Measuring the potential for growth in populations investing in diapause☆

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ABSTRACT

The intrinsic rate of population increase (r) is a common performance measure in many ecological and evolutionary studies. However, in life cycles with diapause investment resources are split into a short-term (current population growth) and a long-term (population survival through periods of unsuitable habitat conditions) component, which complicates the use of r as a single performance measure. Here we propose a new measure that integrates both performance components into a single parameter, the potential intrinsic growth rate, r_{pot}. This is the rate of increase that a population/genotype would have if no investment in diapausing stages would occur. We show that r_{pot} can be computed using standard demographic data from temporal series or life table experiments and demonstrate the use of the r_{pot} for two common life cycles among zooplanktonic organisms: (1) a cyclically parthenogenetic life cycle where investment in diapause happens only during the sexual phase, and (2) an obligate sexual life cycle with a switch from non-investing females to investing females along the lifespan. Using case studies we show that choosing r_{pot} or the standard r affects comparisons between genotypes/populations or environmental factors. We provide clues on how r_{pot} can be estimated in other life cycles with diapause investment if appropriate assumptions are made.

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1. Introduction

Many organisms rely on resistant diapausing stages to cope with the variability in their environments through dispersal in time and space (Brendonck and De Meester, 2003; Cohen and Levin, 1987; Hairston, 1996). However, investment in diapause results in a direct reduction of the current population growth rate because a fraction of resources is allocated to the production of diapausing stages, which do not reproduce immediately. Consequently, it affects the per capita population growth rate, which is a central parameter in population and evolutionary biology. This tradeoff between production of diapausing stages and current population growth has been well studied by applying life-history theory, for instance to zooplankton life cycles (Ellner, 1997; Serra et al., 2005; Spencer et al., 2001), and has major evolutionary and

ecological implications. For example, it might promote coexistence of competitive species (Montero-Pau and Serra, 2011).

Under the exponential growth model, the per capita population growth rate becomes the intrinsic rate of increase (r). Obviously, exponential growth cannot last forever. However, biological relevance of both, the exponential model and the intrinsic rate of population increase holds in many situations. Consequently, many empirical and theoretical studies observe or assume density-independent growth during relevant periods of the population dynamics. First, the intrinsic rate of increase is a predictor for the population recovery from low densities, as stressed in the r–K theory (Pianka, 1970; Roughgarden, 1971), in the concept of fugitive species (Hutchinson, 1951), or in invasion analysis (Chesson, 2000). Moreover, mechanistic resource competition theory relays on the response of the intrinsic rate of population increase to food level (Ciros-Pérez et al., 2001; Rothhaupt, 1990; Tilman, 1982). Second, as pointed out by (Caswell, 2001, p. 29), the exponential growth model can be interpreted as a projection rather than as a forecasting – i.e., the model describes what would happen if all the conditions remained constant. On that sense, the exponential model has parallels to the role of Newton's law of inertia (Turchin, 2003, p. 22). Consequently, the intrinsic rate of population increase has been widely used as a performance measurement to compare environmental effects, or the differences between species, populations or genotypes under the same conditions (Deutsch et al., 2008;

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e.g., Girma et al., 1990; Kocourek et al., 1994; Roy et al., 2003). Not surprisingly, the intrinsic growth rate has also been used to assess the chronic effects of toxicants (Biesinger and Christensen, 1972; Forbes and Calow, 1999; Mount and Norberg, 1984; Snell and Carmona, 1995).

The investment in diapause, however, entangles the interpretation of the biological meaning of the intrinsic rate of population increase. This problem is especially important when the intrinsic growth rate is used to compare the performance of populations or genotypes with different diapause investment, or to compare environmental conditions (e.g., experimental treatments) resulting in a differential diapause investment. It may happen that a population/genotype in any given conditions has a lower current population growth rate than another not because it is performing worse, but because it is investing more in diapause – i.e. future growth. Also, the interpretation of the intrinsic rate of population increase is affected by how this parameter is estimated. Two common methods are normally used to estimate population growth rate: (1) from population density time series as the slope of the log-density with time in a culture growing exponentially (Lampert and Sommer, 2007), or (2) performing life-table experiments (Carey, 1993). Both methods estimate the same rate of increase if in the life table experiment individuals investing in diapausing stages are included for calculations but the fertility fraction allocated into diapause is discounted, since they do not contribute to the current population growth in the time-series experiment. By contrast, if in the life-table experiment the diapausing-stage producers are dropped for data analysis, then a different parameter is estimated; the intrinsic rate of population increase when there is no investment in diapause. This parameter although is not useful to predict population dynamics under exponential growth (forecasting), it is still useful to assess the population performance for the environmental conditions in the experiment. The different meaning of the growth rates resulting from the different experimental and estimation approaches points out the importance of reporting what approach was used. However, this caution is not always found in the literature. For instance, when reviewing the use of life tables to estimate the intrinsic growth rate for rotifers (a major zooplankton group), some studies distinguish between both intrinsic growth rate estimates (Miracle and Serra, 1989), others just perform one of the two estimates but they provide enough methodological information to differentiate which one (Hummon and Bevelhymer, 1980; Sarma et al., 2003), whereas in others studies, this information is lacking (Conde-Porcuna, 1998; Oltra and Todolí, 1997; Stelzer, 2011).

