Dwarfs and giants: the dynamic interplay of size-dependent cannibalism and competition
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Chapter 6

General discussion

6.1 Introduction

This chapter is essentially the continuation of the General introduction (Chapter 1). It consists of four parts. First, the two questions raised in section 1.3 are reconsidered in the light of the results in this thesis. Second, the results and the mechanisms that cause them are discussed in more detail, comparing the results of two different models (the model of Chapters 2 and 3 and the model of Chapter 4). Third, the comparisons between model predictions and empirical data that are made in this thesis are reviewed. Finally, the results of this thesis are put in a wider perspective, addressing the question whether this thesis has implications for ecological theory, experiments and/or fisheries management.

6.2 Questions revisited

In section 1.3 two questions have been raised: (a) What effect(s) may cannibalism have on population dynamics? (b) What mechanisms or aspects of cannibalism cause these effects? In the absence of cannibalism our models predict generation cycles caused by size-dependent competition (and a juvenile delay). Introducing cannibalism can have a number of consequences, which are listed below; the aspects of cannibalism (cf. section 1.2.1) that cause each effect are given in italics:

(i) Stabilisation (i.e., dampening) of competition-driven generation cycles --- mortality.

(ii) Regulation of population size; occurs in the more or less stable, cannibal-driven population state which results from effect (i) --- mortality.

(iii) Coexistence of a ‘dwarf’ size class and a ‘giant’ size class in competition-driven generation cycles; this size-dimorphism corresponds to a bimodal population size distribution, and may happen if effect (i) fails (temporarily) --- mortality, gain, size-dependent interactions, competition.
(iv) The existence of two population states, one ‘stunted’ and one ‘piscivorous’.
In the stunted state individuals remain small and mainly consume alternative resources. The piscivorous state is characterised by a very wide population size distribution with the largest individuals consuming conspecifics exclusively (i.e., the piscivory niche) — gain, size-dependent interactions.

(v) For the same conditions, coexistence of a ‘stunted’ and ‘piscivorous’ population state, i.e., bistability — mortality, gain, size-dependent interactions.

Finally, we may speculate that the ontogenetic niche shift from feeding on an alternative resource to feeding on conspecifics has the potential to induce

(vi) Evolutionary branching — gain, size-dependent interactions, competition.

It should be kept in mind, however, that the result of evolutionary branching (Chapter 5) was obtained for an ontogenetic shift between heterospecific resources. It remains to be shown that this is also possible if the niche shift involves cannibalism. Results from interspecific predation do not necessarily carry over to intraspecific predation (e.g., section 1.2.2).

A number of the listed effects of cannibalism on population dynamics have not been found before. These are the dwarfs-and-giants dynamics, the piscivory niche, and the ‘Hansel and Gretel’ effect as a possible explanation of bistability. Interestingly, all three relate to the energy gain of cannibalism, and therefore emphasise the important distinction between infanticide and cannibalism.

The other effects of cannibalism that we have found had already been described before. Population regulation by cannibalism has been observed in models by Ricker (1954), Gurtin and Levine (1982), Diekmann et al. (1986) and Cushing (1992). The stabilising effect of cannibalism was already found by Cushing (1991), Kohlmeier and Ebenhöh (1995) and van den Bosch and Gabriel (1997). Both effects are caused by the cannibalism-induced mortality of victims, which is the single aspect of cannibalism that is incorporated in all models of the dynamics of cannibalistic populations (Table 1.1). Cannibalism-induced bistability was found by Fisher (1987), van den Bosch et al. (1988) and Cushing (1992). In all three models bistability results from the presence of a positive effect of cannibalism. In the model of Fisher (1987) the positive effect of cannibalism is indirect and mediated through competition for shared resources. In his model, a high cannibalistic mortality rate leads to a high density of alternative food, and hence large cannibals that cause high cannibalistic mortality. In the other two models the positive effect of cannibalism is the direct cannibalistic energy gain. Apparently, cannibalism can give rise to bistability in at least two different ways; via shared resources and through cannibalistic gain. In our case bistability is closely associated with the size-dependent nature of the cannibalistic interaction (the Hansel and Gretel effect, see section 6.3.3). This effect highlights that the population size distribution itself may modify the balance of the cost and benefits of cannibalism.

It should be noted that in the list of the effects of cannibalism displayed above the details of the individual-level model, such as the type of functional response and energy allocation, do not appear as explanatory mechanisms. Rather, different aspects of the ecological interactions between individuals are forwarded as such:
the size-dependent nature of cannibalism and competition, the energy gained by cannibals and the mortality suffered by victims. In the next section it is investigated to what extent the results depend on the ecological interactions alone, or whether they are influenced by the specifics of the bioenergetics.

### 6.3 Bioenergetics versus interactions

The aim of this section is to investigate whether the results obtained in chapters 2, 3 and 4 depend on the specific assumptions of the individual-level model, in particular the channelling of energy to growth, maintenance and reproduction, or whether they are intrinsic to the ecological interactions between individuals. In the latter case the results have more general implications, as many different cannibalistic species, which differ by the specifics of their bioenergetics, engage in similar size-dependent cannibalism and size-dependent competition.

