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Review Paper

Population dynamic theory of size-dependent cannibalism

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Cannibalism is characterized by four aspects: killing victims, gaining energy from victims, size-dependent interactions and intraspecific competition. In this review of mathematical models of cannibalistic populations, we relate the predicted population dynamic consequences of cannibalism to its four defining aspects. We distinguish five classes of effects of cannibalism: (i) regulation of population size; (ii) destabilization resulting in population cycles or chaos; (iii) stabilization by damping population cycles caused by other interactions; (iv) bistability such that, depending on the initial conditions, the population converges to one of two possible stable states; and (v) modification of the population size structure. The same effects of cannibalism may be caused by different combinations of aspects of cannibalism. By contrast, the same combination of aspects may lead to different effects. For particular cannibalistic species, the consequences of cannibalism will depend on the presence and details of the four defining aspects. Empirical evidence for the emerged theory of cannibalism is discussed briefly. The implications of the described dynamic effects of cannibalism are discussed in the context of community structure, making a comparison with the community effects of intraguild predation.

Keywords: size-dependent cannibalism; structured population models; Eurasian perch; infanticide; energy gain; competition

1. INTRODUCTION

A central hypothesis in community ecology is that the structure of ecological communities is a resultant of the dynamics of the constituting populations, which in turn are determined by the interactions within and between those populations (Polis & Strong 1996). Ecological interactions, such as competition, predation, parasitism, mutualism, etc., hence determine community structure in conjunction with abiotic factors. A mechanistic understanding of the dynamic consequences of ecological interactions is therefore an important goal for ecological theory. Such theory requires (i) a precise description of ecological interactions relevant to a particular ecological system; and (ii) prediction of the potential dynamic consequences of these interactions. For example, investigations into the dynamic consequences of competition have produced some of the most important theories in ecology, e.g. competitive exclusion (Tilman 1982) and competitive coexistence (Armstrong & McGehee 1980; Huisman & Weissing 1999). A second example is the theory of interspecific predation, of which the most notable population dynamic effect is predator–prey cycles (Lotka 1925; Volterra 1926; Rosenzweig 1971), which result from the delayed numerical response of predators to changes in the prey population.

Cannibalism can be seen as a short-circuited predator–prey system, in which predator and prey belong to the same population. It is a common ecological interaction in the animal kingdom (Fox 1975; Polis 1981; Elgar & Crespi 1992) and, because it occurs within a single population, it is one of the simplest of trophic interactions. It has often served as a biological example during the development of mathematical models of age- and size-structured populations from the early 1980s until today (e.g. Gurtin & Levine 1982; Diekmann *et al.* 2003). The literature on population dynamic models of cannibalism (table 1) contains a range of interesting implications of cannibalism for population dynamics. However, a comprehensive overview of the emerged ecological theory is lacking. Our aim is to identify the potential ecological consequences of cannibalism and to relate them to four defining aspects of cannibalism, and thus to contribute to a mechanistic understanding of this ecological interaction.

Cannibalism is often defined as: (i) killing and (ii) eating of conspecifics and both are likely to affect the population dynamics of cannibalistic species. Two perhaps equally important but less obvious aspects of cannibalism are: (iii) size-dependent interactions; and (iv) intraspecific competition. The former is implicated because cannibals are generally larger than their victims (Polis 1981), while the latter is implicated because cannibals and victims are the same species and therefore usually share common resources.

Killing and eating need not both be present in particular cannibalistic species, such as in 'intraspecific scavenging' in anuran larvae (Elgar & Crespi 1992), where the victim has died of other causes, or in 'infanticide' in lions, where the victim is killed but not consumed (Hausfater & Hrdy 1984). It is generally assumed that cannibals can capture only victims that are smaller than some critical body size

