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Evolutionary dynamics of exploited populations selected by density dependent competitive interactions

Lars Witting

Greenland Institute of Natural Resources, Box 570, DK-3900 Nuuk, Greenland

Abstract Life-history models have traditionally dealt with short-term evolution where evolutionary equilibria arise from genotypic and phenotypic covariance that have evolved by natural selection. For the case of body mass evolution in mobile organisms with non-overlapping generations, I analyse an alternative model of long-term evolution by the ecological constraint of density dependence in the number of intra-specific competitive interactions per individual. The model is based on the principle that phenotypic constraints that may explain the evolution of life-histories shall not be assumed unless the constraints reflect laws that lie outside the domain of evolutionary biology. It is argued that the model may explain population dynamic cycles either by selection acting directly on genotypic variation or by long-term selection for inheritable phenotypic responses that react to the density dependent changes in the ecology.

The model has an evolutionary equilibrium that is a Continuously Stable Strategy (CSS) when, at equilibrium abundance, the second derivative of the density regulation function with respect to the intra-population variation in ln body mass is smaller than the density regulation function or the first derivative of that function. On the time-scale of population dynamics the model shows inertial dynamics with damped, stable, or repelling cycles in population abundance and life-history traits like the body mass and the intrinsic population dynamic growth rate.

For harvested populations that are allowed sufficient time to equilibrate at the CSS, the equilibrium abundance is constant and independent of the harvest while the intrinsic growth rate is positively related to the harvest. This implies no upper limit to the long-term sustainable harvest of individuals, although there is an upper limit to the sustainable harvest of biomass. It is also shown that the evolutionary maximal harvest does generally not coincide with the maximal sustainable yield. Aand that harvest functions that increase more than proportional with the abundance will stabilise the cyclic population dynamics, while harvest functions that increase less than proportional will destabilise the dynamics.

Keywords: Fishing, sustainable yield, body mass, life-history evolution, population dynamics, population cycles, inertial growth

1 Introduction

Population dynamic models for resource management have traditionally assumed that the life-history and, thus, the relationship between population density and sustainable yield, is evolutionarily fixed for a given population. More resent studies have considered resource management in evolutionary contexts, where harvest induces selection on the life-history traits that determine the sustainable yield (e.g., Bergh and Getz 1989; Law and Grey 1989; Blythe and Stokes 1990; Stokes et al. 1993; Heino 1998; Martínez-Garmendia 1998; Law 2000). With selection the range of possible exploitation patterns increases, with some harvest regimes selecting for a decline in sustainable yield and others for an increase.

There is much evidence showing changes in life-history traits like body mass and age of maturation of commercially harvested populations (e.g., Murphy 1967; Borisov 1978; Haugen and Vøllestad 2001; reviewed by Law 2000). But there is no general agreement why these changes occur. Density regulation is one potential cause, where the reduction in population abundance caused by harvest generates a release in intra-specific competition and thus improved feeding conditions for the remaining individuals. The increase in the available resource may then be transferred to life-history traits by a plastic phenotypic response that generates faster growth, larger body masses, and earlier maturation.

A decline in the age of maturation of harvested populations is often observed, but increased harvest also tends to coincide with a decline in the body mass at a given age (e.g., Rijnsdorp 1989, 1993; Ricker 1981). Thus, at least for body mass, harvest tends to induce a change that is diametrically opposite to that expected by competition release. One explanation for a decline in mass is direct size-selective harvesting, where larger individuals are harvested more frequently than smaller individuals (e.g., Law and Grey 1989; Blythe and Stokes 1990, 1993; Stokes and Blythe 1993; Heino

1998; Martínez-Garmendia 1998; Law 2000). Another possibility is indirect selection where the harvest rate alters a selection optimum of a trade-off between the chance of surviving to the reproductive age and the reproductive output at that age (Brown and Parman 1993). If reproduction is positively related to body mass, and body mass is positively related to age, individuals that reproduce late will have a higher reproductive output but also a lower chance of reproducing. And with increased harvest the mortality penalty of late reproduction increases inducing selection for earlier reproduction at a lower body mass.

In this paper I consider a second mechanism of indirect harvest selection, where the removal of individuals reduces the number of density dependent competitive interactions per individual inducing selection for smaller body masses and increased reproduction. Individuals with larger body masses are often interactively superior to smaller individuals and, thus, they can have more resource available for reproduction than the smaller individuals if they monopolise the resource during competitive interactions. But energetic trade-offs implies that the smaller individuals are expected to have a higher reproductive rate for a given amount of resource. At evolutionary equilibrium the energetic trade-off is balanced against the bias in interactive quality and with a harvest induced decline in the level of interactive (interference) competition this balance becomes biased in favour of the smaller and faster reproducing individuals.

The underlying mechanisms and the evolutionary scales of these two models of indirect harvest selection are quite different. The model of Brown and Parman (1993) resembles traditional life-history models (reviewed by Roff 1992; Stearns 1992; Bulmer 1994; Charlesworth 1994), in the sense that the evolutionary optimum of a trait is determined by genotypic and phenotypic covariance that most likely have evolved by natural selection themselves. The proposed model of density dependent competitive interactions, on the other hand, explains life-history evolution by ecological constraints that lie outside the evolving phenotype. Hereby the latter model aims to avoid a somewhat circular mechanism where evolutionary predictions arise from intrinsic constraints that are evolutionarily determined and evolutionarily unexplained.

On shorter time-scales, where evolutionary changes are restricted to gene frequency changes in the alleles that already exist in the population, the traditional approach with selection by genotypic and phenotypic covariance seems to be appropriate. But for long-term evolution we should aim for predictions that are valid independently of the genotypic and phenotypic variation that are evolutionarily modifiable. And even on faster time-scales it may be that it are the ecological constraints of long-term evolution that modify the dynamics of the population: It has been shown theoretically that cyclic population dynamics may arise from both genotypic and phenotypic responses to selection (Ginzburg and Taneyhill 1994; Ginzburg 1998; Inchausti and Ginzburg 1998; Witting 2000b). And if the density dependent environment fluctuates with a period that exceeds the generation time of the organism, then, on the longer time scale we can expect selection for inheritable phenotypic responses that react directly to the changes in the density dependent ecology (Lachmann and Jablonka 1996). Hence, if cyclic dynamics is driven by inheritable phenotypic responses it is likely that the overall response is determined by the long-term constraints of the density dependent ecology.

The model developed in this paper is part of a larger theory (Witting 1995, 1997, 2000a,b, 2002) where the selection pressure of density dependent competitive interactions is used to explain both the evolution of major life-history traits in mobile organisms and the evolution of cyclic population dynamics. The complete model has been developed for life-history traits as diverse as body mass, metabolic rate, age of maturation, senescence, kin group size, sex ratio, and sexual reproduction. All these traits are related to the intrinsic population dynamic growth rate by a negative trade-off. And they may all be considered as interactive traits that can be used to enhance the interactive quality of the organism, i.e., to enhance the ability by which the organism can monopolise the resource during competitive interactions. As all the traits have these two relations in common their evolution by density dependent competitive interactions is relatively similar.

