increase in minimum temperature. The results of both scenarios indicate that any stochasticity may lead to population extinction.

4.1 Introduction

An increase in temperature on a global scale can have several effects on freshwater ecosystems, varying from changes in periods and frequency of drought and flooding to changes in water chemistry, water temperature and the period of ice cover (Carpenter et al. (1992); Schindler (1997); Hughes (2000); Magnuson et al. (2000)). In more maritime temperate regions where the water surface does not freeze during winter, higher air-temperatures in winter will result in increased water-temperatures because these temperatures are closely linked (Easterling et al. (1997); Schindler (1997); Hughes (2000)). In boreal and continental temperate regions the duration of the period of ice cover on lakes is expected to decrease, as has been documented in several studies (Magnuson et al. (2000); Hodgkins et al. (2002)). Historical data on the Northern Hemisphere show that not only has the ice breakup date become earlier, the freeze date has shifted towards a later date in the year (Magnuson et al. (2000)). Ice breakup is an abrupt event in temperate regions and determines the onset of the growth season. It has been shown that the phytoplankton peak and the abundance of zooplankton have shifted in time, and that fish recruitment shows a response to the earlier breakup dates (Nyberg et al. (2001); Weyhenmeyer (2001); Schindler et al. (2005)).

Aquatic species are usually poikilothermic and their level of activity depends on the temperature of the environment. A reduction of activity with temperature decrease implies a reduction of all physiological rates, including maintenance and foraging activity. At the same time, maintenance and foraging activity scale with body size. Persson et al. (1998) show that, in absence of temperature variation, the difference in scaling of maintenance and food intake with body size has consequences for the population dynamics. Larger individuals have higher maintenance costs and cannot sustain low resource levels as can smaller individuals of the same species (Hamrin and Persson (1986); Persson et al. (1998)). However, large individuals have more fat reserves than small individuals, which allows them to survive longer during periods of starvation. As a consequence, a size threshold for small individuals is present, which they need to reach in order to survive winter. This size threshold has been shown in several studies (Shuter et al. (1980); Post et al. (1998), Chapter 3, this thesis).

Global warming could have a positive effect on small individuals when a longer growth season allows them to reach the size threshold that is needed to survive winter (Shuter et al. (1980); Post et al. (1998); Chapter 3, this thesis). In contrast, McDonald et al. (1996) show that a temperature increase can lead to a higher food demand based on increased metabolic rates, resulting in increased starvation mortality of small individuals. A prolonged growth season might imply that predators are active for a longer period, in which case small individuals are exposed to predation mortality longer. An increase in growth season is likely to have a positive effect on large individuals with respect to growth, as they can grow to larger sizes and accumulate more energy for reproduction. Increased reproduction, however, can have a negative effect on recruitment when it results in higher resource competition amongst the offspring.

Temperature can affect individuals in a different manner, depending on their size, which may in turn affect the response of the population. Hence, changes in temperature due to global warming should be studied at the individual level in order to make any comments about the response at the population level. Unfortunately, studies dealing with the effect of temperature on individual level processes often do not consider population dynamics in the context of global warming (Hamrin and Persson (1986); Post and Evans (1989); Blaxter (1992)) or do not include seasonal variation in temperature (Vasseur and McCann (2005)). Most studies dealing with extinctions due to global warming use a descriptive and population level approach (Hughes (2000); Crozier (2004); Thomas et al. (2004), but see McDonald et al. (1996)). To capture the effects of global warming on differently sized individuals and the population dynamics, we use a physiologically structured population model, which allows for a mechanistic approach to study the effect of global warming on the dynamics of a consumer population and its resource. Two different warming scenarios are studied. In the first scenario, the duration of the growth season is increased, based on the trends towards earlier ice breakup and later ice cover in boreal temperate regions (Nyberg et al. (2001); Schindler et al. (2005)). In the second scenario the minimum winter temperature is increased, simulating the trend that the minimum temperature increases more rapidly than the maximum temperature, which would occur at more maritime temperate regions (Easterling et al. (1997); Schindler (1997)).

4.2 Model

We use a physiologically structured population model (PSPM) to study this consumer-resource system, which describes the population dynamics in terms of physiological processes at the individual level (Persson et al. (1998); Claessen et al. (2000); de Roos and Persson (2001)). Different levels of organization are recognized, the individual state, or *i*-state, which describes the individual physiological characteristics and the population state, *p*-state, which represents the frequency distribution over all *i*-states at a particular time. The *e*-state describes the environment, and includes resource and temperature dynamics. The consumer population is size-structured and feeds on an unstructured resource. The model is parameterized for Eurasian perch (*Perca fluviatilis*) and its resource *Daphnia spp* (1.0 mm) (Table 4.2). The size-structured model was studied with the use of a numerical method for integration of physiologically structured population models (de Roos et al. (1992)).

Consumer physiology

The physiological characteristics of the consumer, describing the individual state, are determined by two state variables, irreversible mass (x) and reversible mass (y), which sum up to total body weight. The irreversible mass x consists of material like bone and vital organs which cannot be used to prevent starvation, while reversible mass y is the mass that can be used to prevent starvation such as fat, muscle tissue and gonad mass. The ratio reversible/irreversible mass (y/x) is a measure of the condition of the individual. Allometric functions that depend on both size and condition of an individual are a function of weight, while functions that do not depend on condition are a function of irreversible mass (Table 4.1).

Individuals forage following a Type II functional response, with handling time and attack rate as a function of irreversible mass (Table 4.1)(Persson et al. (1998)). Consumed food is converted into energy with a constant conversion efficiency, after which maintenance costs are subtracted. The remaining net energy is allocated in to growth of reversible and irreversible mass, with a ratio depending on the condition of the individual (Table 4.1). Consumer energetics, hence, follow a net production model (Lika and Nisbet (2000)). Adult individuals can invest more energy into reversible mass than juveniles, which is reserved as gonad mass. Gonad mass is allocated at the onset of winter. All individuals within a cohort are identical and the population is built up by different cohorts.

Individuals that have a fat ratio (y/x) below a threshold value suffer from starvation

Table 4.1: Model equations describing the individual-level model of perch (*Perca fluviatilis*) and the dynamics of the unstructured resource population. The index i refers to perch cohorts, and each cohort consist of N_i individuals.

Subject	**Equation**
Attack rate	$a(x) = A(\frac{x}{x_{opt}} exp(1 - x/x_{opt}))^{\alpha}$
Handling time	$h(x) = \xi_1 x^{\xi_2}$
Maintenance	$E_m(x, y, \tau) = \gamma(\tau)\rho_1(x + y)^{\rho_2}$
Ingestion	$I(x, \tau) = \gamma(\tau)a(x)R/(1 + a(x)h(x)R)$
Net energy	$E_n(x, y, \tau) = k_e I(x, \tau) - E_m(x, y, \tau)$
Energy allocation to irreversible mass	$\kappa(x, y) = \begin{cases} \frac{1}{(1+q_j)q_j}\frac{y}{x} & \text{if } x \leq x_m \\ \frac{1}{(1+q_a)q_a}\frac{y}{x} & \text{if } x > x_m \end{cases}$
Fecundity	$f = \begin{cases} \frac{k_r(y-q_j x)}{w_b} & \text{if } x > x_m \text{ and } y > q_j x \\ 0 & \text{otherwise} \end{cases}$
Starvation mortality	$\mu_s = \begin{cases} s(x/y - 1) & \text{if } y < q_s x \\ 0 & \text{otherwise} \end{cases}$
Background mortality	$\mu_b = \begin{cases} \gamma(\tau)(\mu_0 + \mu_j) & \text{if } x < x_m \\ \gamma(\tau)\mu_0 & \text{otherwise} \end{cases}$
Resource dynamics	$\frac{dR}{dt} = r(\chi(\tau)K - R) - \frac{1}{V}\sum_i I(x)N_i$

mortality. This function is modeled such that death is imminent when all reversible mass is depleted (Table 4.1). Adults use gonad mass when all other somatic tissue is depleted to cover maintenance costs in order to prevent starvation (Schwalme and Chouinard (1999)). Individuals suffer from background mortality (μ_b) that represents a chance to die of causes other than starvation mortality. Juveniles ($x < x_{mat}$) suffer a higher background mortality because small individuals have a bigger chance to die than larger ones, *e.g.* due to predation by, for example, aquatic insect larvae.

Consumer environment

The resource follows semi-chemostat dynamics in the absence of consumption. This is based on the argument that such dynamics describe more realistically the growth of a prey population with invulnerable, but mature, size classes (Persson et al. (1998); Claessen et al. (2000)). Both the resource and the consumer experience the same temperature regime which is modeled as a sinusiodal function. In the reference situation temperature is assumed to fluctuate between a 4°C minimum in winter and a 20°C maximum in summer, which resembles water temperatures in temperate zones (Persson et al. (1998); Claessen et al. (2000)). The physiological rates of the consumer and resource productivity are based on summer estimates, i.e. for when $T = 19 - 20$°C, and slow down when temperature decreases. We will first briefly discuss the sinusoidal function used to model seasonality and how it affects the physiological rates of the consumer and resource productivity, for a more elaborate description we refer to Chapter 3, this thesis. Thereafter we discuss the different global warming scenarios.

The annual change in temperature is described by a sinusoidal function, which we adapted from Turchin and Hanski (1997):

$$T(\tau) = \begin{cases} T_{min} + \dfrac{T_{max} - T_{min}}{2}\left(1 + \left(\sin \frac{\pi\tau}{S}\right)^{\Theta}\right) & \text{if } 0 \leq \tau < S \\ T_{min} + \dfrac{T_{max} - T_{min}}{2}\left(1 - \left(\sin \frac{\pi(\tau - S)}{(Y-S)}\right)^{\Theta}\right) & \text{if } S \leq \tau < Y \end{cases} \tag{4.1}$$

$T(\tau)$ represents the temperature at a particular day of the year τ, with $0 \leq \tau < 365$ days. $T(\tau)$ fluctuates between $T_{min} = 4$°C in winter and $T_{max} = 20$°C in summer. To represent summer and winter periods of unequal lengths the sinusoidal function (4.1) is a composition of two parts, each incorporating a sine function on the interval $[0;\pi]$ raised to the power Θ. The two sine functions have different periods S and $Y - S$, respectively, representing the parts of the year during which temperature is above (for $0 < \tau < S$) and below (for $S < \tau < Y$, $Y = 365$ days) the midpoint temperature $T_{min} + (T_{max} - T_{min})/2$. Notice that the time point $\tau = 0$ is chosen equal to the start of the growth period. The shape of the sinusoidal function can be manipulated with Θ (Turchin and Hanski (1997)). When Θ equals 1 the two parts of the temperature regime are pure sine functions. With decreasing Θ the slope at the transition point where $T(\tau)$ crosses the midpoint $(T_{min} + (T_{max} - T_{min})/2)$ becomes more steep, resembling a step function near $\Theta = 0$. Here $\Theta = 0.2$ is used (Turchin and Hanski (1997)).

All parameter values for the individual-level physiological processes of the consumer and the productivity of the resource presented in Table 4.2 represent estimates for summer conditions, i.e. for when $T = 19 - 20$°C. We assume that in winter the physiological rates of the consumer and the resource productivity slow down with decreasing temperature. This species specific reduction of all physiological rates is described using the Arrhenius

Table 4.2: Model parameters for perch and its resource (*Daphnia* sp. 1mm)(Claessen et al. (2000); Persson et al. (2003, 2004)), and the temperature function.

Symbol	**Value**	**Unit**	**Interpretation**
i-state			
x_m	4.6	g	Irreversible mass at maturation
w_b	0.0018	g	Weight of a neonate
k_r	0.5	-	Gonad egg conversion
x_{opt}	4.7	g	Optimal consumption weight
μ_0	0.01	d^{-1}	Background mortality rate
μ_j	0.015	d^{-1}	Added juvenile mortality rate
s	0.2	d^{-1}	Starvation coefficient
A	3.0E+4	L/d	Attack rate constant
α	0.5	L/d	Attack rate exponent
ξ_1	3.2	$\mathrm{d/g}^{(1+\xi_2)}$	Digestion time constant
ξ_2	-0.8	-	Digestion time exponent
ρ_1	0.033	$\mathrm{g}^{(1-\rho_2)}/\mathrm{d}$	Maintenance allometric constant
ρ_2	0.77	-	Maintenance allometric exponent
k_e	0.61	-	Food conversion efficiency
q_j	0.74	-	Juvenile reversible/irreversible mass ratio
q_a	1.37	-	Adult reversible/irreversible mass ratio
q_s	0.2	-	Starvation condition
e-state			
r	0.1	d^{-1}	Resource growth rate
K	3.0E-3	g/L	Resource carrying capacity
V	1.0E+9	L	Total lake volume
S	varied	d	Summer duration
Y	365	d	Year length
T_{max}	20	^{o}C	Maximum summer temperature
T_{min}	varied	^{o}C	Minimum winter temperature
T_{ref}	4	^{o}C	Reference value minimum temperature
Θ	0.2	-	Steepness seasonality shift
γ_c	0.02	-	Consumer min. winter rate reduction
χ_r	1E-4	-	Resource min. winter rate reduction

equation (Kooijman (2000a)). At a temperature of $T(\tau)$ the physiological rates of the consumer are hence scaled by the following multiplication factor:

$$\gamma(\tau) = \gamma_c^{\left(\frac{1.0-\frac{T_{max}}{T(\tau)}}{1.0-\frac{T_{max}}{T_{ref}}}\right)} \tag{4.2}$$

$\gamma(\tau)$ denotes the reduction of all physiological rates in winter as a percentage of the summer maximum at time τ. The function is such that for $T(\tau) = T_{max}$, $\gamma(\tau) = 1$ (100% of summer maximum), and for $T(\tau) = T_{ref}$, $\gamma(\tau) = \gamma_c$. We assume that at lower temperatures consumer mortality, maintenance and ingestion rate (attack rate and handling time) decrease, and hence we scale the rates of these processes with the factor $\gamma(\tau)$ (see Table 4.1). A lower value of γ_c implies that consumers are more able to reduce their physiological rates.

Resource productivity follows a similar regime during the year is described by the product $rK\chi(\tau)$, in which $\chi(\tau)$ can vary from χ_r in winter when $T(\tau) = T_{ref}$ to $\chi(\tau) = 1$ in summer when $T(\tau) = T_{max}$. $\chi(\tau)$ is the actual value with which resource productivity is scaled at temperature $T(\tau)$ at time τ:

$$\chi(\tau) = \chi_r^{\left(\frac{1.0-\frac{T_{max}}{T(\tau)}}{1.0-\frac{T_{max}}{T_{ref}}}\right)} \tag{4.3}$$

If γ_c and χ_r are equal the ratio between consumer rates and resource productivity does not change throughout the year. The decreasing temperature during winter in this case only implies a slowing down of dynamics, which is identical for consumers and resource. Temperature variation hence represents a scaling of time. This scaling is such that population changes during that winter period with slow dynamics are identical to the changes that would occur in during a shorter period at faster rates. Therefore, for $\gamma_c = \chi_r$ incorporating a winter period in the size-structured model has the same effect as choosing a slightly longer interval between consumer reproduction pulses in the size-structured models that consider winter to be a period of complete stasis (Persson et al. (1998)).

When $\gamma_c > \chi_r$, an unequal scaling of consumer physiology and productivity occurs, which turns out to be disadvantageous for the consumer. Consider the net energy production of a consumer individual of size x:

$$E_n(x, y) = \gamma(\tau)(k_e(a(x)R/(1 + a(x)h(x)R)) - \rho_1(x + y)^{\rho_2}) \tag{4.4}$$

With decreasing temperature $\gamma(\tau)$ decreases, which scales down both maximum ingestion capacity as well as the metabolic energy demands of the consumer. Simultaneously, however, the resource density R will decline as the decreasing temperature also reduces resource productivity by the factor $\chi(\tau)$. When $\gamma_c > \chi_r$ the decline in resource productivity will be more rapid then the decrease in maximum ingestion capacity and metabolic demands of the consumer. As a consequence, the consumer will experience periods of food limitation, while its energy demands are still relatively high. These periods with low food availability and high demands, *i.e.* with a large discrepancy between the actual values of $\gamma(\tau)$ and $\chi(\tau)$, specifically occur during spring and autumn. During autumn resource productivity drops quickly, but consumer rates are still relatively high, while in spring consumer rates jump ahead of resource productivity when temperature rises.

The effect of two different global warming scenarios on the annual change in temperature is shown in Figure 4.1 and Table 4.3. In scenario 1 summer duration (S)is increased, while the minimum winter temperature remains constant. This leads to an increase of the period for which $T \geq 17$°C and $T \geq 19$°C (Table 4.3). Hence, this scenario provides a longer growth season with increasing summer duration. Consumer reproduction occurs as a pulsed event at $\tau*$, 45 days before midsummer, regardless of summer duration (Figure 4.1, top panel), which is based on the duration of the growth season in temperate regions (90 days)(Persson et al. (1998); Claessen et al. (2000)). This assumption implies that consumer reproduction does not respond to changes in temperature.

In the second scenario the minimum winter temperature (T_{min}) is increased, while summer duration remains constant. When the minimum temperature reached in winter increases (T_{min}), so do the minimum values attained by $\gamma(\tau)$ and $\chi(\tau)$. T_{ref}, γ_c and χ_r remain the reference values for scaling consumer physiology and resource productivity with increasing temperature. The bottom panel (Figure 4.1) shows the effect of the annual temperature change for scenario 2, for three values of minimum winter temperature. Besides the effect on the minimum winter temperature, the duration of the growth period also increases with increasing T_{min}, which is apparent in the increase in the number of days that the temperature is equal to, or above 19°C (Table 4.3). This increase, however, is not as strong as for scenario 1.

