

# Population dynamical consequences of gregariousness in a size-structured consumer–resource interaction

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## Abstract

Many animal species live in groups. Group living may increase exploitation competition within the group, and variation among groups in intra-group competition intensity could induce life-history variability among groups. Models of physiologically structured populations generally predict single generation cycles, driven by exploitation competition within and between generations. We expect that life-history variability and habitat heterogeneity induced by group living may affect such competition-driven population dynamics. In this study, we vary the gregariousness (the tendency to aggregate in groups) of a size-structured consumer population in a spatially explicit environment. The consumer has limited mobility, and moves according to a probabilistic movement process. We study the effects on the population dynamics, as mediated through the resource and the life-history of the consumer. We find that high gregariousness leads to large spatial resource variation, and highly variable individual life-history, resulting in highly stochastic population dynamics. At reduced gregariousness, life-history of consumers synchronizes, habitat heterogeneity is reduced, and single generation cycles appear. We expect this pattern to occur for any group living organism with limited mobility. Our results indicate that constraints set by population dynamical feedback may be an important aspect in understanding group living in nature.

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## 1. Introduction

In many species, individuals grow in size during a significant part of their life (Werner, 1988; Ebenman and Persson, 1988). This growth is usually associated with changes in morphology and metabolics, which in turn affect important ecological properties such as foraging rate, competitive ability and predation risk (for references see de Roos et al., 2003). Hence, in many species, ecological performance or even function is size-dependent (Persson, 1985; Werner, 1988; Persson, 1988; Lundberg and Persson, 1993). The dependence of foraging and competitive ability on size has important consequences for population dynamics. In a size-structured consumer population, size-

dependence in foraging or metabolic properties tends to induce population dynamical cycles driven by the dominance of a single cohort or generation of similar-sized individuals (de Roos et al., 2002; Murdoch et al., 2002; de Roos and Persson, 2003; Murdoch et al., 2003). In this type of population dynamics, which has been coined single generation cycles, a single, large yearclass is able to reduce the resource to such low levels that they themselves barely survive, and all less efficient foragers starve. The growth of individuals of the dominant yearclass is severely slowed down due to within-generation exploitation competition, and the period of these cycles is generally determined by the mortality in the dominant cohort. Single generation cycles have been observed in a variety of natural and lab populations (Murdoch et al., 2002). The characteristics of such cycles depend on the exact relation between size and competitive ability (Persson et al., 1998; de Roos and Persson, 2003).

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The mechanisms that lead to generation cycles have been studied under the assumption that the environment is well-mixed, i.e. all individuals in the population experience an identical environment, with the same resource and predator density, etc. Such a system satisfies the mass-action law (DeAngelis and Rose, 1992; Metz and de Roos, 1992), which states that the system can be fully described in terms of the average densities of each type of particle (individual, resource particle, etc.) if each particle in a population has an equal chance of ‘meeting’ every other particle. This assumption leads to models that are mathematically tractable in so far that numerical methods for their analysis are available (de Roos et al., 1992; Kirkilionis et al., 2001; Diekmann et al., 2003). While few would argue that natural habitats, as perceived by individual organisms, are really homogeneous, the mass-action assumption is often justified on methodological grounds. In many natural systems, individuals interact with the environment on a local rather than on a global scale. A heterogeneous environment offers scope for size diversity among its inhabitants, because it may provide a favorable habitat for more than one size class simultaneously. Recently, van Kooten et al. (2004) studied the effect of relaxing the mass-action assumption in a model of a consumer–resource interaction with a size-structured consumer. They used the mobility of consumers as a measure of mixing; high mobility corresponds to a well-mixed system, decreased mobility relaxes the mass-action assumption. They found that the single generation cycles produced by size scaling of individual characteristics are surprisingly robust to the facilitation of size diversity provided by reduced mixing. Only at strongly reduced mixing did they find increased coexistence of differently sized individuals.

However, reduced individual mobility is only one way to limit the level of mixing in a population. Another mechanism is group living or aggregation of individuals. Group living occurs in many species throughout the animal kingdom, from killer whales (Baird and Dill, 1996) to many bird species (Kenward, 1978; Caraco, 1979a) and is often associated with increased fitness through increased vigilance (Kenward, 1978; Bertram, 1980), foraging efficiency (for extensive references see Roberts, 1996; Krause and Ruxton, 2002), risk dilution (Roberts, 1996; Bednekoff and Lima, 1998) and interference competition (Magurran and Seghers, 1991; Booth, 1995; Krause and Ruxton, 2002). In organisms that deplete their resource, group living can lead to local competition that is stronger than what may be expected on the basis of global population characteristics. This can lead to local overexploitation of resources, which may stabilize global population dynamics (Myers, 1976; de Roos et al., 1991; Basset et al., 1997; Blaine and DeAngelis, 1997; Cuddington and Yodzis, 2000).

The fact that individuals live together in a group evidently implies that they do *not* interact directly with the rest of the population. Hence, an individual’s environment is determined in a large part by the characteristics of the group that it is part of. In this sense, aggregation is

another mechanism, analogous to limited mobility, which can be hypothesized to facilitate size variation in a population. It is this property of group formation, the implicit introduction of a new interaction scale and the relaxation of the mass-action assumption that is central to the current study. Previous studies that address the population dynamical effects of aggregation either deal with small population sizes which may lead to a strong influence of stochasticity (Myers, 1976; Basset et al., 1997; Blaine and DeAngelis, 1997), do not incorporate life-history of individuals (de Roos et al., 1991; Cuddington and Yodzis, 2000), use a resource-dependent spatial movement rule for individuals (Basset et al., 1997), or incorporate other behavioral processes such as interference competition (Cuddington and Yodzis, 2000) which cloud the effect of aggregation *per se* on the dynamics of the population.