To this end we compare the results obtained with two size-structured population models which differ in several important aspects, but which both incorporate size-dependent cannibalism as outlined in section 1.4. Also, in both models size-dependent competition emerges from the size-dependent scaling of vital rates and the exploitative foraging on a dynamic, alternative resource. A detailed description of the first model is presented in chapters 2 and 3, of the second model in chapter 4. Here we limit ourselves to the description of the differences and similarities in terms of the underlying, biological assumptions.

#### 6.3.1 Different bioenergetics

In the first model mature individuals are assumed to reproduce in synchronised pulses at the beginning of each growing season. Consequently the population consists of discrete age cohorts. Within growing seasons the state of individuals changes continuously depending on resource levels and their body size. At reproduction, individuals are assumed to convert their accumulated gonad mass into new offspring. Hence it is necessary to keep track of the amount of accumulated gonad tissue, as well as somatic body mass. Moreover, in this model individuals are assumed to be able to starve away part, but not all, of their body mass when the energy requirements for body maintenance exceed the assimilation rate. In order to incorporate both accumulated gonads and the possibility of starvation into the model, the state of individuals is characterised by two state variables; these are referred to as irreversible body mass and reversible body mass, respectively. Gonad tissue is assumed to be a fraction of the reversible body mass. The rules for channelling of energy in this model are summarised graphically in Fig. 6.1.

By contrast, in the second model individuals are assumed to reproduce continuously. As a result, the emerging population size distribution is also continuous. Continuous reproduction allows for a much simpler individual-level model, since there is no need to keep track of accumulated gonad tissue, nor (explicit) energy reserves for starvation. Rather, the assimilation rate can be channelled instanta-
Figure 6.1: Energy channelling and growth in the pulsed model. Arrow (1): Individuals are born with a fixed amount of irreversible body mass \( x = x_b \) and reversible mass such that \( y / x = q_j \). As they grow, the ratio \( y / x \) approaches (or remains at) the maximum ratio for juveniles, \( q_j \). (2): Upon reaching \( x = x_f \), they mature. If they are not starving, the ratio \( y / x \) now approaches the maximum ratio for adults, \( q_A \). (3): At the start of a growing season, adults convert all their reversible body mass in excess of \( y = q_j x \) into offspring. Resource densities permitting, they start growing again after reproduction. (4): If, however, the assimilation rate is insufficient to cover metabolism, they starve away reversible body mass. Below the ratio \( y / x = q_S \) their mortality rate increases steeply with decreasing \( y / x \).

neously to reproduction, metabolism and somatic growth. Starvation can then be incorporated by decreased growth and reproduction rates, and possibly a negative somatic growth rate. In the model in Chapter 4, we assumed that a fixed fraction \((1 - \kappa)\) of the energy assimilation rate is allocated to reproduction, whereas the other fraction \((\kappa)\) is used for metabolism and somatic growth. This type of energy channelling has been referred to as the \(\kappa\)-rule (Kooijman and Metz, 1984; Kooijman, 1986, 1993, 2000, 2001), and falls in the category of assimilation allocation, as opposed to net-production allocation (Gurney and Nisbet, 1998). In the continuous model the state of individuals is hence characterised by a single state variable: length.

As described above, the two models differ most fundamentally in their energy channelling. Furthermore, the two models incorporate different functions to describe the relation between body size and vital rates, such as handling time and metabolic rate. The pulsed model was designed to be parameterised with experi-
menta ll data on individual-level performance. In the continuous model most of the parameterised functions of the pulsed model have been approximated by simpler functions. For example, in the pulsed and continuous models the metabolic rate is given by, respectively:

\[ M(x, y) = \rho_1 (x + y)^{\rho_2} \]

and

\[ M(l) = \rho l^3 \]

where \( x \) and \( y \) are irreversible and reversible body mass, respectively (Fig. 6.1), \( \rho_1 \) and \( \rho_2 \) are two allometric constants, \( l \) is body length and \( \rho \) an allometric constant. Both models assume a Holling type II functional response.

6.3.2 Similar interactions

The ecological interactions in the two models are essentially the same. Size-dependent competition for the alternative resource results from the size-scaling of foraging rate and metabolic requirements. It is best captured by the relation between the minimum resource density required for growth (the 'critical resource density') and body size. In both models, this is an increasing function of body size, implying that smaller individuals are competitively superior to larger ones (Persson et al., 1998). Both models assume semi-chemostat dynamics of the alternative resource.

