

Predicting shifts in dynamics of cannibalistic field populations using individual-based models

Lennart Persson^{1*}, André M. de Roos² and Andrea Bertolo^{1†}

¹Department of Ecology and Environmental Science, Umeå University, SE-90187 Umeå, Sweden

²Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, POB 94084, NL-1090 GB Amsterdam, The Netherlands

The occurrence of qualitative shifts in population dynamical regimes has long been the focus of population biologists. Nonlinear ecological models predict that these shifts in dynamical regimes may occur as a result of parameter shifts, but unambiguous empirical evidence is largely restricted to laboratory populations. We used an individual-based modelling approach to predict dynamical shifts in field fish populations where the capacity to cannibalize differed between species. Model-generated individual growth trajectories that reflect different population dynamics were confronted with empirically observed growth trajectories, showing that our ordering and quantitative estimates of the different cannibalistic species in terms of life-history characteristics led to correct qualitative predictions of their dynamics.

Keywords: nonlinear dynamics; individual-based model; cannibalistic capacity; cannibalistic population dynamics; growth curve predictions; rule of thumb

1. INTRODUCTION

Nonlinear, ecological models that describe entire populations as trophic units predict that populations may exhibit shifts in dynamics from equilibria to cycles, or even chaos (May 1976; Ellner & Turchin 1995; Costantino *et al.* 1997; Fussmann *et al.* 2000; Turchin & Ellner 2000). Empirical tests of *a priori* model predictions are, however, restricted to a few, tightly controlled laboratory systems of moderate complexity (Costantino *et al.* 1997; Fussmann *et al.* 2000; McCauley *et al.* 1999). Evidence from field populations is based on fitting population dynamic time series to estimate model parameters (Ellner & Turchin 1995; Costantino *et al.* 1997; Turchin & Ellner 2000; Turchin *et al.* 2000; Turchin & Hanski 2001; Björnstad *et al.* 2002), an approach that is open to alternative explanations. Using a modelling approach, which is explicitly based on individual life histories (Metz & Diekmann 1986; de Roos 1997; Claessen *et al.* 2000), we predict the shifts in dynamics occurring in field populations of cannibalistic fishes, where the community is shaped by complex interactions among individuals with different body sizes. Our study considers the dynamics of cannibalistic populations where cannibals generally share a common resource with their victims (Polis 1988; Claessen *et al.* 2000; Persson *et al.* 2000). Predicted and empirically observed population dynamics are traced via changes in individual growth of different year cohorts. We argue that even shifts in dynamics of complex ecological systems can be predicted on the basis of relatively simple rules of thumb, and that modelling approaches explicitly based on individual life histories are pivotal for deriving these rules as well as for unravelling the mechanisms causing the shifts.

2. METHODS

We assembled time-series data for three cannibalistic fish populations extending at least 8 years and where the fish community was essentially a one-species system with no other piscivorous interactions than cannibalism. The systems included a lake population of yellow perch (*Perca flavescens*) (Sanderson *et al.* 1999), a lake population of Eurasian perch (*Perca fluviatilis*) (Persson *et al.* 2000, 2003) and a stream population of northern pike (*Esox lucius*) (Persson *et al.* 2004a). Sampling of Eurasian perch was based on intensive trap fishing including estimates of absolute population densities (mark-recapture) between 1991 and 2003 (Persson *et al.* 2000, 2004b). Age and growth of individual fishes were determined by calculating the size of the fish backwards in time using opercular bones. Northern pike were sampled by electrofishing during the pike spawning season (February to April) between 1985 and 1992 (Persson *et al.* 2004a). Pike age was assessed by scale analyses. Age determination was confirmed by comparing scale analyses conducted on the same tagged individuals in different years. The abundance and size structure of the yellow perch population was based on a combination of trapping with fyke nets, beach seines and minnow traps and hydroacoustic surveys (see Sanderson *et al.* 1999). Because of strong cohort dominance in this system (see § 3), mean growth rates of cohorts could be determined from length distributions. We predicted population dynamics based on the ‘cannibalism window’ describing (i) the lower limit for victim size below which a cannibal of a specific size does not encounter (see) victims because of the latter’s small size, and (ii) the upper limit above which the cannibals cannot capture victims because of escape abilities of victims or gap morphological constraints in the cannibal (Claessen *et al.* 2002; Persson *et al.* 2004b). In addition, we provide data on hatching size, the size at which individuals switch to piscivory, and maximum length.