We study the population dynamical and life-history consequences of aggregation. We focus on the feedback of such aggregation on individuals through the population dynamics, without assuming a specific mechanism for the aggregation. We vary the level of ‘gregariousness’, the tendency of consumer individuals to form groups. On an individual level, the food deprivation that may result from exploitation competition may lead to reduced, or even negative growth. The size-structured consumer population in our model allows us to study such aggregation-induced effects on the growth trajectories of individuals. In the model we present here, all individuals within each group (or school, as we will use in the following) are considered identical, and experience an identical environment. In addition, we assume that individuals stay in the same school throughout their life. The combination of these assumptions implies that increased gregariousness and hence concentration of individuals in relatively few large schools on one hand gives rise to strong homogeneity. On the other hand, it increases the potential for globally stabilizing spatial heterogeneity to develop, as has been found in other studies (Myers, 1976; de Roos et al., 1991; Basset et al., 1997; Blaine and DeAngelis, 1997; Cuddington and Yodzis, 2000).

## 2. Model formulation

We model the interaction between a size structured consumer and a resource in a spatially structured environment, as developed in van Kooten et al. (2004). We use the parameter set for Eurasian perch (*Perca fluviatilis*) that is used in Claessen et al. (2000), de Roos et al. (2002) and van Kooten et al. (2004). Perch is a well-studied organism, and is a very common species in temperate aquatic systems throughout Europe. In our model, consumer individuals are aggregated in schools. These schools develop and move through space independently, and interact with each other only through their effect on the resource. All individuals in a school are identical, and remain so for the duration of their lives. All individual level processes in the model are

continuous, except for reproduction and movement of consumers through space. Reproduction is a pulsed event, occurring once per growth season. The parameter set stems from central Sweden, where the growth season lasts 90 days due to low temperatures and ice cover during the rest of the year. We will only briefly summarize the basic model formulation and its assumptions. A technical summary of the model, including the population level formulation is in the appendix, for a more detailed discussion of assumptions see Persson et al. (1998), Claessen et al. (2000) and van Kooten et al. (2004). For reference, all parameters of the model are listed in Table 1.

Consumer individuals in our model are characterized by their irreversible mass (all vital organs such as bones, heart, intestines, etc.), reversible mass (fat, muscles, gonads, and all other tissue that can serve as emergency fuel in times of starvation), and their location in space. Energy intake is first used to cover basic metabolism, and any surplus energy intake that is left goes into growth. A fraction of this energy is always converted to irreversible mass, independent of the condition of individuals. Individuals mature upon reaching a threshold irreversible mass. Adult individuals are assumed to spend a larger fraction of acquired energy on reversible mass, due to gonad investments. For the resource consumption we use a type II functional response, with a size-dependent attack rate and a size-dependent handling time. The attack rate is a hump-shaped function of consumer size. Handling time decreases with irreversible mass, due to gape and gut size increases. The energy allocation rule, attack rate and handling time are discussed extensively in Persson et al. (1998) and Claessen et al. (2000), and their functional forms are given in the appendix. The combination of our parameter set with the attack rate, handling time and energy allocation functions leads to a size-based competitive asymmetry, where small individuals are at an advantage compared to large ones (Persson et al., 1998; de Roos and Persson, 2001), because they can persist at lower resource densities.

Reproduction in perch, as in many fish species, is a pulsed event that occurs once per year. At these events, all gonad mass is removed from all adult consumers, and is converted to a number of offspring. Newborn individuals are allocated to a fixed number of newly formed schools, which are added to the population (see the appendix for details).

We model a structured environment which consists of 40 separate resource populations, interlinked in a circular fashion, forming a one dimensional circular space. Each resource grows according to semi-chemostat dynamics, as described in Persson et al. (1998). Semi-chemostat dynamics is presumed to be an appropriate description for a resource population with smaller sizes that are invulnerable to predation. We assume diffusive flow between resource compartments. Consumers feed in the compartment they occupy, but also in the two neighboring compartments. Biologically, this assumption reflects spatial

wandering of schools on time scales smaller than we use for modeling consumer dispersal. Numerically, it avoids extreme differences between adjacent compartments which are likely to introduce numerical artifacts. We model dispersal of consumers as a random probabilistic process. Once per day all schools in the population move. At each opportunity to move, each school has a  $\frac{2}{3}$  chance to stay in the current location, and a  $\frac{1}{6}$  chance each to move one compartment to the left or right. van Kooten et al. (2004) show that this level of mobility can significantly affect life-history and population dynamics.

Upon reproduction, all newborn individuals are divided into a fixed number of equally sized schools. Each of these schools is then assigned a random initial resource compartment. This initial location is independent of the location of all schools that may already be present in the population. The initial location of offspring schools is hence uncorrelated to the location of the parent schools. There is no mixing between schools, and all individuals in a school are considered identical. In other words, *within-school* dynamics is by definition well-mixed. We use this initial number of schools as a measure of gregariousness. High gregariousness means that individuals are concentrated in a few schools, while the limit of low gregariousness is when each school consists of only one individual. We explore the effects of gregariousness on life-history (variability) and population dynamics, under the conditions of low individual mobility as described above.

To test the robustness of our results to our specific assumptions about allocation of newborn individuals to schools, we have repeated our analysis with an alternative allocation scheme. In our original scheme, the number of schools that is added at each reproductive event is fixed. The number of newborns allocated to each of these schools is determined by the total number of offspring produced. This allows us to vary gregariousness by varying the initial number of schools. In the alternative scheme, we keep constant the number of newborns assigned to a school, and let the total number of reproduced offspring determine the initial number of schools. We then vary gregariousness by varying the size of schools of newborn individuals, rather than the number of such schools. Using this alternative newborn allocation scheme does not qualitatively alter the results presented here.