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Table 1. *Chronological list of theoretical studies of population dynamic models of cannibalism, classified according to the four aspects of cannibalism mentioned in the text: (i) victim mortality, (ii) energy extraction, (iii) size dependence and (iv) competition. ('+' indicates that an aspect is incorporated and '−' indicates that it is not incorporated. '(+)' indicates that cannibalism is modelled as age-dependent (hence implicitly size-dependent). Column (iv) indicates which vital rate is affected by competition: g, growth rate; m, mortality; f, fecundity.)*

| reference | aspect of cannibalism | | | | population dynamics |
	(i)	(ii)	(iii)	(iv)	
Ricker (1954)	+	−	(+)	−	fixed point, cycles, chaos
Landahl & Hansen (1975)	+	−	(+)	−	fixed point, cycles
DeAngelis *et al.* (1979)	+	+	+	−	within-year size distribution
Botsford (1981)	+	−	+	g	bistability
Gurtin & Levine (1982)	+	+	(+)	m	population control, population cycles
Frauenthal (1983)	+	−	(+)	m	bistability, population cycles
Diekmann *et al.* (1986)	+	−	(+)	−	population cycles
Fisher (1987)	+	−	+	g	bistability
Hastings (1987)	+	−	(+)	−	population cycles, bistability
Hastings & Costantino (1987)	+	−	(+)	−	population cycles, bistability
Van den Bosch *et al.* (1988)	+	+	(+)	−	lifeboat effect, bistability
Van den Bosch & Gabriel (1991)	+	+	(+)	f	cannibalism dampens predator–prey cycles
Hastings & Costantino (1991)	+	−	(+)	−	population cycles, no bistability
Cushing (1991)	+	+	(+)	f	fixed point, cycles, lifeboat effect, bistability
Cushing (1992)	+	+	+	−	control, lifeboat, bistability
Crowley & Hopper (1994)	+	+	+	−	size distribution, stock–recruitment overcompensation
Kohlmeier & Ebenhöh (1995)	+	+	−	+	cannibalism dampens predator–prey cycles
Fagan & Odell (1996)	+	+	+	+	within-season size structure
Costantino *et al.* (1997)	+	−	(+)	−	nonlinear dynamics, chaos
Van den Bosch & Gabriel (1997)	+	−	(+)	f	cannibalism dampens generation cycles
Henson (1997)	+	+	(+)	−	lifeboat effect
Dong & DeAngelis (1998)	+	+	+	g	size distribution, stock–recruitment overcompensation
Henson (1999)	+	−	(+)	−	equilibrium, cycles
Magnússon (1999)	+	+	(+)	+	population cycles
Briggs *et al.* (2000)	+	−	(+)	m	generation cycles
Claessen *et al.* (2000)	+	+	+	gmf	cannibalism dampens cycles and induces size-dimorphism
Lantry & Stewart (2000)	+	−	(+)	−	population cycles
Claessen *et al.* (2002)	+	+	+	gmf	stabilization, dimorphism, gigantism
Claessen & De Roos (2003)	+	+	+	gmf	bistability, gigantism
Diekmann *et al.* (2003)	+	+	+	−	lifeboat effect

owing to morphological limitations such as gape width or the ability of prey to escape from cannibals (Christensen 1996). The upper limit to victim size is often assumed to be a fixed ratio of cannibal size (DeAngelis *et al.* 1979; Cushing 1992; Fagan & Odell 1996; Dong & DeAngelis 1998) but the precise relationship between cannibal size and victim size is rarely known. Notable exceptions are four marine piscivorous gadoids (Juanes 2003), the snow crab *Chionoecetes opilio* (Lovrich & Sainte-Marie 1997), Eurasian perch *Perca fluviatilis* (figure 1; Popova & Sytina 1977; Persson *et al.* 2000), Arctic char *Salvelinus alpinus* (Amundsen 1994; Hammar 1998) and other piscivorous freshwater fishes (Mittelbach & Persson 1998). These studies provide evidence that there is also a lower limit to the victim sizes that cannibals can take, which has been explained in terms of difficulties in the detection and retention of very small prey (Lundvall *et al.* 1999), and evidence that the capture rate reaches a maximum at an intermediate ratio of victim length to cannibal length (Amundsen 1994; Lovrich & Sainte-Marie 1997; Lundvall *et al.* 1999).

There are exceptions to this pattern of size dependence, such as larger individuals falling victim to 'group cannibalism' by smaller ones in *Notonecta* backswimmers (Polis 1981). There is plenty of evidence for competition between cannibals and their victims (Persson *et al.* 2000). Direct resource overlap can be completely absent, however, as in egg cannibalism. However, even in these cases, by reducing the number of individuals that reach the cannibal stage, cannibalism still influences competition.