Size-dependent cannibalism is modelled in exactly the same way in both models. The cannibalistic attack rate of a cannibal of length \( c \) and a victim of length \( v \) is given by:

\[ A_c(c, v) = C_{max}(c) T(c, v) \]  \( \tag{6.1} \)

where the function \( C_{max}(c) \) describes the maximum possible attack rate of a cannibal of length \( c \), attained for optimal victim sizes only, which is given by:

\[ C_{max}(c) = \beta c^\sigma \]  \( \tag{6.2} \)

The function \( T(c, v) \) takes into account the effect of suboptimal victim sizes and is given by:

\[ T(c, v) = \begin{cases} \frac{v - \delta c}{(\delta - \delta)c} & \text{if } \delta c < v \leq \phi c \\ \frac{x - v}{(\epsilon - \phi)c} & \text{if } \phi c < v < \epsilon c \\ 0 & \text{otherwise} \end{cases} \]  \( \tag{6.3} \)

which is a tent-shaped function that takes values between one when the ratio between victim and cannibal length is optimal \((v/c = \phi)\), and zero at the lower and upper limits of the cannibalism window \((v/c = \delta \text{ or } \epsilon, \text{ respectively})\). Outside this window \( T(c, v) \) is zero.

With respect to how cannibalism is incorporated, the only difference between the two models is in the parameter value of \( \sigma \), which is assumed to be 0.6 in the pulsed model and 2 in the continuous model. Note that for individual of 140 mm,
$C_{\text{max}}$ in the continuous model and in the pulsed model differ by a factor 1000. For example, $C_{\text{max}}$ in the continuous model with $\beta = 0.8$ is comparable to $C_{\text{max}}$ in the pulsed model with $\beta = 800$. A second difference results indirectly from the different timing of reproduction. Whereas in the continuous model (at least some) victims are available continuously, in the model with pulsed reproduction the availability of victims varies strongly within seasons.

6.3.3 **Similar results?**

The list of effects of cannibalism (section 6.2) does not differentiate between the two different models with which the results were obtained. Below we discuss the first five effects on that list, and compare the results obtained with the pulsed and the continuous models. The comparison will show to what extent the results are determined by the ecological interactions or by the bioenergetics.

(i) **Stabilisation**

One of the most striking results obtained with the pulsed model is the critical dependence of population dynamics on the lower limit of the cannibalism window, $\delta$ (Chapter 3). Above a critical value of $\delta$ competition-induced, single-cohort cycles are found, whereas below it either dwarfs-and-giants dynamics are found or cannibalism stabilises dynamics in which case a more or less stable population size distribution is found. A remarkably similar result is found with the continuous model, as is shown in Fig. 6.2. Cannibal-driven dynamics are found for small $\delta$, dwarfs-and-giants dynamics for intermediate $\delta$, and the equivalent of single-cohort cycles for high $\delta$. There are, however, interesting differences. First, dwarfs-and-giants dynamics are found for much higher values of $\delta$ (up to $\delta \approx 0.15$). Second, the critical value of $\delta$ below which cannibal-driven dynamics occur is also higher in the continuous model ($\delta \approx 0.095$). Third, in between these two critical values of $\delta$, both dwarfs-and-giant dynamics and single-cohort dynamics can be found, depending on initial conditions. Bistability of these types of population dynamics is not found with pulsed reproduction.

The explanation of these differences lies in the timing of reproduction and the consequence it has on the resulting population size distribution. Clearly, pulsed reproduction results in a pulsed population size distribution where each pulse is a discrete age class. Continuous reproduction gives rise to a continuous size distribution. It should be noted, however, that even with continuous reproduction the size-distribution may consist of discrete size classes, separated from each other by ‘empty’ size intervals (i.e., no individuals in that size interval). The competition-induced population cycles that result with a high $\delta$ (e.g., $\delta > 0.15$ in Fig. 6.2) are the equivalent of ‘single-cohort cycles’ discussed in Chapter 3. Competition between newborns and larger individuals is so strong that, regularly, a high density of newborns causes starvation mortality of large juveniles and adults. As a consequence, the population consists of discrete age classes or ‘generations’. In such population cycles periods without any reproduction due to the absence of adults
Figure 6.2: The effect of the lower limit of the cannibalism window, $\delta$, on population dynamics, characterised by the maximum length at time of censussing. Both bifurcation diagrams are constructed from simulations (i.e., not continuation) with: $\beta = 500$, $\epsilon = 0.5$, $\phi = 0.2$. In both (a) and (b), from low to high $\delta$ the type of population dynamics are cannibal-driven, dwarfs-and-giants (obvious from gigantic lengths), and single-cohort cycles, respectively. (a) Pulsed model ($\delta_1 = 0.077$); censussed at the first day of each growing season. Single-cohort cycles are evident from the regular 7-year cycles. (b) Continuous model ($\delta_1 = 0.11$); output generated at local minima and maxima of the alternative resource. The arrow indicates the lowest value of $\delta$ ($= 0.095$) for which single-cohort cycles are found. In the interval $\delta \in (0.095, 0.15)$ both dwarfs-and-giants dynamics and single-cohort cycles are possible, depending on initial conditions.

are alternated by periods of continuous reproduction. Because there is a time interval between maturation of the first individuals in a generation and the death of the last ones, the next generation will consist of a range of ages and sizes. Smaller individuals grow faster, however, and therefore the width of the size distribution of a generation decreases over time. Therefore, continuous reproduction may lead to either a continuous or a nearly pulsed size distribution, which may explain the of bistability of single-cohort cycles and dwarfs-and-giants dynamics.