In this paper the analysis is restricted to body mass keeping in mind that the model will also reflect the dynamics of the other interactive traits. For this case I incorporate harvest into the model in order to describe the potential influence that the removal of individuals may have on the equilibria and dynamics of mobile species with non-overlapping generations and density dependent competitive interactions. I describe the general selection framework in Section 2.1. Some conceptual differences between traditional single species population dynamic models and the model with superimposed selection by density dependent competitive interactions are described in Section 2.2. In Section 2.3 I develop the population dynamic selection model before the different harvest patterns are considered in Section 3. Section 3.1 describes the sustainable harvest of

populations in evolutionary equilibrium. Section 3.2 describes the harvest of populations that are in population dynamic equilibrium but not in evolutionary equilibrium. And Section 3.3 considers the case of evolutionary population dynamics in the aim of identifying harvest functions that stabilise the dynamics.

The evolutionary equilibrium and population dynamics for the case with no harvest have been considered in detail in other papers (e.g., Witting 1997, 2000b, 2002). But these studies were based on a power density regulation function. In the present paper I extend the density regulation model to a more general function that assumes only that the population dynamic growth rate is a continuously declining function of the population abundance.

2 The model

2.1 Density dependent selection

Classical models of density dependent selection are based r- and k-selection (reviewed by Mueller 1997). The basic idea of r- and k-selection was considered by Fisher (1930) [Witting 2000a], but the concept was proposed by MacArthur (1962) and MacArthur and Wilson (1967) and developed theoretically by others (e.g., Anderson 1971; Charlesworth 1971, 1994; Roughgarden 1971; Clarke 1972). The mechanism of r- and k-selection operates through an increase in the intrinsic growth rate, which implies an increase in the population dynamic growth rate (r) and/or the carrying capacity (k) [I define the intrinsic growth rate as explained in Witting (2000a)]. This principle can be seen as a reflection of Fisher's (1930) Fundamental Theorem of Natural Selection (Witting 2000a), and it is based on the assumption that the relative fitnesses are constant at a specific population density, which is inappropriate whenever competitive interactions play an essential role in density regulation. For cases with density dependent competitive interactions the intrinsic growth rate may decline (Witting 2000a), and we need to apply the game theoretical concepts of Evolutionary Stable Strategies (ESSs) [Maynard Smith and Price 1973; Maynard Smith 1982] and Continuously Stable Strategies (CSSs) [Eshel and Motro 1981; Eshel 1983].

For the case with harvest, Law and Grey (1989) have extended the concept of an ESS into the concept of the Evolutionary Stable Optimal Harvest Strategy (ESOHS), which is the ESS that maximises the sustainable yield. Like the ESS, the ESOHS does not consider the possibility that the population evolves to an ESS; both concepts only establish the equilibrium conditions when the population is at the ESS. To determine the possibility of evolution toward equilibrium we need to apply the selection concept of a CSS, with the Continuously Stable Optimal Harvest Strategy (CSOHS) being the CSS that maximises the sustainable yield.

Evolutionary and Continuously Stable Strategies are genetic-free concepts that, at least in principle, deal with long-term evolutionary equilibria. It has been shown that the long-term convergence to a CSS is independent of the genetic structure for a wide range of genetic assumptions (Eshel and Feldman 1984; Liberman 1988; Matessi and Di Pasquale 1996; Eshel et al. 1997; Eshel et al. 1998). For the case of a one-dimensional continuity of pure strategies, as considered in this paper, the long-term convergence is deterministic and virtually independent of the distribution of mutations (Eshel et al. 1997). This implies that the phenotypic and genetic constraints that have evolved during earlier evolutionary processes cannot generally be expected to ultimately constrain the process of long-term evolution. Although phenotypic and genetic constraints put the evolutionary process in a historical framework that influences the evolutionary trajectory toward the long-term equilibrium, the constraints are expected to vanish on the longer-time scale if there is selection against them.

The suggestion that the equilibria of long-term evolution are independent of the evolutionarily determined phenotypic constraints is generally not reflected in models of life-history evolution. Traditional life-history models (reviewed by e.g. Roff 1992; Stearns 1992; Bulmer 1994; Charlesworth 1994) tend instead to focus on a shorter time-scale, where the equilibria of some life-history traits are determined by the constraints imposed by other traits (see Witting 1997 for details). For the case of body mass considered here, it is traditionally assumed that larger body masses evolve from a proportional relationship between the body mass and the rate of reproduction (McLaren 1966; Schoener 1969; Case 1979; Roff 1981, 1986; Lundberg and Persson 1993). Although this relationship is confirmed empirically in many species (Peterson 1950; Robertson 1957; Wooton 1979; Roff 1982; Peters 1983; Reiss 1989), the relationship has never been explained as an ultimate evolutionary constraint that exists independently of frequency dependent selection. There is instead some evidence that the proportional relation may arise from selection by the density and frequency dependent ecology (Witting 1997) and, thus, that it is a local constraint that evolves in response to ongoing selection. The proportional relationship is also the assumption upon which most of the models on evolutionary optimal harvest

strategies are based (e.g., Law and Grey 1989; Heino 1998; Law 2000).

For models of long-term evolution it is instead more appropriate to assume a complete absence of evolutionarily determined constraints so that it is clear that model predictions are independent of local constraints. The difficulty with the latter approach is to construct life-history models where the relationships among the different traits reflect only true constraints that cannot be altered by natural selection, i.e., constraints that are evolutionarily fixed because they arise from laws that lie outside the domain of evolutionary biology. A first attempt for such models were developed for mobile organisms by Witting (1997, 2002), who assumes that life-history traits evolve independently of each other unless we have a non-biological law that clearly explains why the different traits should trade-off against one another. This approach is adopted here where it is the ecological constraints of a limited world that explains the evolution of energy demanding traits like body mass, while the intrinsic constraints on body mass are restricted to an energetic trade-off. This approach depends on the assumption that there are no extra significant constraints by which the body mass is related to fitness. This assumption might not hold, but until such extra constraints have been explicitly identified the proposed model can be seen as a first attempt towards a better understanding of the long-term evolution of body mass. A more detailed discussion on the use of constraints in the life-history model is given in Section 2.3.

The time it will take a population to evolve to a long-term equilibrium depends on many factors, which include both the amount of additive genetic variation in the population and the mutation rate. For harvested populations the time will also depend on changes in the harvest rate, and the time required may well be magnitudes longer than the time spans usually considered in relation to the exploitation of natural resources. But although the evolutionary equilibria of large transitions in the harvest rate may not be attainable in the near future, short-term selection responses that interact with the current harvest regime might also be expected. If the transitions in harvest rate are so small that the predicted evolutionary changes easily can be obtained from the additive genetic variation available in the population, then, the evolutionary optimal harvest strategies may be of relevance also for relatively short-term commercial considerations.