To test whether our results are dependent on the size of the spatial domain, we have repeated our simulations for a full factorial design, testing all combinations of 10, 40 and 400 spatial compartments (SC) and 40, 400 and 1600 schools per yearclass. When we increase the number of compartments, the total resource carrying capacity is kept constant. We then performed autocorrelation analysis on the resource time series (series of  $1.8e4$  days after transients have died out). We report the dominant period and the corresponding autocorrelation coefficient. Furthermore, we report the coefficient of variation (CV) (standard deviation divided by the mean) as a measure of variability. To further explore a trend we find in our factorial design,

Table 1  
Model variables and parameters

Subject	Symbol	Value	Unit	Interpretation	Ref.
Consumer variables	$N$	–	#	Number of consumers in a school	
	$x$	–	g	Irreversible mass of a consumer	
	$y$	–	g	Reversible mass of a consumer	
Season	$Y$	90	day	Length of year	
Ontogeny	$w_b$	$1.8e - 03$	g	Egg mass	Byström et al. (1998), P. Byström (unpublished data)
	$x_f$	4.6	g	Maturation size	Byström et al. (1998), P. Byström (unpublished data)
	$q_J$	0.74	–	Juv. max condition	Treasurer (1981)
	$q_A$	1.37	–	Adult max condition	L. Persson (unpublished data)
	$k_r$	0.5	–	Gonad-egg conversion	
Planktivory	$\alpha$	0.62	–	Allometric exponent	Byström et al. (1998), P. Byström (unpublished data)
	$\hat{A}$	$3.0e + 04$	$L d^{-1}$	Max attack rate	Persson (1987)
	$w_{opt}$	8.2	g	Optimal forager size	Persson and Greenberg (1990)
Handling	$\xi_1$	5.0	$d g^{-(1+\xi_2)}$	Allometric scalar	P. Byström (unpublished data), Lessmark (1983)
	$\xi_2$	–0.8	–	Allometric exponent	P. Byström (unpublished data), Lessmark (1983)
Metabolism	$\rho_1$	0.033	$g^{(1-\rho_2)} d^{-1}$	Allometric scalar	Karås and Thoresson (1992), Kitchell et al. (1977), Elliott (1976), Beamish (1974)
	$\rho_2$	0.77	–	Allometric exponent	Karås and Thoresson (1992), Kitchell et al. (1977), Elliott (1976), Beamish (1974)
	$k_e$	0.61	–	Intake coefficient	Karås and Thoresson (1992), Elliott (1976), Beamish (1974), Solomon and Brafield (1972), Rice et al. (1983)
Mortality	$\mu_0$	0.01	$d^{-1}$	Background rate	Byström et al. (1998), P. Byström (unpublished data), B. Christensen (unpublished data)
	$\mu_j$	Varied	$d^{-1}$	Additional juvenile background rate	
	$q_s$	0.2	–	Starvation condition	
	$s$	1.0	–	Starvation coefficient	
Resource	$r$	0.1	$d^{-1}$	Population growth rate	
	$K$	100.0	$L^{-1}$	Carrying capacity	E. Wahlström (unpublished data), L. Persson (unpublished data)
	$m$	$3.0e - 5$	g	Wet wt 1.0 mm <i>Daphnia</i>	Byström et al. (1998), P. Byström (unpublished data)

we also present results for a simulation with 1600 schools per yearclass and 1600 SC.

### 3. Results

At high gregariousness (40 schools per yearclass, SPY) (Fig. 1a), the population dynamics shows a strong influence of stochasticity. Reproduction occurs each year, and the number of individuals in the newborn cohorts is highly

variable, with most newborn yearclasses being relatively small. Considerable variation in life-histories exists both between and within yearclasses, and a broad spectrum of different sizes is present in the population. Autocorrelation analysis on the dynamics of the model at 40 SPY confirms that there is no dominant periodic component (Table 2). At 40 SPY the environment is characterized by large spatial variation in local resource density (Fig. 2). Accordingly, the variability in life-history of individuals in the different