In Chapter 3 it is shown that in the pulsed model the expected value of $\delta$ below which cannibalism can stabilise single-cohort cycles is

$$\delta_1 = \frac{L_s}{L_1}$$

where $L_1$ is the length at first reproduction and $L_s$ the length of newborns at the moment the last adults die of starvation (see section 3.3.1). In the continuous model the maturation size is assumed to be 115 mm. From time series of single-cohort cycles in the continuous model we can determine that the largest adults become only 116.5 mm. Furthermore, we find that the starvation period is $\tau_s \approx 16$ days and that the maximum length of recruits at that moment is 12.5 mm. Thus,
the lengths of the offspring generation are distributed between 7 mm (the length at birth) and 12.5 mm. If we substitute $L_s = 12.5$ mm and $L_1 = 116.5$, the rule derived for the pulsed model hence predicts a critical value of $\delta_1 = 0.107$ for the continuous model. Note, however, that the recruits have a length distribution rather than a single length, and therefore this estimate of $\delta_1$ should be considered as an upper estimate of the critical value. As an alternative, we may substitute the average length of the recruits (10.5 mm) for $L_s$, which gives $\delta_1 = 0.09$. If we compare these two estimates of $\delta_1$ with Fig. 6.2, it appears that they are indeed very close to the lower boundary of single cohort dynamics ($\delta = 0.095$, in Fig. 6.2b indicated with an arrow). Although we cannot make a precise estimate of $\delta_1$ in the continuous model, the estimates (i.e., 0.107 and 0.09 from the rule and 0.095 from the simulation) are consistently higher than in the pulsed model, where $\delta_1 = 0.077$. This difference may be a result of differences at the bioenergetic level; adults starve to death earlier in the continuous model, but newborns grow faster. While this may explain the quantitative difference between the critical values of $\delta$ in the pulsed and continuous models, the similar, drastic change of population dynamics around the critical $\delta$ is determined by the ecological interactions.

Surprisingly, with continuous reproduction dwarfs-and-giants dynamics are found for $\delta$ values above the critical value, rather than below it as is the case in the pulsed model (Fig. 6.2a). Why this is the case is discussed under point (iii).

(ii) Population regulation

In the absence of cannibalism the size-structured population does not grow out of bounds because survival, growth and reproduction of individuals are limited by the amount of alternative food they consume. Competition for the alternative resource hence regulates the population.

In the cannibal-driven population state which results with sufficiently low $\delta$ as discussed under point (i), the cannibalistic mortality rate of small individuals is very high (e.g., Fig. 2.4). Despite a high population birth rate the severe mortality results in a low number of (competitively superior) small individuals. Competition for the alternative resource is hence weak and juveniles grow quickly due to the high level of alternative food. Another effect of weak competition is the lack of starvation mortality, resulting in the coexistence of old and young individuals. Although adult reproduction is determined by both the amount of alternative food and the amount of conspecific food, cannibalism indeed acts as a mechanism of population regulation in these circumstances because it is the main cause of mortality. With non-fixed point dynamics, occasional high pulses of newborns are also killed-off and regulated by the existing size class of cannibals.

The main aspects of the cannibal-driven population state, i.e., fast juvenile growth, high juvenile mortality and coexistence of many age classes, are observed in cannibal-driven dynamics in both the pulsed model (Fig. 2.4, Fig. 3.5) and the continuous model (Fig. 4.2, Fig. 6.2).
An interesting result from the pulsed model are the dwarfs-and-giants cycles (Chapter 2, 3, Fig. 6.3a), found in a range of δ values in between the critical values δ₁ and δ₂ (Chapter 3, Fig. 6.2). This type of dynamics is characterised by competition-induced population cycles, in which the (numerically) dominant cohort cannibalises the first pulse of offspring whereas the next pulse of offspring outcompetes the adult size class. During their first year, the few survivors of the first pulse of offspring (referred to as giants) grow fast until the resource is depressed by the next cohort. Their body size allows them to cannibalise the later offspring (referred to as dwarfs). The dwarfs grow slowly due to intense competition for the alternative resource. They serve as cannibalistic food to the slightly older but much larger giants, which continue to feed on the dwarfs (Fig. 6.2a).