2.2   Population dynamic model

At the time-scale of population dynamics there may also be significant interactions between selection responses and optimal harvest strategies. This may be surprising as it has been argued that selection hypotheses for population dynamics have been experimentally rejected because the level of additive genetic variation tends to be so low that genetic changes at the time scale of population dynamics is insignificant (e.g., Boonstra and Boag 1987; Boonstra and Hochachka 1997). Nevertheless, empirical studies have found that genotypic changes to selection can indeed occur at the time-scale of population dynamics (e.g, Krebs et al. 1973; Sinervo et al. 2000). Furthermore, for population dynamics it is the phenotypic response to selection that matters and phenotypic responses need not depend on evolutionary changes in the genotype. The phenotype may instead have a plastic response to selection, or it may respond by inherited environmental effects, where an epigenetic inheritance system transfers plastic phenotypic responses from parent to offspring generations (e.g., Jablonka and Lamb 1989, 1998; Rossiter 1996). Maternal effect is one example of an epigenetic inheritance system that has now been shown to have the potential to explain cyclic population dynamics in animal species (Ginzburg 1980, 1998; Ginzburg and Taneyhill 1994; Inchausti and Ginzburg 1998).

Instead of theoretically deducing the maternal effects from the density dependent ecology, the population dynamic models of Ginzburg and Taneyhill (1994), Ginzburg (1998), and Inchausti and Ginzburg (1998) have assumed that the population has the density dependent maternal effect that is required for cyclic dynamics. Recently it has been shown that the selection pressure of density dependent competitive interactions may be the ecological factor that induces the correct form of density dependent response, where cyclic dynamics may arise either from selection responses in genotypes and/or from phenotypic responses of epigenetic inheritance systems (Witting 1997, 2000b). Especially if the density dependent environment fluctuates with a period that exceeds the generation time of the organism, then, on the time scale of long-term evolution, we may expect the evolution of an inheritable phenotypic response that reacts on the density dependent changes in the ecology (Lachmann and Jablonka 1996). In this way the ecological constraints that define the long-term evolutionary equilibria may also be the constraints that determine the short-term response of population dynamics.

The traditional consensus of population dynamics is

that the abundance is an initial condition while the intrinsic growth rate is a fixed parameter for given environmental conditions. This results in an actual growth rate that changes as a function of the abundance of the species (and maybe of the abundance of other species). The population dynamic models of maternal effect and selection by density dependent competitive interactions belong to an alternative set of models that have become known under the concept of inertial growth (Ginzburg 1980, 1998). In these models the intrinsic growth rate is a second initial condition so that changes in the actual growth rate may arise not only from density dependent changes in the environment but also from density dependent changes in the intrinsic growth rate.

Inertial growth was proposed by Ginzburg who developed the concept into maternal effect models with cyclic population dynamics (Ginzburg 1980, 1998; Ginzburg and Taneyhill 1994; Inchausti and Ginzburg 1998). Both the maternal effect model and the selection model deduced in this paper define the density dependent changes in the intrinsic growth rate as a continuously declining function of density with the equilibrium defined for the density with no change. The result is an inertia response that relative to the dynamics of traditional density regulation models tends to maintain current abundance changes in the vicinity of the population equilibrium. The consequence is cyclic or overcompensatory dynamics where depleted populations increase beyond the equilibrium because the depleted state has selected for an intrinsic growth rate that is larger than the intrinsic growth rate at equilibrium.

Where the inertia model of maternal effect recognises the Malthusian law of exponential increase as the density independent fundament (e.g., Ginzburg 1998), the most basic principle of the inertia based selection model is Fishers Fundamental Theorem of Natural Selection (Fisher 1930) that generates a hyper-exponential increase in abundance (Witting 2000a,b). Another difference between the two models is that the maternal effect model deals not only with a density dependent change in the intrinsic growth rate but also with a growth dependent change (see Ginzburg 1998). The growth dependent change ensures that the intrinsic growth rate will never exceed an upper limit, and it is through this limit that the maternal effect models recognise the Malthusian law as the density independent principle. With no growth dependence and thus no upper limit to the intrinsic growth rate the density independent principle changes from exponential to hyper-exponential growth.

For the case of long-term evolution the selection model does not allow for an upper limit to the intrinsic growth rate. However, for cases of short-term evolution it may provide a mechanism: If the rate of change in the intrinsic growth rate declines significantly at the limit where selection has exhausted the selection response of the additive genetic variation and the epigenetic inheritance systems, and if the mutation dependent rate of evolution is so low that it can be ignored, it follows that the intrinsic growth rate can be viewed as constrained within the limits of the short-term dynamic process.

2.3 Population equations

In this section I define the density dependent ecology and the constraints of the life-history model. I then use the selection pressure of the density dependent competitive interactions to deduce the evolution of a balanced life-history and the evolution of a population dynamic model with inertial growth.

Let there be non-overlapping generations, and let $f(N)$ be a multiplicative density regulation function that declines monotonically from one to zero as the population density N increases from zero to infinity. Let the total catch c_t at time t be a fraction q_t of the population abundance immediately after reproduction, i.e., let

$$c_t = N_t \lambda_m f(N_t) q_t \tag{1}$$

with the intrinsic population dynamic growth rate being represented here by the maximal growth rate $\lambda_m = p R_m$, where R_m is maximal reproduction and p is natural survival given as the probability that a non-caught new-born at time $t-1$ will survive and reproduce at time t. Thus, we obtain the following population dynamic equation

$$N_{t+1} = N_t \lambda_m f(N_t) s_t \tag{2}$$

where $s_t = 1 - q_t$ is the fraction of the newborn individuals that survive the harvest. Let the carrying capacity k be the population dynamic equilibrium for the case with no harvest, i.e., let $k = f^{inv}(1/\lambda_m)$ where f^{inv} is the inverse function of f. And let the curve of sustainable yields sy be the equilibrium harvest c^* over all possible population dynamic equilibria N^*, i.e., let

$$sy = N^*[\lambda_m f(N^*) - 1] \tag{3}$$

with equilibrium abundance $N^* = f^{inv}(1/\lambda_m s)$. The curve of eqn 3 has a maximum known as the maximum sustainable yield (msy) and the abundance at which this maximum occurs is the maximum sustainable yield level ($msyl$).

Equation 2 represents the case with no selection and a maximal growth rate λ_m that is non-evolving and constant for a given set of ecological conditions. For the

case of selection let selection operate indirectly on λ_m through its effects on the interactive quality of the individual, and consider the case where it is only the body mass w that represents interactive quality. The body mass may act as an interactive trait as it can be selected so that the individuals with the larger body masses can dominate the smaller individuals during competitive interactions. And with respect to intrinsic trade-offs, for the case where the offspring are reared by the parents, we may expect that the population dynamic growth rate is related to body mass as

$$\lambda_m = \rho/w \qquad (4)$$

where $\rho = p\epsilon$ is the product between the average probability p that an offspring will survive and reproduce and the average amount of energy ϵ that an individual on an unexploited resource allocates to reproduction. With ϵ amounts of energy allocated to reproduction ϵ/w offspring can be produced and, thus, the organism can choose to allocate resource either to the body mass w or to the population dynamic growth rate λ. The inverse relationship of eqn 4 holds only for cases where offspring are reared by the parents. Not only is this case reflected in many species of higher animals, but it is also the expectation for simple self-replicators that reproduce by binary fission. Thus, it may be argued that the energetic trade-off reflects a basic reproductive constraint from which other reproductive modes have evolved.