In 30 articles about the population dynamics of cannibalism (table 1) only aspect (i) is always taken into account. Sixteen studies include aspect (ii) as well. Most studies assume size dependence but only implicitly, by letting cannibalism depend on age. Fifteen articles include competitive interactions as well as cannibalism. Few theoretical studies take all the aspects into account.

In this review we seek to answer the following questions.

(i) What effects may cannibalism have on population dynamics?

Table 2. Population dynamic effects of cannibalism. For each effect, the combination of defining aspects required for its occurrence is indicated.

((i) victim mortality, (ii) energy extraction, (iii) size dependence and (iv) competition.)

effect	aspect of cannibalism				comment
	(i)	(ii)	(iii)	(iv)	
population control	✓				if maximum kill rate sufficient
destabilization	✓		✓		interplay of cannibalism and time delays
	✓		✓	✓	if (i) reinforces (iv)
stabilization	✓		✓[a]	✓[a]	if (i) weakens (iv)
	✓			✓[a]	if (i) weakens (iv)
bistability	✓		✓	✓	by 'indirect positive effect'
		✓			by 'direct positive effect'
	✓	✓	✓		by 'Hansel and Gretel effect'
size-distribution effects	✓		✓		generation separation
	✓	✓	✓		stunted versus gigantic populations
	✓	✓	✓	✓	'dwarfs and giants' bimodality

[a] Not required for stabilizing effect but required for induction of cycles.
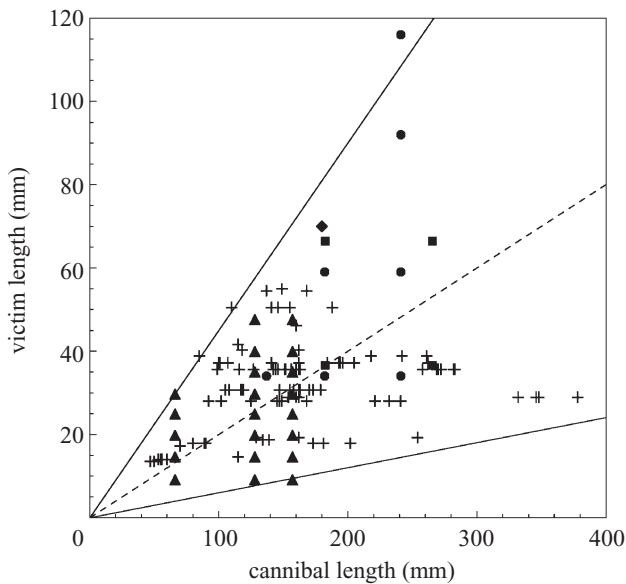

Figure 1. Victim length plotted against cannibal length for observed cases of successful cannibalistic attack in Eurasian perch. Symbols refer to sources of data, see references in Claessen *et al.* (2000). Solid lines: the assumed lower limit ($y = \delta x$) and upper limit ($y = \varepsilon x$) of the cannibalism window, as used in the model in Claessen *et al.* (2000). Dotted line: estimated optimal victim length ($y = \phi x$) for a given cannibal length. Parameters are $\delta = 0.06$, $\varepsilon = 0.45$ and $\phi = 0.2$.

(ii) Which aspects of cannibalism cause these effects?

Classification of the different effects according to the four aspects of cannibalism that cause them provides a framework in which to evaluate particular cannibalistic species. Depending on the specific nature of cannibalism in a particular species, this classification shows which consequences may be expected. Although this review focuses on theory, some empirical evidence supporting the theoretical predictions will also be discussed briefly.

2. CONSEQUENCES OF CANNIBALISM

The consequences of cannibalism as predicted by population dynamic models fall into five categories (table 2). Each is discussed in more detail below.