The direct comparison between observed and predicted population dynamics included coefficient of variation (CV) in mean individual size over time and individual growth rates of different cohorts. The comparison thus included both individual and

* Author for correspondence (lennart.persson@eg.umu.se).

† Present address: Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P.500, Trois-Rivières, Québec G9A 5H7, Canada.

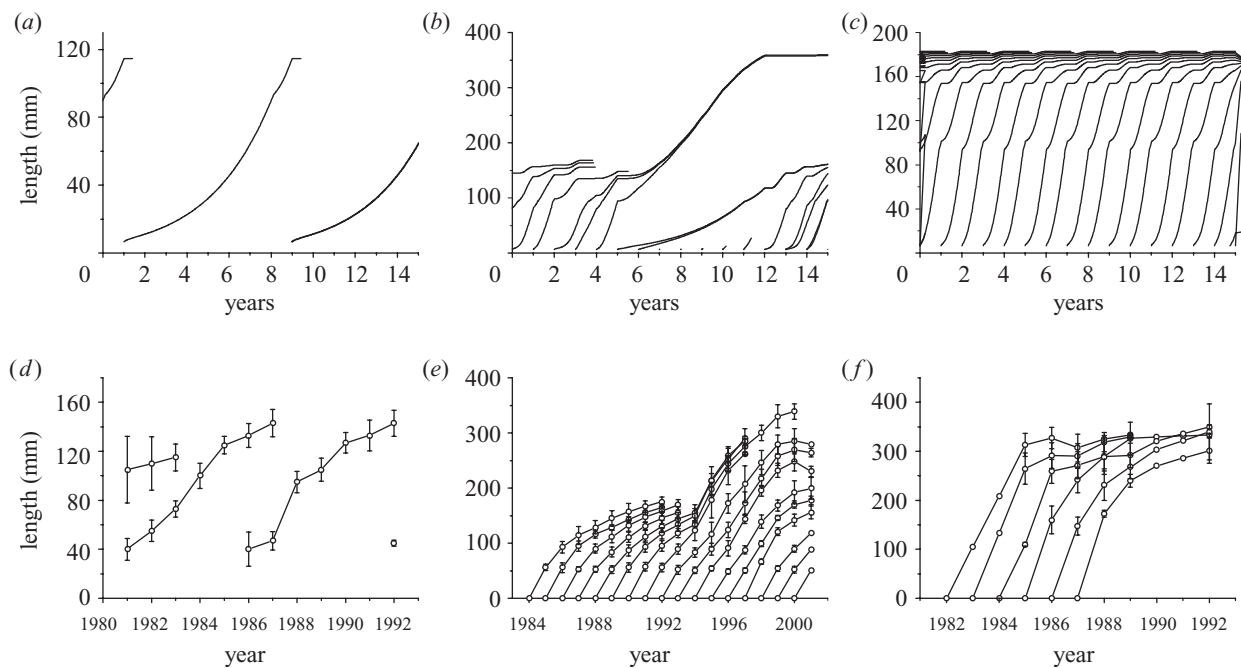


Figure 1. (*a-c*) Predicted growth trajectories of cannibalistic populations with a lower and upper victim–cannibal size ratio, respectively, of (*a*) 0.08 and 0.4 (cohort competition), (*b*) 0.056 and 0.45 (cannibal driven–cohort competition), and (*c*) 0.03 and 0.7 (cannibal driven) (see table 1). (*d-f*) Growth trajectories of different age cohorts of (*d*) yellow perch, (*e*) Eurasian perch, and (*f*) northern pike; based on Sanderson *et al.* (1999), Persson *et al.* (2003) and Persson *et al.* (2004a). Model parameters other than the lower and upper size limits are based on data from Eurasian perch (Claessen *et al.* 2002). Growth trajectories of Eurasian perch and northern pike are based on readings of operculum bones (Eurasian perch) or scales (northern pike) where error bars are ± 1 s.d. For sample sizes of less than four, no error bars are given. Growth trajectories (mean ± 1 s.d.) of yellow perch are based on length frequency data showing dominating cohort.