The life-history constraints of eqn 4 differ somewhat from those of traditional life-history models. Usually it is assumed that the reproductive rate R is approximately proportional to body mass (e.g., McLaren 1966; Roff 1981, 1986; Gerritsen 1984; Stearns and Koella 1986; Lundberg and Persson 1993) which, for eqn 4, is the case if the energy available for reproduction scales to the second power of body mass, i.e., if $\epsilon \propto w^2$. However, as there seems to be no general non-biological law to explain this relationship I follow the principle of Witting (1997) by assuming evolutionary independence between ϵ and w.

By eqn 4 I assume that the survival probability p is independent of body mass, which is also in contrast to more traditional life-history models. At the within-population scale in nature the survival rate is often observed to increase with body mass (McGurk 1986). Nevertheless, the assumption in traditional life-history models has been that the survival probability declines with body mass because larger individuals tend to reproduce at a later age. But at larger evolutionary scales, as revelled by between species comparisons, the probability of survival to reproductive age seems to be
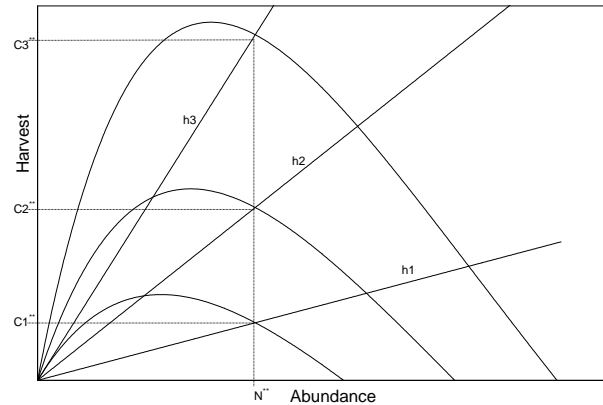

Figure 1: The sustainable yield at the evolutionary equilibria for a case where the evolutionary optimal harvest in terms of individuals is an infinite catch that coincides with the maximum sustainable yield. The three harvest functions $h1$, $h2$ and $h3$ specifies the harvest $c1$, $c2$ and $c3$ as a function of the abundance N, with double stars indicating evolutionary equilibria.

independent of body mass [Fig. 1 in Witting (1995)]. Also, for a general class of age-structured models, where the survival probability p reflects survival at the time-scale of the organism, p is expected to be independent of lifespan and absolute reproduction (Witting 1995, 1997) suggesting that p is invariant among organisms with similar bauplans. Thus, in the absence of a clear and general constraint relating body mass to the survival probability at the time-scale of the organism, I follow the principle of long-term evolution assuming independence between p and w.

By eqn 4 the smaller individuals have a higher reproductive rate provided that there are no competitive interactions. With competitive interactions, however, the larger individuals may out-reproduce the smaller individuals if they monopolise the resource. In this case the density regulation function of an individual in the population will depend not only on the population density as illustrated by eqn 2, but also on the individuals body mass relative to the average body mass in the population. The density regulation function f may thus be extended to

$$f_i[N_t, \ln(w_{i,t}/w_t)] \qquad (5)$$

where w_t is the average body mass in the population at time t, $w_{i,t}$ is the body mass of the ith body mass variant, and f_i is the density regulation function of that variant. The density regulation function of eqn 5 will decline with N, increase with $\ln(w_i/w)$, and reduce into $f(N)$ at the limit $w_i = w$. Note also that the intra-population slope in the density

regulation function over body mass, i.e., $\dot{f}_i(N_t) = \partial f_i[N_t, \ln(w_{i,t}/w_t)]/\partial \ln w_{i,t}|_{w_{i,t}=w_t}$, is an increasing function of N that takes the value of zero at the lower limit $N = 0$ where there are no competitive interactions ($|w_i = w$ denotes that the partial derivative is to be taken at the limit $w_i = w$).

In the appendix I use the constraints of eqns 2, 4, and 5 to show that populations at population dynamic equilibrium have an evolutionary equilibrium that is a Continuously Stable Strategy when, at equilibrium, the second derivative of the density regulation function with respect to the intra-population variation in ln body mass is smaller than the density regulation function or the first derivative of that function. It is also noted that for the case with no competitive interactions there is no equilibrium but a continuous decline in the body mass. For the general case with competitive interactions and a population that do not need to be in population dynamic equilibrium, it is shown that the population dynamic equation of eqn 2 extends into

$$\begin{aligned} \lambda_{m,t+1} &= \lambda_{m,t} g(N_t) \qquad (6) \\ N_{t+1} &= N_t \lambda_{m,t} f(N_t) s_t \end{aligned}$$

where $g(N_t) = e^{-\sigma^2[\dot{f}_i(N_t)/f(N_t)-1]}$ is a density dependent selection function that operates on λ_m, with $\sigma^2 = \hat{\sigma}^2 + \tilde{\sigma}^2$ representing the potential by which w and λ_m responds to selection, where $\hat{\sigma}^2$ is the additive genetic variance in $\ln w$ and $\tilde{\sigma}^2$ is a plastic response of inherited environmental effects. An age-structured version of eqn 6 was deduced by Witting (2002), and it has been applied to the dynamics of bowhead whales *Balaena mysticetus* (Punt and Witting 2002) and gray whales *Eschrichtius robustus* (Witting 2001).

The function $g(N)$ is defined for all positive abundances, and it is either one for all N or a continuously declining function of N with the slope of the function being defined both by the strength of selection and by the populations ability to respond to selection. The function g is one for all N when there is no response to selection, which is the case when there is no additive genetic variation and no epigenetic inheritance system ($\sigma^2 = 0$). In this case eqn 6 reduces to the classical model of eqn 2. Whenever there is a selection response the function g is one at the evolutionary equilibrium N^{**}, it is larger than one for abundances that are below the evolutionary equilibrium, and it is smaller than one for abundances that are above the evolutionary equilibrium. This relationship reflects the deduction that density dependent competitive interactions selects for a decline in the population dynamics growth rate when the abundance is above the abundance at evolutionary equilibrium, while it selects for an increase in the

growth rate when the abundance is below the evolutionary equilibrium.

In this paper it is assumed that the function g is constant over time which implies that the populations ability to respond to selection remains constant. A constant selection response is a simplifying assumption that will not affect the long-term equilibrium predictions, although it is likely to have some effect on the dynamics. If the major contribution to the phenotypic selection response is additive genetic variation the selection response is likely to decline over time, at least for the case of directional selection. But the cyclic dynamics of eqn 6 and the associated shifts in the direction of selection may maintain some genetic variation in the population despite of continuously ongoing selection and evolution. And for cases where the major selection response is due to epigenetic inheritance systems the assumption of a constant selection response is likely to hold as an approximation as long as the predicted dynamics is within the potential of the plastic respond.