4.3 Results

In scenario 1 the summer duration, S, is increased, which means that the period with a high temperature is prolonged (see also Figure 4.1, top panel). In figure 4.2, the population dynamics resulting from an increase in summer duration (S) (scenario 1) are shown. Apart

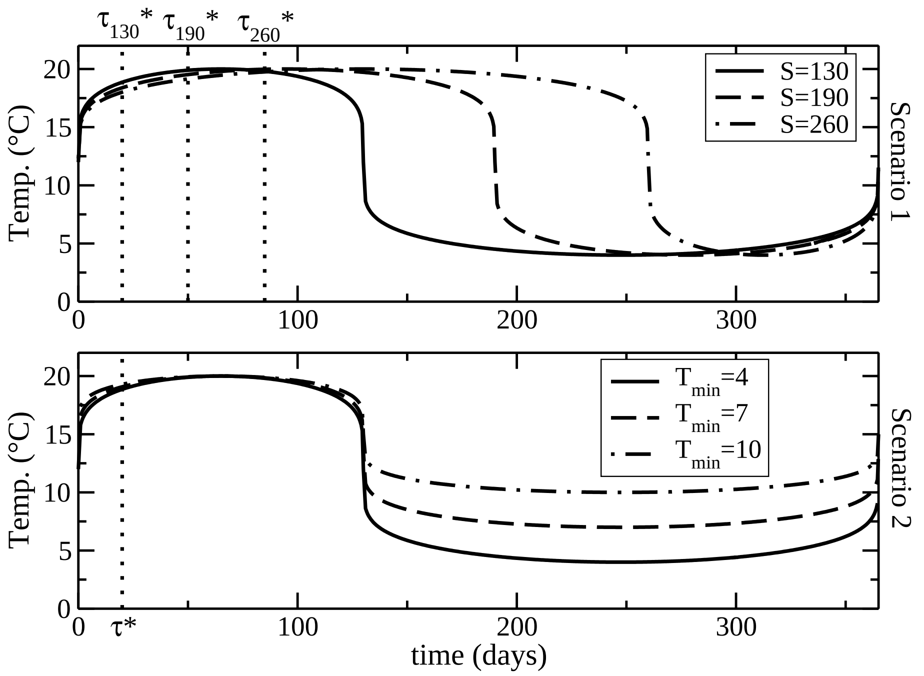

Figure 4.1: The yearly change in temperature for different values of summer duration S (scenario 1, $T_{min} = 4°C$), top panel, and for different values of minimum winter temperature (scenario 2, $S = 130$ days), lower panel. At $\tau = 0$ the summer period starts (Equation 3.2), $\tau*$ denotes the date at which reproduction occurs, 45 days before mid-summer.

from some parameter regions with irregular dynamics, the population exhibits mostly recruitment driven cycles. The competitive ability of small individuals over larger ones, due to the higher scaling of maintenance over ingestion with size, gives rise to these recruitment drive cycles (Persson et al. (1998)). Reproduction is a pulsed event and the high numbers of offspring reduce the resource density to a level at which adults cannot sustain. The latter are outcompeted and die of starvation imposed on them by their own offspring. As a consequence, the cohort of newborns is now the only cohort in the population, and is outcompeted by their own offspring. The cycle repeats it self resulting in stable recruitment driven single cohort cycles. For summer duration S between 140 and 175 days these cycles have a period of 3 years, while for summer durations S between 175 and 335 the period is 2 years. For $S > 335$ days the population exhibits some irregular but recruitment driven dynamics. The decrease in cycle length in a stepwise manner observed here is similar to the results shown by de Roos et al. (2002), where with increasing juvenile mortality the same bifurcation pattern was obtained. For $175 < S < 260$ the biomass of young of the year (YOY), juveniles and adults increases. Adult size and fecundity

Table 4.3: The effect of the two global warming scenarios used in this study on mean temperature and duration of the period for which $T \geq 17°C$ and $T \geq 19°C$.

S (d)	**T$_{min}$(°C)**	**Mean T (°C)**	**T $\geq$ 17°C (d)**	**T$\geq$ 19°C (d)**
Scenario 1				
130	4	9.95	122	85
190	4	12.29	179	125
260	4	14.99	245	171
Scenario 2				
130	4	9.95	122	85
30	7	12.53	127	93
130	10	13.73	128	103

increase with an increasing growth season duration (represented by adult biomass), while the number of adults decreases (not shown)(Figure 4.2). YOY survival, measured from $\tau*$ to $\tau*$, decreases, which is due to the increase of summer duration. The YOY suffer longer from the (high) summer mortality rates. The surviving YOY do not suffer from winter mortality because they experienced a long growth season and high resource densities (not shown). For $S > 275$ first year survival no longer decreases with increasing summer duration. These individuals do not suffer from juvenile mortality any longer in spring, as they have reached the size of maturation after winter but before they are one year old. They cannot reproduce at the coming reproduction date since they could not allocate gonad mass before winter, hence the three year cycle stays intact. The juveniles grow into large and highly fecund adults. These few but large adults reproduce as much offspring as many smaller adults, although for $S > 260$ the size of the adults is no longer sufficient to compensate for the loss in numbers, which leads to a decrease in YOY biomass. The pattern in population dynamics, observed with increasing summer duration, thus results directly from the temperature scenario rather than from a population feedback.

With the second scenario the minimum winter temperature increases, while summer duration is kept constant. For $4°C \leq T_{min} \leq 8°C$ the population dynamics are irregular (Figure 4.3). For $8°C < T_{min} \leq 9°C$ the population dynamics alternate between a two year and a one year cycle, after which some irregular dynamics occur. For $T_{min} > 9.7°C$ the population exhibits fixed point dynamics. Changing the minimum number of individuals

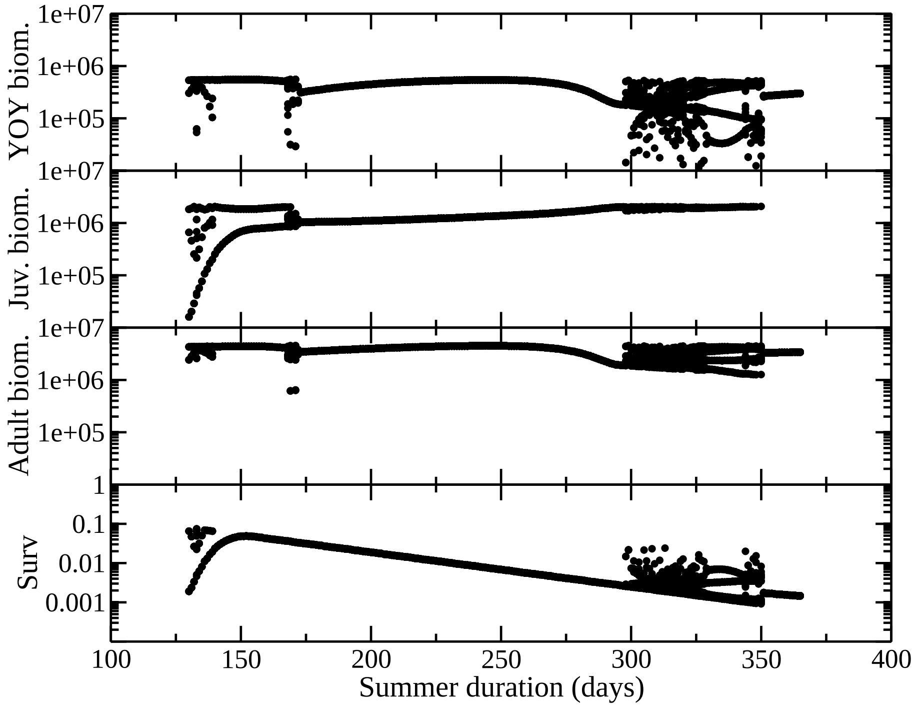

Figure 4.2: The change in biomass of the consumer population (top: YOY (at $\tau*$), second from top: juveniles (at $\tau(0)$), second from bottom: adults (at $\tau(0)$)), and first year survival (bottom panel) as a function of increasing summer duration (scenario 1)(T_{min} = 4.0°C).

allowed in a cohort has no influence on the irregularity of the dynamics. The amount of biomass of YOY, juveniles and adults fluctuates heavily. Moreover, the first year survival fluctuates with 9 orders of magnitude.

Figure 4.4 shows the recruitment driven dynamics of the consumer population for T_{min} = 6.0°C. The dynamics are irregular and on several occasions the population goes through a bottleneck with very low numbers at t = 7 years, t = 13 years and t = 40 years. These bottlenecks occur after a high reproduction pulse, and result in low first year survival. The size of YOY at the start of their first winter reflects their resource intake during summer (Figure 4.4, bottom panel). Small sizes at the onset of winter correspond with the low survival, which is due to high starvation mortality in winter. YOY need to reach a size threshold in order to survive their first winter, and when they do not reach that threshold they suffer from starvation mortality. The effect of an increasing minimum temperature on population fecundity, adult fecundity, YOY survival and the size reached by YOY at the start of winter was studied for T_{min} = 4.5°C and T_{min} = 6.0°C (Figure 4.5). The Box-Whisker plots of population fecundity and YOY survival show a higher variation for T_{min} = 6.0°C than T_{min} = 4.5°C within the 25% and 75% interval, and

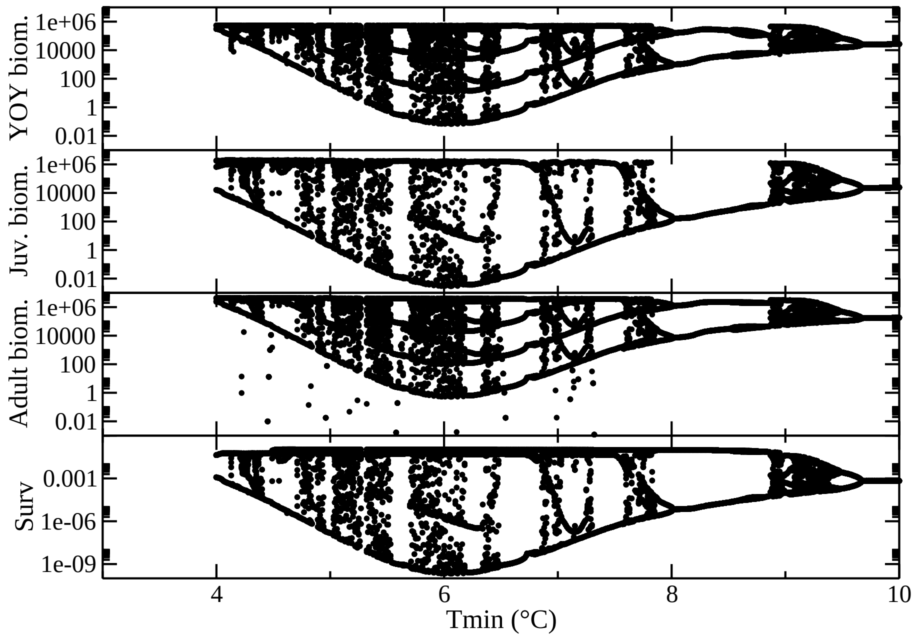

Figure 4.3: Similar to Figure 4.2, but now using scenario 2, an increase of the minimum winter temperature ($S = 130$ days).

also a lower minimum and a higher maximum (cross correlation -0.97 for $T_{min} = 4.5$°C and -0.87 for $T_{min} = 6.0$°C). Adult fecundity has lower variability within the 25% and 75% interval for $T_{min} = 6.0$°C, but does have a lower minimum and a higher maximum than for $T_{min} = 4.5$°C. The size of YOY at the onset of winter has a larger variation within the 25% and 75% interval but the minimum and maximum are similar to $T_{min} = 4.5$°C. The results presented in Figure 4.5 illustrate that population feedback plays a more important role for the population dynamics than the direct effect of temperature acting on the individual level.

With our assumption that reproduction occurs at a certain date, we assume that consumers are not responding to temperature concerning reproduction. In contrast to a fixed reproduction date we can assume that consumers reproduce when a temperature threshold is reached, *i.e.* when individuals can track seasonality. However, using a temperature threshold for reproduction ($T = 15.0$°C) instead of a fixed date does not alter the results in a quantitative way for both scenarios (results not shown). With the assumption that individuals first use the energy reserves they have accumulated as gonad mass to prevent starvation during winter, the population goes extinct with increasing winter temperature (results not shown). This outcome is independent of whether reproduction occurs at a

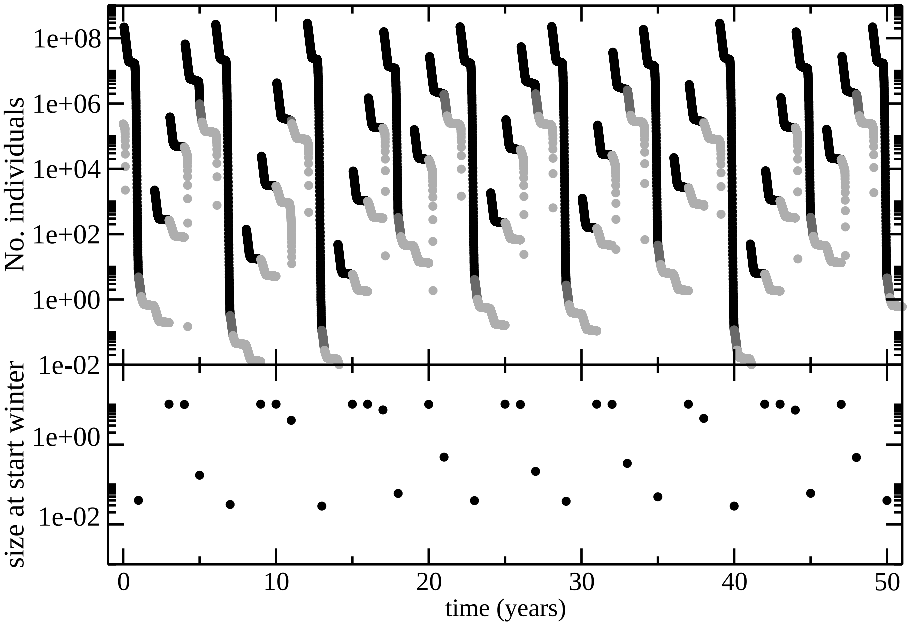

Figure 4.4: The population dynamics in number of individuals (black: YOY, dark grey: juveniles, light grey: adults), and irreversible mass x of YOY reached at the age of 1 year for $T_{min} = 6.0°\text{C}$ ($S = 130$ days).

fixed date during the year or whether individuals can track the seasonality and reproduce when the ambient temperature reaches a threshold of 15.0°C. The extinction occurs at a high minimum winter temperature ($T_{min} = 10.2°\text{C}$) and is due to adult maintenance and not due to YOY starvation mortality during winter. Because adults first use their gonad mass to cover maintenance requirements during periods of starvation, they fail to reproduce in spring. As a consequence the population does not go extinct due to recruitment failure, but due to reproductive failure. The minimum number of individuals allowed in a cohort does not influence the occurrence of extinction.

4.4 Discussion

The two global warming scenarios studied here show that adults benefit while YOY suffer. However, the mechanism is different for the two scenarios. In scenario 2, an increase of the minimum winter temperature, the YOY suffer from starvation mortality in winter due to the high population fecundity and the resulting high number of competitors. Individuals benefit as adult from the low resource competition and the high food intake, and, hence, benefit due to a population feedback. In this scenario, individuals are affected by a

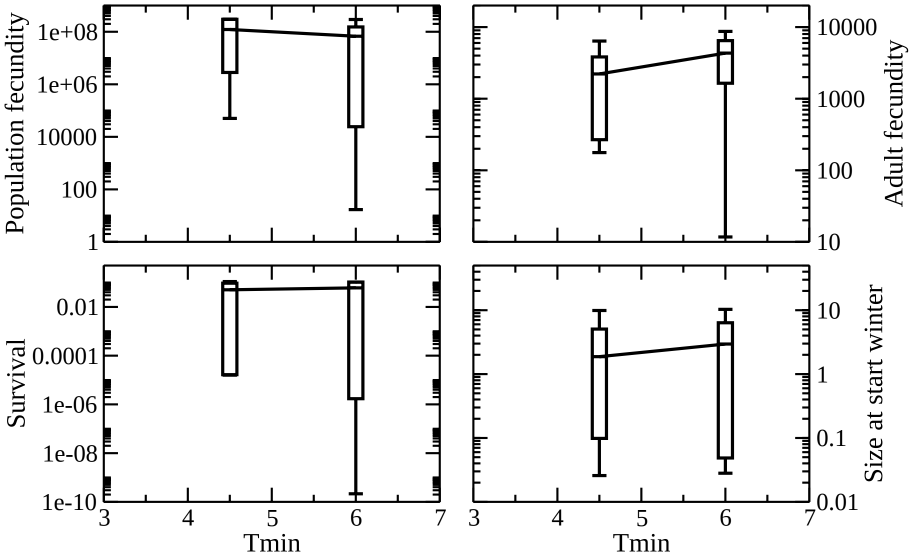

Figure 4.5: Box-Whisker plots of population fecundity, adult fecundity, first year survival and irreversible mass x of YOY reached at the age of 1 year for $T_{min} = 4.5$°C and $T_{min} = 6.0$°C. Shown are the mean, the 25% to 75% interval, and the minimum and maximum value ($S = 130$ days).

population feedback, rather than directly by the change in temperature. In scenario 1, an increase of summer duration, YOY suffer as a direct effect from summer prolongation via longer exposure to high mortality. The surviving individuals benefit from the low number of competitors.

The increased exposure to mortality in scenario 1 is a direct result from our model assumption that mortality scales with temperature and the use of a fixed value for juvenile mortality. These assumptions are based on the fact that active individuals are more likely to be noticed by predators. As for the fixed value of juvenile mortality, an increase in summer duration may not lead to a reduced predation risk if predators also benefit from the prolonged growth season, *i.e.* when YOY do not outgrow their predators. Assuming a size-dependent juvenile mortality could affect the model outcome if that mortality would only affect very small YOY. However, if the size for which juvenile mortality no longer plays a role, is reached after the first winter of YOY, our results will not be quantitatively different.

