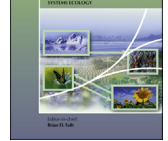




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Measuring the potential for growth in populations investing in diapause



Javier Montero-Pau*, Carmen Gabaldón, María José Carmona, Manuel Serra

Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, A.O.22085, 46071 Valencia, Spain

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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;

* Corresponding author. Tel.: +34 963543664; fax: +34 963543670.

E-mail addresses: javier.montero@uv.es (J. Montero-Pau), carmen.gabaldon-tebar@uv.es (C. Gabaldón), maria.j.carmona@uv.es (M.J. Carmona), manuel.serra@uv.es (M. Serra).

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 Bevelhimer, 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 anostracans (e.g. *Artemia*) (Dodson and Frey, 2001) or calanoid copepods (Santer, 1998). We will illustrate this life cycle with the calanoid copepod *Onychodaptomus* (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

Box 1: Procedure to obtain r_{pot} from life table and time series experiments (see details in the text).

Life table approach

1. Exclude diapausing investing individuals from data set.
2. Calculate r from data by using Euler–Lotka’s equation.
3. $r = r_{pot}$.

Time series

1. Obtain theoretical expression of r for your system: $r = b(1 - \delta) - d$ where b is the intrinsic birth rate, δ the diapause investment ratio and d the intrinsic death rate.
2. Calculate r from data.
3. Calculate intrinsic birth rate with diapausing investment by using Edmonson–Paloheimo’s equation: b_{EP} .
4. Calculate intrinsic birth rate without diapause investment: $b = b_{EP}/(1 - \delta)$.
5. Obtain intrinsic death rate: $d = b_{EP} - r$.
6. Calculate $r_{pot} = b - d$.

Note: convergence to exponential growth of the system is required.

rates estimated for females (i.e., discounting male production from the offspring). This model assumes that the contribution of diapausing-egg hatching to the current population growth is negligible after the growing season has started. Assuming that b , d and δ are density-independent, which may be true for an observation period, this model reduces to the standard exponential growth model ($dF/dt = rF$), with intrinsic growth rate of population increase $r = b(1 - \delta) - d$. Therefore, the potential intrinsic rate of population increase (i.e., if no investment in diapause is assumed, $\delta = 0$) will be $r_{pot} = b - d$, assuming that b and d are not dependent on δ (e.g., a higher proportion of diapausing eggs has no cost for female survival, or the production of a diapausing egg is as costly as the production of a subitaneous egg). For some species, departure from this assumption could introduce an important bias. In these cases, the model may be corrected by introducing relevant life-cycle information (e.g., an estimation of the relative cost of a diapausing egg compared to a subitaneous one). This issue is fatherly addressed in Section 5.

2.2.2. Cyclical parthenogens with investment during the sexual phase

This life cycle is characteristic of many cladocerans and monogonont rotifers (De Meester et al., 2004). We will use the life cycle of monogonont rotifers of the genus *Brachionus* as a model here (Wallace and Snell, 1991) (Fig. 1). The growing season of the population begins with asexual female hatching from diapausing eggs. These females produce genetically identical daughters by ameiotic parthenogenesis during several generations. When sexual reproduction is induced by environmental factors such as population density, asexual females start producing both asexual and sexual daughters. Sexual females produce haploid eggs that develop into haploid males or, if fertilized, diploid diapausing eggs. Diapausing eggs usually hatch after a dormant period of variable length. As in

exists, which can lead to the problems stated above for comparing performance.