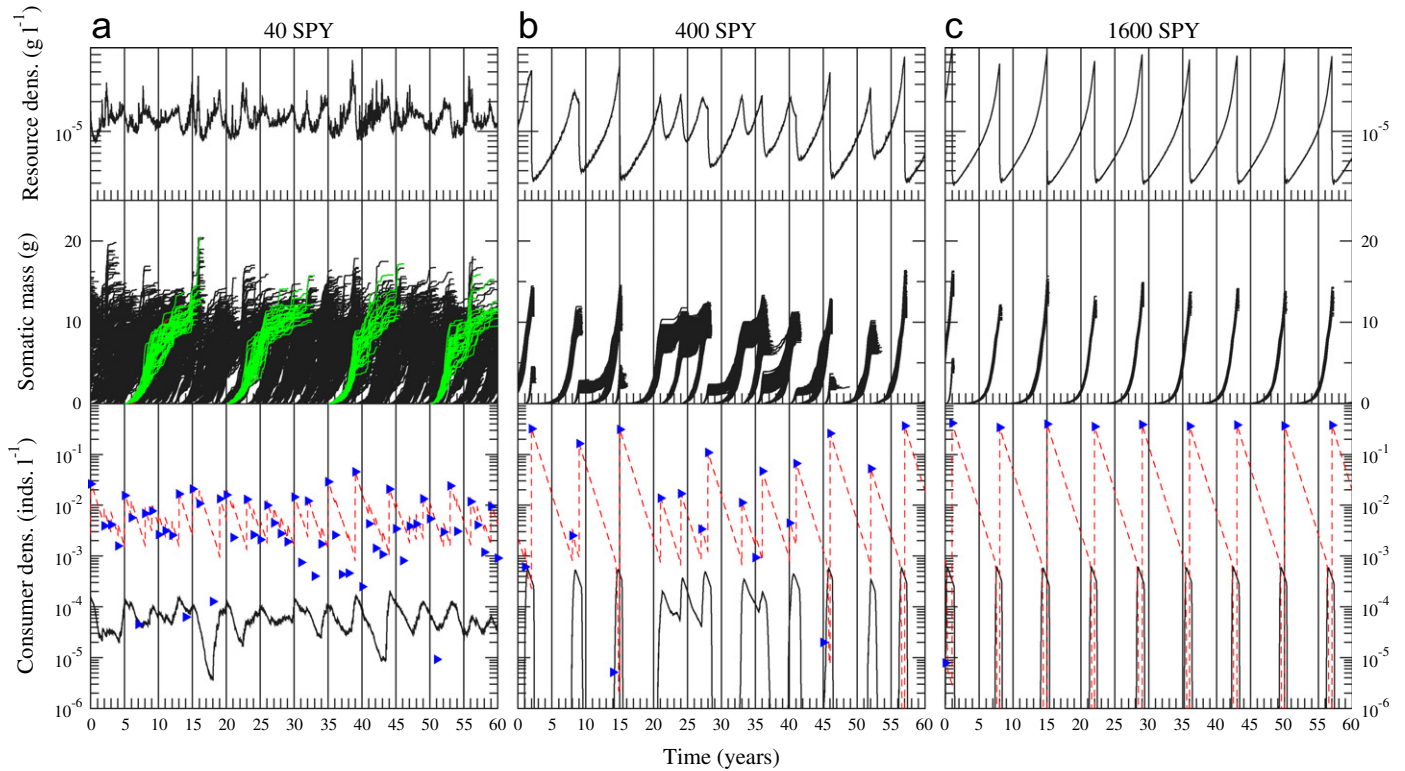


Fig. 1. The dynamics of the model when all newborn individuals are grouped into 40 (a), 400 (b) or 1600 (c) schools, exemplary for the three types of dynamics the model exhibits. Upper panels: global resource biomass. Middle panels: growth curves of each school in the population. For clarity, we have highlighted the trajectories of all schools for each of 4 yearclasses (only at 40 SPY). Lower panels: population dynamics; solid lines—adults, dashed lines—juveniles, triangles—newborns.

Table 2  
Periodicity and stability characteristics of simulations

SPY	No. of spatial compartments			
	10	40	400	1600
1600	160	40	4	1
	0.94098	0.96423	0.84435	*
	7	7	6	*
	1.01458	1.01043	0.61298	0.04325
400	40	10	1	SPY/SC
	0.94536	0.76259	*	ACF maximum
	7	7	*	Dominant period
	0.98024	0.77931	0.08546	CV
40	4	1	0.1	
	0.80278	*	*	
	7	*	*	
	0.89389	0.27184	0.26733	

SPY/SC: number of schools per yearclass/number of spatial compartments. ACF maximum: Highest absolute autocorrelation coefficient found for lags of an integer number of years. Dominant period: the lag in number of years for which the ACF maximum occurs. CV: coefficient of variation, the standard deviation as a fraction of the mean. All statistics are calculated from the resource density of a 200-year time series after transients have died out, with output generated every day. For entries listed as ‘\*’, the (absolute) autocorrelation coefficient decreases monotonically with lag, indicating no periodicity.

schools is large. Although the population continuously consists of a relatively large number of generations (5–10), the total number of schools making up the population is relatively small (200–400 schools) compared to intermediate and low gregariousness (see below). Consequently, the

mean number of schools occupying a resource patch is relatively low. This implies that the chance that a particular resource compartment is relatively empty (and hence ‘undergrazed’) for some time is higher. In addition, because each school consists of a relatively large fraction of the

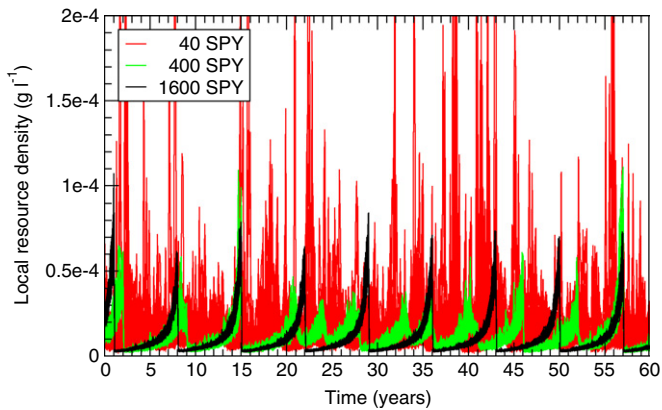


Fig. 2. The local resource density in each of the 40 compartments for 40, 400 and 1600 SPY (schools per yearclass), as shown in Fig. 1. Each line shade is made up of 40 lines, one for each resource compartment.

total consumer population, the chance that a certain resource compartment is ‘overgrazed’ for some time period is also relatively high. The concentration of many individuals in a few schools that occurs at high gregariousness (40 SPY), renders the consumers unable to ‘control’ (maintain at a relatively stable level) the local resource densities. Resource density in many patches is either too low or too high, resulting in high spatial resource variation (Fig. 2). This explanation is supported by the observation that at intermediate gregariousness (400 SPY), the highest variation in local resource density generally coincides with the highest variation in individual life-history.

The spatial resource variation affects the consumer population via two mechanisms. First, high spatial resource variation means a relatively high number of patches with low resource density. Schools that run into such a patch suffer starvation mortality. The numerical effect of this starvation mortality on the total population increases when the particular school represents a larger fraction of the population. Second, individuals from the same yearclass, but in different schools, are likely to encounter strongly different environments during their juvenile period, which leads to highly diversified size-at-age relations among schools within yearclasses (Fig. 1a). Since in perch, maturation is related to size rather than age, this induces variation in the maturation age of consumers from the same yearclass, and hence promotes asynchronous reproduction of yearclasses. The effects of exploitation competition on the consumer population are strongest at high consumer density. Such high densities are attained when all schools from one yearclass reproduce synchronously. Because we assume that consumers only compete via the resource, and small consumers can persist at lower resource density than larger conspecifics, a large enough pulse of newborns can reduce the resource globally to such low levels that all larger individuals in the population starve to death. High variance in maturation age, leading to asynchronous reproduction of schools within a yearclass, prevents such large offspring

pulses, and hence facilitates the persistence of life-history variation.

The induction of asynchronous reproduction through resource heterogeneity is very strong at high gregariousness (40 SPY). If we start a simulation with a population consisting only of one very large yearclass of newborn individuals, the accumulation of life-history variability among the different schools is so large that it induces asynchronous reproduction already within one generation. In only very few generations, the population distribution returns to the highly diversified state shown in Fig. 1a, at 40 SPY. The results for 40 SPY are exemplary for all simulations we have done up to approximately 200 SPY.