population level information, and was based on predictions about population dynamics of a physiologically structured population model. Physiologically structured population models are based on a two state description: an *i*-state which represents the state of the individual in terms of a collection of characteristic physiological traits (size, age, sex, energy reserves, etc.) and a *p*-state which is the frequency distribution over the space of possible *i*-states (Metz & Diekmann 1986; de Roos 1997; Claessen *et al.* 2000). A complete derivation of model assumptions including parameterization can be found in Claessen *et al.* (2000). In the model, all processes are assumed to be continuous except reproduction, which is assumed to take place once a year (see Claessen *et al.* 2000). Deriving the individual level functions essentially involves deriving functions for size-dependent metabolism and food gathering, functions describing allocation of energy intake to somatic and gonad growth, respectively, and functions for starvation mortality (see Persson *et al.* 1998; Claessen *et al.* 2000). Two size-dependent functions describe the interactions between cannibals, victims and their resources. One function relates to the interaction between the consumer and the resource (zooplankton) that is shared between cannibals and victims (Claessen *et al.* 2000). The second function describes the interaction between cannibals and victims as a function of the body size of both. The ‘cannibalism window’ determines all size combinations of cannibals and victims for which cannibalistic interactions are possible (Claessen *et al.* 2000; Persson *et al.* 2004b).

Parameters used for the physiologically structured model were based on perch values except the parameters describing the rate by which the lower and upper size boundaries increase with cannibal size, which was varied according to species-specific values (table 1). Model runs with different values for other parameters of the

model have shown that the parameter describing the rate by which the lower size boundary increases with cannibal size is the paramount parameter yielding shifts in dynamical regimes. In addition, the overall rate by which the cannibalistic attack rate increases with cannibal size will affect the dynamics and also the maximum length obtained by the cannibal. As the parameter describing the change in this rate is known only for Eurasian perch (Claessen *et al.* 2002), we used the parameter value for Eurasian perch for all three species.

3. RESULTS

Analysis of a physiologically structured population model (Metz & Diekmann 1986; de Roos 1997; Claessen *et al.* 2000), which is based on the explicit modelling of the individual life history, has shown that in particular, the size range of cannibal and victim sizes that allow cannibalistic interactions to take place (the ‘cannibalism window’) strongly determines which kind of population dynamics is observed (Claessen *et al.* 2002). Depending on the width of this cannibalistic window, three basic dynamical regimes can be distinguished. For a small width (i.e. cannibals cannot consume very small victims), the dynamics are characterized by high amplitude *cohort competition-driven* cycles where smaller recruiting individuals out-compete older and larger individuals (Persson *et al.* 1998; Claessen *et al.* 2002). A single, slowly growing cohort dominates the population dynamics, because right after its birth it suppresses resource densities to such low levels that all other cohorts of older and larger individuals die of starvation. Upon maturation it gives rise to the next dominating cohort (figure 1*a*). For a large width, cannibals impose a

Table 1. Life-history characteristics related to cannibalism capacity for three different piscivore fish species.

species	minimum victim–cannibal size ratio	maximum victim–cannibal ratio	size when switching to piscivory (mm)	hatching size (mm)	maximum length (mm)
yellow perch (<i>Perca flavescens</i>)	0.08 ^{a,b}	0.4 ^{a,b}	100–170 ^b	4.8–6.0 ^b	345 ^b
Eurasian perch (<i>Perca fluviatilis</i>)	0.05–0.06 ^{c,d}	0.45 ^{c,d}	110–160 ^b	4.1–6.6 ^b	500 ^b
northern pike (<i>Esox lucius</i>)	0.03 ^e	0.7 ^e	45–100 ^b	6.0–8.0 ^b	1295 ^b

^a Knight *et al.* (1984); ^b Mittelbach & Persson (1988); ^c Claessen *et al.* (2000); ^d Persson *et al.* (2004b); ^e Persson *et al.* (2004a).