Temperature affects reproduction, growth and mortality. By bridging the gap between individual responses to temperature and population responses to global warming, we demonstrate that global warming affects individuals differently depending on their size. Moreover, we show that mechanisms operating at the individual level influence the effect of global warming on population dynamics. Taking the individual level into account when studying the effects of global warming on population dynamics may result in extinction when large individuals do well, while their offspring starves to death. Severe resource competition among offspring, which may result in recruitment failure, is caused by large reproduction pulses of well fed adults. This mechanism, which is based on food dependent development, has not been proposed before but is likely to occur for species for which reproductive output increases with adult size and a minimum size is needed for winter survival, which is the case for many species, f.e. fish, amphibians and many invertebrates (Werner and Gilliam (1984)).

While an increase in winter temperature resulted in highly fluctuating population dynamics, an increase in the duration of the growth season resulted in stable cyclic dynamics. Cycle length decreased from a three year to a two year cycle and to fixed point dynamics when growth season duration was close to year length, which corroborates with the expectation that age at maturity decreases and the completion of life cycles will accelerate with global warming (Choi (1996); Schindler (1997)). Both scenarios show that YOY survival decreases, which can be argued to translate into an increased risk of recruitment failure. In scenario 2 the internal dynamics are sufficiently irregular to cause extinction due to recruitment failure, whereas in scenario 1 this is not the case. However, also in scenario 1 we hypothesize to see an increased incidence of recruitment failure when the low YOY survival combines with external, stochastic perturbations to the dynamics. Vasseur and McCann (2005) used a consumer resource model that included a temperature and body mass dependent scaling for biological rate functions (growth, metabolism and ingestion rate), but no body size variation within a species. They predict that extinction of the consumer population will not occur with increasing temperature (no seasonality included), but the presence of cyclic dynamics might increase.

Whether reproduction occurred on a fixed date or dependent on the ambient temperature did not matter for the population dynamics in our model results. Differences in timing between resource availability and consumer reproduction has proven to be an important element for recruitment success, and can occur when different species respond to different environmental cues that mark the beginning of their growth season (Nyberg et al. (2001)). A good example of a potential mismatch due to different cues is that plankton responds to a light cue and their (fish) predators to a temperature cue. Beaugrand et al. (2003) show that the timing of spawning and algae blooms plays a crucial role in the recruitment success of young cod (*Gadus morhua*). Match-mismatch effects on recruitment, possibly due to global warming, are not limited to ectotherms, but can also occur for endotherms, for example for insect-feeding birds (Both and Visser (2005)), but is not likely to be present for mammals for which recruitment success to a large extend depends on the condition of the mother that produces the food (Durant et al. (2005)).

Unfortunately, the change in temperature due to global warming is generally reported as annual average or trend (Easterling et al. (1997); Hughes (2000)). Often, information on for example the duration of the growing season for consumers, their resources and their predators and the amplitude of the temperature fluctuations between summer and winter is not available (but see Easterling et al. (1997); Schindler (1997); Hughes (2000); Nyberg et al. (2001); Schindler et al. (2005)). These aspects will vary on a more local scale and may hence cause populations to go extinct at certain localities, but to thrive at other places. Only more detailed information on changes in these characteristics with global warming in combination with a careful consideration of individual-level and population-level responses to these changes may help to make our predictions and our understanding of the important mechanisms better. Evidence for more subtle changes in seasonality associated with a global temperature increase, such as earlier dates for ice break-up in more boreal and continental temperate regions (Magnuson et al. (2000)), supports the need for more detailed information to estimate extinction risks.

4.5 Acknowledgements

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Chapter 5

Effects of life history omnivory and food-dependent growth on community structure

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Unpublished manuscript

Abstract

Growth in body size during ontogeny often results in changes in diet and thus to life history omnivory. In addition, growth is often dependent on food density. Using a physiologically structured population model we investigated the effects of these two size-structured processes in a system consisting of two populations, an omnivorous top predator and an intermediate consumer. In the simplest intraguild predation system (IGP), with one shared resource, we found that life history omnivory decreases the likelihood of coexistence between top predator and intermediate consumer. This result contrasts to previous unstructured models and stage-structured models without food dependent development. Food dependent development and size-dependent foraging abilities of the predator resulted in a positive feedback between foraging success on the shared resource at an early life stage, and foraging success on the intermediate consumer later in life. We show that the negative effect of this feedback on coexistence is robust, as it also demotes coexistence when the feedback is incorporated in other unstructured models. When an additional, exclusive resource for the top predator was included coexistence was more likely to occur and patterns of equilibria resembled community patterns predicted by earlier non size-structured models. It is argued that the additional resource weakens the competitive dominance of the intermediate consumer and thereby negatively affects its occurrence in favor of persistence of the top predator.

5.1 Introduction

Intraguild predation, where two species are not only engaged in a predator-prey relationship but also compete for a basic resource (Holt and Polis (1997); Mylius et al. (2001)), represents the simplest omnivorous type of species' interaction. Intraguild predation is commonly found in many natural systems (Arim and Marquet (2004)) and for a variety of different species such as insects, amphibians and fish (Werner and Gilliam (1984); Byström et al. (1998); Walls and Williams (2001)). A number of experimental (e.g. Morin (1999); Diehl and Feißel (2000, 2001)) as well as theoretical studies (e.g. Holt and Polis (1997); Diehl and Feißel (2000); Mylius et al. (2001)) have focused on intraguild predation, primarily addressing the issue of coexistence and possible extinction of predator and prey species along a productivity gradient. Most models used to study intraguild predation are based on Lotka-Volterra type interactions (Holt and Polis (1997); Diehl and Feißel (2000); Mylius et al. (2001)). Frequently, these models predict that coexistence of the predator and the prey population is possible for a narrow range of intermediate productivities only. At low productivity food availability is too low for the predator to persist, analogous to the predictions of simple models for linear food chains (Oksanen et al. (1981)). For high productivity the prey population is driven to extinction by the predator population, which can sustain itself on the basic resource alone and thereby impose too large a predation pressure on the prey.

These predictions of limited prey and predator coexistence over a narrow range of productivities are in line with the general theoretical insights about the role of omnivory in food webs. Omnivory has been found to have a destabilizing influence on food web models (*e.g.* Pimm and Lawton (1977, 1978); Pimm (1982)), especially when the omnivorous feeding relationships are strong (*e.g.* McCann et al. (1998); Neutel et al. (2002)). The theoretical predictions regarding the role of intraguild predation are partially supported by experimental results (Morin (1999); Diehl and Feißel (2000, 2001)). Using microcosm experiments, these study results show coexistence of predator and prey at intermediate productivity. In addition, recent results from whole lake experiments indicate that the presence of a top predator may considerably limit the establishment of a prey population in an intraguild prey-predator system (Persson et al. unpublished).

In contrast to the theoretical expectations and the experimental evidence from laboratory systems, a number of empirical overviews have suggested omnivory to be common in natural systems (Polis et al. (1989); Polis and Strong (1996); Arim and Marquet (2004)). Persson et al. (1991) and Jeppesen et al. (2000) analyzed aquatic systems over a wide range of productivity levels, showing that coexistence between an intraguild predator and its prey is common. All these empirical studies, however, mainly assess whether or not omnivory occurs in documented natural food webs, but are inconclusive about its dynamic importance or strength.

The apparent prevalence of omnivory in natural systems is not in agreement with theoretical predictions and experimental findings that intraguild predation limits coexistence. One possible explanation for this discrepancy is that in natural systems intraguild predation often occurs as life history omnivory, in which an individual organism exhibits shifts in diet during ontogeny, while it is not represented as such in models. Ontogenetic diet shifts are frequently associated with accompanying shifts in habitat use and generally imply a change in the interaction pattern of the individual with its environment. Life history omnivory differs from omnivory in that the feeding on different resources and/or trophic levels does not occur simultaneously in time, but sequentially in the course of an individual's life. In theoretical studies of food webs, life history omnivory has been found to have less of a destabilizing influence than omnivory (Pimm and Rice (1987)). These authors found that life history omnivory in combination with a food-dependent maturation rate generally led to less stability compared to a fixed stage duration, especially when adult fecundity was food dependent as well. Mylius et al. (2001) also investigated simple forms of life history omnivory with food- and environment dependent maturation rates, but this did not change the results compared to a fixed stage duration to a large extent.

The ontogenetic diet shifts that form the basis of life history omnivory generally result from growth and development of the individual organism. An increase in body size changes the rates of foraging and handling food, as well as most other physiological rates. In addition, it increases an individual's capacity to exploit new resources. Although the studies of Pimm and Rice (1987) and Mylius et al. (2001) did represent changes in diet, they ignored the changes in body size that give rise to them. Therefore, a drawback of the models used to study intraguild predation is that they either ignore life history omnivory altogether (Holt and Polis (1997); Diehl and Feißel (2000)) or represent it in a rather phenomenological way (Pimm and Rice (1987); Mylius et al. (2001)), without capturing the essence, namely changes in body size during ontogeny.

Here, we use a size-structured population model to study life history omnivory in a system with an omnivorous top predator (TP) and an intermediate consumer (IC). This modeling framework allows us to explicitly model the changes in body size that give rise to the change in diet, while both TP and IC experience food dependent growth rates and have size-dependent foraging capacities. The interaction between two structured populations allows for size-dependent inter- and intra-specific relationships such as piscivory and competition to play a role in the life-history of individuals of both species. We analyzed how the size-structured interactions affect the community structure and the occurrence of coexistence. The results of this model are being compared with results from existing unstructured models. We also investigate the effect of an alternative resource exclusively available for the top predator on coexistence of top predator and intermediate consumer. An exclusive resource can enhance predator persistence for low levels of the shared resource, and therefore potentially facilitate of coexistence for a wider range of productivity levels. Any effects of an exclusive resource for the intermediate consumer and/or cannibalism on coexistence of IC and TP where not included in this study, they are however the subject of future research. To allow comparison with results of other studies we investigate the persistence of the top predator and the intermediate consumer as a function of the carrying capacity of the shared resource, as a measure of productivity, and the ability of the top predator to forage on the shared resource.

5.2 Model

The model studied here describes the interactions between a size-structured consumer population, a size-structured predator population and two non-structured resource populations, extending and combining the single species models described by Persson et al. (1998) and Claessen et al. (2000). Below we give a general verbal description of the model, for a more detailed description, equations and parameter values we refer to the Appendix: Size-structured Model. The two species used to parameterize the model are perch (*Perca fluviatilis*) as the top predator (TP) and roach (*Rutilus rutilus*) as intermediate consumer (IC). Roach and perch are commonly found together in freshwater lakes in boreal regions (Persson (1988); Persson et al. (1991)). Perch is an omnivore and undergoes two major ontogenetic niche shifts, shifting from planktivory to benthivory and from benthivory to piscivory (Persson (1983b, 1988); Persson and Greenberg (1990b); Byström et al. (1998)). Roach is a planktivorous fish that mainly feeds on zooplankton (Persson (1988)). Zooplankton is considered the shared resource and for the parameterization *Daphnia* sp. are used as they are generally found in roach and perch diet (Persson and Greenberg (1990b); Hjelm and Persson (2001)). Mayfly larvae *Cloeon*, which is one of the main species commonly found in perch' diet (Persson (1983b); Persson and Greenberg (1990b); Persson et al. (1996)), represent the macro-invertebrates as exclusive TP-resource. When the exclusive resource is included in the model, the carrying capacity is set to a level at which an individual perch cannot reach maturity when solely feeding on the exclusive resource. With this assumption we want to assure that competition for the shared resource plays a role in the life history of individuals of both species. Both resources are modeled as unstructured populations and follow semi-chemostat dynamics (Persson et al. (1998); Claessen et al. (2000); de Roos et al. (2002)). All parameter values are based on a freshwater lake in central Sweden, with a volume of $10^9 L$ and a littoral bottom surface area of $5.0 \cdot 10^4 m^2$ (Persson et al. (1998); Claessen et al. (2000); de Roos et al. (2002)). Only the growth season is considered, with a duration of 90 days. The rest of the year lake is covered with ice reducing activity to a minimum (Persson et al. (1998)).

Both the TP and the IC annually reproduce in a pulsed event. All individuals of a species that are born at the same time belong to the same cohort, and all individuals within a cohort are identical. As a result, a population consists of different cohorts, and size differences occur between individuals of different cohorts. Individuals are characterized by two measures of body size, structural mass and reserves, which sum up to total mass, where structural mass relates to body length following an allometric relationship. Foraging of all individuals follows a Holling type II functional response, and feeding is assumed to be limited by digestive constraints, *i.e.* handling times are identical for different food items but differ for differently sized individuals (Claessen et al. (2000)). The IC is assumed to be the better competitor for the shared resource (Byström et al. (1998)). The attack rate of an individual on its resource depends on its size, while the attack rate of a top predator on an intermediate consumer depends on the length of both predator and prey. The predation attack rate has a tent-like shape (see Figure 5.4 for an illustration) which is based on the assumption that the attack rate is bounded by a minimum, an optimum and a maximum ratio of prey and predator length, due to physiological constraints (*e.g.* gape size)(Claessen et al. (2000)).

The life history of an individual, which is made up by all events and processes occurring during an individuals life, is modeled using a dynamic energy budget model that describes the rate at which individuals acquire energy and how that energy is divided between maintenance, growth and reproduction (Kooijman (2000b); Lika and Nisbet (2000)). Here a net production model is used, which means that from the acquired energy through foraging, maintenance is covered first. The remaining net energy is allocated to growth of both structural mass and reserves where the latter includes energy reserved for reproduction. In case the energy needed to cover maintenance exceeds the acquired energy, reserves are used as energy source. When an individual cannot acquire enough energy through feeding and reserves are low, it will suffer from starvation mortality. In the case that no reserves are left the individual will die for certain. Background mortality is accounted for by a size-dependent mortality rate, assuming that small individuals have a bigger chance of dying than larger ones, *e.g.* due to predation by insect larvae (de Roos and Persson (2001)).

Because this size-structured model cannot be solved analytically, we use the numerical technique developed by de Roos et al. (1992) for simulations. We will use this technique to determine the persistence of TP and IC within a parameter space, with resource carrying capacity and TP attack rate on the shared resource. We first investigate for which parameter values a species goes extinct. We assess the extinction boundaries of the IC and the TP population without the other species present, and the extinction boundary of a species when coexisting with the other. A species is considered extinct if the number of individuals is less than 1. We also determine for which parameter values an invading species (TP or IC) can successfully establish itself in an environment set by the resident species (see Appendix: Invasion and Extinction). We assume that the number of invaders is small and hence any feedback from the invader on the resident is removed. This implies that the invading species does not affect resource densities or causes predation mortality in case the invading species is the top predator. Invading consumers do suffer from predation mortality inflicted by the resident predator. Invasion is successful when the population growth rate of the invading species is positive (criteria in Appendix: Invasion and Extinction).

5.3 Results

Single population dynamics

In the absence of the other species both an IC and a TP population exhibit fixed point dynamics, with yearly reproduction. The IC population only exhibits fixed point dynamics throughout the zooplankton carrying capacity range used in this study, while for the TP population an alternative type of dynamics may occur for $K_Z > 2.5 \cdot 10^{-5}$, in which reproduction occurs only every third year. Since the results we present below are only marginally affected by the type of single-species dynamics of the TP, we will not discuss nor distinguish between these alternative dynamics any further.

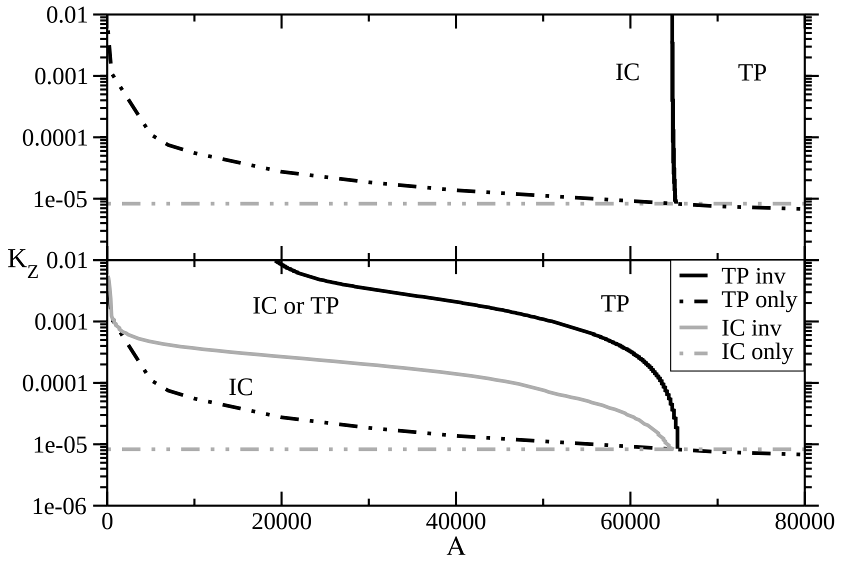

Figure 5.1: The solid lines denote the invasion thresholds, top predator invasion occurs on the right side of the TP threshold (dark), the IC can invade on the left side of the IC threshold (light), as a function of the maximum attack rate of TP on the shared resource (A (Ld^{-1})) and the carrying capacity of the shared resource (K_Z (gL^{-1})). Top graph without piscivory; bottom graph with piscivory. Dashed-dotted lines delineate the single-population extinction thresholds, below which the population can no longer exist. The exclusive resource for TP is not included.

Competition and predation

When TP and IC both only feed on zooplankton, and predation of TP on IC does not occur, coexistence of the two competing species is not possible (Figure 5.1, top panel). Figure 5.1 (top panel) shows that for $A < 6.5 \cdot 10^4$, where A represents the attack rate of the TP on zooplankton, IC is the superior competitor and excludes the TP population (region IC). For $A > 6.5 \cdot 10^4$ TP is the superior competitor and it can hence invade a resident IC population and drive it to extinction. The boundary between the parameter regions where TP or IC dominates is independent of the zooplankton carrying capacity. Moreover, invasion of the dominant competitor will always lead to exclusion of the other species.