At lower gregariousness (higher number of SPY), the effects of resource competition are more clearly visible in the consumer population dynamics. At 400 SPY (Fig. 1b), the population on average consists of only 1 or 2 generations (400–800 schools), but occasionally reaches up to 5 generations. Reproduction occurs in only a fraction of the years. When reproduction occurs, the reproduced generation is in general significantly larger than the generations produced at higher gregariousness (compare Fig. 1a and b, lower panels). The large reproduction pulses lead to strong competition, both within and between yearclasses. Between yearclasses, it leads to the starvation of larger individuals because the newborns reduce the global resource density to very low levels (Fig. 2). Within the newborn yearclass, the reduced resource density generates strong size similarity between schools. No school can grow faster than the rest of its yearclass, due to the competitive disadvantage of being large. The growth rate of the newborns is determined by their mortality rate, which acts to release the scramble competition. When no variation between schools develops at all, the yearclass eventually matures, produces a new dominant offspring generation, and starves as a result. This competition-mediated cycle is known as a single generation cycle (Murdoch et al., 2002; de Roos and Persson, 2003). In general, dynamics at 400 SPY is dominated by the mechanisms leading to single generation cycles. However, Fig. 2 shows that considerable local resource density variation develops within a generation. This leads to ‘imperfect’ generation cycles, where the largest individuals in the population starve, but smaller-sized individuals survive the resource depression (at  $t = 9, 28, 36$  and  $41$  in Fig. 1b). In general we conclude that at this level of gregariousness, individuals within yearclasses show relatively little life-history variation until late in life, whereas life-history trajectories of schools from different yearclasses can be quite dissimilar.

At even lower gregariousness (1600 SPY, Fig. 1c), pure single generation cycles emerge. The population consists of only one generation that lives for seven years, reproduces, and is outcompeted by its offspring in a matter of days. These single generation cycles are the type of dynamics that have been found for purely deterministic models. The high similarity in the life-history of individual schools, both

within and between generations, confirm the absence of stochastic effects in the population at low gregariousness. Spatial resource variation is continuously very low at such low gregariousness (Fig. 2). This dynamics is identical to what is found in non-spatial models (Persson et al., 1998; de Roos and Persson, 2003), or for a highly mobile consumer population (van Kooten et al., 2004).

### 3.1. Robustness and generality

To compare gregariousness in simulations with a different number of spatial compartments (SC), we need to redefine our measure of gregariousness. To this end, we introduce the ratio of SPY to the number of SC. This ratio gives the average number of cohorts added to each SC at each reproduction event. For the simulations presented in Figs. 1 and 2, this ratio is 40, 10 and 1, with high gregariousness indicated by a low value. Table 2 lists some key aspects of time series generated for different combinations of SPY and number of compartments. The simulations presented in Figs. 1 and 2 are on the vertical line at 40 SC. The stabilizing effect of higher gregariousness is apparent from the loss of periodicity and a decrease in the CV. It is clear from Table 2 that a decrease in SC has a similar effect as an increase in SPY. The ratio between the two determines the type of dynamics that the population exhibits. High SPY/SC ratios (40 and 160, the top left entries in Table 2) are characterized by a very strong periodic component with period 7 years. Low SPY/SC ratios ( $\leq 1$ , the bottom right of Table 2) have a strongly

reduced CV, indicating more stable dynamics. For these ratios, autocorrelation of the resource density over time is a monotonously decreasing function, indicating no periodicity. The combinations for which the ratio SPY/SC is either 4 or 10 are in between these extremes, with both reduced strength of periodicity and somewhat more stable dynamics. This analysis furthermore shows that the stabilizing effect of high gregariousness increases strongly in a system consisting of more spatial components. This result, which is suggested in the factorial design (compare the CV for the combinations [40,40] and [400,400]) is further confirmed by the simulation for 1600 SPY with 1600 SC (Table 2). This result has a purely statistical cause. By definition, the global resource density equals the average over the resource densities in all SC and its standard deviation will therefore scale inversely with the square root of the number of compartments.

As a further test of the robustness of these results, we have repeated all simulations using a fixed initial number of individuals per school. Instead of distributing all newborns into a fixed number of schools, we fix the number of newborns per school, and add as many of these schools as is necessary to accommodate all newborn individuals. The initial number of schools (SPY) now depends on the number of individuals in the newborn yearclass. With this alternative handling of newborns, gregariousness is high when newborn individuals are put in large schools (resulting in low SPY), and low if newborns are assigned to smaller schools (and hence a high SPY). The results are qualitatively identical to those with the reproductive