Fig. 6.3b shows that the continuous models exhibits very similar dynamics. This may come as a surprise, since the above described mechanism is hard to imagine with continuous reproduction. If, with continuous reproduction, small adults are able to cannibalise newborns, this is sufficient to prevent starvation mor-
tality of adults, and thus sufficient to lead to cannibal-driven dynamics. This is illustrated by the occurrence of cannibal-driven dynamics up to the critical value $\delta_1$ (Fig. 6.2b). One might expect, therefore, that dwarfs-and-giants dynamics are impossible in the continuous model. Indeed, starting from single-cohort cycles with $\delta = 0.19$, one can gradually lower $\delta$ without changing population dynamics down to 0.095 (the arrow in Fig. 6.2b), at which value the dynamics change to cannibal-driven dynamics, without ever spotting a giant cannibal. However, starting from the cannibal driven dynamics with $\delta = 0.05$, and gradually increasing $\delta$, it is impossible to miss the dwarfs and giants dynamics. It appears that in the single-cohort cycles (in the range $\delta \approx 0.1 \ldots 0.15$) there is a ‘niche’ for giant cannibals, but that the individuals of the dwarf cohorts and their offspring cannot enter it. As discussed under point (i), the size distribution of the population in single-cohort cycles is nearly pulsed, and therefore reproduction occurs discontinuously in time. While an individual can enter the ‘giant cannibal niche’ if it is born at the right moment (that is, in a certain phase of the cycle), this does not occur due to the absence of adults in this phase of the cycle. If, however, by a perturbation some individuals of adequate size are added to the system, they thrive well because they cannibalise the abundant dwarf cohort. Once mature, the individuals in the giant cannibal niche reproduce during a prolonged period. Their reproductive period includes the timing required for entering the next giant cannibal niche, and therefore the giants can form a persisting subpopulation. Interestingly, the giant cohorts in the continuous model are not the offspring of dwarf cohorts, which contrasts with the pulsed model, in which giants and dwarfs are nearly 100% full-sibs from dwarf-sized parents. Rather, every generation of giants is produced by the previous generation of giants (while most dwarfs are produced by dwarfs). It should be noted, however, that ‘genetically’ segregated subpopulations of dwarfs and giants occur only in very stable dwarfs-and-giants cycles, such as depicted in Fig. 6.3b. For many parameter values the dynamics are not regular, and mixing occurs frequently. Unstable dwarfs-and-giants dynamics are expected if the subpopulation in the giant cannibal niche becomes abundant enough to have a dynamic impact on the dwarf cohort.

In summary, the occurrence of dwarfs-and-giants dynamics depends critically on the dynamic interplay of size-dependent cannibalism and competition (i.e., interactions, not bioenergetics). Time series of this type of dynamics, obtained with the two models, are very similar. Yet, there are subtle but important differences, which can be attributed to the mode of reproduction (pulsed vs. continuous) and the resulting population size distribution.

Already in the discussion of Chapter 2 a continuous-time model has been presented (Fig. 2.9), which is similar to the continuous model in Chapter 4 except that it assumes a linear functional response. The occurrence of dwarfs and giants hence seems independent of the shape of the functional response as well.
(iv) Stunted and piscivorous population states

A conspicuous result found with the pulsed model is the dependence of the population size distribution on the upper limit of the cannibalism window, $\epsilon$ (Chapter 3). In bifurcation runs the maximum size attained in the population increases quickly from around 18 cm to over 30 cm around a critical value of $\epsilon$ (Fig. 6.4a). A similar result is found with the continuous model (Fig. 6.4b), although the effect is more drastic because the equilibrium curve is folded. In both models we can distinguish between a 'stunted' population state and a 'piscivorous' population state. The stunted state is characterised by small ultimate size, little gain from cannibalism, and a high alternative resource density. Inversely, the piscivorous state is characterised by large ultimate sizes, a high gain and a low resource (although not as low as in the single-cohort cycles or dwarfs-and-giants cycles). The piscivorous state is further characterised by the presence of individuals that consume conspecifics only, because they are too large to consume the alternative resource (i.e., individuals in the piscivory niche).

In order to characterise the role of cannibalism in the different equilibrium states quantitatively, Fig. 6.4 depicts the fraction of population fecundity that is derived from cannibalistic food intake (which equals the fraction of a single individual's expected life time reproduction that is derived from cannibalistic food intake), the probability of an individual to escape cannibalism, and the probability of an adult to fall victim to cannibalism. Of these three aspects, the first relates to the benefit of cannibalism (via the direct energy gain), whereas the latter two relate to the cost of cannibalism (via additional mortality). These data allow us to address the following question: is the stunted (resp., piscivorous) population state in the pulsed model similar to the stunted (resp., piscivorous) state in the continuous model? In other words, are the stunted and piscivorous population states comparable in the two models? As pointed out above, with respect to the ultimate size the stunted and piscivorous states are similar in the two models. Fig. 6.4 shows further that the stunted state in both models is characterised by a small (but increasing with $\epsilon$) contribution of cannibalistic energy intake to reproduction, a high probability to escape cannibalism, and a negligible probability for adults to fall victim to cannibalism.

The figure shows that with respect to the piscivorous state, the pulsed model deviates in two ways from the continuous model. Firstly, in the pulsed model the alternative resource remains an important contribution to population fecundity even in the piscivorous state, whereas in the continuous model reproduction derives for nearly 100% from cannibalistic food intake in the piscivorous state. Apparently, small adults that still have a significantly planktivorous diet deliver the main contribution to population fecundity in the pulsed model. This difference corresponds to a difference in population size distribution, which is roughly exponentially distributed in the pulsed model (Fig. 3.8) and U-shaped in the continuous model (Fig. 4.4). In the latter situation large adults dominate reproduction, whereas in the former one the small adults dominate reproduction. Secondly, the probability to escape cannibalism does not differ spectacularly between the two
Figure 6.4: The effect of the upper limit of the cannibalism window, $\epsilon$. (a) Pulsed model, based on simulations (cf. Fig. 3.7), censused on first day of the growing season, with $\beta = 200$, $\delta = 0$, $\phi = 0.2$. (b) Continuous model, based on continuation with $\beta = 0.8$, $\delta = 0.03$, $\phi = 0.2$. Top panel: maximum length in the population (at the time of censusing). Second panel: fraction of population fecundity that is derived from cannibalistic food intake (which equals the fraction of a single individual’s expected life time reproduction that is derived from cannibalistic food intake). Third panel: the probability of an individual to escape cannibalism. Bottom panel: the probability of an adult to fall victim to cannibalism. Note that in the continuous model the values on the curve of stunted equilibria and on the curve in between the two fold bifurcations lie on the axis.
population states in the pulsed model.