Accounting for predation by the TP on the IC substantially changes the invasion boundaries of the TP and the IC (Figure 5.1 bottom panel). The boundary separating the area where the TP can and cannot invade a resident IC population now depends on the zooplankton carrying capacity. At lower values of A, TP invasion is only possible at a higher value of K_Z. For A close to zero, for which values the model approximates a

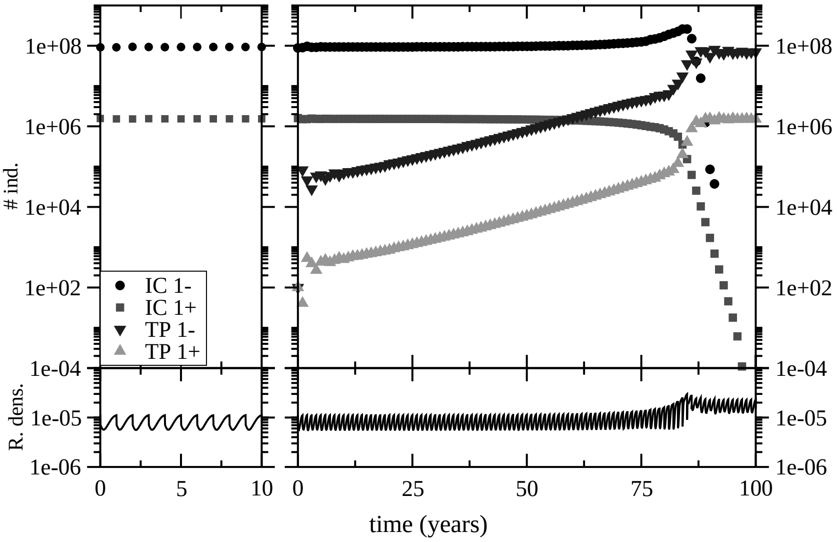

Figure 5.2: The left panel shows the population dynamics of the IC population in absence of the TP, the right panel shows the dynamics of IC and TP after the invasion of 100 YOY and 100 adult TP individuals. $A = 3.0 \cdot 10^4 Ld^{-1}$ and $K_Z = 3.7 \cdot 10^{-3} gL^{-1}$. For both populations, the number of young of the year (1-) and one year old and older (1+) present at the first day of the year are plotted (top panels), while the resource density (gL^{-1}) is plotted for every day of the year (lower panels).

linear food chain system, coexistence of the IC and the TP does not occur at all, because newborn TP require prey smaller than the size of a newborn IC. Hence, without an alternative resource to forage on for newborn TP, the TP population cannot persist for such low A values.

In a large region of parameter values bistability occurs where neither species can invade the others species' equilibrium. A TP invasion in an established IC population is not possible because both the shared resource density, which is depressed to low densities by the IC, and the low number of IC individuals within the TP predation window are not sufficient to support the TP population. An established TP population, on the other hand, prevents IC invasion through high predation mortality inflicted on small IC individuals. Outside the bistable parameter region the IC dominates for low values of K_Z and A, while for high values of K_Z and A the TP dominates. Our model results hence predict that the occurrence of coexistence of IC and TP is reduced when size-structure is taken into account, compared to predictions of unstructured and stage-structured models of intraguild predation (Holt and Polis (1997); Diehl and Feißel (2000); Mylius et al. (2001)).

Figure 5.2 shows the population dynamics of TP and IC when an invasion of the TP into a resident IC population occurs, for fixed values of A and K_Z above the TP invasion boundary. For reference the IC population dynamics prior to the TP invasion are shown as well. We have found that the dynamics presented in Figure 5.2 is representative for all parameter combinations for which TP can invade a resident IC population and drive it to extinction. Figure 5.2 shows that two distinct phases can be distinguished in the TP invasion dynamics. In the initial phase (phase 1) the dynamics of both IC and the shared resource remain by and large the same as before TP invasion, while the density of TP steadily increases. The rate of increase of the TP population and hence the duration of phase 1 depends on the parameter values: for parameter combinations close to the TP invasion boundary the initial phase can last up to several hundred years. The second phase (phase 2) of the invasion dynamics is invariably short, lasting up to 10 years, irrespective of the parameters. This second phase is characterized by a very rapid increase of TP densities, an increase in IC reproduction, declining numbers of IC with age 1+ and large fluctuations in resource density. The increase in IC newborns produced increases their competition for shared resource in the beginning of the growing season and causes a depletion of resource just after reproduction. However, due to predation mortality the density of YOY IC rapidly decreases during their initial year, allowing the resource density to recover quickly. The increase in resource densities in the second half of the growing season benefits the fecundity of IC with age 1+ to such an extent that it more than compensates for the decrease in density of these older individuals. Thus, the total reproduction of the IC population increases.

The mechanism behind the exclusion of the IC by the TP and hence the lack of coexistence is revealed in Figure 5.3 and Figure 5.4. Figure 5.3 (left panel) shows that during phase 2 of the invasion, the length-age relationship of TP changes substantially (compare the curves for $t = 82$ and $t = 65$), whereas it is not changing as much during phase 1 (compare the curves for $t = 65$ and $t = 12$). The body size of TP-individuals up to three years old increases, while the size of older individuals decreases. The increase in resource density during the second half of the growth season benefits especially small TP, rather than large TP (Figure 5.2). After the IC exclusion TP grow rapidly in their first 2 years, after which growth slows down considerably ($t = 87$). Figure 5.3 (right panel) shows that while the amount of IC biomass consumed yearly by the total TP population increases, this is mainly due to an increase in consumption by one year old TP. The proportion IC biomass consumed by one year old TP increases from initially 20% upto 80% just before IC extinction (Figure 5.3 bottom right panel). The increase results from the positive effect that predation of one year old TP on newborn IC have on the size, and with that the attack rate, of the next cohort of one year old TP. This positive feedback from predation by one year old TP to the predation by the next one year old TP cohort

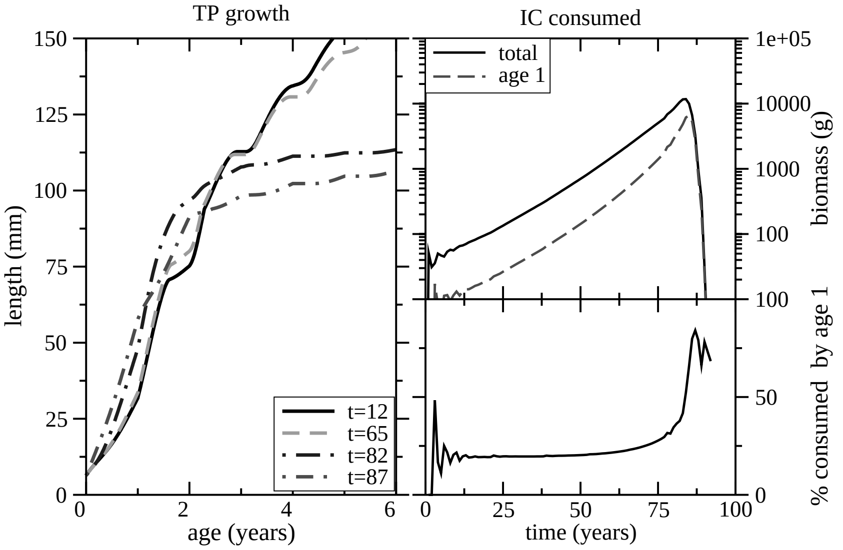

Figure 5.3: Left panel: length-age relationships for TP cohorts born at different times during the TP invasion (Figure 5.2). Right top panel: yearly IC biomass consumed by the total TP population (solid line) and the one year old TP individuals. Right bottom panel: percentage IC biomass eaten by one year old TP.

operates via the increased resource density and drives the IC population extinct.

The increase in resource density does not only result in increased growth rates of YOY TP but also in increased growth rates of YOY IC. If the latter grow fast, they could in principle outgrow their one year old predators and escape from their predation. Figure 5.4 depicts the tent-like function of the predation attack rate (see Appendix: Size-structured Model for equations, Table 5.2) as a function of prey and predator length. Plotted on this function are two trajectories showing the dynamics of the lengths of one year old TP, their YOY IC prey and the realized piscivorous attack rate. These trajectories represent the dynamics in two years during the invasion dynamics exemplified in Figure 5.2. The first trajectory (triangles up) represents the dynamics in phase 1 of the invasion, preceding the major change in the length-age relationship of the TP (t = 12 years). Throughout the year the length-ratio between YOY IC and YOY TP is such that the attack rate is on the down-sloping part of the tent function. The attack rate declines during the year as the YOY IC grow, and they escape predation by one year old TP around day 52. The second trajectory (triangles down, t = 82 years) shows the corresponding dynamics just before IC extinction. The size of one year old TP at the start of the growing season is larger and the length ratio of IC and TP is now such that the attack rate is on the increasing slope of the attack rate function. The attack rate on YOY IC is therefore not only higher due to the increased size of one year old TP, but it also increases at the start of the year. In

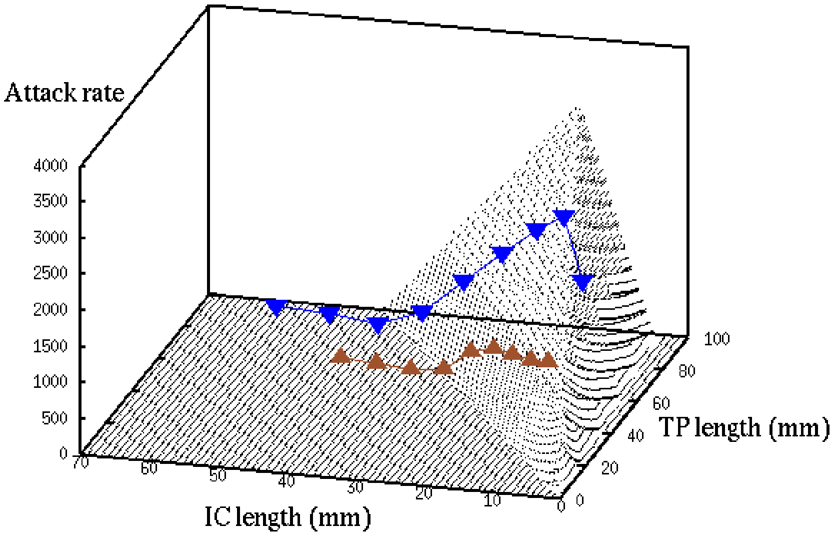

Figure 5.4: The predation attack rate as a function of prey and predator length (tent shaped function), and trajectories of the length of IC young of the year, TP one year old and the realized attack rate, in two particular years during the invasion dynamics (Figure 5.2). Symbols are plotted on every tenth day. The trajectories correspond to $t = 12$ years (triangles up) and $t = 82$ years (triangles down) in Figure 5.2.

absolute sense the attack rate of one year old TP on YOY IC is twice as high at the end of phase 2 than during phase 1 of the invasion dynamics. This doubling of attack rate results from the increase in resource density, which at the end of the growing season is almost three times as high at the end of phase 2 than during phase 1. The higher attack rate implies exposure to more intense predation for YOY IC, which translates into higher resource densities and more rapid growth of the survivors. They escape from predation by one year old TP around day 56. During phase 2 of the invasion the YOY IC thus grow more rapidly and reach larger body sizes at the end of their first year than previous cohorts did. However, the consequent gain in size at age 1 of predators not only increases the rate with which they can attack the next cohort of newborn consumers, but also increases the range of consumer sizes they can forage on. Together these factors result in IC exclusion.

We hence predict that life history omnivory reduces the possibility of coexistence because it enables a positive feedback between foraging success on different resources. To assess the robustness of this prediction we provide 3 lines of evidence. First, we studied the invasion of a TP population into a resident IC population with identical parameter values as used for the invasion shown in Figure 5.2, but in which we assumed a fixed length-age

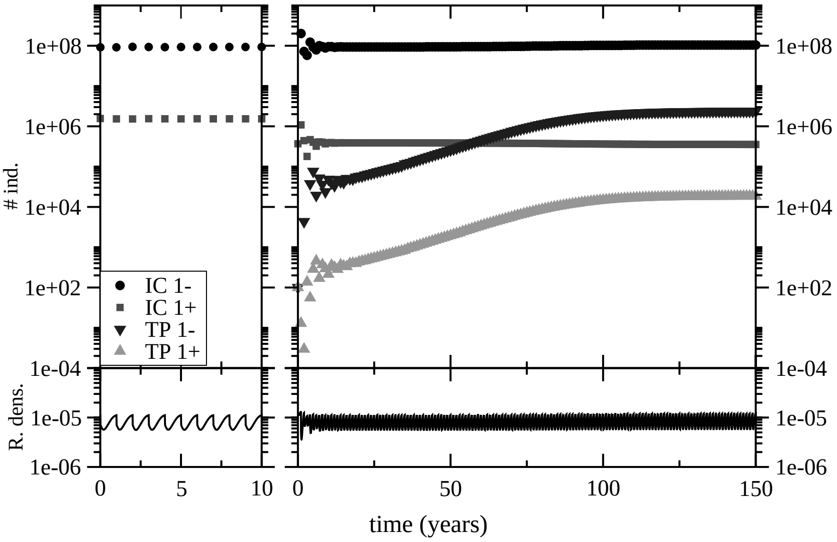

Figure 5.5: As Figure 5.2, but now using a fixed length-age relationship for the TP. The fixed length-age relationship assumed equals the relationship at $t = 12$ shown in Figure 5.3, left panel.

relationship of the TP. The fixed length-age relationship is taken identical from to one at the start of TP invasion (Figure 5.3, $t = 12$). Figure 5.5 shows that enforcing such a fixed length-age relationship resulted in coexistence of TP and IC, because it prevented the positive feedback of foraging success on the shared resource and predation ability as one year old TP. Second, we reanalyzed the unstructured intraguild predation model studied by Mylius et al. (2001) (see Appendix: Unstructured Model for equations). In Figure 5.6 (top panel) we show which equilibria are possible for different values of the predator maximum attack rate on the consumer (a_{cp}) and the shared resource carrying capacity (K_Z)(cf Figure 5.1). Identical to the results of Mylius et al. (2001) we find for low values of K_Z and a_{cp} an C equilibrium while for high values of K_Z and a_{cp} we find a P equilibrium. These two regions are separated by a coexistence equilibrium and a region with bistability between a coexistence equilibrium and a P equilibrium. The results of the size-structured model show a doubling of the attack rate of one year old TP on YOY IC just before IC extinction. Figure 5.6 (top panel) makes clear that for a large range of K_Z values a doubling of a particular value of the maximum attack rate a_{cp}, for which C and P coexistence can occur, would yield a value for which the C population is predicted to go extinct. Third, we phenomenologically incorporated the positive correlation between foraging success on the shared resource and C predation into the unstructured model by assuming that the maximum attack rate of P on C increases with the resource density relative to the resource density for which a consumer equilibrium is present: $\alpha = a_{cp}(1 + Z - Z_C)$, where

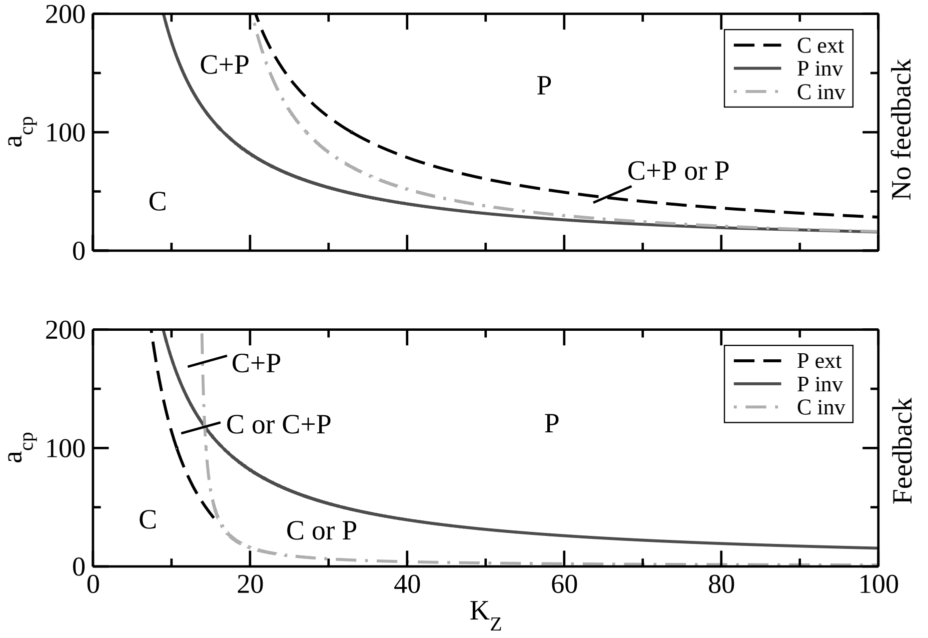

Figure 5.6: Possible equilibria for different values of the maximum ingestion rate of P on C (a_{cp} ($Ld^{-1}ind_P^{-1}$)) and the resource carrying capacity (K_Z ($ind_Z L^{-1}$)) in the unstructured IGP model of Mylius et al. (2001). Top panel: the thresholds below and above which C and P, respectively, can invade the other species' equilibrium. The dashed line delineates the threshold above which the C goes extinct. Bottom panel: similar to the top panel, but now using a maximum ingestion rate of P on C that scales with shared resource density following $\alpha = a_{cp}(1 + Z - Z_C)$. Note that the C extinction threshold no longer occurs, but that there is now a P extinction threshold present.

α is the maximum attack rate and Z_C represents the resource density for the consumer equilibrium. In Figure 5.6, bottom panel, the effect of this resource dependence in the predator attack rate on the occurrence of the different equilibria is shown. Notice that the model of Mylius et al. (2001) predicts that the value of Z in an equilibrium with only C is in the order of 1 (measured in individuals per liter), such that a doubling of resource density implies roughly a doubling of the maximum attack rate of P on C. Compared to the model results without the feedback (Figure 5.6 top panel), the region with a P equilibrium has increased, while the region with a C equilibrium has decreased. The bistable region with either coexistence or a P equilibrium is no longer present, instead bistability occurs between coexistence and a consumer equilibrium. Overall, the occurrence of coexistence has decreased. We also incorporated the positive feedback into the (predator) stage-structured model studied by Mylius et al. (2001), which also resulted in a reduction of the occurrence of coexistence (results not shown). Together, these three different lines of evidence demonstrate the generality of our prediction that a positive feedback between food-dependent growth and size-dependent predation demotes coexistence of the IC and TP.