(a) *Population regulation*

A very basic population dynamic effect of cannibalism is the regulation of population size. This has been shown in several population models in which cannibalism is the only density-dependent process (e.g. Ricker 1954; Diekmann *et al.* 1986; Hastings & Costantino 1991; Cushing 1992). The classical model of Ricker (1954) describes the relationship between the density of the present stock of fishes, $N(t)$, and that of next year's:

$$N(t + 1) = N(t) \, a \, e^{-bN(t)}, \tag{2.1}$$

in which a is the number of offspring produced per adult and b is the cannibalistic tendency of adults. The probability that a newborn escapes cannibalism by adults decreases exponentially with adult density. This model implicitly incorporates size dependence of cannibalism, because all cannibals are (at least) 1 year old and all victims are newborns, but ignores the energy gain from cannibalism. For large values of a the dynamics are complex (May 1974), but abundance can never exceed the maximum of the right-hand side of equation (2.1), that is $N_{max} = a/(b \, e)$. This shows that for all $b > 0$ cannibalism works as a self-regulating mechanism.

In the age-structured population model of Diekmann *et al.* (1986) cannibalism regulates population density if the maximum number of victims that a cannibal can eat in its entire lifetime is sufficiently high. If the cannibalistic voracity is too small, cannibalism fails to control population size because of the saturating functional response, which is absent in Ricker's model. The regulation of population density is obviously a result of cannibalism-induced mortality.

(b) Destabilization

An important question is whether cannibalism stabilizes or destabilizes population dynamics. To answer it we first consider models in which no other density-dependent processes are incorporated (table 1). In the model of Ricker (1954), cannibalism causes over-compensation in the stock–recruitment relationship. The stability of the internal equilibrium of the Ricker model, however, is independent of the cannibalism parameter b, and fully determined by the fecundity parameter a (equation (2.1)). With increasing a, the equilibrium is destabilized by a sequence of period doublings, eventually leading to deterministic chaos—a bifurcation pattern similar to that of the logistic map (May 1974). In the models of Landahl & Hansen (1975) and Costantino *et al.* (1997), cannibalism serves as a mechanism of population control. As in the Ricker model, it also provides a form of density dependence, which, with sufficiently high fecundity, may produce population cycles and possibly chaos. Both models are essentially stage-structured extensions of the Ricker model, with cannibalism modelled as a survival rate of victims that decreases exponentially with cannibal density, and without any other density-dependent process. The model of Landahl & Hansen (1975) includes two larval stages and an adult class, while the model of *Tribolium* population dynamics (Costantino *et al.* 1997) includes larvae, pupae and adults.

It should be noted that, in general, time-delayed density-dependent processes are likely to induce population cycles (Gurney & Nisbet 1985; De Roos & Persson 2003). The continuous-time age-structured population model of Hastings (1987) incorporates a time delay as an egg stage in which individuals are vulnerable to cannibalism but not able to cannibalize, followed by a fixed age interval (the larval stage) in which individuals do cannibalize but are invulnerable themselves. Even with a constant total birth rate and in the absence of non-cannibalistic density-dependent processes, this model produces population cycles with a period approximately that of the total juvenile period. This shows that the combination of density-dependent cannibalistic mortality and a time delay is sufficient to produce population cycles (see also Hastings & Costantino 1987, 1991). Similarly, in the age-structured model of Diekmann *et al.* (1986) cannibalism induces population cycles. In their model the vulnerable life stage (eggs) is assumed to be infinitesimally short and it is followed by an invulnerable non-cannibalistic life stage. Their model incorporates an additional time delay: a juvenile life stage. As in the model of Hastings (1987), the cycle length depends on the length of the non-cannibalistic life stage.

In summary, in models of age-dependent cannibalism without other density-dependent interactions, the interplay between cannibalistic mortality and time delays may induce population cycles.

(c) Stabilization

By contrast, cannibalism may be stabilizing in population models that incorporate other density-dependent processes. Cushing (1991) studies a discrete-time model of cannibalism that has a non-cannibalistic juvenile age class and a cannibalistic adult age class. This model is mechanistically more elaborate than the discrete-time models of Ricker (1954), Landahl & Hansen (1975) and Costantino *et al.* (1997) because it incorporates a nonlinear functional response, an energy gain from cannibalism and competition among adults for an alternative resource. In the absence of cannibalism, the model shows the familiar period-doubling route to chaos. Introducing cannibalism drastically reduces the parameter range in which oscillations occur, showing that cannibalism can have a stabilizing effect. For the case where competition is weak, the model of Cushing (1991) predicts that cannibalism induces population cycles with a period equal to the juvenile delay, corroborating the results discussed in § 2b.