high cannibalistic mortality on victims from birth onwards, which prevents strong competition from and among the recruits. Because of the small sizes at which they consume their victims, however, cannibals gain most of their energy from the shared resource. These *cannibal-driven* dynamics lead to an equilibrium or low-amplitude dynamics where different year classes grow at similar rates (figure 1c; Claessen *et al.* 2002). For an intermediate width, cannibals control recruiting victims through heavy cannibalism for some period but this dynamic is intermitted by a dynamic where a strong recruiting cohort breaks through and, by depleting the shared resource, out-competes most of the cannibals. This cohort dominates the system until they mature, whereafter the dynamics return to a cannibal-driven dynamic (figure 1b; Claessen *et al.* 2002). The few adults that survive the recruitment of the strong cohort gain a lot of energy from cannibalism and become ‘giants’, but owing to their low numbers they impose only a negligible mortality on the dominating cohort.

Overall, the dynamics of the model thus shows a shift from competition control to cannibal control with increasing cannibal efficiency including a range with mixed dynamics. As shown in figure 1, the physiologically structured model not only predicts population level dynamics, but also has the advantage of generating predictions about individual-level growth trajectories that can be compared with and tested against empirical data on growth trajectories. Specifically, depending on the width of the cannibalism window, cannibalistic fish populations are hence expected to exhibit distinct and predictable dynamics of the length–age relationship, relating to the extent to which the population dynamics is shaped by either competition or cannibalism.

The three cannibalistic fish species, yellow perch (*P. flavescens*), Eurasian perch (*P. fluviatilis*) and northern pike (*E. lucius*), were ordered according to their minimum and maximum victim–cannibal size ratios (table 1). On the basis of this order of size ratios, we derived the following order in expected degree of cannibal control: yellow perch, Eurasian perch and northern pike, with northern pike having the highest cannibalistic capacity (lowest lower limit and highest upper limit). This order is supported by the facts that (i) the manipulation time for handling prey fishes differs between these species, being longest for yellow perch and shortest for northern pike and (ii) gape width for a specific cannibal size is larger for northern pike than for Eurasian perch and smallest for yellow perch (Mittelbach & Persson 1998). The expectation of a lower cannibal efficiency of yellow perch and Eurasian perch than

northern pike is further borne out in a larger size when switching to piscivory in these two species (table 1). It is noteworthy that the different values for the lower and upper size limits generating different population dynamics in the model (figure 1a–c) were based on estimates for yellow perch, Eurasian perch and northern pike (table 1).

Empirical data on growth trajectories of yellow perch, Eurasian perch and northern pike show that we correctly ordered them with respect to the expected population dynamics. The dynamics of yellow perch was characterized by dominating cohorts, which give rise to new dominating cohorts when maturing (figure 1d). The growth trajectories clearly resemble those of cohort competition-driven cycles (figure 1). Growth trajectories of northern pike did not vary over time. Growth was rapid early on, with individuals quickly approaching an asymptotic size of 330 mm (figure 1f). Growth trajectories thus clearly resemble model predictions of cannibal-driven dynamics (figure 1c), although the model predicted a smaller maximum size than that observed. The latter is probably a result of the fact that the parameter used for overall cannibalistic rate based on Eurasian perch gives an underestimate of maximum size of northern pike (see model description above). Eurasian perch, with life-history characteristics intermediate between yellow perch and northern pike, exhibited growth dynamics shifting between those expected from cannibal control and a phase with the appearance of gigantic individuals that gain most of their energy from strong recruiting cohorts (figure 1e). The observed individual growth trajectories were thus overall in qualitative correspondence with the dynamics in growth trajectories, as predicted on the basis of the three species’ life-history characteristics. This interpretation is further reinforced by the variation in individual mean size, which is expected to be higher for populations driven by cohort competition or a mixture of cannibal-driven dynamics and giants than for cannibal-driven dynamics (Claessen *et al.* 2002). The CV in mean size of yellow perch and Eurasian perch was 0.17 and 0.34, respectively, whereas that for northern pike was only 0.07 (table 2).