Including the exclusive TP resource

Naturally, the presence of an exclusive resource allows TP to persist for lower values of A and K_Z (Figure 5.7 top panel), when not exposed to competition with the IC. Hence, the persistence threshold of a single TP population intersects the persistence threshold of a single IC population at a lower value of A, compared to the case without the exclusive resource (Figure 5.1 top panel). Likewise, for the pure competition case the boundary delineating the parameter range for which the TP can successfully invade a resident IC population shifted towards lower values of A. As a consequence, the TP invasion boundary ends up to the left of the IC invasion boundary, and coexistence is possible. The exclusive resource allows the TP to compensate for the disadvantage it has competing with IC for the shared resource. For low values of A an IC-only equilibrium is the only possible outcome of the species interaction, while for high values of A TP dominates.

When accounting for predation by TP on IC the presence of an exclusive TP resource results in the occurrence of some new type of equilibria (Figure 5.7 bottom panel) in addition to the types of equilibria found in the absence of an exclusive TP resource (Figure 5.1 bottom panel). Similar to the results presented above, an IC-only equilibrium and a TP-only equilibrium occur for low and high values of K_Z and A, respectively. Stable coexistence of IC and TP is possible and the only outcome of the species interaction for a small set of parameter values ($8.3 \cdot 10^{-6} < K_Z < 1.3 \cdot 10^{-4}$ and $3.0 \cdot 10^{4} < A < 3.6 \cdot 10^{4}$). Compared to the case without an exclusive resource the parameter range with mutual non-invasibility has decreased. Instead, for a range of parameter values, a TP-only equilibrium exists next to a coexistence equilibrium (Figure 5.7 bottom panel, region TP or IC-TP). Nonetheless, compared to the pure competition case, predation of TP on IC reduces the parameter range with a coexistence equilibrium. The boundary separating the areas for which the IC can or cannot invade a resident TP population is shifted to lower values of A and K_Z more than the boundary delineating the parameter range for which TP can invade a resident IC population. The differential effect that TP predation on IC has on these two boundaries is due to changes in the TP population size-structure. These changes are such that the IC faces severe predation of a stunted TP population when invading a TP-only equilibrium, whereas the TP population is not stunted when it invades a resident

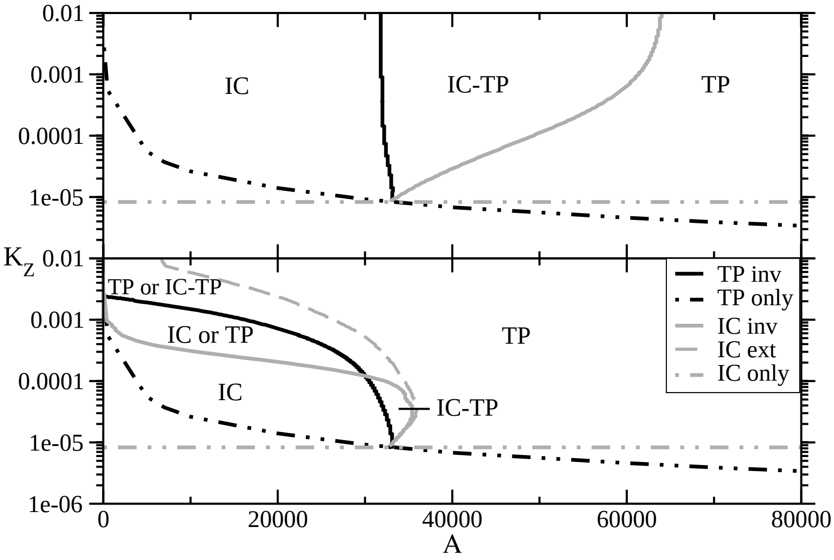

Figure 5.7: Invasion (solid lines) and extinction (dashed lines) thresholds of the top predator (TP invasion possible above the threshold)(dark) and the intermediate consumer (IC invasion below the threshold)(light) without (top graph) and with piscivory (bottom graph) as a function of the maximum attack rate of TP on the shared resource (A) and the carrying capacity of the shared resource (K_Z). The dashed line represents the extinction boundary of the IC above which coexistence is no longer possible. Dashed-dotted lines delineate the single-population extinction thresholds below which a population cannot exist. The exclusive resource for TP is available for consumption, $K_M = 1gm^{-2}$.

IC population. We will discuss the size-structure of IC and TP elsewhere in more detail (this thesis Chapter 6).

Finally, when the TP does not forage on the shared resource, $A = 0.0$, a single TP population cannot exist on its own since we set the carrying capacity of the exclusive resource to a value too low for population persistence. In this case coexistence of the TP and the IC is possible and the only outcome of the interaction when the carrying capacity of the shared resource is above a threshold value such that the IC density is sufficient to allow TP persistence on a mixed diet of exclusive resource and the IC ($A = 0.0$ and K_Z is high, not visible in Figure 5.7).

5.4 Discussion

Through the segregation in time of the competitive and predatory interaction between TP and IC, life history omnivory allows for a positive feedback between performance during a juvenile predator phase with resource competition and performance during a later phase where predation by TP in IC occurs. When TP do well in competition for the shared resource at an early life stage, they might perform better as a predator later on (Persson (1988)). We have shown that, for all parameters we investigated, such a positive feedback between the competitive and predatory capabilities of the TP reduces coexistence of IC and TP, especially in a system where a single resource is available for IC and TP. However, the feedback also reduces the possibility for coexistence when an exclusive resource for the TP present. In our model the positive feedback between competition and predation is mediated by food dependent growth during early ontogeny and size-dependent predation performance later on, and works over consecutive generations. The intraguild predation models studied earlier have only accounted for life history omnivory to a limited extent. The stage-structured IGP-models analyzed by Mylius et al. (2001) did segregate the competition and predation aspect of the IGP interaction over the TP life history, but the predation capacity of an adult was independent of its performance as a juvenile. Hence, Mylius et al. (2001) found that the predictions of a stage-structured IGP-model were not significantly different from those without stage-structure. However, Mylius et al. (2001) did hint at the negative effect of a resource-dependent maturation rate on coexistence: 'A resource-dependent maturation rate, . . . , shows a smaller productivity window for the consumer-predator equilibrium, if the latter exists at all'. We showed that incorporating the feedback-loop between the performance on one resource and a second resource into the unstructured model of Mylius et al. (2001) had a similar detrimental effect on coexistence of predator and prey. These results demonstrate the robustness of our prediction that life history omnivory demotes coexistence between predator and prey.

During the process of IC exclusion, an 'arms-race' occurs between newborn consumers and one year old predators. Due to a release in resource density and food dependent growth, growth rates of YOY IC and YOY TP increase with increasing predation mortality. The interaction between growing prey and predators has been discussed by Wilbur (1988) and Rice et al. (1997). Unfortunately, these studies do not present any empirical data, that would allow a comparison with our model results, on the dynamics of the size-dependent interaction between predators and consumers within a growing season (but see Wilbur (1988) for a theoretical example), even though it is recognized that the interaction changes within this period (Rice et al. (1993); Brabrand (2001)). As shown in our study, the within-season dynamics of the predation rate of growing predators on their growing prey may have significant consequences for community structure.

Walters and Kitchell (2001) proposed that a 'cultivation-depensation' mechanism might be crucial for the persistence of species exhibiting life history omnivory, and especially for species exhibiting a niche shift between a resource feeding stage and a predatory stage. Adult predators may 'cultivate' their own offspring by predating on, and hence cropping down, species that potentially compete for the same resource as juvenile predators. On the other hand, such predatory species may exhibit reduced growth rates at low densities ('depensation') when the number of adult predators is not sufficient to crop down a consumer species. Concerning the system studied in this paper, the 'cultivation-depensation' hypothesis would predict a consumer-only equilibrium, when the consumer population can monopolize the shared resource, next to a coexistence equilibrium in which the consumer population is cropped down sufficiently by adult predators. In the case with only a shared resource present, we find that the cropping of the consumer population by predators does not lead to coexistence, but to the extinction of the IC. This result depends, however, on the model assumption that TP individuals can reach maturation while feeding on the shared resource alone, such that the IC is not a necessary food source for TP persistence. Clearly when adult TP can only forage on the IC and not on basic resources, TP persistence is only feasible in coexistence with the IC.

Optimal foraging has been shown to enhance persistence in an intraguild predation system in case foraging on one resource excludes foraging on the other (Krivan (2000)). However, when optimal foraging concerns adaptive omnivory, *i.e.* when predators only feed on the less profitable prey if the profitable prey is rare, the effect is less (Krivan and Diehl (2005)). Interestingly, Krivan and Diehl (2005) find that adaptive omnivory does not promote IC persistence, but promotes TP persistence into to the region where the IC would dominate otherwise. In our study we find similar results when comparing the intraguild predation system with and without the exclusive resource for the predator. For $A < 3.0{\cdot}10^4$ the IC invasion threshold has not changed much compared to when the exclusive TP resource is present, but the TP invasion threshold has shifted downwards considerably, resulting in coexistence. Apparent competition between the exclusive resource and the IC is a possible explanation for the increase of the TP domain, especially for $A > 3.0 \cdot 10^4$ where the TP can endure lower values of shared resource carrying capacity. If apparent competition would play an important role we would expect the IC invasion threshold for $A < 3.0 \cdot 10^4$ to shift downwards due to an increase in predation mortality. An other possible explanation is that the TP is less dependent on the shared resource with the exclusive resource present, which weakens the competitive dominance of the IC. The reduced IC dominance would then allow for establishment of the predator under conditions for which it would be outcompeted in the absence of the exclusive resource. Given that the IC invasion threshold for $A < 3.0 \cdot 10^4$ is hardly changing due to the presence of an exclusive TP resource, we speculate that reduced IC dominance is a more important factor in the increased TP persistence than apparent competition.

While in this study only an exclusive resource for the top predator was considered, the intermediate consumer can also have an exclusive resource. Mylius et al. (2001) argue that an exclusive resource for the consumer would not promote coexistence since the consumer's functional response is already close to a maximum when they are close to extinction at high productivity levels. We hypothesize that the effect of an exclusive consumer resource on coexistence may not be as straightforward as suggested by Mylius et al. (2001). Following McCann et al. (1998) we argue that an exclusive IC resource may promote coexistence as it reduces the efficiency with which the consumer attacks the shared resource. However, when the addition of an exclusive resource for the consumer leads to an increase in the number of consumers, the density of the shared resource will be depressed even more, promoting consumer dominance and prohibiting coexistence.

Intraguild predation has been claimed to be the simplest form of omnivory. Modeling studies have led to the hypothesis that omnivory should be rare in natural systems (Pimm and Lawton (1977, 1978); Holt and Polis (1997); Diehl and Feißel (2000)) as it is detrimental to community stability. In contrast to these unstructured models, Pimm and Rice (1987) studied the influence of life history omnivory on community stability and concluded that its effect on community stability is less detrimental than when omnivores feed simultaneously on different food sources, an effect which was reduced when food dependent development and reproduction were included in the model. These findings corroborate with the results from Mylius et al. (2001), who found that consumer presence was possible for higher productivity levels when an invulnerable stage was introduced for the consumer as well as when a non-predatory stage was introduced for the predator. Our results contrast with these two studies as we find that life history omnivory is detrimental to community complexity. This contrast may result from the fact that we explicitly model food dependent development and size-dependent foraging capacities for both consumer and predator. Hence, the interaction between growing consumers and growing predators is incorporated in the model, the mechanism which is eventually responsible for the lack of coexistence.

Our size-structured model accounts explicitly and in detail for life history omnivory in a way that is based on field and experimental data of the species involved (e.g. Persson and Greenberg (1990a); Persson et al. (1996); Holt and Polis (1997); Byström et al. (1998)). Its analysis allowed us to disclose the precise mechanism that is fundamental to the interaction between the growing prey and predators in the model. This mechanistic understanding of the exclusion dynamics of the IC by the TP we subsequently exploited to incorporate a phenomenological representation of the mechanism in a simpler, unstructured model. The latter model showed comparable behavior, demonstrating the robustness of our conclusion that life history omnivory demotes coexistence. These steps in our opinion illustrate the usefulness and functionality of detailed, size-structured models of a particular ecological system. Their analysis allows us to identify the relative importance for the system's dynamics of the various mechanisms that operate during an individual life history. Once a particular mechanism has been identified as having a major influence compared to other model aspects, an unstructured model incorporating this mechanism may provide insight about the way it changes systems dynamics. More specifically, the unstructured model we studied allowed us to assess how a positive correlation between foraging success on the shared resource and predation capacity influences population dynamics, but in contrast to the size-structured model it does not reveal whether the positive correlation will arise in the first place.

5.5 Acknowledgements

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5.6 Appendix: Model Descriptions

Size-structured Model

The model studied here describes the interactions between a size-structured consumer population, a size-structured predator population and two non-structured resource populations, extending and combining the single species models described by Persson et al. (1998) and Claessen et al. (2000). The size-structured population model used in this study has two levels of organization, the individual state and the population state. The population state represents the frequency distribution of all individual states. Its dynamics are described by ordinary differential equations for the abundances and physiological traits of individuals in the cohorts that make up the populations (Persson et al. (1998); de Roos and Persson (2001). As the number of cohorts in the population varies over time, so does the number of ODE's describing the population dynamics. This two-level modeling approach ensures that results on the population level are emergent properties of modeling the individual states.

The physiological characteristics of an individual are determined by the size of that individual. Total individual body mass is assumed to consist of structural mass and reserves. Structural mass uniquely determines length via an allometric relationship (Table 5.2 Eq. 1). The individual model that makes op the core of the size-structured population model combines and extends the models formulated by Persson et al. (1998) and Claessen et al. (2000). Foraging of both TP and IC follows Holling type II functional responses, in which handling time and resource specific attack rates depend on individual size. The attack rate on the shared resource (zooplankton) for both TP and IC is described by a hump-shaped function (Table 5.2 Eq. 2, see Persson et al. (1998) for justification and generality of this hump-shaped function). The TP attack rate on its exclusive resource (macroinvertebrates) is described by a power function of individual size (Table 5.2 Eq. 3)(de Roos et al. (2002); Persson et al. (2004)). The attack rate for TP on IC is a function of both predator and victim length (Claessen et al. (2000)). For optimally sized victims the predator attack rate increases with predator length following an allometric function. This maximum attack rate is adjusted for non-optimally sized prey using a tent-like function of the ratio between victim and predator length (see Claessen et al. (2000) for its derivation and empirical support). The upper limit of the victim-predator length ratio for which a predator can successfully attack its victim, ϵ, represents the catchability of prey, narrowing the size range of prey to individuals smaller than the predator itself. The lower limit δ delineates the detectability of the prey by a certain sized predator (Table 5.1).

Table 5.1: Model parameters for roach (*Rutilus rutilus*)(de Roos and Persson (2001); Hjelm and Persson (2001)) and Eurasian perch (*Perca fluviatilis*)(Claessen et al. (2000); Persson et al. (2003, 2004)) foraging on zooplankton (*Daphnia* sp. 1mm) and macroinvertebrates (*Cloeon*).

Symbol	**Value**		**Unit**	**Interpretation**
	Roach	***Perch***		
μ_b	0.01	0.01	d^{-1}	background mortality rate
μ_0	0.034	0.034	d^{-1}	scaling const. size-dep. mort. rate
x_μ	0.5	0.5	g	shape param. in size-dep. mort. rate
x_m	5.0	4.6	g	irreversible mass at maturation
w_b	0.0014	0.0018	g	total mass of a neonate
q_j	0.74	0.74	-	juvenile y/x mass ratio
q_a	1.0	1.37	-	adult y/x mass ratio
q_s	0.2	0.2	-	starvation threshold
s	0.2	0.2	d^{-1}	starvation coefficient
k_r	0.5	0.5	-	gonad egg conversion
λ_1	58.9	57.7	mm $g^{-\lambda_2}$	length allometric constant
λ_2	0.29	0.32	-	length allometric exponent
A	1.5E+5	varied	L/d	maximum attack rate on zoopl.
α	0.5	0.62	-	allometric exp. zoopl. attack rate
x_{opt}	28.7	4.7	g	optimum consumption size zoopl.
ξ_1	3.8	3.2	$d/g^{(1+\xi_2)}$	handling time allometric constant
ξ_2	-0.81	-0.8	-	handling time allometric exponent
ρ_1	0.022	0.022	$g^{(1-\rho_2)}/d$	maintenance allometric constant
ρ_2	0.77	0.77	-	maintenance allometric exponent
k_e	0.61	0.61	-	food conversion efficiency
ν_1		0.12	$m^2\ d^{-1}g^{-\nu_2}$	all. const. macro-inv. attack rate
ν_2		0.4	-	all. exp. macro-inv. attack rate
β		2.0E+2	$Ld^{-1}mm^{-\sigma}$	piscivory all. constant
σ		0.6	-	piscivory all. exponent
δ		0.05	-	minimum prey/predator ratio
ϵ		0.45	-	maximum prey/predator ratio

Table 5.1 – Continued

Symbol	Value		Unit	Interpretation
	Roach	***Perch***		
φ		0.16	-	optimum prey/predator ratio
Zooplankton				
r_Z	0.1		d^{-1}	regrowth rate zooplankton
K_Z	varied		g/L	carrying capacity zooplankton
Macro-inv.				
r_M	0.1		d^{-1}	regrowth rate macro-inv.
K_M	1.0		g/m^2	carrying capacity macro-inv.
Environment				
V	1.0E+9		L	lake volume
B	5.0E+4		m^2	lake bottom surface
Y	90		d	duration of growing season

The total food encounter rate is used in the functional response to determine food intake (Table 5.2 Eq. 5). All resources are assumed to be equally digestible and the intake is assumed to be limited by the digestion capacity of an individual which is an allometric function of its size (Table 5.2 Eq. 6)(Claessen et al. (2000)). The consumed food is converted into energy with a constant conversion efficiency, after which maintenance costs are subtracted. The remaining net energy is used for growth and allocated to structural or irreversible mass (x), and reserves or reversible mass (y), with a ratio that depends on the condition of the individual (Table 5.2 Eq. 10). Adults allocate more energy to reserves than juveniles targeting for an optimal ratio $y/x = q_a$. This additional energy is reserved as gonad mass and converted into offspring at the beginning of a new year, making reproduction a discrete event. As a consequence of pulsed reproduction all newborns are born at the same time, with identical but species specific body mass, making a population consist of discrete cohorts.