Kohlmeier & Ebenhöh (1995) study an unstructured predator–prey model in which the cannibalistic predator consumes both alternative prey and conspecifics. In the absence of cannibalism the model reduces to the McArthur–Rosenzweig model and predicts predator–prey cycles. If cannibalism is introduced, the cycles are damped, and with a sufficient cannibalistic voracity the internal equilibrium is stable. Age-structured equivalents of this model were studied by Van den Bosch & Gabriel (1991, 1997). In their models, both predator–prey cycles and population cycles caused by time delays resulting from the age structure of the cannibal population can be stabilized by cannibalism.

The model of Claessen *et al.* (2000) incorporates both size-dependent cannibalism and size-dependent competition for an alternative resource. In the absence of cannibalism single-cohort cycles are found, caused by a mechanism described as a size-dependent analogue of R^* competition (Persson *et al.* 1998). Intermediate levels of cannibalism dampen these cycles, resulting in stable coexistence of individuals of all ages. The stabilizing effect works through the killing of competitively superior juveniles by adult cannibals.

A model in which not the victims but the cannibals are competitively superior was studied by Briggs *et al.* (2000). In the absence of cannibalism, the competitive superiority of old larvae induces generation cycles. As long as there is a numerically dominant cohort of old larvae in the population, it suppresses the following cohort by causing high starvation mortality of young larvae. A new successful cohort cannot emerge until the old larvae have matured into the next life stage, relaxing competition. In contrast to the results of Van den Bosch & Gabriel (1997) and Claessen *et al.* (2000), Briggs *et al.* (2000) found that cannibalism increases the region of parameter space in which generation cycles occur. In their model the life stage that is competitively superior (the old larvae) is also the most cannibalistic. Introducing cannibalism hence does not remove the mechanism causing generation cycles, but reinforces it.

In summary, in systems where population cycles are induced by density-dependent effects other than cannibalism, cannibalism can stabilize these cycles. Specifically, this occurs if cannibalistic mortality weakens the mechanisms causing population cycles.

(d) Bistability

Cushing (1991) argues that 'the interplay between positive and negative effects [of cannibalism] can result in multiple steady states' (p. 48). The negative effect of cannibalism is the mortality of victims. The positive effects

of cannibalism can be subdivided into direct and indirect positive effects and both can lead to multiple stable states.

First, the indirect positive effect of cannibalism is mediated through competition for shared resources. In Fisher's (1987) discrete-time model, cannibalism is restricted to 1 year olds feeding on young-of-the-year (YOY) with an attack rate that is assumed to be an increasing function of cannibal body size. Competition affects growth and occurs within the YOY age class only, determining the body size of 1 year olds. The cannibalistic mortality rate is the product of: (i) the number of cannibals; and (ii) their *per capita* cannibalistic attack rate, mediated by body size. Both depend indirectly on the size of the previous YOY cohort. If the effect of YOY abundance on (ii) outweighs the effect on (i), there is a negative relationship between YOY abundance and next year's cannibalistic mortality. This translates into a positive relationship between consecutive YOY numbers, and hence results in a positive feedback loop. This is the case only if the cannibalistic activity increases sufficiently fast with cannibal body size. Thus, from the interaction of cannibalism, competition and individual growth, a positive feedback loop can emerge, which induces bistability. It should be noted that the indirect positive effect does not benefit the cannibal itself, but benefits the potential victims that survive. Botsford (1981) found bistability induced by a similar interplay of cannibalism, competition and growth.