Overall, Fig. 6.4 suggests that the results from the two models are qualitatively similar. The stunted state is associated with (relatively) low benefit and low cost of cannibalism, whereas in the piscivorous state both the benefit and the cost of cannibalism are high. (Note that the net benefit of cannibalism is always negative in both stunted and piscivorous states, in the continuous model; Fig. 4.5). Yet the quantitative differences concern two factors which are likely to affect population dynamics: reproduction and the probability to escape cannibalism (the middle two panels in Fig. 6.4). In Chapter 3 we argue that the effect of $\epsilon$ on population dynamics is small because it mainly affects old cohorts with little dynamic influence.

The reason why young, cannibalistic cohorts are more important for population dynamics in the pulsed model than in the continuous model may be due to the pulsed nature of reproduction itself. As pointed out above, pulsed reproduction results in a pulsed population size distribution (e.g., Fig. 2.5, Fig. 3.8). This has three important consequences for the cannibalistic interactions. (1) The availability of victims varies strongly within a growing season as victims move through the cannibalism window. For small cannibals, this means that part of the year there is no conspecific food available and they have to rely on alternative food or, if alternative food is scarce, they starve away reserves. (2) The pulsed availability of food means that cannibals are more handling time limited, and hence kill fewer victims per year than cannibals in a continuously reproducing population. (3) Individuals cannot start cannibalising before reaching the age of one year, when the first cohort of potential victims is produced. With pulsed reproduction the size of one-year-old individuals is between 60-100 mm, in both the stunted and piscivorous population states (Fig. 2.5, Fig. 3.8). Consequently, individuals are obligatory planktivorous up to that size. By contrast, in the continuous model individuals start cannibalising upon reaching length $x_b/\epsilon$; with $\epsilon = 0.5$ and $x_b = 7$ mm, this equals 14 mm. These aspects may explain why the adult subpopulation is dominated by small adults in the pulsed model, rather than large adults as in the continuous model. In turn, the smaller contribution of cannibalism to the energy balance of small adults may explain the quantitative difference observed in Fig. 6.4.

(v) **Bistability of stunted and piscivorous states**

The most striking difference between the results of the two models is the presence of bistability in the continuous model and its absence in the pulsed model (Fig. 6.4). In certain parameter ranges, the continuous model predicts that the population can either converge to a stunted state or a piscivorous state, depending on initial conditions. In Chapter 4 we argue that the driving force of the bistability is the Hansel and Gretel effect. In the continuous model, the net benefit of cannibalism is much higher in the piscivorous state than in the stunted state (Fig. 4.5, and see Fig. 6.4: large contribution of cannibalism to reproduction). The net benefit of cannibalism depends on the size distribution of cannibals. Due to the cannibalism window, if cannibals are larger they have a larger gain from cannibalism because on average the cannibals consume victims when the victims are larger and contain...
hence more energy. This effect is called the ‘Hansel and Gretel’ effect (Chapter 4), named after the tale which, to our best knowledge, is the first account of the idea to postpone cannibalism until the victim has become more nutritious (Grimm and Grimm, 1884).

Why is this bistability not observed in the pulsed model? With respect to the cannibalistic interaction, there are two main differences between the two models. The first is simply the difference in the exponent of the size-scaling of the maximum cannibalistic attack rate ($\sigma = 0.6$ in the pulsed model, $\sigma = 2$ in the continuous model). Simulation of the pulsed model with $\sigma = 2$, however, show that the pattern depicted in Fig. 6.4a does not change significantly, and hence the value of $\sigma$ cannot explain the absence of bistability. The second difference is the pulsed vs. continuous size distribution, with the three consequences for cannibalism discussed under point (iv). As pointed out above, we argue in Chapter 4 that the observed bistability in the continuous model may be the consequence of a positive feedback loop created by the Hansel and Gretel effect. Compared to a small cannibal, a large cannibal gains more energy from its victims because its victims are, on average, larger. More energy may result in individual growth. As the large cannibal becomes even larger it gains even more energy, as its victims are even larger, etc. We conjecture that bistability is absent in the pulsed model because with a pulsed size distribution a cannibal of a larger size does not necessarily have access to larger victims, simply because the set of available victim sizes is limited. This conjecture, however, remains to be established more firmly.

In summary, we conclude that most results that we have found are independent of the specifics of the individual-level model. In particular, the results that relate to cannibalistic mortality rather than cannibalistic gain are very robust. Where we found differences between the continuous and pulsed models, this appears to be due to the timing of reproduction and the resulting population size distribution, rather than due to the allocation of energy or other bioenergetic aspects.