Individuals that have a condition (*i.e.* reserves-structural mass ratio) below the threshold value q_s suffer from starvation mortality μ_s, which increases with decreasing condition. The starvation mortality function μ_s is such that individuals die with certainty when reserves are depleted (Table 5.2 Eq. 12). All individuals suffer from a size-dependent background mortality, which represents a chance to die of causes other than starvation or predation. Small individuals have a bigger chance to die than large individuals, *e.g.* predation mortality caused by insects larvae or birds, hence mortality decreases with increasing size (Table 5.2 Eq. 11). The size-dependent background mortality does not include predation mortality inflicted by the TP on the IC. IC mortality due to predation is a function of the density and the functional response of all TP cohorts (Table 5.2 Eq. 13).

Both resources are modeled as unstructured populations and follow semi-chemostat dynamics (Persson et al. (1998); Claessen et al. (2000); de Roos et al. (2002)). The shared resource is measured in densities per volume, since zooplankton is present in the water column. Macro-invertebrates occur on the lake bottom and are therefore measured as density per square meter. The IC and the TP are measured in absolute numbers of individuals in the entire lake (volume 10^9 L).

Table 5.2: Model equations, describing the individual-level, life-history model of roach and perch and the dynamics of the two unstructured resource populations. The variables c and v refer to the length of the piscivore predator and its victim, respectivily. The indices i and j refer to cohorts of perch and roach, respectivily. These cohorts consist of N_i (N_j) individuals with structural mass x_i (x_j) and reserves y_i (y_j), and hence a body length equal to $c_i = l(x_i)$ ($v_j = l(x_j)$).

Subject	**Equation**		**Eq. nr**
	Roach	***Perch***	
Length-structural mass	$l(x) = \lambda_1 x^{\lambda_2}$	$l(x) = \lambda_1 x^{\lambda_2}$	1
Zooplankton attack rate	$a_Z(x) = A(\frac{x}{x_{opt}} exp(1 - x/x_{opt}))^{\alpha}$	$a_Z(x) = A(\frac{x}{x_{opt}} exp(1 - x/x_{opt}))^{\alpha}$	2
Macroinv. attack rate		$a_M(x) = \nu_1 x^{\nu_2}$	3
Piscivorous attack rate		$a_P(c, v) = \begin{cases} \beta c^{\sigma} \frac{v - \delta c}{(\varphi - \delta) c} & \text{if } \delta c < v \leq \varphi c \\ \beta c^{\sigma} \frac{\epsilon c - v}{(\epsilon - \varphi) c} & \text{if } \varphi c < v \leq \epsilon c \\ 0 & \text{otherwise} \end{cases}$	4
Total encounter food rate	$\gamma_T(x) = a_Z(x) Z$	$\gamma_T(x_i) = a_Z(x_i) Z + a_M(x_i) M$ $+ \sum_j a_P(l(x_i), v_j)(x_j + y_j) N_j$	5
Handling time	$h(x) = \xi_1 x^{\xi_2}$	$h(x) = \xi_1 x^{\xi_2}$	6
Maintenance	$E_m(x, y) = \rho_1 (x + y)^{\rho_2}$	$E_m(x, y) = \rho_1 (x + y)^{\rho_2}$	7
Energy assimilation	$E_a(x) = k_e (\frac{\gamma_T(x)}{1 + h(x) \gamma_T(x)})$	$E_a(x) = k_e \frac{\gamma_T(x)}{1 + h(x) \gamma_T(x)}$	8
Net energy	$E_n(x, y) = E_a(x) - E_m(x, y)$	$E_n(x, y) = E_a(x) - E_m(x, y)$	9

Table 5.2 – Continued

Subject	**Equation**		**Eq. nr.**
	Roach	***Perch***	
Energy all. to x	$\kappa(x,y) = \begin{cases} \frac{1}{(1+q_j)q_j}\frac{y}{x} & \text{if } x \leq x_m \\ \frac{1}{(1+q_a)q_a}\frac{y}{x} & \text{if } x > x_m \end{cases}$	$\kappa(x,y) = \begin{cases} \frac{1}{(1+q_j)q_j}\frac{y}{x} & \text{if } x \leq x_m \\ \frac{1}{(1+q_a)q_a}\frac{y}{x} & \text{if } x > x_m \end{cases}$	10
Size dep. backgr. mort.	$\mu(x) = \mu_0^{(-\frac{x}{x_\mu})} + \mu_b$	$\mu(x) = \mu_0^{(-\frac{x}{x_\mu})} + \mu_b$	11
Starvation mortality	$\mu_s(x) = \begin{cases} s(x/y-1) & \text{if } y < q_s x \\ 0 & \text{otherwise} \end{cases}$	$\mu_s(x) = \begin{cases} s(x/y-1) & \text{if } y < q_s x \\ 0 & \text{otherwise} \end{cases}$	12
Piscivorous mortality	$\mu_p(x_j) = \sum_i \frac{a_P(c_i,l(x_j))N_i}{1+h(x_i)\gamma_T(x_i)}$		13
Total mortality	$\mu_T(x) = \mu(x) + \mu_s(x) + \mu_p(x)$	$\mu_T(x) = \mu(x) + \mu_s(x)$	14
Fecundity	$f(x,y) = \begin{cases} \frac{k_r(y-q_j x)}{w_b} & \text{if } x > x_m \text{ and } y > q_j x \\ 0 & \text{otherwise} \end{cases}$	$f(x,y) = \begin{cases} \frac{k_r(y-q_j x)}{w_b} & \text{if } x > x_m \text{ and } y > q_j x \\ 0 & \text{otherwise} \end{cases}$	15
Zooplankton dynamics	$\frac{dZ}{dt} = r_Z(K_Z - Z) - \frac{Z}{V}\sum_j \frac{a_Z(x_j)N_j}{1+h(x_j)\gamma_T(x_j)} - \frac{Z}{V}\sum_i \frac{a_Z(x_i)N_i}{1+h(x_i)\gamma_T(x_i)}$		16
Macroinvertebrate dynamics	$\frac{dM}{dt} = r_M(K_M - M) - \frac{M}{B}\sum_i \frac{a_M(x_i)N_i}{1+h(x_i)\gamma_T(x_i)}$		17

Invasion and Extinction

To locate the invasion thresholds of the species, long numerical integrations were carried out during which one of the system parameters, from here on referred to as bifurcation parameter, was increased in small steps at regular intervals. After a change in the bifurcation parameter transient dynamics in the resident system were first allowed to dissipate during a fixed period of time (x years). At the end of this period 10 newborn individuals of the invading species were introduced on the first day of each year for 10 consecutive years. With this repeated introduction any influence of cyclic behavior of the resident population is circumvented. An invasion is considered successful if the population growth of the invader, considered over a 30 year interval, is significantly positive, and hence the following condition holds:

$$\frac{1}{20} \cdot \ln \frac{N_{20}}{N_0} > 0.0001 \tag{5.1}$$

Here, N_0 represents the total number of invaders 10 years after the last invasion event. This choice of N_0 aims at providing an unbiased estimate of the initial number of invaders and hence of the population growth rate. N_{20} is the total number of invaders 20 years later. The numerical integration was stopped at the first parameter value for which invasion was found to be successful according to the criterion above. The parameter combination found provided one point of the invasion boundary. Following this method a two parameter plane was scanned to reconstruct the invasion boundary as a function of two system parameters. The determination of the extinction thresholds of a population within the parameter space was carried out in a similar manner as the invasion thresholds, except for that the starting situation was now a system in which a particular population is present, as opposed to a system in which it has to invade. A population is considered extinct when the number of individuals drops below 1. Both the extinction thresholds of a population in absence of the other species, and the extinction thresholds of a population while coexisting with the other species where determined.

Unstructured Model

We adapted the model of Mylius et al. (2001) to assess the robustness of our claim that life history omnivory demotes coexistence through the correlation between foraging success on the shared resource and predation. These authors use a system of three ordinary differential equations to describe the dynamics of a predator (P), a consumer (C) and their shared resource (Z). Foraging of the predator and the consumer follows a Holling type II functional response. The parameter values are based on predator individuals with a body mass of $184g$ (perch), consumer individuals with a body mass of $3g$ (roach), and zooplankton of $0.5mm$, and are listed in Table 5.5, for more details we refer to Mylius et al. (2001). Here we will only show the equations we used for which dependence of the ingestion rate of P on C on the shared resource density (Z) was incorporated into the original model:

$$\frac{dP}{dt} = \frac{e_{zp}a_{zp}Z + e_{cp}\alpha C}{1 + h_{zp}a_{zp}Z + h_{cp}\alpha C}P - \mu_p P \tag{5.2}$$

$$\frac{dC}{dt} = \frac{e_{zc}a_{zc}Z}{1 + h_{zc}a_{zc}Z}C - \frac{\alpha C}{1 + h_{zp}a_{zp}Z + h_{cp}\alpha C}P - \mu_c C \tag{5.3}$$

$$\frac{dZ}{dt} = \rho(K_Z - Z) - \frac{a_{zc}Z}{1 + h_{zc}a_{zc}Z}C - \frac{a_{zp}Z}{1 + h_{zp}a_{zp}Z + h_{cp}\alpha C}P \tag{5.4}$$

With:

$$\alpha = a_{cp}(1 + Z - Z_C) \tag{5.5}$$

Z_C is the minimum resource density for which the C equilibrium can exist. The attack rate of P on C depends on the relative value of the resource density. In this manner the positive feedback from foraging on the shared resource on foraging on the C is included phenomenologically. The invasion boundaries of P and C are determined by the zero population growth conditions $\frac{1}{P}\frac{dP}{dt} = 0$ and $\frac{1}{C}\frac{dC}{dt} = 0$, respectively. Mylius et al. (2001) referred to the P and C invasion boundaries and the extinction boundaries as the BP2-, BP3- and LP-curves, respectively (see for example figure 3 in Mylius et al. (2001)).

Table 5.5: Definitions of model variables and parameters for the unstructured model (Mylius et al. (2001))

Symbol	Value	Unit	Description
Predator			
P	-	$ind_p \cdot L^{-1}$	Population density
a_{cp}	varied	$L \cdot d^{-1} \cdot ind_p^{-1}$	Consumer attack rate
h_{cp}	0.11	$d \cdot ind_p \cdot ind_c^{-1}$	Consumer handling time
e_{cp}	0.3	$ind_p \cdot ind_c^{-1}$	Consumer conversion efficiency
a_{zp}	$5E2$	$L \cdot d^{-1} \cdot ind_p^{-1}$	Resource attack rate
h_{zp}	$5E-5$	$d \cdot ind_p \cdot ind_z^{-1}$	Resource handling time
e_{zp}	$1E-5$	$ind_p \cdot ind_z^{-1}$	Resource conversion efficiency
μ_p	0.05	d^{-1}	Natural mortality rate
Consumer			
C	-	$ind_c \cdot L^{-1}$	Population density
a_{zc}	$5E3$	$L \cdot d^{-1} \cdot ind_c^{-1}$	Resource attack rate
h_{zc}	$5E-5$	$d \cdot ind_c \cdot ind_z^{-1}$	Resource handling time
e_{zc}	$1E-5$	$ind_c \cdot ind_z^{-1}$	Resource conversion efficiency
μ_c	0.05	d^{-1}	Natural mortality rate
Resource			
Z	-	$ind_z \cdot L^{-1}$	Population density
ρ	0.5	d^{-1}	Semichemostatic inflow rate
K_Z	varied	$ind_z \cdot L^{-1}$	Stand-alone equilibrium density

Chapter 6

Interspecific competitive bottlenecks in intraguild predation systems - model predictions and field data

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Unpublished manuscript

Abstract

Field observations of aquatic systems show an increasing consumer (vertebrate planktivores) dominance with increasing productivity. This dominance of consumers over predators has been explained by an interspecific juvenile bottleneck that demotes predator recruitment. Often juvenile stages of a predator species compete for resource with their future prey. Simple models on intraguild predation, where consumer and predator have both a competitive and a predator-prey relationship, do not account for juvenile bottlenecks as they model single-stage omnivory. The community pattern found in these models contrasts to field observations, *i.e.* predator dominance is found instead of consumer dominance with increasing productivity. Here, we use a size-structured population model that explicitly models food dependent development and size-dependent foraging capacities of an intermediate consumer and a top predator. The intermediate consumer forages on the shared resource, while the top predator undergoes two ontogenetic niche shifts, from foraging on the shared resource, to foraging on an exclusive resource, to piscivory. When cannibalism for the top predator is included, coexistence of consumer and predator is promoted. Moreover, we find that a juvenile bottleneck emerges from the model results for a large range of productivity levels and also we find an increase in the percentage consumer biomass, as observed in the field. Although a percentage decrease in top predator biomass in relation to consumer biomass is observed, no absolute decrease was observed in the model results.

6.1 Introduction

Predators growing in size during ontogeny often undergo niche shifts towards larger prey to meet the increasing metabolic demand that results from the increase in individual size (Werner and Gilliam (1984); Persson (1988); Byström et al. (1998)). Feeding on different prey types brings about morphological consequences that constrain the predator's foraging ability during ontogeny (Werner and Gilliam (1984); Byström et al. (1998). During early ontogeny predators often compete for the same resource as their future prey whose morphology is usually better adapted to foraging on that resource (Werner and Gilliam (1984); Persson (1988)). Field and laboratory experiments have suggested that interspecific competitive interactions between size-structured populations can induce a juvenile bottleneck for the predator which can have major consequences for the life history and survival of individuals (Neill (1975); Persson and Greenberg (1990b); Byström et al. (1998)). For example, Persson and Greenberg (1990b) showed that a juvenile bottleneck induced by interspecific competition between perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) resulted in an earlier ontogenetic niche shift at a smaller size for perch. Due to the smaller size at which predators started to forage on the second ontogenetic resource, this resource was less profitable, and individuals were hence less able to grow into sizes large enough to predate on the competing prey. Byström et al. (1998) showed that this early niche shift for small perch when competing with roach increased first winter mortality. Thus, a juvenile bottleneck imposed by future prey can have a severe impact on the predator population and on interspecific relationships (Persson and Greenberg (1990b); Byström et al. (1998)).

It has been argued that interspecific juvenile bottlenecks result in an asymmetry in predatory and competitive interactions between competing prey and predators, and that the relative strength of the competitive and predatory interaction, respectively, determines species dominance (Persson (1988)). Furthermore, Persson (1988) discussed how the balance between predator dominance or consumer dominance depends on the productivity of the system. In highly productive lakes, the consumer was argued to dominate the system because of its ability to induce a juvenile bottleneck for the predator. The bottleneck was suggested to affect predator size in a negative manner by reducing the number of individuals that reach sizes allowing for predation on the consumer. In less productive lakes, on the other hand, the juvenile bottleneck for the predator population was not established due to a lower productivity of the resource for which juvenile predators and prey compete. Without the bottleneck, predators could reach sizes that allow predation on the consumer, and therefore the predator dominated the system (Persson (1988)). This community pattern where consumers dominate at higher productivities and predators dominate at lower productivities has been supported in a number of studies on European freshwater lake fish communities (Persson (1983a, 1988); Persson et al. (1991); Persson (1994); Jeppesen et al. (1997)). Jeppesen et al. (1997) most recently did a survey of more than 200 lakes demonstrating that the carnivorous biomass percentage decreases from over 90% to nearly zero of the total fish biomass with increasing productivity, thus supporting the theory on fish communities and the asymmetry in predation and competition introduced by Persson (1988).

Mathematical theory on the type of interaction where an omnivorous predator shares a resource with its consumer prey, which is characteristic for the above systems, are mostly based on unstructured models which do not take life history omnivory into account (Holt and Polis (1997); Diehl and Feißel (2000), but see Mylius et al. (2001) for a stage-structured example). The general outcome of these models is that predator and consumer can only coexist in a narrow range of intermediate productivity levels. For low values of productivity, the consumer dominates because it is a better forager on the shared resource and outcompetes the predator. At high productivity levels the predator excludes the consumer by predation. When predator and consumer do coexist, typically the number of consumers decreases while the number of predators increases with increasing productivity. These model results are thus in sharp contrast to the community patterns observed in the field (Persson et al. (1991); Jeppesen et al. (2000)). Moreover, the juvenile bottleneck supposed to be responsible for the patterns found in natural systems does not occur, even when stage-structure is added to the model (Mylius et al. (2001)).

A possible reason for the discrepancy between model results and field observations may be that the models do not properly incorporate important elements of the size-structured interactions. One such a mechanism lacking in the above models is food dependent development. However, in Chapter 5 (this thesis) we showed that coexistence was reduced to almost zero in a model that included food dependent development. Introducing an exclusive resource for the predator allowed for some coexistence, albeit for a small parameter range. Another interaction generally lacking in the IGP-models is cannibalism, which is common in the empirical systems studied (Persson (1988)). Cannibalism affects population structure and can reduce the number of individuals in the cannibalistic population (Salvanes et al. (2004)). By reducing the number of predators, cannibalism could be a mechanism that promotes coexistence of predator and consumer in an intraguild predation system.

The purpose of our paper was to investigate whether a juvenile bottleneck could emerge as a model result in a model with food dependent development, this in contrast to previous modeling studies of IGP systems. We also asked the question whether a juvenile bottleneck, if it emerges, was sufficient to explain the community patterns observed in the field. To answer these questions, we used the size-structured population model analyzed in Chapter 5 to study the interactions between an omnivorous top predator (TP) and an intermediate consumer (IC). We included (1) an exclusive resource for the predator as it has been shown to promote coexistence and (2) cannibalism since cannibalism is present in the top predator's life history in the studied lake systems. Food dependent development and size-dependent foraging capacities were explicitly modeled for both the IC and the TP. Life history omnivory is hence an implicit result of these two assumptions. The persistence of the top predator and the intermediate consumer was investigated as a function of the carrying capacity of the shared resource, which allows for comparison with other results.