Second, the direct positive effect of cannibalism arises from the energy extracted from consuming conspecifics. Through its effects on fecundity and survival, the energy gain from cannibalism enhances the production of new victims. If the production of new victims outweighs the victim deaths, cannibalism may induce a positive feedback loop and cause bistability (Cushing 1991, 1992; Van den Bosch *et al.* 1988). A special case of bistability caused by the direct gain of cannibalism is the 'lifeboat mechanism'. It enables a cannibalistic population to persist under food conditions in which a non-cannibalistic but otherwise identical population would go extinct. Under these conditions there are hence two stable states, the extinct state and the persistent state, separated by a saddle point. The lifeboat effect amounts to a positive feedback, which results from the costs of cannibalism (e.g. additional mortality) being smaller than the benefits (e.g. additional reproduction). For a population in which juveniles are victims and adults are cannibals and in which juveniles consume an external resource inaccessible to adults, Van den Bosch *et al.* (1988) and Diekmann *et al.* (2003) determined the conditions that give rise to the lifeboat effect. One essential condition for the lifeboat effect is that victims grow in energy content between their birth and the average age at which they fall victim to cannibalism. With a modified version of Cushing's (1991) discrete-time model, Henson (1997) showed that if the density of alternative food fluctuates periodically (by external forcing), such that, repeatedly, food is scarce during a couple of years, a cannibalistic population may persist while a non-cannibalistic population goes extinct. She found that this can occur even if the expected energy gain from cannibalizing a single juvenile is insufficient to produce a single new offspring.

The expected lifetime energy gain from cannibalism depends on the size and abundance of potential victims but also on the body size of the cannibal itself, which determines the range of victim sizes it can consume (figure 1). Claessen & De Roos (2003) found that, for certain parameter values and depending on initial conditions, a size-structured cannibalistic fish population can converge to either a 'stunted' state, with small ultimate body sizes, or a 'piscivorous' state, with giant ultimate sizes. Underlying the bistability is the interplay between cannibal body size and energy gain from cannibalism: (i) a larger body size results in a larger cannibalistic energy gain; and (ii) an increased energy gain results in increased growth. Because the bistability is the result of the cannibals 'sparing' their victims until they are more nutritious, it was termed the 'Hansel and Gretel' effect.

In summary, alternative stable states can be induced by direct (via cannibalistic energy gain) and indirect (via competition) positive effects of cannibalism. Whereas the latter can occur in models of infanticide (as well as of cannibalism), the former is possible only in models of cannibalism that incorporate an energy gain.

(e) *Size-distribution effects*

Effects of cannibalism on the population size distribution have received much less attention than its effects on stability. It has been observed that cannibalism (Hastings 1987) or the combination of cannibalism and competition (Briggs *et al.* 2000) can lead to almost discrete generations in continuous-time age-structured population models (i.e. generation separation). Also, recall that cannibalism-induced bistability is often associated with profound size-distribution effects.

Size-structured models show that there can be strong interplay between cannibalism and the population size distribution, with implications for individual growth trajectories. Based on empirical evidence DeAngelis *et al.* (1979), Fagan & Odell (1996) and Dong & DeAngelis (1998) assume that cannibalism is possible only if the ratio of victim length to cannibal length is below a critical value (0.625, 0.4 and 0.73, respectively). These authors and Crowley & Hopper (1994) focus on the within-season dynamics of a single cohort of YOY individuals. They find nonlinear effects of the initial size distribution on life history in terms of age at maturation and survival to maturation (Fagan & Odell 1996), or on growth rate and final size distribution (DeAngelis *et al.* 1979; Crowley & Hopper 1994). DeAngelis *et al.* (1979) set out to test the effect of alternative food on the short-term dynamics of a single YOY cohort of cannibalistic largemouth bass (*Micropterus salmoides*). Both experiments and model analysis showed that not the presence or absence of alternative food, but slight differences in the initial size distributions were decisive for the dynamics of the cohorts. In the case of a wider size distribution only a very few, but very large, individuals remained at the end of the season, whereas with a narrower distribution a larger number of smaller individuals survived. Because these studies focus on within-season dynamics, the implications for long-term population dynamics remain unclear.

The interplay between size-dependent cannibalism and competition can result in population cycles with a marked bimodal size distribution (Claessen *et al.* 2000). These cycles originate when cannibalism is potentially strong but, owing to size-dependent or other constraints, fails to dampen generation cycles caused by size-dependent

competition. Every 'generation' then consists of two distinct size classes: a dense class of dwarf-sized individuals and a sparse one of giants. Giants have a predominantly cannibalistic diet, while dwarfs feed mostly on the alternative resource. This type of dynamics depends critically on the size-dependent nature of cannibalism.

3. THEORY AND EMPIRICAL EVIDENCE

A logical step following a summary of theoretical predictions is to consider the empirical evidence for or against them. We do this briefly, by focusing on studies that specifically address the theory reviewed here.