The aim of this paper is to clarify the biological meaning of the intrinsic rate of population increase in organisms investing in diapause, and how this meaning is affected by the assumptions and methods used to estimate this parameter. We focus on zooplanktonic organism investing in diapausing eggs, and propose a new measure to estimate the intrinsic growth rate when the interest is to assess performance. Our approach is to propose a demographic measure of the resources captured by organisms and made available to invest either in current growth or in diapause. We propose that potential intrinsic rate of population increase (r_{pot}) is a suitable comparative measure of performance when an effect of diapause investment on population growth is suspected. We define r_{pot} as the rate of increase that a population/genotype would have if no investment in diapausing stages would occur. That means that r_{pot} cannot be measured directly in a population dynamics, but inferred. Here, we show a methodology to integrate the diapause investment into the intrinsic rate of population increase to obtain r_{pot}. Estimation of this parameter is depending on the lifecycle of the organism on focus. For this reason, we concentrate our analysis in a functional group of organisms – i.e., zooplankters –, which, being short-life animals, are commonly used in demographic experiments.

2. Theory

2.1. Procedure

The integration of diapause investment into the intrinsic rate of population increase is not trivial as both measures may have different metrics when estimated in an experiment. Moreover, the estimation of r_{pot} is strongly dependent on both features of the life cycle and the type of demographic data available, and might require simplifying assumptions. The intrinsic rate of population increase is commonly estimated from data obtained either by following the population dynamics or by a life table experiment. When using data from time series, parameters (i.e., birth and death rate) are required to be density-independent. Normally, this requirement is accomplished by (1) using data from populations growing at low densities or (2) selecting those data showing a linear variation between log-density and time (Lampert and Sommer, 2007). In the case of using data from life table experiments density-independence is guaranteed by an appropriate experimental set-up, particularly by approaching a constant environment through frequent medium renovation and offspring removal.

Life cycle features also play a decisive role when estimating r_{pot}. Important features are which stages contribute to the diapausing investment and when this investment occurs along the lifespan. For example, investing individuals can be females producing diapausing eggs, whereas, in organisms like cyclical parthenogens, diapause-investing individuals are females producing either males – which allocate their gametes only into diapausing eggs – or diapausing eggs. Also, diapause investment may or may not vary along an individual lifespan. In some organisms females are born determined to contribute uniquely either to current population growth or to diapausing stages (e.g., asexual vs. sexual females in rotifers), while in other organisms the individuals can switch along their lifespan from non-investing to investing in diapause (e.g., cladocerans, anostracans, and copepods). The diapause stage can also vary; in rotifers, cladocerans and calanoid copepods generally this stage is the diapausing egg, whereas in cyclopoid copepods normally it is the copepodid which enters into diapause. As the diversity of life cycles among zooplanktonic organisms is enormous, we demonstrate the computation of the r_{pot} for two common life cycles among zooplanktonic organisms: (1) an obligate sexual life cycle with a switch from non-investing females to investing females along the lifespan, and (2) a cyclically parthenogenetic life cycle where investment in diapause occurs only during the sexual phase. We will show how to obtain r_{pot} using data from both, time series and life table experiments (Box 1). Before dealing with these case studies, we develop the equations describing the exponential growth for these two life cycles.

2.2. Exponential growth

2.2.1. Obligate sexuals with diapause investment switching

This kind of life cycle is common for many zooplanktonic organisms like anostraceans (e.g. *Artemia*) (Dodson and Frey, 2001) or calanoid copepods (Santer, 1998). We will illustrate this life cycle with the calanoid copepod *Onychodiaptomus* (formerly *Diaptomus*) *sanguineus* (Hairston et al., 1995) (Fig. 1). Active individuals reappear in the water column when diapausing eggs begin to hatch. Females produce subitaneous eggs resulting in both females and males during several generations. Associated to habitat deterioration, some environmental cues – variation of photoperiod and temperature – induce females to switch from producing subitaneous eggs to producing diapausing eggs that do not hatch immediately. Interestingly, variation in the timing of diapause has been described in this species (Hairston and Olds, 1984). Consequently, a differential investment in diapause among genotypes