3 Results

For eqn 6 there are two equilibrium conditions: $g(N) = 1$ and $\lambda_m f(N)s = 1$ and, thus, there are four state combinations to consider. Section 3.1 describes the state where the population is in both population dynamic and evolutionary equilibrium, i.e., where $\lambda_{m,t} f(N_t)s_t = 1$ and $g(N_t) = 1$. Section 3.2 describes the state where the population is in population dynamic equilibrium but not in evolutionary equilibrium, i.e., where $\lambda_{m,t} f(N_t)s_t = 1$ and $g(N_t) \neq 1$. And Section 3.3 describes the case of population dynamics, which includes the case where the population is neither in population dynamic or evolutionary equilibrium [$\lambda_{m,t} f(N_t)s_t \neq 1$ and $g(N_t) \neq 1$] as well as the case where the abundance is at the evolutionary equilibrium but not in population dynamic equilibrium [$\lambda_{m,t} f(N_t)s_t \neq 1$ and $g(N_t) = 1$].

3.1 Evolutionary equilibrium

In classical density regulation theory with no selection it is the population abundance that trade-offs against the mortality rate, given here by the harvest level. In this case the abundance at population dynamic equilibrium will decline as the sustainable harvest is increased. For the equilibrium harvest of eqn 6 it is not the abundance but the maximum growth rate, or more generally the life-history traits, that trade-off against the sustainable harvest. This results in an equilibrium abundance that remains constant while the maximal growth rate

increases as the sustainable harvest is increased. And for the case with no evolutionarily imposed phenotypic constraints on the growth rate it is impossible to over-exploit the population as long as it is allowed sufficient time to equilibrate at the evolutionary equilibrium.

To see this theoretically note that the evolutionary equilibrium of eqn 6 is defined by the equilibrium constraint $\lambda_m^{**} = \lambda_m^{**} g(N^{**})$ on the maximal growth rate. Thus, the equilibrium abundance $N^{**} = g^{inv}(1)$ is independent of the harvest. And with the equilibrium abundance being a constant $g^{inv}(1)$ it follows from the second equilibrium constraint $N^{**} = N^{**}\lambda_m^{**}f(N^{**})s$ that the evolutionary equilibration of the maximal growth rate is determined by the fraction of the population that is harvested $q = 1 - s$. Thus, the evolutionary equilibrium is characterised as

$$
\begin{aligned}
N^{**} &= g^{inv}(1) \\
c^{**} &= \frac{N^{**}q}{1-q} \\
\lambda_m^{**} &= \frac{1}{f(N^{**})(1-q)} \\
w^{**} &= \rho/\lambda_m^{**}
\end{aligned}
\tag{7}
$$

That is, as the harvest fraction increases toward the upper limit $q = 1$ the abundance remains constant, while both the number of individuals harvested and the maximal population dynamic growth rate increase toward infinity and the body mass decreases toward zero. Since the harvest of individuals can be increased indefinitely at the evolutionary equilibrium of eqn 7 it follows that there is no Evolutionarily or Continuously Stable Optimal Harvest Strategy. It is instead optimal to continue to increase the harvest. However, if we look at the harvest in terms of biomass we find that the sustainable harvest is

$$
\begin{aligned}
c^{**}_{\text{mass}} &= w^{**}c^{**} \\
&= \rho N^{**}f(N^{**})q
\end{aligned}
\tag{8}
$$

Thus, the harvested biomass stabilises at $\rho N^{**}f(N^{**})$ as the harvest fraction q goes toward one.

As the carrying capacity $k = f^{inv}(1/\lambda_m)$ is positively related to the intrinsic growth rate λ_m it follows that the depletion ratio $D = N^{**}/k^{**}$ decreases as the harvest increases, even though the equilibrium abundance $N^{**} = g^{inv}(1)$ at which the population is harvested remains constant. Note also from eqn 3 that the sustainable yield at a give abundance is positively related to the intrinsic growth rate $(\partial sy/\partial \lambda_m > 0)$ and thus to the harvest, at least for density regulation functions f that are independent of λ_m. This furthermore im-

plies that the maximum sustainable yield is positively related both to λ_m and to the harvest.

When may we expect that the population is exploited at the maximum sustainable yield level? From eqn 3 we note that

$$
\partial sy/\partial N = \lambda_m[f(N) + Nf'(N)] - 1
\tag{9}
$$

with $f'(N) = \partial f/\partial N$. Thus, as the *msyl* is given by the intercept $\partial sy/\partial N = 0$ of eqn 9 and as $f(N) + Nf'(N)$ is a declining function of N that is positive for small enough N, it follows that $\partial msyl/\partial \lambda_m > 0$ when the density regulation function f is independent of λ_m. Hence, when $msyl < N^{**}$ for $q^{**} = 0$ and $msyl > N^{**}$ for $q^{**} \to 1$ we can expect a single harvest level at which the maximum sustainable yield level and the harvest equilibrium N^{**} coincide. An interesting special case is when $msyl \to N^{**}$ for $q^{**} \to 1$. Then, at the limit $q^{**} \to 1$ the harvest will be at the evolutionary optimum, the catch will be the *msy*, and the population will be harvested at the *msyl*. The following model

$$
\begin{aligned}
\lambda_{m,t+1} &= \lambda_{m,t}e^{1-\gamma N} \\
N_{t+1} &= N_t\lambda_{m,t}e^{-\gamma N}s_t
\end{aligned}
\tag{10}
$$

has this behaviour, as illustrated in Fig. 1.

3.2 Population dynamic equilibrium

For the model with superimposed selection the population may be exploited at a constant abundance, i.e., at a population dynamic equilibrium, even when the population is not in evolutionary equilibrium. This is possible when $N^*\lambda_{m,t}f(N^*)s = N^*$ and $g(N^*) \neq 1$. When N^* is constant and different from N^{**} it follows from eqn 6 that the maximal growth rate increases or decreases geometrically as

$$
\lambda_{m,t} = \lambda_{m,0}g(N^*)^t
\tag{11}
$$

and that the body mass decreases or increases geometrically as

$$
w_t = w_0/g(N^*)^t
\tag{12}
$$

where $\lambda_{m,0}$ and w_0 are the growth rate and body mass at time $t = 0$. Thus, the equilibrium abundance N^* can be maintained constant if the harvest rate $c_t = N^*[\lambda_{m,t}f(N^*) - 1]$ is continuously adjusted to the changes in the maximal growth rate, i.e., if

$$
c_t = N^*[\lambda_{m,0}g(N^*)^t f(N^*) - 1]
\tag{13}
$$

This mode of harvest can be maintained only when the equilibrium abundance is below the abundance at

the evolutionary equilibrium, i.e., for cases where the growth rate and the harvest increase geometrically. When instead the abundance is above the evolutionary equilibrium the harvest rate will eventually cross the lower limit $c = 0$, and then the geometric decline in λ_m will cause the abundance to decline to or below the evolutionary equilibrium N^{**}.