6.2 Model

The model studied here describes the interactions between a size-structured consumer population, a size-structured predator population and two non-structured resource populations, extending and combining the single species models described by Persson et al. (1998) and Claessen et al. (2000). Because this size-structured model cannot be solved analytically, we use the numerical technique developed by de Roos et al. (1992) for simulations. Below we give a general verbal description of the model, for a more detailed description, equations and parameter values we refer to the Appendix. The two species used to parameterize the model are perch (*Perca fluviatilis*) as the top predator (TP) and roach (*Rutilus rutilus*) as intermediate consumer (IC). Roach and perch are commonly found together in freshwater lakes in temperate regions (Persson (1988); Persson et al. (1991)). Perch is an omnivore and undergoes two major ontogenetic niche shifts, shifting from planktivory to benthivory and from benthivory to piscivory (Persson (1983b, 1988);

Persson and Greenberg (1990b); Byström et al. (1998)). Roach is a planktivorous fish that mainly feeds on zooplankton (Persson (1988)). Zooplankton is considered the shared resource and for the parameterization *Daphnia* sp. are used as they are commonly found in roach' and perch' diets (Persson and Greenberg (1990b); Hjelm and Persson (2001)). Mayfly larvae *Cloeon*, which is a macroinvertebrate species commonly found in perch' diet (Persson (1983b); Persson and Greenberg (1990b); Persson et al. (1996)), represent the macro-invertebrates modeled as an exclusive TP-resource. When the exclusive resource is included in the model, the carrying capacity is set to a level at which an individual perch cannot reach maturity when solely feeding on the exclusive resource. With this assumption we want to assure that competition for the shared resource plays a role in the life history of individuals of both species. Both resources are modeled as unstructured populations and follow semi-chemostat dynamics (Persson et al. (1998); Claessen et al. (2000); de Roos et al. (2002)). All parameter values are based on a freshwater lake in central Sweden, with a volume of $10^9 L$ and a littoral bottom surface area of $5.0 \cdot 10^4 m^2$ (Persson et al. (1998); Claessen et al. (2000); de Roos et al. (2002)). Only the growth season is considered, with a duration of 90 days. The rest of the year the lake is assumed to be covered with ice reducing activity to a minimum (Persson et al. (1998)).

Both the TP and the IC reproduce annually in a pulsed event. All individuals of a species that are born at the same time belong to the same cohort, and all individuals within a cohort are identical. As a result, a population consists of different cohorts, and size differences occur between individuals of different cohorts. Individuals are characterized by two measures of body size. The two measures are structural mass and reserves, which sum up to total mass, where structural mass relates to body length following an allometric relationship. Foraging of all individuals follows a Holling type II functional response, and feeding is assumed to be limited by digestive constraints, *i.e.* handling times are identical for different food items but differ for differently sized individuals (Claessen et al. (2000)). The IC is assumed to be the better competitor for the shared resource (Persson (1988)). The attack rate of an individual on its resource depends on its size, while the attack rate of a top predator on an intermediate consumer depends on the length of both predator and prey. The predation attack rate has a tent-like shape which is based on the assumption that the attack rate is bounded by a minimum, an optimum and a maximum ratio of prey and predator length, due to physiological constraints (*e.g.* gape size)(Claessen et al. (2000)).

The life history of an individual, which is made up by all events and processes occurring during an individual's life, is modeled using a dynamic energy budget model that describes the rate at which individuals acquire energy and how that energy is divided between main-

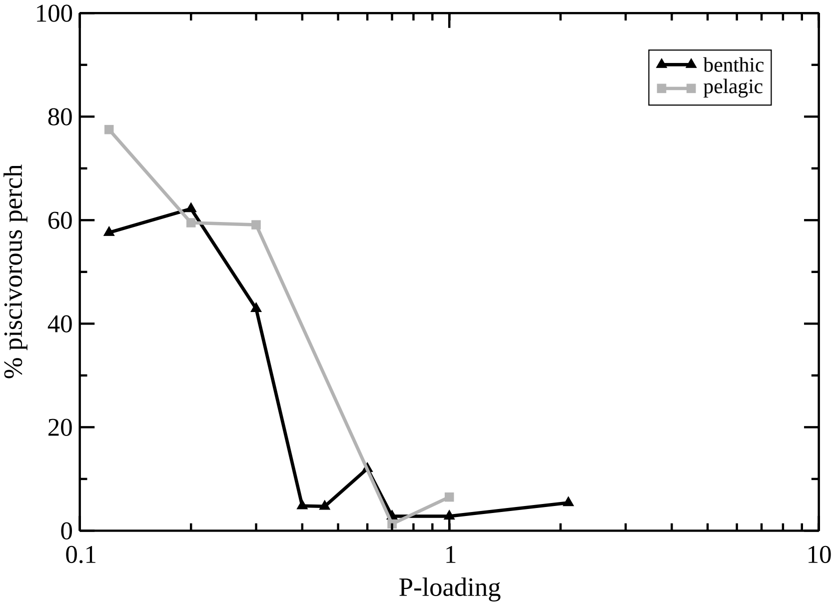

Figure 6.1: The change in the percentage of piscivorous perch biomass along a productivity gradient (phosphorous loading $gm^{-2}yr^{-1}$) in lakes in benthic and pelagic habitats. (Data from Persson (1994)).

tenance, growth and reproduction (Kooijman (2000b); Lika and Nisbet (2000)). Here a net production model is used, which means that from the acquired energy through foraging, maintenance is covered first. The remaining net energy is allocated to growth of both structural mass and reserves, where the latter includes energy reserved for reproduction. In case the energy needed to cover maintenance exceeds the acquired energy, reserves are used as energy source. When an individual cannot acquire enough energy through feeding and reserves are low, it will suffer from starvation mortality. In the case that no reserves are left the individual will die for certain. Background mortality is accounted for by a size-dependent mortality rate, assuming that small individuals have a bigger chance of dying than larger ones, *e.g.* due to predation by insect larvae (de Roos and Persson (2001)).

6.3 Results

Field data representing the change in the percentage of piscivorous perch present in the fish community along a productivity gradient (Figure 6.1) show that the percentage of piscivorous perch sharply decreases with increasing productivity. In the benthic habitat the percentage of piscivorous perch drops from almost 80% to 3%, and in the pelagic habitat a similar pattern occurs (from 60% to 4%).

Figure 6.2 (top panel) shows the biomass percentage of the IC and the TP (only individuals with age 1+ are included) as a function of the shared resource carrying capacity in the absence of cannibalism. At low carrying capacity, the IC is not present, while for intermediate carrying capacity ($1.4 \cdot 10^{-5} < K_Z < 2.6 \cdot 10^{-4}$) stable coexistence of the IC and the TP occurs, with both populations exhibiting fixed point dynamics and yearly reproduction. With increasing carrying capacity of the shared resource the percentage of IC biomass increases rapidly from zero to almost 90%. For $2.6 \cdot 10^{-4} < K_Z < 4.5 \cdot 10^{-4}$ bistability occurs between a coexistence equilibrium and a TP equilibrium, and for $K_Z \geq 4.5 \cdot 10^{-4}$ only a TP equilibrium occurs.

The pattern in biomass percentage is similar with cannibalism for the TP population (Figure 6.2, bottom panel), as without cannibalism. Again, at low carrying capacity only TP is present ($K_Z \leq 1.2 \cdot 10^{-5}$). However, coexistence is now possible for a larger region of parameter values than without cannibalism. For the major part of the parameter range, the populations exhibit fixed point dynamics with yearly reproduction ($1.2 \cdot 10^{-5} < K_Z < 5.8 \cdot 10^{-4}$), but some irregular dynamics also occur for $1.2 \cdot 10^{-5} < K_Z < 1.7 \cdot 10^{-5}$ and $2.3 \cdot 10^{-3} < K_Z < 3.2 \cdot 10^{-3}$. Bistability between a coexistence equilibrium and a TP equilibrium occurs for $5.8 \cdot 10^{-4} < K_Z < 5.2 \cdot 10^{-3}$. Cannibalism results in a reduced predation mortality for the IC due to a reduction in the total number of predators, and the fact that the predation pressure is shared with small TP. As a consequence, cannibalism allows for an increase in IC persistence with increasing carrying capacity of the shared resource.

To study the interaction between (cannibalistic) TP and IC the size structure of the population was studied at two different levels of resource carrying capacity (marked by $\bigwedge$ in Figure 6.2). The top four graphs in Figure 6.3 show the population states of the TP and the IC as single populations and when coexisting at $K_Z = 2.0 \cdot 10^{-3}$. For this value of carrying capacity bistability occurs between coexistence and a TP equilibrium, which implies that the single TP population can refrain an IC population from invading due to high predation mortality. When the IC and the TP do coexist, the size structure of the TP population has shifted towards smaller and fewer individuals. Young-of-the-year (YOY) TP suffer from retarded growth compared to the situation when only TP is present, due to low resource densities induced by IC consumption, and they only reach half the size of the YOY when TP and IC do not coexist. Because the total number of TP individuals and their reproduction pulse are lower when coexisting, the retarded growth of the YOY cannot be due to an increased intraspecific bottleneck. The size distribution of the IC also differs between a single population and a population coexisting with TP (Figure 6.3 top right graphs). Due to predation mortality, fewer YOY IC survive their first

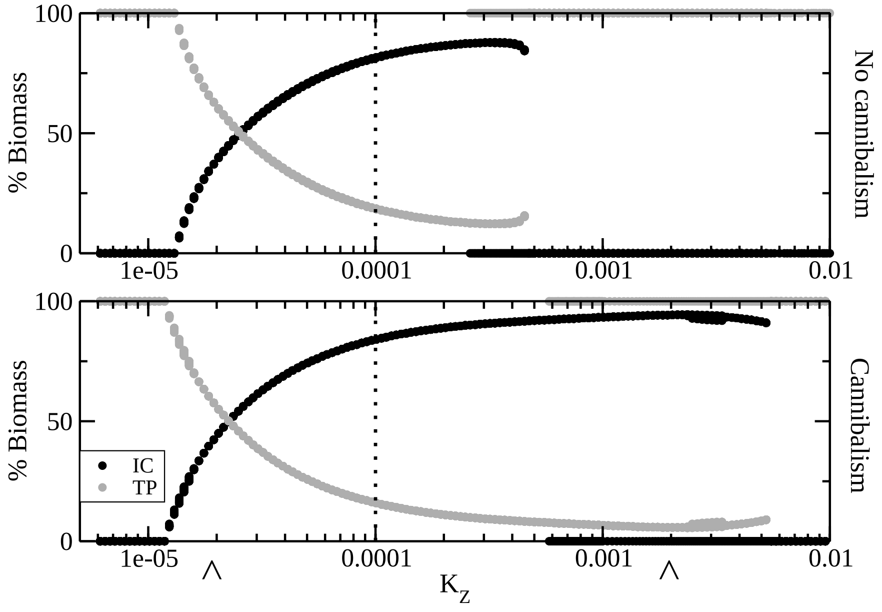

Figure 6.2: Biomass percentage of the intermediate consumer (black dots) and the top predator (grey dots) as a function of the shared resource carrying capacity. YOY are excluded. Top graph: no cannibalism; Bottom graph: including cannibalism. The marks ($\bigwedge$) on the x-axes of the bottom graph denote the K_Z values used in Figure 6.3.

year, but the individuals that do survive reach a larger size compared to individuals in a single IC population. This relates to that predation mortality leads to increased density of the shared resource by reducing the number of (small) individuals. As a result, adult IC grow into larger sizes and exhibit increased population fecundity. By predating on small IC, predators thus stimulate the total population reproduction of the IC and hence increase their own food availability ($5.4 \cdot 10^7$ YOY IC in single situation vs $5.8 \cdot 10^7$ YOY IC when coexisting with TP). However, the large reproduction pulse of the IC, which is promoted by predation mortality inflicted by the TP who are 'growing' their own food, also promotes an interspecific bottleneck in the TP, which is reflected in that one-year-old TP only reach a size of $50mm$ when coexisting with IC compared to $150mm$ when alone (Figure 6.3, upper two left panels). Because of their large numbers the YOY IC have the highest resource intake of the IC cohorts present (result not shown). One effect of this interspecific juvenile bottleneck is that YOY TP spend more time in the predation window vulnerable to cannibalism. However, the cannibalistic mortality suffered by YOY TP is still less than with the single population due to the lower absolute numbers of predator individuals and the shared predation attack rate with the IC.

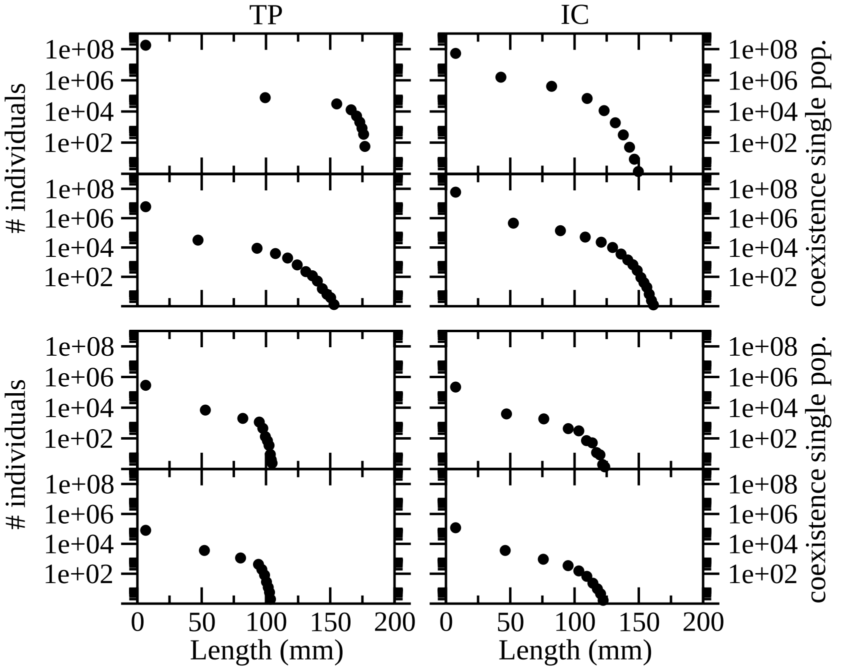

Figure 6.3: Population states of TP and IC at the first day of the year, derived from the single population dynamics or the dynamics when coexisting. Population are displayed with length and the number of individuals, where each dot represents a cohort. The TP is cannibalistic. Top 4 graphs: $K_Z = 2.0 \cdot 10^{-3}$. Bottom 4 graphs: $K_Z = 2.0 \cdot 10^{-5}$.

For a low value of shared resource carrying capacity ($K_Z = 2.0 \cdot 10^{-5}$) the size structures of the single and the coexisting TP populations do not differ as much as for a high value of the carrying capacity ($K_Z = 2.0 \cdot 10^{-3}$). The maximum size reached does not differ, however, the number of individuals and the reproduction pulse decrease when TP coexists with the IC (Figure 6.3 bottom graphs). The YOY TP do not show retarded growth when coexisting with IC compared to the single population situation, hence, there is no interspecific juvenile bottleneck present. The IC population size distribution also does not differ much between coexisting or a single population situation but the number of individuals is less when coexisting. In contrast to the population states at $K_Z = 2.0 \cdot 10^{-3}$, the reproduction pulse is lower when IC coexist with TP, and YOY IC reach similar sizes. At low carrying capacity, there is thus mostly a numerical difference between coexisting and single populations for both IC and TP.

The retarded growth of YOY TP and the accelerated growth of YOY IC resulting from coexistence at different productivities are shown in Figure 6.4. At low values of the carrying capacity of the shared resource both populations show irregular dynamics, but

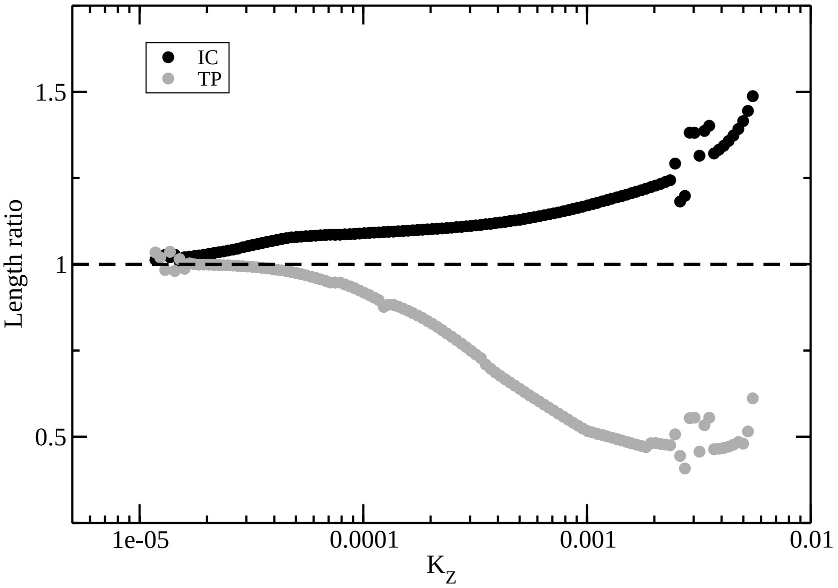

Figure 6.4: The length ratio at age 1 between a population when coexisting with the other species and the single population as a function of the shared resource carrying capacity. Each dot represents the length ratio, taken at the first day of the year and several years for each value of K_Z. IC: black dots. TP: grey dots. The dashed line denotes a ratio of 1.

the length-ratio of age-1 individuals in coexisting versus single populations is close to one for both species. With increasing carrying capacity, the juvenile bottleneck for the TP becomes more apparent, and the length-ratio drops and reaches a minimum around 0.5 for $1.3 \cdot 10^{-3} < K_Z < 5.0 \cdot 10^{-3}$. The increase in IC growth during the first year as a result of predation mortality also increases with increasing carrying capacity. The effect of the interactions between IC and TP thereby shifts along the productivity gradient, from mostly a numerical effect at low K_Z values to an effect on population size distributions at higher K_Z values.