The current dynamics of the copepod females in the water column can be described as

$$\frac{dF}{dt} = b(1 - \delta)F - dF \tag{1}$$

where F is female density, δ is the proportion of eggs going into diapause, and b and d are the instantaneous birth and death

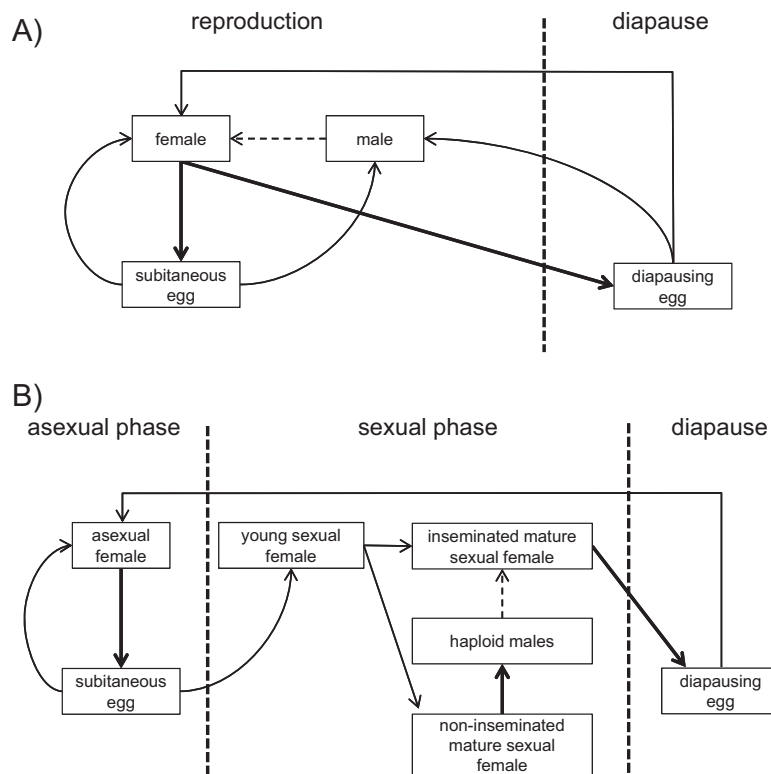


Fig. 1. Schematic representation of two different life cycles with investment in diapause: (A) obligate sexuals with diapause investment switching and (B) cyclical parthenogens with investment during the sexual phase. See text for details (Sections 2.2.1 and 2.2.2). Thick solid arrows represent reproduction; thin solid arrows, development and dashed arrows, insemination. Two arrows from a single box are mutually exclusive.

the case of the copepod, variation in both timing and investment in diapause has been observed among clones and populations (Aparici et al., 2001; Campillo et al., 2011; Carmona et al., 2009).

The population dynamics in the water column can be described by the number of asexual females (F_σ , for females producing daughters subitaneously) and sexual females (F_δ , for females investing in diapause, either directly or mediated by male production). A model after Serra and King (1999) is

$$\frac{dF_\sigma}{dt} = b(1 - \delta)F_\sigma - dF_\sigma \quad (2)$$

$$\frac{dF_\delta}{dt} = b\delta F_\sigma - dF_\delta \quad (3)$$

where b and d are the intrinsic birth and death rates for females, and δ is now the proportion of eggs from non-investing females that develop into females investing in diapause. As in the copepod model, contribution to population from diapausing egg hatching after the growing season starts is assumed to be negligible. Following the same reasoning as above, the first equation in the model tells us that F_σ grows exponentially with $r = b(1 - \delta) - d$. By contrast, this model could raise concern about whether the whole female population ($F = F_\sigma + F_\delta$) grows exponentially. Nevertheless, it can be proved (see Appendix A) that F converges to be

$$\frac{F_\sigma}{1 - \delta}$$

Therefore, F converges to exponential growth as it converges to F_σ , with $r = b(1 - \delta) - d$. This convergence is analogous to the convergence to a stable age distribution and exponential growth in age-structured populations with density-independent age-specific fertility and age-specific mortality (Caswell, 2001).

Keeping the assumption that b and d are independent of δ , $r_{pot} = b - d$. Notice that, although the cost of producing diapausing egg would be higher than the cost of a subitaneous egg (e.g., Serra et al., 2005), here δ is the proportion of eggs developing into sexual females, so the assumption that b is not dependent on δ is reasonable.