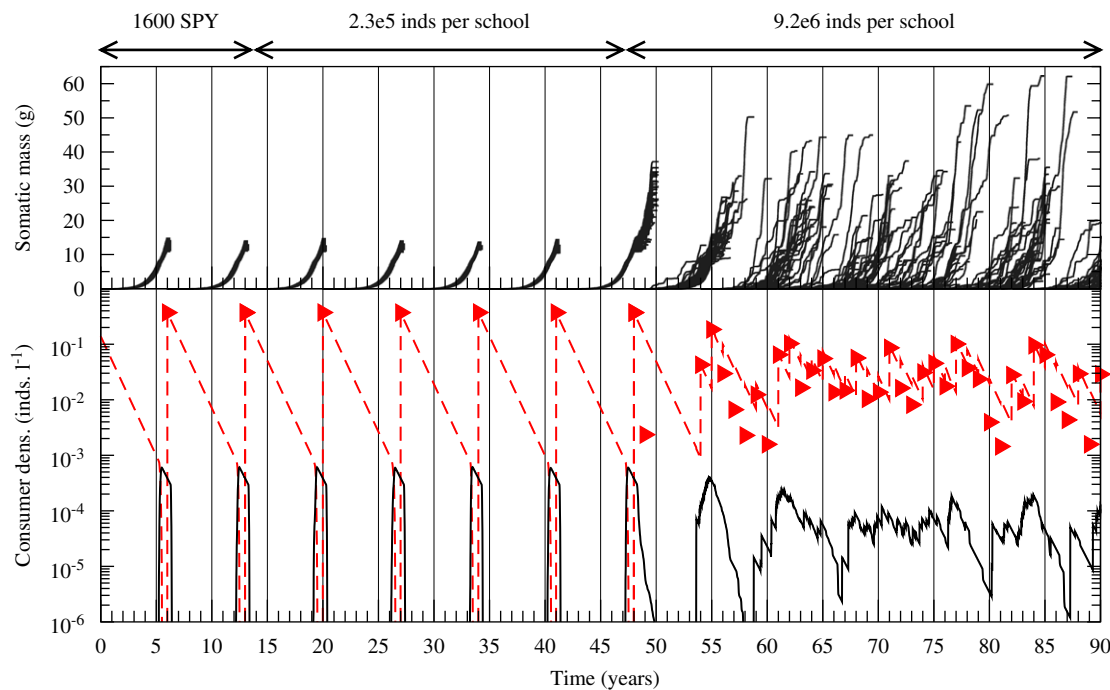


Fig. 3. Illustration of the robustness of results to an alternative allocation of newborn individuals. For  $0 \leq t < 13$ , newborns are distributed equally over 1600 schools. In the interval  $13 \leq t < 47$ , newborn individuals are distributed over a variable number of schools containing  $2.3e5$  individuals each. For  $t \geq 47$ , the initial school size is increased by a factor 40, to  $9.2e6$ . Upper panel: growth curves of all schools. Lower panel: population dynamics; solid lines—adults, dashed lines—juveniles, triangles—newborns.

scheme we have used in all other simulations. As an illustration of the similarity, we present the time series shown in Fig. 3. This simulation starts out identical to the one presented in Figs. 1c and 2 (1600 SPY). However, just before the reproduction pulse at  $t = 13$ , we change the reproductive scheme to the use of a fixed number of newborn individuals per school. We set this number to  $2.3e5$ , equal to the number of newborns divided by 1600. This hence results in 1600 schools in the reproductive pulse at  $t = 13$ . This way, we change the reproductive scheme, but not the gregariousness. This has no effect on population dynamics: the single generation cycle continues undisturbed. At  $t = 47$ , we increase the number of individuals per school by a factor 40, effectively reducing by the same factor the number of schools added to the population in the next reproduction event. This sets the gregariousness equal to that in Fig. 1a (40 SPY). After the first reproductive event, the population dynamics become highly similar to those at 40 SPY when the original reproduction scheme is used.

With the alternative reproduction scheme, we find the same transition from erratic dynamics and strong spatial heterogeneity to globally synchronous generation cycles as gregariousness is reduced. The transition is more abrupt than when newborns are put in a fixed number of schools. This is because the constant school size allocation rule introduces a new interaction between the size of a newborn yearclass and the number of schools in the population. A large reproduction pulse has a strongly homogenizing effect on the resource as well as on the consumer population in both reproduction schemes. In the constant school size scheme, this effect is amplified because a large newborn yearclass increases the number of schools in the population more than a small yearclass. The result is stronger consumer life-history convergence and hence population homogeneity.

#### 4. Discussion

The effect of gregariousness on population dynamics is apparent from Fig. 1. At high gregariousness (40 SPY), the population dynamics are, both locally and globally, strongly affected by stochasticity. This is expressed as highly variable life-history trajectories for schools both within and between generations, and noisy, erratic global dynamics.

With decreased gregariousness, the influence of stochasticity is reduced, life-history variability is reduced, and the generation cycles that are expected for a well-mixed population dominate the population dynamics. At reduced gregariousness, the habitat is highly homogeneous and our model produces single generation dynamics identical to those found at high consumer mobility in van Kooten et al. (2004), and similar to those found in well-mixed physiologically structured models (Persson et al., 1998).

Two mechanisms form the basis of these results. First, we implicitly assume a relation between mobility and the

level of gregariousness. While the mobility at the individual level is independent of the number of schools per yearclass, at the population level the total number of ‘moves’ (the number of schools that change location per time step) increases linearly with the number of schools in the population. Hence, there is an interaction term between the gregariousness and the level of mixing in the population. This effect is present irrespective of which scheme is used to add newborn individuals to the population, a constant number of schools per yearclass or a constant number of individuals per school. This implicit coupling of gregariousness and population mixing is purely a result of the probabilistic movement rule. It is therefore not specific to perch. We expect the phenomenon to occur for any group-living organism with limited mobility compared to the size of its environment. A second factor that contributes to the appearance of the single generation cycles is the global reproduction process. All newborn schools are randomly placed in the environment. At low gregariousness, when there are many schools to distribute, this process dampens local differences, because it decreases the relative difference between patches. This process may act to increase habitat homogeneity and global coupling of population dynamics in species with global reproduction. While truly global reproduction may not be the most common form of procreation, the reproductive process of many aquatic and marine organisms can hardly be qualified as local. Barnacles, mussels, and many other sessile benthic invertebrates have free-floating planktonic larval stages, that become sedentary upon metamorphosis (Gaines and Bertness, 1992; Pawlik, 1992). Many fish species, including perch, produce massive amounts of eggs, and have no or hardly any parental care. In these cases, newly hatched individuals rapidly spread out in the pelagic water column, leading to a weak coupling between hatching (and parent spawning) location and the foraging area of these newly hatched individuals. In the current study, we have not tested the effects of local reproduction. We speculate that it can either dampen or amplify spatial heterogeneity, depending on the reproductive energetics of the consumer. Perch quickly lose their gonad mass to cover maintenance costs when starved, which would most probably lead to a decrease in reproduction in bad resource patches, and hence lead to reduced heterogeneity. For species that first lose somatic mass, and conserve gonads when starved, reproduction and local resource density may be less tightly coupled, possibly leading to different results.