Two ways in which cannibalism can have a destabilizing effect (via its interplay with time delays, or via its interplay with size-dependent competition; table 2) are supported by empirical evidence. First, experiments with the *Tribolium* system have confirmed that the nonlinear cannibalistic interaction in an age-structured population can induce complex dynamics, including chaos (see § 2b) (Costantino *et al.* 1997; Benoît *et al.* 1998; Dennis *et al.* 2001). This was also shown by Higgins *et al.* (1997) who obtained a good fit of a stochastic population model to a long-term time series for the Dungeness crab (*Cancer magister*). An important result in their work is that the destabilizing effect of cannibalism is enhanced by its interaction with environmental perturbations. Second, in a study of the Indian meal moth (*Plodia interpunctella*) the best fit to the observed time series was provided by a model that included both asymmetric competition and cannibalism (Briggs *et al.* 2000). Although it does not directly confirm the destabilizing effect of cannibalism through reinforcement of the competitive asymmetry, it does suggest that the interplay between size-dependent competition and cannibalism determines the population dynamics of this species, as was also found by Bjørnstad *et al.* (1998).

A criterion derived by Van den Bosch *et al.* (1988) (see also Henson 1997; Diekmann *et al.* 2003) allows one to calculate for a particular species whether cannibalism can work as a lifeboat mechanism. Empirical estimates of the criterion have not been made, so at present there is no evidence for the existence of the lifeboat effect. However, a study of the copepod *Cyclops abyssorum* suggests that the energy gain from cannibalism may be crucial for population persistence through periods of low alternative food availability (Van den Bosch & Santer 1993).

A detailed comparison between model predictions and field data on Eurasian perch was reported in Claessen *et al.* (2000). Owing to size-dependent constraints the potential of cannibalism to stabilize generation cycles was predicted to be limited. As discussed in § 2e, the loss of stability was predicted to be associated with the emergence of gigantic cannibals in the population. Indeed, in the observed time series, a period of stability, during which stunted cannibals controlled the competitively superior recruits, was destabilized and followed by a period of intense competition. The moment of destabilization was marked, as predicted, by the emergence of gigantic cannibals. Together with the results of DeAngelis *et al.* (1979) and LeCren (1992) this lends strong support to the discussed effects of cannibalism on population structure.

Further empirical evidence for strong effects of cannibalism on the population size distribution, specifically revealing the importance of cannibalistic energy gain (i.e.

the 'Hansel and Gretel' effect), was presented by Persson *et al.* (2003). In a 10 year time series of a whole-lake food web they found that the perch population switches between two alternative phases. One of them is characterized by low YOY survival resulting from cannibalism, low energy gain from cannibalism and many but stunted cannibalistic adults. The other phase has high YOY survival, a high gain from cannibalism and few but gigantic cannibalistic adults. The difference between the phases cascades down the food web to the zooplankton and phytoplankton communities. Although these are not alternative stable states, they are reminiscent of the 'stunted' and 'piscivorous' population equilibria predicted by Claessen & De Roos (2003). Persson *et al.* (2003) showed that despite their low number the gigantic cannibals produced larger pulses of offspring than when the population was dominated by many stunted cannibals, an effect that was unequivocally shown to depend on the energy gain from cannibalism. Together, these data and the model results show that details in the individual life history may have substantial consequences for the dynamics of the population and community as a whole.

The effects of cannibalism are predicted to depend to a large extent on the rate of cannibalism. The empirical observations of the dynamic effects of cannibalism described above indicate that cannibalistic rates in many species are sufficient to have an impact on population dynamics.

4. MECHANISTIC THEORY AND COMMUNITY STRUCTURE

We have identified four aspects that together define cannibalism and have reviewed their individual and collective dynamic consequences (table 2). This review shows that it is necessary to analyse an ecological mechanism in detail because its consequences may depend on how its defining aspects interact with each other. In addition, our review highlights the importance of considering the entire life history, as the ecological role of an individual is likely to change during its life history. This is illustrated by the question of whether cannibalism has a stabilizing or destabilizing effect. The answer depends on: (i) whether or not competition is present in the system; and, if it is, (ii) whether the potential victims of cannibalism are competitively superior or inferior.