For the case $N^* < N^{**}$, note also from eqns 12 and 13, that the harvest in terms of biomass is

$$c_{\mathrm{mass},t} = N^* w_0 [\lambda_{m,0} f(N^*) - 1/g(N^*)^t] \qquad (14)$$

This implies that the harvested biomass will stabilise at $N^* w_0 \lambda_{m,0} f(N^*) = \rho N^* f(N^*)$ as $1/g(N^*)^t \to 0$ when $t \to \infty$. Thus, even though the harvest increases geometrically in terms of the number of animals harvested, the harvested biomass will stabilise because the body mass of the harvested individuals declines geometrically.

For exploitation at the population dynamic equilibrium relatively high rates of geometrical increase in the harvest and growth rates may be expected only initially on a short-term time scale. Whenever the responses of the additive genetic variance and the epigenetic inheritance systems of the initial population has been exhausted by selection, the rate of change can be expected to decline drastically as it becomes dependent on the mutation rate.

3.3 Population dynamics

Traditional density regulation models with no selection returns monotonically towards the equilibrium when the density regulation function $f(N)$ is not too strongly non-linear (May 1974; May and Oster 1976). The more general inertial model with selection has cyclic dynamics with periods between two and an infinite number of generations (Witting 2000b). These cycles may be damped with the population showing a cyclic return to the evolutionary equilibrium, or they may be stable showing no return, or repelling with a cyclic increase away from equilibrium. When harvest is added to such systems an essential first question is whether the harvest will make the dynamics more stable and increase the probability that the population will return to some harvest equilibrium.

To address this question assume that the harvest fraction is a function of the population abundance, i.e., $q(N) = 1 - s(N)$, and let

$$\begin{aligned} G &= \lambda_m^{**} g(N^{**}) \qquad (15) \\ F &= N^{**} \lambda_m^{**} f(N^{**}) s(N^{**}) \end{aligned}$$

The local dynamics around the evolutionary equilibrium is then given by the eigenvalues of the Jacobian matrix

$$\begin{bmatrix} \partial G/\partial \lambda_m^{**} & \partial G/\partial N^{**} \\ \partial F/\partial \lambda_m^{**} & \partial F/\partial N^{**} \end{bmatrix} \qquad (16)$$

For the case with complex eigenvalues and cyclic dynamics induced by selection (Witting 2000b), the local dynamics is repelling cycles when the absolute value of the dominant eigenvalue is larger than one, neutrally stable cycles when the value is one, and damped cycles when the value is less than one (Bulmer 1994). For the matrix eqn 16 the eigenvalues are

$$(T \pm \sqrt{T^2 - 4D})/2 \qquad (17)$$

where D is the determinant and T the trace of that matrix. For the case $T^2 - 4D < 0$ with complex eigenvalues and $D > 0$, it follows from the calculus of complex numbers that the absolute value z of the eigenvalues of eqn 17 reduces to $\sqrt{D}$. And for eqn 16 the determinants is

$$\begin{aligned} D &= g(N^{**})\lambda_m^{**}[f(N^{**})s(N^{**}) \qquad (18) \\ &+ N^{**} f'(N^{**})s(N^{**}) \\ &+ N^{**} f(N^{**})s'(N^{**})] \\ &- N^{**} \lambda_m^{**} f(N^{**})s(N^{**})g'(N^{**}) \end{aligned}$$

with $h'(N^{**}) = \partial h(N)/\partial N|_{N=N^{**}}$ and $h \in \{f, g, s\}$. As $g(N^{**}) = 1$ and $\lambda_m^{**} f(N^{**})s(N^{**}) = 1$, it follows that eqn 18 reduces to

$$\begin{aligned} D &= 1 + N^{**}[f'(N^{**})/f(N^{**}) \qquad (19) \\ &+ s'(N^{**})/s(N^{**}) \\ &- g'(N^{**})/g(N^{**})] \end{aligned}$$

Hence, for the case of no harvest [where $s(N) = 1$ for all N] the local dynamic is cyclic and neutrally stable when the relative change in the density regulation function (f) and the selection function (g) are the same around the equilibrium, i.e., when

$$f'(N^{**})/f(N^{**}) = g'(N^{**})/g(N^{**}) \qquad (20)$$

And the local dynamics is damped when $f'(N^{**})/f(N^{**}) < g'(N^{**})/g(N^{**})$ and repelling when $f'(N^{**})/f(N^{**}) > g'(N^{**})/g(N^{**})$. For cases with harvest we note that the harvest will stabilise the dynamics when

$$s'(N^{**})/s(N^{**}) < 0 \qquad (21)$$

i.e., when the chance that an individual will survive the harvest declines with N, which is the case when the catch increases more than proportionally with the abundance.

4   Discussion

Classical life-history models are generally based on short-term evolution, where traits evolve from constraints that have themselves evolved by natural selection. A constraint that has often been used to select for a large body mass is a reproductive rate that increases proportionally with body mass, a relationship that is confirmed in many species at the scale of intra-population variation [summarised by Peters (1983) and Reiss (1989)]. When this increase is traded-off against survival that is assumed to decline with body mass we obtain the well-established result of a body mass and an age of maturation in evolutionary equilibrium (e.g., Case 1979; Roff 1981, 1986; Stearns and Koella 1986; Lundberg and Persson 1993). Due to the constrained relationships between the body mass and the rate of reproduction and survival it follows that the body mass and age of maturation will decline if the harvest rate is increased (Brown and Parman 1993), although an increase may occur if it is only the reproducing individuals that are harvested (Heino 1998; Law 2000).

Although this life-history model can explain the often-observed decline in body mass with increase harvest (e.g., Rijnsdorp 1989, 1993; Ricker 1981), the model seems to be based on a fragile concept. First of all the prediction depends on the fixed constraints between body mass, reproduction and survival, but the model provides no general mechanism that will explain the relationship between reproductive rate and body mass as a non-evolving constraint. And as short-term evolution is constrained to occur within the global constraints of long-term evolution, the short-term models should be evolutionarily stable if they are to represent a driving force in the evolutionary process. But on the scale of long-term evolution the traditional models of body mass evolution tend to be evolutionarily unstable. At least for one class of phenotypic constraints it has been shown that if selection operates not only on body mass and age of maturation, but also on the trade-off between reproduction and survival, then, we expect the trade-off to decline so that the body mass collapses toward zero and the reproductive rate increases toward infinity (Witting 1997).