The implicit coupling of the level of mixing and the level of gregariousness explains the mismatch between our results and those found by de Roos et al. (1991), McCauley et al. (1993), and more recently Hosseini (2003). They study population dynamics of models with local reproduction. They find, at low mobility and *no* gregariousness, global dynamics that are strongly stabilized due to spatial asynchrony. In our model system, spatial asynchrony disappears at low gregariousness. Myers (1976) shows that an increasingly clumped distribution of mobility-limited



consumers leads to increasingly stable global population dynamics. However, Myers (1976) defines stability as generation-to-generation population fluctuation. Under this definition, the single generation cycles we observe at low gregariousness are an example of highly stable population dynamics, and increased gregariousness leads to decreased population stability. Other studies that focus on the relation between aggregation, heterogeneity and stability are Basset et al. (1997), Blaine and DeAngelis (1997) and Cuddington and Yodzis (2000). In these studies, aggregation is an emergent result of the spatial movement patterns of individuals. Individuals are together in a certain location because there is plenty of food, for example. Hence, in these studies the effect of aggregation *per se* on population dynamics cannot be assessed. In this work, we can independently study the effects of aggregation of individuals on the dynamics and heterogeneity of the population, because the measure of gregariousness that we use imposes a certain controlled level of aggregation on the consumer population. Our results indicate that a tendency to aggregate does not automatically lead to spatial heterogeneity; for such heterogeneity to develop, aggregation has to be strong enough to counteract the homogenizing effect of exploitation competition.

The strong feedback of aggregation, through the population dynamics, on the life-history of individuals which occurs at intermediate and low gregariousness, adds an important perspective to the existing work on advantages and disadvantages of group living. The scramble competition that on a global scale produces single generation cycles strongly synchronizes population dynamics of the schools in the population. In this population dynamical regime, schools tend to converge in terms of their constituency, mediated through the life-history. Larger schools (larger compared to the other schools in the population) are at a disadvantage, because individuals in such schools suffer increased scramble competition, resulting in slower growth, higher maturation age, and hence longer exposure to relatively high juvenile background mortality. Individuals in smaller schools grow faster due to reduced competition, and hence suffer juvenile background mortality for a shorter period, allowing these schools to catch up with larger schools in terms of the number of constituents. These mechanisms, and the resulting convergence could limit the effectiveness of positive aspects of group living. For example, a larger than average group may benefit from increased vigilance (Caraco, 1979a, b; Magurran and Seghers, 1991; Ranta et al., 1993), but might also grow more slowly and individuals may take longer to reach maturity. In other words, the instantaneous mortality rate of individuals in such a group may be lower as a result of the increased vigilance, but as a consequence of increased scramble competition for food and hence slower growth, these individuals will endure this mortality for a longer time before reproduction.

At high gregariousness, the environmental variability is large, which offers scope for 'lucky' schools, that produce

many offspring, and 'losers' that do not reproduce at all. This is reflected by the wide range of physiological states of the individuals in the population and the sizes of the groups in which these individuals live. In this highly diverse environment, there may be scope for fitness increase through active choice of individuals. However, as Sibly (1983) argues, when free choice is considered from an individual rather than from a group perspective, it generally leads to 'stable' group sizes, where no individual can gain by moving, rather than a situation with 'optimal' group sizes. Along this line of reasoning, free choice of individuals to leave or join schools may be expected to increase habitat homogeneity and hence population dynamical synchrony. This expectation is based on the premises that individuals are ideal (i.e. omniscient) and free to move instantaneously and without a cost (Fretwell and Lucas, 1970). However, since the choice to freely leave and join schools effectively changes the level of gregariousness, such optimal behavior may lead to shifts in global population dynamics that are beyond the scope of even ideal and free (*sensu* Fretwell and Lucas, 1970) organisms.

Further analysis shows that our results hold for larger numbers of SC when gregariousness is defined relative to the number of compartments (i.e. the average number of schools added to each spatial patch per reproductive event). This implies that the transition from stable dynamics to single generation cycles and vice versa can also be induced by manipulating the homogeneity of the environment (i.e. the number of SC). This generalization increases the scope for experimental testing of our results, as the spatial homogeneity of the environment seems to be easier to manipulate than the innate tendency of individuals to form schools.

Concluding, we can state that the tendency of individuals to aggregate (i.e. their gregariousness) has important consequences for both the life-history of individuals, and global population dynamics. The individual variability introduced by limited mobility, as studied by van Kooten et al. (2004) can be counteracted by the statistical averaging effect caused by low gregariousness. Gregariousness, which is often studied from an individual-based perspective strongly affects the individual through the population dynamical feedback loop. While the specific effects of the feedback may change with model assumptions, especially consumer energetics and reproductive process, we expect the presence of a population dynamical effect of gregariousness *per se* to be independent of the specific assumptions.

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## Appendix A. Model formulation

### A.1. Individual state

Individuals are described by their reversible mass ( $y$ ) and irreversible mass ( $x$ ). The ratio of reversible to irreversible mass ( $y/x$ ) is a measure of the physical condition of the individual. For size-dependent processes that are independent of the condition of an individual we use the standardized mass,

$$w = x(1 + q_J). \quad (1)$$

We use a fixed maturation size threshold  $x_f$ . Individuals larger than the threshold allocate a larger fraction of their energy to reversible mass, since they must invest in gonads. For adults, any reversible mass in excess of the standardized mass ( $y - q_J x$ ) is considered gonad mass. At reproduction events, this mass is removed from the adults, and converted to offspring (see below).