### 6.4 Testable hypotheses - the link with empirical data

One of the aims of this thesis has been to develop testable hypotheses which can be compared with empirical data. Physiologically structured population models are defined primarily at the individual level, specifying how the state of an individual changes with time in response to environmental conditions. This approach allows one to develop a model which is easily parameterised because model ‘ingredients’ can be formulated in terms of experimentally measurable quantities, such as size-dependent attack rates, handling times, and fecundity. This contrasts with population models that are formulated at the population level, which are the more commonly used models in ecology. These are necessarily more phenomenological and therefore less testable.

The model developed in Chapter 2 is based on Eurasian perch (*Perca fluviatilis*) feeding on zooplankton. The models in the other chapters are all based on this
model and its parameterisation, and their results should therefore be comparable with empirical data on perch population dynamics. However, by changing model parameters, the model represents the biology of other, related species, such as yellow perch (*P. flavescens*), pikeperch (*Sitzostedion lucioperca*), pike (*Esox lucius*), roach (*Rutilus rutilus*) or arctic char (*Salvelinus alpinus*). At least qualitatively, our model should be able to predict differences between population dynamics of these species by comparing results with different parameter values.

Of the chapters in this thesis, Chapter 2 contains the most extensive comparison between model predictions and empirical data. In a comparison of cannibal-driven and dwarfs-and-giants dynamics with an empirical time series of perch in Lake Abborrtjärn 3 it was shown that the (population dynamic) mechanism of induction of giant growth is remarkably similar in model and data. Thus, our model offers a population dynamic explanation for the occurrence of giant cannibals. Yet, there were also discrepancies between model results and data, particularly with respect to the dynamics following the induction of giant growth. To understand these discrepancies is one of the goals of ongoing research (Persson et al, in prep).

Based on the analyses in Chapter 3 we can make predictions about differences in population dynamics in related cannibalistic species. Chapter 3 focuses on the relation between the size-dependent nature of cannibalism and the emerging population dynamics. A comparison is made between two closely related species, Eurasian perch and yellow perch. The latter species has a higher value of $\delta$ and cannibalism is hence predicted to have a smaller stabilising effect than in Eurasian perch. Comparison of time series appears to confirm this prediction. Further, the chapter contains a more speculative discussion of arctic char population dynamics.

The population model studied in Chapter 5 is simplified to such an extent that it cannot be readily compared with empirical data. In order to obtain tractable results it has been stripped of some biological assumptions such as a juvenile delay (but see appendix 5.B). Yet, it contains mechanistic ingredients, such as the size-scaling of the functional response, which can be parameterised with experimental data. This means that the model predictions can be linked to these parameters. However, comparisons with observations should be made with reservation. Testable predictions cannot be made before a more system-specific model has been developed, tailored for a particular species of interest.

Essentially, Chapter 5 shows that the presence of an ontogenetic niche shift in the life history can result in evolutionary branching. It remains to be shown, however, that this is also the case if the second resource consists of conspecifics. In this case the situation is more complex due to a number of feedback mechanisms between the evolutionary trait and population size distribution. The most obvious difference with the model in Chapter 5 is that with cannibalism the mortality rate in the evolving population depends strongly on the evolutionary trait, which almost certainly has important consequences.
6.5 This thesis in perspective

The ‘discovery’ of giants (Chapter 2) leads to a search image, i.e., the conspicuous pattern of growth curves such as shown in Figures 2.8, 2.9 and 2.10, which allows for testing of predictions. If another population were found exhibiting a similar growth pattern (e.g., LeCren, 1992), our model predicts that a very specific sequence of population dynamic ‘events’ would be associated with the acceleration of giant growth. If time series of the population dynamics are available it can be checked whether the predicted series of events has occurred or not. Alternatively, if a lake contains a ‘stunted’ population, our model predicts that removing the bulk of the cannibal size class results in the emergence of dwarfs and giants. Our model also predicts, however, that the existence of giants is transient, which may limit the interest of fisheries managers. Thus, our model of size-dependent cannibalism and competition provides testable predictions. Besides Eurasian perch candidate species include yellow perch, arctic char, brown trout and pikeperch. Interestingly, giant growth patterns have already been described for arctic char (Hammar, 1998) and ferox trout (Campbell, 1979).

Despite its potentially transient effect, removing the bulk of the cannibal size class may be a manipulation by which fisheries managers can transform a commercially uninteresting, stunted fish population into one with at least some gigantic individuals, interesting for sports fishing. Removing the bulk of the cannibals reduces the cannibalistic mortality rate of small juveniles. The resulting high density of small juveniles leads to a depletion of the alternative resource, but provides the few surviving cannibals with sufficient food to become giants. This manipulation stands in sharp contrast to the standard solution for management of stunted fish populations, which consists of removing the bulk of the small juveniles, in order to release the alternative food, which may increase the growth rate of all remaining individuals.