In this paper I used an alternative model of indirect harvest selection to circumvent these problems with the classical models. Being based on long-term evolution by the density dependent ecology of competitive interactions, the model was first proposed by Witting (1997) under the assumption of density regulation by a power function. This assumption was relaxed here where density regulation can take any form as long as the pop-ulation dynamic growth rate is continuously declining with an increasing population. To avoid the problem that predictions arise from unexplained constraints, the model was based on the principle that phenotypic constraints that may explain the evolution of large body masses shall not be assumed unless they arise from laws that lie outside the domain of evolutionary biology. For the case of mobile organisms and no competitive interactions the proposed model predicts that only organisms at the level of negligible-sized self-replicators should evolve. But when the feedback ecology of density dependent competitive interactions is added it follows that large bodied organisms evolve as a density dependent balance between an intrinsic energetic trade-off and the enhanced interactive quality of a larger body mass. In line with the classical model, the proposed model predicts that the body mass will decline when the harvest rate is increased.

Although the proposed model circumvents some problems of classical life-history theory it does not clearly suggest how far towards the long-term equilibrium we may expect the process of short-term evolution to run. And in relation to the problem of sustainable harvest it is typically on the time scale of long-term evolution that the classical predictions from population dynamic theory with no selection will brake down. But dependent upon the situation the predictions of short-term evolution may resemble traditional non-selection predictions or the suggested long-term predictions. The response of short-term evolution to a change in the harvest level will have a certain resemblance with non-selection predictions when the change it takes to reach the new evolutionary equilibrium is much larger than the short-term response expected by the additive genetic variation and the epigenetic inheritance systems of the population. In such cases we can expect an initial and relatively fast response toward the new equilibrium before the population hits the wall of slow mutation limited evolution. Thereafter the life-history traits will be relatively fixed and the remaining short-term response will occur through the traditional trade-off between the harvest and the abundance, and not through the selection trade-off between the harvest and the life-history traits. When instead the change it takes to reach the new long-term evolutionary equilibrium is within the range of the short-term response of the population we may expect that the population will adjust to the new equilibrium within a relatively short time scale. Relatively fast changes in the intrinsic production rate of a population as an apparent response to changes in the mortality rate has been observed for natural populations. Reznick and Bryga (1987) and Reznick et al.

(1990) have shown that guppies that are transferred from a high predation locality to a low predation locality evolve a significantly lower rate of reproduction within few generations.

It is though important to note that the prediction in Sections 3.1 and 3.2 of no limit to the long-term sustainable harvest relates to a time scale that is so long that it is basically irrelevant for commercial fisheries. The prediction may also depend on the assumption that the amount of energy that the organism can allocate to reproduction is independent of body mass when there are no intra-specific interactions among the individuals in the population. Although this assumption is likely to hold as an approximation when the deviation in body mass is not too large, on a larger scale we may expect that non-biological laws impose a net assimilation rate that declines significantly with a decline in body mass. Such a relationship will tend to limit the maximal harvest, although it will generally not affect the prediction that increased harvest selects for a decline in body mass and an increase in both the reproductive rate and the sustainable yield.

The long-term prediction of an equilibrium abundance that is independent of the harvest depends on the assumption that the density dependence in the level of interactive competition is independent of body mass. This assumption is likely to hold as an approximation for small to moderate deviations in mass. On larger scales however we may expect that the number of competitive interactions per individual at a given population density will be somewhat positively related to body mass. Thus, as the level of interactive competition at evolutionary equilibrium can be expected to be body mass invariant (Witting 1997, 2000a), we may expect that the equilibrium abundance will decline with body mass, as established by Damuth's (1981, 1987) empirical allometry where the population abundance scales to the negative 3/4 power of body mass. And indeed, when a density dependent foraging process that generates intra-specific interactive competition is taken into account it is possible to theoretically deduce the empirically established population abundance allometry as an evolutionary optimum that arises from first principles of the foraging process in mobile organisms (Witting 1995, 1998). This suggests that the population abundance allometry may indeed capture an essential trade-off between body mass and the level of interactive competition. The theoretical deduction, however, suggests that the allometric exponents of 1/4 and 3/4 hold only for organisms that forage in two spatial dimensions, while the expectations for three-dimensional foragers are 1/6 and 5/6. Although there seems to have been no study that have examined if this holds for the population abundance allometry, the 1/4 to 1/6 power transition is empirically supported by the life-time allometry in mammals, given that terrestrial mammals forage in two dimensions and pelagic mammals in three dimensions (Witting 1995, 1998). Other recent studies suggest instead that the 1/4 and 3/4 power exponents arise from physiological constraints on branching vascular systems (West et al. 1997; Brown and West 2000). The latter model is applicable also to sessile organisms (Enquist et al. 1998), but it does not explain the apparent 1/4 to 1/6 power transition between terrestrial and pelagic mammals.

In relation to population dynamics it is now evident that selection by density dependent competitive interactions implies inertial dynamics, with damped, stable, or repelling cycles in the population density and life-history traits like the body mass and the intrinsic growth rate. This was first shown by Witting (1997, 2000b) for the case of a power density regulation function, and it was confirmed here for the general density regulation function.

The odds that the population dynamics in many natural species is more like inertial dynamics than traditional density regulated dynamics might be rather high. The frequency and density dependent selection of competitive interactions has now been shown to promote an evolutionary game with two-generation oscillations in lizards (Sinervo et al. 2000). And where traditional density regulated models cannot reconcile the catch history and the abundance data for eastern North Pacific gray whale, the data are easily explained by inertial dynamics (Witting 2001). The decline in the cyclic dynamics of the lach budmoth *Zeiraphera diniana* and the Canadian lynx *Lynx canadensis* tends also to continue even after the population density is very low, and the initial recovery from low densities is often slower than exponential in hares and voles (Ginzburg 1998). And population cycles have often been found to be associated with cyclic changes in life-history traits like body mass, kin group size, age of maturation, and the level of aggression (e.g., Krebs and Myers 1974; Krebs 1978; Boonstra and Krebs 1979; Stenseth 1982; Stenseth and Ims 1993; Lidicker and Ostfeld 1991; MacColl et al. 2000).

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A   Appendix

In this appendix I use the model of selection by density dependent competitive interactions to deduce the evolution of a balanced life-history and to deduce a population dynamic model with inertial growth.