4. DISCUSSION

Communities of planktivorous and piscivorous fishes are characterized by complex networks of intra- and inter-specific interactions, which strongly depend on the body size of the organisms involved. Because individuals grow sometimes orders of magnitude in size, the interaction between them changes in strength and may even change in type from competitive to predator–prey during ontogeny

Table 2. CV in mean individual size for individuals 1 year old or older over time, maximum individual size (mm) and length of time series for the three studied populations of piscivorous species.

species	CV	maximum length	time series (years)	source
yellow perch	0.17	175	12 ^a	Sanderson <i>et al.</i> (1999)
Eurasian perch	0.34	180/320 ^b	10	Persson <i>et al.</i> (2003)
northern pike	0.07	500	8	Persson <i>et al.</i> (2004a)

^a Data after the system became dominated by the invading rainbow smelt (Beissner *et al.* 2003) not included.

^b Giant phase.

(Claessen *et al.* 2000, 2002; de Roos *et al.* 2003; Persson *et al.* 2003). Despite these complexities relating to population size structure, previous analyses have shown that the dynamics of these systems may follow simple rules of thumb. In size-structured consumer–resource systems, different types of generation cycles will result, depending on whether juvenile and small, or adult and large, individuals require the lowest level of resource to cover their maintenance requirements, while stable population equilibria are predicted to occur only when individuals are competitively similar. This ‘minimum resource requirement’ rule (Persson *et al.* 1998) is an intraspecific analogue of the well-known R^* -rule governing the outcome of interspecific competition. The predicted generation cycles have recently been shown to be a dominant type of dynamics occurring in many different systems (Murdoch *et al.* 2002). Cannibalistic populations where victims and cannibals share a common prey differ from consumer–resource systems by incorporating size-dependent cannibalism as an additional mechanism. Our analysis shows that even the dynamics of these more complex systems may also be *a priori* predicted on the basis of relatively simple measures of victim–cannibal size relationships. These measures represent an assessment of the extent to which large individuals can balance their disadvantage in the resource competition (expressed by the ‘minimum resource requirement’ rule) with smaller conspecifics by cannibalizing the latter.

A number of field studies have presented evidence for shifts in dynamical regimes. Tests of model predictions and assumptions have, however, in these studies generally been based on statistical fits of data from the system under study at best comparing fits of different models (Ellner & Turchin 1995; Turchin & Ellner 2000; Turchin & Hanski 2001). This leads to a fundamental problem of interdependence between model assumptions and the dynamics of the system to be predicted. By contrast, physiologically structured population models are formulated by explicitly modelling the individual life history, and all assumptions pertain to individual-level processes independent of the system whose dynamics is to be predicted (de Roos 1997; Persson *et al.* 2004b)). Our results illustrate that this modelling approach also has the advantage of generating a wide array of predictions at both the population and individual level, although studies of more populations and of other cannibalistic species will still be needed to corroborate our findings about the predictability of cannibalistic population dynamics. This ability to predict details of dynamics in complex ecological communities will allow more critical analyses of field data. The physiologically structured population model was especially useful to discern the different

dynamics in the field populations, because of its capacity to predict individual growth trajectories. Individual-based approaches may therefore prove to be an indispensable tool to provide more conclusive evidence for shifts in population dynamical regimes outside the limited domain of laboratory populations.

L.P. was supported by the Swedish Research Council and the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning; A.M.d.R. by the Netherlands Organization for Scientific Research; and A.B. by the European Science Foundation.