6.4 Discussion

Intraguild predation models predict that the probability of exclusion of the intermediate consumer by the top predator increases with productivity (Pimm and Lawton (1977, 1978); Pimm and Rice (1987); Holt and Polis (1997); Diehl and Feißel (2000); Mylius et al. (2001)). These model results contrast to observed community patterns where the consumer dominates at high productivity levels (Persson (1994); Jeppesen et al. (1997)). The model results presented here do agree with field observations with respect to that the intermediate consumer biomass increases with increasing productivity, although the

TP does again dominate the community at very high productivity. The difference in model predictions between the unstructured models and the size-structured model can be related to presence of size-dependent foraging and food dependent development in the model presented here. The inclusion of cannibalism and an exclusive resource for the top predator are important elements in increasing the likelihood for coexistence between IC and TP, but the increase in dominance of IC within a considerable productivity range is largely due to food dependent development. However, although increased IC dominance with productivity was seen in the model results, model results and observed data still differ in that in the latter an absolute decrease in TP is observed.

One possible explanation for this remaining discrepancy between model results and data may be related to that the carrying capacity of the exclusive predator resource is not fixed in natural systems, but varies with productivity. Persson (1994) suggested, based on literature data, that the zone with littoral habitat, which provides shelter and resources for the predator, will decrease at high productivities leading to a dominance of pelagic productivity. With a decrease of the littoral zone, the availability of macro-invertebrate prey that occupy the littoral zone and which are a more important resource for the top predator perch than for the intermediate consumer roach, will decrease. This shift in habitat availability for both intermediate consumer and top predator in combination with the decrease in macro-invertebrate density with increasing productivity, will favor consumer dominance. Vadeboncoeur et al. (2005) studied the coupling between the pelagic and the littoral food web via a generalist top predator (foraging in littoral and pelagic habitat, analogous to our top predator) along a productivity gradient. They found that at intermediate productivity this coupling had a stabilizing effect on the combined food webs, while for high productivity switching occurred between a generalist top predator controlled system and a system controlled by the pelagic top predator (analogous to our intermediate consumer). When a parameter was incorporated to scale decreasing visibility with increasing productivity for the generalist predator, the control of the pelagic predator increased (Vadeboncoeur et al. (2005)). We did not model a simultaneous increase in shared resource (zooplankton) productivity and decrease in exclusive TP resource (macro-invertebrates) productivity with increasing productivity as such, but such a shift is likely to promote consumer dominance.

Besides an increase in pelagic productivity at the expense of littoral productivity, leading to a decrease in an exclusive resource for TP, an other resource, blue-green algae, becomes available exclusively for the intermediate consumer with increasing productivity (Persson (1988, 1994)). This exclusive IC resource is common in highly productive lakes and has been proposed to be a major mechanism behind the shift from predator to consumer dominance with increasing productivity, leading to increased consumer numbers and thereby increased control of the shared resource, strengthening the juvenile bottleneck imposed on the top predator (Persson (1994)). In contrast, Mylius et al. (2001) suggested that an exclusive resource for the consumer will not promote consumer presence at high productivity since the consumer's functional response is already at its maximum at intermediate productivities. We did not analyze the effect of an exclusive resource for the IC on community structure, and we anticipate that the impact on the TP-IC relationship may be hard to predict. On the one hand, feeding on more than one resource will decrease the attack rate of consumer individuals on the shared resource, which can have a positive effect on juvenile TP if the interspecific bottleneck is relaxed. On the other hand, the presence of an exclusive resource for the consumer is likely to result in an increase in IC numbers leading to an intensification of the TP juvenile bottleneck.

An important aspect of our model results was the negative effect of IC on small TP growth performance, *i.e.* we provided evidence for the presence of an interspecific competitive juvenile bottleneck (cf Werner and Gilliam (1984) and Persson (1988)). Interspecific juvenile bottlenecks have been suggested to be common in natural systems, especially for predator species that only become predacious after a juvenile stage during which they rely on a different resource that is often shared with species that become their prey later in life (Werner and Gilliam (1984)). Field data show that juvenile bottlenecks can have a negative effect on growth and survival of small predators (Byström et al. (1998); Persson and Greenberg (1990b)), but juvenile bottlenecks can also have negative effects on consumer species. For example, Neill (1975) showed that in a system with two consumer species, the adults of one of the species, that foraged on larger food particles than their juveniles, were reproducing successfully. Nonetheless, recruitment of those juveniles to the adult stage did not occur since these juveniles where inferior competitors for their required resource and died a few days after hatching. Such an interspecific juvenile bottleneck effect thus observed in empirical systems is lacking in other IGP-models, including stage-based versions. In contrast, we found it to occur in our model throughout the parameter range explored. We also found in accordance with Persson (1988) that the juvenile bottleneck was more pronounced at high productivity levels.

The interspecific juvenile bottleneck was mainly imposed by YOY consumers, who with their large numbers depressed resource density which in turn resulted in reduced growth rates of YOY predators. Thus the predation on IC leads to an increase in fecundity of adult IC, but at the same time as large TP 'cultivate' their own food, they also promote the juvenile bottleneck imposed on their own offspring. This indirect manner in which the bottleneck is affected is opposite to the hypothesis by Walters and Kitchell

(2001) stating that a high number of adult predators may keep the number of consumers down thereby promoting the development and survival of their own offspring that would otherwise compete for resources with the consumers. However, as clearly shown by our analysis, consideration of all feedbacks including the effect of TP predation on their own reproduction yield a different result.

6.5 Acknowledgements

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6.6 Appendix

The model studied here describes the interactions between a size-structured consumer population, a size-structured predator population and two non-structured resource populations, extending and combining the single species models described by Persson et al. (1998) and Claessen et al. (2000). The size-structured population model used in this study has two levels of organization, the individual state and the population state. The population state represents the frequency distribution of all individual states. Its dynamics are described by ordinary differential equations for the abundances and physiological traits of individuals in the cohorts that make up the populations (Persson et al. (1998); de Roos and Persson (2001). As the number of cohorts in the population varies over time, so does the number of ODE's describing the population dynamics. This two-level modeling approach ensures that results on the population level are emergent properties of modeling the individual states.

The physiological characteristics of an individual are determined by the size of that individual. Total individual body mass is assumed to consist of structural mass and reserves. Structural mass uniquely determines length via an allometric relationship (Table 6.2 Eq.1). The individual model that makes up the core of the size-structured population model combines and extends the models formulated by Persson et al. (1998) and Claessen et al. (2000). Foraging of both TP and IC follows Holling type II functional responses, in which handling time and resource specific attack rates depend on individual size. The attack rate on the shared resource (zooplankton) for both TP and IC is described by a hump-shaped function (Table 6.2 Eq. 2, see Persson et al. (1998) for justification and generality of this hump-shaped function). The TP attack rate on its exclusive resource (macro-invertebrates) is described by a power function of individual size (Table 6.2 Eq. 3)(de Roos et al. (2002); Persson et al. (2004)). The attack rate for TP on IC is a function of both predator and victim length (Claessen et al. (2000)). For optimally sized victims the predator attack rate increases with predator length following an allometric function. This maximum attack rate is adjusted for non-optimally sized prey using a tent-like function of the ratio between victim and predator length (see Claessen et al. (2000) for its derivation and empirical support). The upper limit of the victim-predator length ratio for which a predator can successfully attack its victim, ϵ, represents the catchability of prey, narrowing the size range of prey to individuals smaller than the predator itself. The lower limit δ delineates the detectability of the prey by a certain sized predator (Table 6.1).

Table 6.1: Model parameters for roach (*Rutilus rutilus*)(de Roos and Persson (2001); Hjelm and Persson (2001)) and Eurasian perch (*Perca fluviatilis*)(Claessen et al. (2000); Persson et al. (2003, 2004)) foraging on zooplankton (*Daphnia* sp. 1mm) and macro-invertebrates (*Cloeon*).

Symbol	**Value**		**Unit**	**Interpretation**
	Roach	***Perch***		
μ_b	0.01	0.01	d^{-1}	background mortality rate
μ_0	0.034	0.034	d^{-1}	scaling const. size-dep. mortality rate
x_μ	0.5	0.5	g	shape par. in size-dep. mortality rate
x_m	5.0	4.6	g	irreversible mass at maturation
w_b	0.0014	0.0018	g	total mass of a neonate
q_j	0.74	0.74	-	juvenile y/x mass ratio
q_a	1.0	1.37	-	adult y/x mass ratio
q_s	0.2	0.2	-	starvation threshold
s	0.2	0.2	d^{-1}	starvation coefficient
k_r	0.5	0.5	-	gonad egg conversion
λ_1	58.9	57.7	$mm\ g^{-\lambda_2}$	length allometric constant
λ_2	0.29	0.32	-	length allometric exponent
A	1.5E+5	varied	L/d	maximum attack rate on zooplankton
α	0.5	0.62	-	allometric exp. zoopl. attack rate
x_{opt}	28.7	4.7	g	optimum consumption size zoopl.
ξ_1	3.8	3.2	$d/g^{(1+\xi_2)}$	handling time allometric constant
ξ_2	-0.81	-0.8	-	handling time allometric exponent
ρ_1	0.022	0.022	$g^{(1-\rho_2)}/d$	maintenance allometric constant
ρ_2	0.77	0.77	-	maintenance allometric exponent
k_e	0.61	0.61	-	food conversion efficiency
ν_1		0.12	$m^2\ d^{-1}g^{-\nu_2}$	all. const. macro-inv. attack rate
ν_2		0.4	-	all. exp. macro-inv. attack rate
β		2.0E+2	$Ld^{-1}mm^{-\sigma}$	piscivory all. constant
σ		0.6	-	piscivory all. exponent
δ		0.05	-	minimum prey/predator ratio
ϵ		0.45	-	maximum prey/predator ratio

Table 6.1 – Continued

Symbol	Value		Unit	Interpretation
	Roach	***Perch***		
φ		0.16	-	optimum prey/predator ratio
Zooplankton				
r_Z	0.1		d^{-1}	regrowth rate zooplankton
K_Z	varied		g/L	carrying capacity zooplankton
Macro-inv.				
r_M	0.1		d^{-1}	regrowth rate macro-inv.
K_M	1.0		g/m^2	carrying capacity macro-inv.
Environment				
V	1.0E+9		L	lake volume
B	5.0E+4		m^2	lake bottom surface
Y	90		d	duration of growing season

The total food encounter rate is used in the functional response to determine food intake (Table 6.2 Eq. 5). All resources are assumed to be equally digestible and the intake is assumed to be limited by the digestion capacity of an individual which is an allometric function of its size (Table 6.2 Eq. 6)(Claessen et al. (2000)). The consumed food is converted into energy with a constant conversion efficiency, after which maintenance costs are subtracted. The remaining net energy is used for growth and allocated to structural mass (x), and reserves (y), with a ratio that depends on the condition of the individual (Table 6.2 Eq. 10). Adults allocate more energy to reserves than juveniles targeting for an optimal ratio $y/x = q_a$. This additional energy is reserved as gonad mass and converted into offspring at the beginning of a new year, making reproduction a discrete event. As a consequence of pulsed reproduction all newborns are born at the same time, with identical but species specific body mass, making a population consist of discrete cohorts.

Individuals that have a condition (*i.e.* reserves-structural mass ratio) below the threshold value q_s suffer from starvation mortality μ_s, which increases with decreasing condition. The starvation mortality function μ_s is such that individuals die with certainty when reserves are depleted (Table 6.2 Eq. 13). All individuals suffer from a size-dependent background mortality, which represents a chance to die of causes other than starvation or predation. Small individuals have a bigger chance to die than large individuals, *e.g.* predation mortality caused by insects (larvae) or birds, hence mortality decreases with increasing size (Table 6.2 Eq. 12). The size-dependent background mortality does not include predation mortality inflicted by the TP on the IC. IC mortality due to predation is a function of the density and the functional response of all TP cohorts (Table 6.2 Eq. 14).

Both resources are modeled as unstructured populations and follow semi-chemostat dynamics (Persson et al. (1998); Claessen et al. (2000); de Roos et al. (2002)). The shared resource is measured in densities per volume, since zooplankton is present in the water column. Macro-invertebrates occur on the lake bottom and are therefore measured as density per square meter. The IC and the TP are measured in absolute numbers of individuals in the entire lake (volume 10^9 L).

Table 6.2: Model equations, describing the individual-level, life-history model of roach and perch and the dynamics of the two unstructured resource populations. The variables c and v refer to the length of the piscivore predator and its victim, respectively. The indices i and j refer to cohorts of perch and roach respectively. These cohorts consist of N_i (N_j) individuals with structural mass x_i (x_j) and reserves y_i (y_j), and hence a body length equal to $c_i = l(x_i)$ ($v_j = l(x_j)$).

Subject	**Equation**		**Eq. nr**
	Roach	***Perch***	
Length-structural mass	$l(x) = \lambda_1 x^{\lambda_2}$	$l(x) = \lambda_1 x^{\lambda_2}$	1
Zooplankton attack rate	$a_Z(x) = A(\frac{x}{x_{opt}} exp(1 - x/x_{opt}))^{\alpha}$	$a_Z(x) = A(\frac{x}{x_{opt}} exp(1 - x/x_{opt}))^{\alpha}$	2
Macroinv. attack rate		$a_M(x) = \nu_1 x^{\nu_2}$	3
Piscivorous attack rate		$a_P(c, v) = \begin{cases} \beta c^{\sigma} \frac{v - \delta c}{(\varphi - \delta) c} & \text{if } \delta c < v \leq \varphi c \\ \beta c^{\sigma} \frac{\epsilon c - v}{(\epsilon - \varphi) c} & \text{if } \varphi c < v \leq \epsilon c \\ 0 & \text{otherwise} \end{cases}$	4
Total encounter food rate	$\gamma_T(x) = a_Z(x) Z$	$\gamma_T(x_i) = a_Z(x_i) Z + a_M(x_i) M$ $+ \sum_j a_P(l(x_i), v_j)(x_j + y_j) N_j$	5
Handling time	$h(x) = \xi_1 x^{\xi_2}$	$h(x) = \xi_1 x^{\xi_2}$	6
Maintenance	$E_m(x, y) = \rho_1 (x + y)^{\rho_2}$	$E_m(x, y) = \rho_1 (x + y)^{\rho_2}$	7
Energy assimilation	$E_a(x) = k_e(\frac{\gamma_T(x)}{1 + h(x)\gamma_T(x)})$	$E_a(x) = k_e \frac{\gamma_T(x)}{1 + h(x)\gamma_T(x)}$	8
Net energy	$E_n(x, y) = E_a(x) - E_m(x, y)$	$E_n(x, y) = E_a(x) - E_m(x, y)$	9

Table 6.2 – Continued

Subject	**Equation**		**Eq. nr.**
	Roach	***Perch***	
Energy all. to x	$\kappa(x,y) = \begin{cases} \frac{1}{(1+q_j)q_j}\frac{y}{x} & \text{if } x \leq x_m \\ \frac{1}{(1+q_a)q_a}\frac{y}{x} & \text{if } x > x_m \end{cases}$	$\kappa(x,y) = \begin{cases} \frac{1}{(1+q_j)q_j}\frac{y}{x} & \text{if } x \leq x_m \\ \frac{1}{(1+q_a)q_a}\frac{y}{x} & \text{if } x > x_m \end{cases}$	10
Size-dep. backgr. mort.	$\mu(x) = \mu_0^{(-\frac{x}{x_\mu})} + \mu_b$	$\mu(x) = \mu_0^{(-\frac{x}{x_\mu})} + \mu_b$	11
Starvation mort.	$\mu_s(x) = \begin{cases} s(x/y-1) & \text{if } y < q_s x \\ 0 & \text{otherwise} \end{cases}$	$\mu_s(x) = \begin{cases} s(x/y-1) & \text{if } y < q_s x \\ 0 & \text{otherwise} \end{cases}$	12
Piscivorous mort.	$\mu_p(x) = \sum_i \frac{a_P(c_i,l(x))N_i}{1+h(x_i)\gamma_T(x_i)}$	$\mu_p(x) = \sum_i \frac{a_P(c_i,l(x))N_i}{1+h(x_i)\gamma_T(x_i)}$	13
Total mort.	$\mu_T(x) = \mu(x) + \mu_s(x) + \mu_p(x)$	$\mu_T(x) = \mu(x) + \mu_s(x)$	14
Fecundity	$f(x,y) = \begin{cases} \frac{k_r(y-q_jx)}{w_b} & \text{if } x > x_m \text{ and } y > q_jx \\ 0 & \text{otherwise} \end{cases}$	$f(x,y) = \begin{cases} \frac{k_r(y-q_jx)}{w_b} & \text{if } x > x_m \text{ and } y > q_jx \\ 0 & \text{otherwise} \end{cases}$	15
Zooplankton dynamics	$\frac{dZ}{dt} = r_Z(K_Z - Z) - \frac{Z}{V}\sum_j \frac{a_Z(x_j)N_j}{1+h(x_j)\gamma_T(x_j)} - \frac{Z}{V}\sum_i \frac{a_Z(x_i)N_i}{1+h(x_i)\gamma_T(x_i)}$		16
Macroinvertebrate dynamics	$\frac{dM}{dt} = r_M(K_M - M) - \frac{M}{B}\sum_i \frac{a_M(x_i)N_i}{1+h(x_i)\gamma_T(x_i)}$		17

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Curriculum Vitae

Karen van de Wolfshaar was born on the 11th of Februari 1977 in Wageningen, The Netherlands. After graduating from highschool, VWO Streeklyceum Ede, she started Biology at the agricultural university in Wageningen (currently known as Wageningen University). In 2000 she graduated in theoretical biology. At Utrecht University she did a research project on wetland restauration. For the Dutch institute for freshwater and wastewater management (RIZA) she did a short project concerning the life history of the zebra mussel. In 2001 she started her PhD with prof. dr. André de Roos at the Universiteit van Amsterdam at the Population Biology department in cooperation with prof. dr. Lennart Persson from Umeå University in Sweden. At this moment Karen is employed at WL — Delft Hydraulics as reseachter and consultant at the department of Marine and Coastal Management.

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