Summarizing, we conclude that (i) quantitative data on the different aspects of cannibalism, including the role of body size in both cannibalism and competition, are crucial for predicting the population dynamic effects of cannibalism for any particular species. (ii) The inclusion of the energy gain from cannibalism can change predictions of population and even food-chain dynamics. Deceptively, an energy gain from cannibalism ('infanticide') can be a dynamic effect because the cannibalistic gain depends on the state of the population. This may mislead an ecologist into thinking that the energy gain can always be ignored. (iii) The consequences of cannibalism for population dynamics depend to a large extent on its interplay with (size-dependent) competition and time delays. This highlights the importance of considering ecological interactions in conjunction.

Having thus reviewed the population dynamic consequences of cannibalism in single- and two-species models, we can return to the broader perspective and ask ourselves

what the implications are for the influence of cannibalism on community structure. The community effects of cannibalism have not been addressed explicitly in the theoretical literature, presumably because the complexity of the (structured) cannibalistic-population models makes extensions to multi-species systems a daunting task. We can, however, make a comparison with models of intraguild (IG) predation, an interaction that is closely related to cannibalism, and usually modelled with simpler models. IG predation is defined as predation among interspecific competitors and usually modelled as a three-species configuration where the IG predator consumes both a basic resource and another consumer of that resource (Holt & Polis 1997). Such a three-species 'omnivory' community responds differently from classic food chains to enrichment. First, there is the possibility of bistability (Diehl & Feißel 2000; Mylius *et al.* 2001; Kuijper *et al.* 2003). Second, at high productivities, the IG predator tends to outcompete the IG prey, leading to extinction of the latter, as shown by the same authors. Further, in combination with predator-dependent functional responses, a food web with IG predation is unlikely to show trophic cascades (Hart 2002). The work of Kuijper *et al.* (2003) shows that, when the link between the IG predator and the basic resource is weak, IG predation has a stabilizing effect on the food-web dynamics.

Cannibalism can be seen as a special case of IG predation in which the IG predator and the IG prey belong to the same species. There are also analogies between the dynamic effects of cannibalism and those of IG predation. By different mechanisms, cannibalism can give rise to multiple attractors. When the cannibalistic population is an important species in the community, as in the case of freshwater or marine top piscivorous fishes, such bistability may extend to the whole community. Associated with bistability is the risk of catastrophic collapse, with obvious implications for the exploitation of such ecosystems (Scheffer *et al.* 2001; De Roos & Persson 2002). Although the cannibalistic analogue of extinction of the IG prey at high productivities is not possible, the situation where cannibals can outcompete their victims has, however, been studied, and leads to generation cycles enhanced by cannibalism (Briggs *et al.* 2000). The stabilizing effect of IG predation may be valid for cannibalism as well. In the form of cannibalistic self-limitation (regulation) or stabilization via a reduction in the abundance of competitively strong victims, cannibalism tends to reduce the impact of the cannibalistic species on other species in the community, i.e. relieving competition and/or IG predation. The strongly nonlinear density dependence and time-lags caused by cannibalism, however, imply that ecological systems with cannibalism are prone to nonlinear population dynamics and in particular may undergo transitions among different types of dynamics in response to changing conditions (Dennis *et al.* 2001). As stressed by Higgins *et al.* (1997), when nonlinear interactions such as cannibalism are combined with environmental perturbations, the dynamic effect of the deterministic mechanisms can be amplified, producing large fluctuations where in the absence of stochasticity an equilibrium would be found.

Finally, a phenomenon of special interest in the context of community structure is that cannibalism makes trophic structure a variable: as giant cannibals appear and disappear in a population, the length of the food chain increases and decreases accordingly, with effects cascading down to the lowest levels (Persson *et al.* 2003). Correspondingly, a recent review showed that the inclusion of conspecifics in the diet resulted in an increased mean trophic breadth in several piscivorous fish species (Juanes 2003). Whether the effects of cannibalism reviewed here carry over to more complex communities remains a challenge to be addressed in future theoretical work. Also, the roles of other complicating factors such as spatial or genetic structure and the presence of two sexes remain unresolved issues. However, the observation of many of the described effects in lake and marine ecosystems shows that the predicted effects of cannibalism are robust to at least some level of complexity.

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