REFERENCES

- Beissner, E. B., Ives, A. R. & Carpenter, S. R. 2003 The effects of an exotic fish invasion on the prey communities of two lakes. *J. Anim. Ecol.* **72**, 331–342.
- Björnstad, O. N., Finkenstadt, B. F. & Grenfell, B. T. 2002 Dynamics of measles epidemics: estimating scaling of transmission rates using a time series SIR model. *Ecol. Monogr.* **72**, 169–184.
- Claessen, D., de Roos, A. M. & Persson, L. 2000 Dwarfs and giants: cannibalism and competition in size-structured populations. *Am. Nat.* **155**, 219–237.
- Claessen, D., Van Oss, C., de Roos, A. M. & Persson, L. 2002 The impact of size-dependent predation on population dynamics and individual life history. *Ecology* **83**, 1660–1675.
- Costantino, R. F., Desharnais, R. A., Cushing, J. M. & Dennis, B. 1997 Chaotic dynamics in an insect population. *Science* **275**, 389–391.
- de Roos, A. M. 1997 A gentle introduction to physiologically structured population models. In *Structured-population models in marine, terrestrial, and freshwater systems* (ed. S. Tuljapurkar & H. Caswell), pp. 119–204. New York: Chapman & Hall.
- de Roos, A. M., Persson, L. & McCauley, E. 2003 The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecol. Lett.* **6**, 473–487.
- Ellner, S. & Turchin, P. 1995 Chaos in a noisy world: new methods and evidence from time-series analysis. *Am. Nat.* **145**, 343–375.
- Fussmann, G. F., Ellner, S. P., Shertzer, K. W. & Hairston, N. G. 2000 Crossing the Hopf bifurcation in a live predator–prey system. *Science* **290**, 1358–1360.
- Knight, R. L., Margarf, F. J. & Carline, R. F. 1984 Piscivory by walleye and yellow perch in western Lake Erie. *Trans. Am. Fish. Soc.* **113**, 677–693.
- McCauley, E., Nisbet, R. M., Murdoch, W. W., de Roos, A. M. & Gurney, W. S. C. 1999 Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments. *Nature* **402**, 653–656.
- May, R. M. 1976 Simple mathematical models with very complicated dynamics. *Nature* **261**, 459–467.

- Metz, J. A. J. & Diekmann, O. (eds) 1986 *The dynamics of physiologically structured populations. Springer lecture notes in biomathematics*, vol. 68. Heidelberg, Germany: Springer.
- Mittelbach, G. G. & Persson, L. 1998 The ontogeny of piscivory and its ecological consequences. *Can. J. Fish. Aquat. Sci.* **55**, 1454–1465.
- Murdoch, W. W., Kendall, B. E., Nisbet, R. M., Briggs, C. J., McCauley, E. & Bolser, R. 2002 Single-species models for many-species food webs. *Nature* **417**, 541–543.
- Persson, L., Leonardsson, K., de Roos, A. M., Gyllenberg, M. & Christensen, B. 1998 Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theor. Popul. Biol.* **54**, 270–293.
- Persson, L., Byström, P. & Wahlström, E. 2000 Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. *Ecology* **81**, 1058–1071.
- Persson, L., de Roos, A. M., Claessen, D., Byström, P., Lövgren, J., Svanbäck, R., Wahlström, E. & Westman, E. 2003 Gigantic cannibals driving a whole lake trophic cascade. *Proc. Natl Acad. Sci. USA* **100**, 4035–4039.
- Persson, L., Bertolo, A. & de Roos, A. M. 2004a Cannibal-victim size ratios, population dynamics and life-history dynamics in cannibalistic populations. *Oecologia* (Submitted.)
- Persson, L., Claessen, D., de Roos, A. M., Byström, P., Lövgren, J., Svanbäck, R., Sjögren, S., Wahlström, E. & Westman, E. 2004b Cannibalism in a size-structured population: energy extraction and control. *Ecol. Monogr.* **74**, 135–157.
- Polis, G. A. 1988 Exploitation competition and the evolution of interference, cannibalism, and intraguild predation in age/size-structured populations. In *Size-structured populations—ecology and evolution* (ed. B. Ebenman & L. Persson), pp. 185–202. Berlin: Springer Verlag.
- Sanderson, B. L., Hrabik, T. R., Magnuson, J. J. & Post, D. M. 1999 Cyclic dynamics of a yellow perch (*Perca flavescens*) population in an oligotrophic lake: evidence for the role of intraspecific interactions. *Can. J. Fish. Aquat. Sci.* **56**, 1534–1542.
- Turchin, P., Oksanen, L., Ekerholm, P., Oksanen, T. & Henttonen, H. 2000 Are lemmings prey or predators? *Nature* **405**, 562–565.
- Turchin, P. & Ellner, S. P. 2000 Living on the edge of chaos: population dynamics of Fennoscandian voles. *Ecology* **81**, 3099–3116.
- Turchin, P. & Hanski, I. 2001 Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecol. Lett.* **4**, 267–276.