For the case with changes in the intrinsic life-history we find from eqns 2 and 4 that the population dynamic growth rate at time t is

$$\lambda_t = \rho f(N_t) s_t / w_t \qquad (22)$$

if we assume that $\rho = p\epsilon = \lambda_{m,t} w_t$ is a constant. For populations at population dynamic equilibrium $\lambda = 1$ we note that the equilibrium density N^* is negatively related to the average body mass. This is because the intrinsic growth rate is negatively related to mass by the energetic trade-off $\lambda_m = \rho/w$ and because the equilibrium density is positively related to the intrinsic growth rate $[N^* = f^{inv}(1/\lambda_m s)]$. Thus, $\partial N/\partial w|_{N=N^*} < 0$ and consequently

$$\partial f / \partial \ln w|_{N=N^*} > 0 \qquad (23)$$

For the case with intra-specific competitive interactions we have from eqns 5 and 22 that the growth rate of the ith body mass variant at time t can be described as

$$\lambda_{i,t} = \rho f_i[N_t, \ln(w_{i,t}/w_t)] s_t / w_{i,t} \qquad (24)$$

where the density regulation function f_i of the ith variant depends both on the population density (N), the average body mass in the population (w), and the body mass of the ith variant (w_i). As the body mass dependence of f arises from competitive interactions where the larger individuals monopolise the resource, we expect f to be an increasing function of $\ln(w_i/w)$ that reduces into $f(N)$ at the limit $w_i = w$. Now define the partial derivative

$$\dot{f}_i(N_t) = \left. \frac{\partial f_i[N_t, \ln(w_{i,t}/w_t)]}{\partial \ln w_{i,t}} \right|_{w_{i,t}=w_t} \qquad (25)$$

The function $\dot{f}_i(N)$ reflects the within population differentiation in resource access as described by the slope in the density regulation function over ln body mass

at the limit of the average body mass in the population. This function is an increasing function N that takes the value of zero at the limit of zero population density, where there is no interactive competition and thus, at least in principle, equal resource access to all variants. Due to the negative relationship between the population dynamic equilibrium N^* and the average body mass in the population, for populations at population dynamic equilibrium, it follows that $\dot{f}_i$ is a decreasing function of w, i.e., that

$$\partial \dot{f}_i / \partial \ln w|_{N=N^*} < 0 \qquad (26)$$

A.1 The evolutionary equilibrium

In this section I determine the conditions under which the evolutionary equilibrium is an ESS and a CSS, under the assumption that the population is in population dynamic equilibrium. From eqns 22, 24, and 25, and $w = e^{\ln w}$ we find that the selection gradient on ln body mass at the limit of the average body mass is

$$
\begin{aligned}
\dot{\lambda}_i &= \left. \frac{\partial \lambda_i}{\partial \ln w_{i,t}} \right|_{w_{i,t}=w_t} \qquad (27)\\
&= \rho[\dot{f}_i(N_t) - f(N_t)]s_t/w_t\\
&= \lambda_t[\dot{f}_i(N_t)/f(N_t) - 1]
\end{aligned}
$$

Thus, the evolutionary equilibrium $\dot{\lambda}_i = 0$ is defined by the intercept between the density regulation function $f(N)$ and the within-population derivative in that function at the limit of the average variant, here denoted $\dot{f}_i(N)$.

The evolutionary equilibrium is an ESS if the second within-population fitness derivative is negative at equilibrium (Maynard Smith 1982), i.e., if $\ddot{\lambda}_i|_{w=w^{**}} = \partial^2\lambda_i^*/\partial(\ln w_i)^2|_{w_i=w=w^{**}} < 0$. From eqn 27

$$\ddot{\lambda}_i|_{w=w^{**}} = \frac{\rho[\ddot{f}_i|_{w=w^{**}} - 2\dot{f}_i|_{w=w^{**}} + f|_{w=w^{**}}]s}{w^{**}} \quad (28)$$

where $\ddot{f}_i = \partial^2 f_i^*/\partial(\ln w_i)^2|_{w_i=w}$. Then as $\dot{f}_i|_{w=w^{**}} = f|_{w=w^{**}}$ from eqn 27 we find that $\ddot{\lambda}_i|_{w=w^{**}} < 0$, and thus that the equilibrium is an ESS, when $\ddot{f}_i|_{w=w^{**}} < \dot{f}_i|_{w=w^{**}} = f|_{w=w^{**}}$.

The ESS is a CSS when $\partial\dot{\lambda}_i/\partial \ln w|_{w=w^{**}} < 0$ (Eshel 1983; Taylor 1989; Christiansen 1991). From eqn 27

$$\left. \frac{\partial\dot{\lambda}_i}{\partial \ln w} \right|_{w=w^{**}} = \frac{\rho \left(\left. \frac{\partial\dot{f}_i}{\partial \ln w} \right|_{w=w^{**}} - \left. \frac{\partial f}{\partial \ln w} \right|_{w=w^{**}} \right) s}{w^{**}}$$

$$(29)$$

and from eqns 23 and 26 we have that $\partial f/\partial \ln w|_{w=w^{**}} > 0$ and $\partial\dot{f}_i/\partial \ln w|_{w=w^{**}} < 0$

because $N = N^{**}$ at evolutionary equilibrium. Thus $\partial\dot{\lambda}_i/\partial \ln w|_{w=w^{**}}$ is always smaller than zero and the ESSs are also CSSs.

For the case with no competitive interactions we note from eqn 22 that the selection gradient on body mass is negative $[\partial\lambda/\partial \ln w = -\rho f(N)s/w]$. Thus, there is no evolutionary equilibrium but selection for a continuous decline in mass.

A.2 Population dynamic equation with selection

In this section I relax the assumption of a population in population dynamic equilibrium. This is done to deduce the population dynamic equation with superimposed selection. Following Robertson (1968), Charlesworth (1990), Iwasa et al. (1991), Taper and Case (1992), Abrams et al. (1993), and Taylor (1996) the per generation change in $\ln w$ can be approximated as

$$\Delta \ln w_t = \sigma^2 \dot{\lambda}_{i,t}/\lambda_t \qquad (30)$$

with σ^2 representing the potential by which $\ln w$ responds to selection. Normally σ^2 is the additive genetic variance, but assume here that $\sigma^2 = \hat{\sigma}^2 + \tilde{\sigma}^2$ where $\hat{\sigma}^2$ is the additive genetic variance in $\ln w$ and $\tilde{\sigma}^2$ is a plastic response of inherited environmental effects. Assume also that the plastic response can be modelled as the response of quantitative genetics, which implies that the plasticity operates by adjusting the phenotype of the offspring to the selection pressure experienced by the parents. Thus, from eqn 27 we have

$$\Delta \ln w_t = \sigma^2[\dot{f}_i(N_t)/f(N_t) - 1] \qquad (31)$$

Then from eqn 31 and $\ln w_t = \ln w_{t-1} + \Delta \ln w_{t-1}$ we find that

$$w_t = w_{t-1}e^{\sigma^2[\dot{f}_i(N_{t-1})/f(N_{t-1})-1]} \qquad (32)$$

Thus, from eqn 32 and the fact that $\dot{f}_i(N)$ is an increasing function N, and $f(N)$ is a decreasing function of N it follows for constant σ^2 that

$$g(N_t) = e^{-\sigma^2[\dot{f}_i(N_t)/f(N_t)-1]} \qquad (33)$$

is an always positive a decreasing function of N_t, and that $g(N^{**}) = 1$ at the evolutionary equilibrium $\dot{f}_i(N^{**}) = f(N^{**})$. Thus, as $\lambda_m = \rho/w$ we find that the dynamics in the maximal growth rate and the population abundance are described by

$$
\begin{aligned}
\lambda_{m,t} &= \lambda_{m,t-1}g(N_{t-1}) \qquad (34)\\
N_{t+1} &= N_t\lambda_{m,t}f(N_t)s_t
\end{aligned}
$$