Chapter 3 presents a frame of reference for a comparison of population dynamics between different species. We argue that most of the results we find depend on the cannibalistic and competitive interactions. We show that these interactions depend heavily on the size-dependent nature of cannibalism (i.e., on $\delta$ and $\epsilon$). Thus, we can compare the size-dependence of different species and use the results of Chapter 3 to make predictions about their population dynamics. We have done this for two closely related perch species (section 3.4.1). For arctic char the values of $\delta$ and $\epsilon$ can be estimated from literature data (e.g., $\delta = 0.15$ and $\epsilon = 0.47$ based on Amundsen, 1994) and together with estimates of $L_1 \approx 100 - 149$ mm and $L_2 \approx 20$ mm this leads to the prediction of cannibal-driven (CD) population dynamics (cf. Fig. 3.5). For such between-species comparisons the same candidate species as mentioned above are relevant, and relevant size-dependent data from these species would prove most useful.

The development of the continuation methodology of Kirkilionis et al. (2001) and the possibility to include infinite-dimensional interaction environments (Chapter 4) may improve the level of analysis of physiologically structured population models considerably. The development of such techniques for ODEs and discrete
Chapter 6 — General Discussion

maps (e.g., Kuznetsov, 1995) has improved the understanding of these classes of models. From a theoretical point of view, using this method gives more insight in the underlying structure of population dynamics than numerical simulations. PSPMs tend to show rather complicated bifurcation patterns, which are hard to disentangle with simulations alone. From an empirical point of view, this development allows to scan parameter space of mechanistic population models for testable predictions, such as bistability. The use of bifurcation diagrams in a manipulative experimental setting has been shown to be fruitful (Costantino et al., 1997). Finally, the continuation method may facilitate the study of evolutionary dynamics of size-structured populations (appendix 5.B).

In Chapter 4 we speculate that the presence or absence of submerged vegetation may effectively lead to a high and low value of the lower limit of the predation window ($\delta$). The mechanism behind this effect would be that vegetation provides a refuge from cannibalism for YOY fish, effectively increasing the minimum size at which victims can be cannibalised. Decreasing the value of $\delta$ may lead to a catastrophic bifurcation which is associated with a dramatic reduction in the maximum size of fish in the population. Thus, the effect of removing vegetation from a lake with a population with a wide size distribution may have detrimental effects for the existence of commercially interesting, large piscivores. Alternatively, this analogy suggests that by introducing vegetation, it may be possible to move a stunted, commercially (and touristically) uninteresting fish population into the piscivorous state. Although the presence of alternative stable states creates interesting opportunities for fisheries managers (Scheffer, 1998; Scheffer et al., 2001), at the same time they pose a potential problem, as the wrong manipulation may bring the population in the unwanted, stunted population state.

Chapter 5 is one of first examples of a mechanistic and hence testable model studied within the adaptive dynamics framework so far. The use of physiologically structured population models in adaptive dynamics may prove to be very fruitful, as PSPMs are easily linked to empirical data, and fit very well into the individual-based setting of adaptive dynamics. Obviously, our model needs more development before rigorous testing is possible, but nevertheless models like this create opportunities for testing the different concepts developed in the theoretical framework of adaptive dynamics, which may increase its credibility as a scientific theory.

The comparison of cannibalism in the pulsed model and in the continuous model (section 6.3) may be a source of testable hypotheses as well. In that section it is argued that the main differences between the results of the two models stems from the different timing of reproduction and the resulting different population size distributions. For example, dwarfs-and-gians dynamics are expected below and above the critical value of $\delta_1$ with pulsed and continuous reproduction, respectively. Although the stunted and piscivorous population states exist with both types of reproduction, bistability is expected only with continuous reproduction. Thus one could compare of cannibalistic populations with contrasting timing of reproduction. Ideally, one would need data on population dynamics of an organism that lives in a gradient of environments from, for example, seasonal to tropical, which
leads to a gradient from pulsed to continuous reproduction. Potential candidates may be found among squid species, some of which are known to be cannibalistic (Sauer et al., 1992; Santos and Haimovici, 1997). Unfortunately, the commonness of cannibalism among cephalopod species is unknown. Some squid species occur in a range from tropical to temperate seas, such as _Loligo noctiluca_, which occurs from New Guinea to Tasmania (Jackson and Moltschaniwskyj, 2001). Although the life cycle of this particular species may be too short (4 months in tropical populations; Jackson and Moltschaniwskyj, 2001) for the environmental seasonality to impose pulsed reproduction, in the class of Cephalopoda suitable species may be found to test the different predictions related to the timing of reproduction.

Finally, in the theoretical context regarding the dynamics of cannibalistic populations, this thesis points to a conceptual aspect of cannibalism which has rarely been made explicit so far: the distinction between cannibalism and infanticide (or: cannibalism without energy gain). Our results suggest that by neglecting the energy gain a modeller may miss out some of the most exciting effects of cannibalism. Interestingly, ‘infanticide’ may be a dynamic effect in the sense that depending on the state of the population, cannibalism may or may not yield a significant gain. This may mislead an ecologist into thinking that the energy gain can be ignored. Obviously, if this is done the alternative population state, in which the gain is substantial, can never be predicted.