Consumers have an attack rate which is a hump-shaped function of standardized mass:

$$A(w) = \hat{A} \left( \frac{w}{w_{opt}} e^{(1-w/w_{opt})} \right)^\alpha. \quad (2)$$

Handling time is an allometric function of standardized mass.

$$H(w) = \xi_1 w^{\xi_2} \quad (3)$$

due to gut size increases, this is a decreasing function (we assume  $\xi_2 < 0$ ). The resource encounter rate of an individual depends on its location  $u$ , and the local resource density  $R_u$ . We assume that consumer individuals spend a fraction 0.6 of their time foraging in their current location ( $P(0)$ ), and 0.2 in each of the neighboring compartments ( $P(\{-1, 1\})$ ) (see van Kooten et al., 2004, for a discussion). This amounts to an encounter rate which is a weighted sum over the current and adjacent resource compartments  $R_{u+\sigma}$ :

$$\eta_u(x) = \sum_{\sigma=-1}^1 A(w) P(\sigma) R_{u+\sigma} m, \quad (4)$$

where  $m$  refers to the mass of one resource individual. This gives us all the components of the type II functional response of the consumers:

$$I_u(x) = \frac{\eta_u(x)}{1 + H(w)\eta_u(x)}. \quad (5)$$

Hence, the total energy intake of an individual is

$$E_{a,u}(x) = k_e I_u(x), \quad (6)$$

where  $k_e$  is the assimilation efficiency. This energy is used to cover maintenance costs, which we assume to scale with total mass:

$$E_m(x, y) = \rho_1 (x + y)^{\rho_2}. \quad (7)$$

This yields net energy:

$$E_{g,u}(x, y) = E_{a,u}(x) - E_m(x, y). \quad (8)$$

Note that  $E_{g,u}(x, y)$  may be negative, in which case it is amended from the reversible mass, and the individual loses weight. If  $E_{g,u}(x, y)$  is positive, individuals allocate a fraction  $\kappa$  to growth in irreversible mass. Juveniles and adults have different allocation rules:

$$\kappa(x, y) = \begin{cases} \frac{1}{(1 + q_J)q_J x} y & \text{if } x \leq x_f \text{ and } E_{g,u} > 0, \\ \frac{1}{(1 + q_a)q_a x} y & \text{if } x > x_f \text{ and } E_{g,u} > 0, \\ 0 & \text{otherwise.} \end{cases} \quad (9)$$

All individuals suffer a size-independent background mortality. Juvenile individuals suffer an additional (constant) mortality on top of this. Starvation mortality affects individuals in bad condition ( $y \leq q_s x$ ). Total mortality is given by

$$\mu(x, y) = \mu_0 + \mu_s(x, y) + \mu_f(x). \quad (10)$$

We model dispersal of consumers as a random probabilistic process. Once per day all schools in the population may move. Each school has a  $\frac{2}{3}$  chance to stay in the current location, and a  $\frac{1}{6}$  chance to move to each of the adjacent compartments.

Reproduction of consumers occurs once per year, at the beginning of the 90-day growth season. At this time, all gonad mass is removed from all adults, and converted to offspring. Thus adult fecundity equals:

$$F(x, y) = \begin{cases} k_r (y - q_J x) / w_b & \text{if } x > x_f \text{ and } y > q_J x, \\ 0 & \text{otherwise,} \end{cases} \quad (11)$$

where  $k_r$  is the gonad-egg conversion factor.

### A.2. Population level

The dynamics of each local resource population is determined by semi-chemostat growth, diffusion, and feeding by consumers. This leads to the total rate of change

$$\frac{dR_u}{dt} = r(K - R_u) + D(R_{u+1} + R_{u-1} - 2R_u) - \sum_{\sigma=-1}^1 P(\sigma) R_u \sum_{j \in A_{u-\sigma}} \frac{A(w_j) N_j}{1 + H(w_j) \eta_{u-\sigma}(w_j)}, \quad (12)$$

where  $A_{u-\sigma} = \{k \mid \text{school } k \text{ is in compartment } u - \sigma\}$ .

For each compartment  $u$ . The first term in Eq. (12) is the semi-chemostat resource growth. The second term is the discretized diffusion process. The last term is the total consumption by the consumer population. Since we assume that a school in compartment  $u$  will forage in that compartment plus the two adjacent compartments (see Eq. (4)), the rate of change of the resource in compartment  $u$  depends on the feeding by all consumers present in compartments  $u$ ,  $u - 1$  and  $u + 1$ .

Individuals are grouped in schools. All individuals in a school are identical. Thus, we can describe each school by a set of ordinary differential equations describing its  $i$ -state variables ( $x_i$  and  $y_i$ ), and the number of individuals it contains. The change in numbers of individuals in school  $i$  is given by

$$\frac{dN_i}{dt} = -\mu(x_i, y_i)N_i. \quad (13)$$

When the number of individuals in a school drops below 1, it is removed from the population and hence the dimension of the total discrete population distribution is reduced whenever the number of individuals in a given school has become negligible.

The growth of these individuals depends on their energy intake. If food is scarce, and consequently  $E_{g,u}(x_i, y_i) \leq 0$ , then

$$\frac{dy_i}{dt} = E_{g,u}(x_i, y_i), \quad (14)$$

while irreversible mass is invariant ( $dx_i/dt = 0$ ). When energy intake exceeds basic metabolic costs ( $E_{g,u}(x_i, y_i) > 0$ ), the changes in irreversible and reversible mass, respectively, are given by

$$\frac{dx_i}{dt} = \kappa(x_i, y_i)E_{g,u}(x_i, y_i), \quad (15)$$

$$\frac{dy_i}{dt} = [1 - \kappa(x_i, y_i)]E_{g,u}(x_i, y_i). \quad (16)$$

Newborn individuals are added to the population as new schools. The total number of newborn individuals equals the summed fecundity  $F(x_i, y_i)$  (Eq. (11)) of all individuals carrying gonad tissue.

$$N_{tot} = \sum_i F(x_i, y_i)N_i.$$

The converted gonad mass is removed from the reproducing adults, leaving them with reversible mass  $y_i = q_j x_i$ . The newborn individuals are then added to the existing population in the form of  $n$  new schools. The initial state of the newborn schools is

$$\begin{cases} N_i = \frac{N_{tot}}{n}, \\ x_i = \frac{1}{1 + q_j} w_b, \\ y_i = \frac{q_j}{1 + q_j} w_b. \end{cases} \quad (17)$$

Overall, the simulation of physiologically structured populations thus involves the numerical integration of a (large) system of ordinary differential equations, which is extended in dimension at the beginning of each season with a concurrent reset of some of the variables. When the number of individuals in a school falls below 1, it is removed from the system, and the dimension of the system is reduced.

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