3. Calculations

3.1. Calculating r_{pot} from time series

The use of time series is a common and simple procedure to estimate the intrinsic rate of population increase (r). Two main kinds of experiments can be performed. The first one is starting a culture from a known number of individuals and after a given lapse of time (t), to count the number of individuals again. Then, r is estimated as $[\ln F(t) - \ln F(0)]/t$. The second one is monitoring population abundance along time, and then r is estimated by adjusting the function $\ln F(t) = \ln F(0) + rt$ to the time series. In order to estimate r properly, the population in the initial conditions has to be growing exponentially, which means that it must have reached the stable age-distribution (Caswell, 2001). In some long-lived temporary populations this convergence might not occur. Nevertheless, experimental procedures where the convergence does occur are possible.

As shown above, the potential intrinsic growth rate ($r_{pot} = b - d$) cannot be inferred directly from r and δ , but an estimation of b and d is needed. The egg ratio method can be used to obtain b , different implementations have been proposed (Gabriel et al., 1987), but here we will use Edmonson–Paloheimo’s method (EP) (Paloheimo, 1974), which is simple and has been proved to be accurate (Bennett and Boraas, 1989; Gabriel et al., 1987; Lynch, 1982). The EP method has been used to estimate b in both groups, copepods (Castilho-Noll and Arcifa, 2007; e.g., Santos et al., 2003; Strecker and Arnott, 2008)

and rotifers (e.g., Devetter and Sed’a, 2006; Dokulil and Herzig, 2009; Wahl et al., 2008).

EP method estimates instantaneous birth rate as

$$b_{EP} = \frac{\ln((E_{EP}/F_{EP}) + 1)}{D_{EP}} \quad (4)$$

where E_{EP} is the number of eggs, F_{EP} is the number of females and D_{EP} is the egg development time. Estimates for D_{EP} for a range of zooplanktonic organisms are available in the literature (Galkovskaja, 1987; e.g., Herzig, 1983).

In the copepod case, EP method can be applied by ignoring diapausing eggs (i.e., E_{EP} and D_{EP} being respectively the number of observed subitaneous eggs and their development time, and F_{EP} being the total number of females, F). In this way, since the subitaneous eggs are divided by both diapausing investing and non-investing females, the estimation of b_{EP} equals $b(1 - \delta)$ (i.e., the actual birth rate with diapausing investment) and d is estimated as $d = b_{EP} - r$. δ is obtained from identification and counting of eggs (Lohner et al., 1990) as number of diapausing eggs/total number of eggs, and b can be estimated from b_{EP} and δ . Finally, r_{pot} is obtained as $r_{pot} = b - d$.

In the rotifer case, the numbers of sexual F_δ and asexual females F_σ have to be estimated. This can be performed by (1) counting separately the non-egg-bearing females and the egg-bearing females, (2) classifying the latter as sexual and asexual accordingly to the type of eggs carried (e.g., Carmona et al., 1995), and (3) applying the proportion found in the egg-bearing females to the total number of females. Notice that the proportion found in (2) allows estimating δ , as $F_\delta/(F_\delta + F_\sigma)$. Besides counting females, the number of ameiotic subitaneous eggs (i.e., those hatching into asexual females) needs to be recorded. It is important to keep in mind that the rotifer population as a whole grows exponentially with $r = b(1 - \delta) - d$. Hence, as in the copepod case, if E_{EP} is the number of ameiotic subitaneous eggs, F_{EP} is $F_\delta + F_\sigma$, and D_{EP} is the development time of subitaneous eggs, then EP equation gives $b_{EP} = b(1 - \delta)$, again, the actual birth rate. Estimation of d can be carried out as above, and, analogously to the copepod case, b can be obtained from b_{EP} and δ .

3.2. Calculating r_{pot} from life table data

Dynamic life tables are another common technique to calculate r in laboratory studies of zooplanktonic organisms. Typically, a cohort of new-born females is followed until all have died and their survival and offspring recorded. Intrinsic rate of population increase is obtained from life table data by solving Euler–Lotka equation (e.g., Stearns, 1992)

$$1 = \sum e^{-rx} l_x m_x \quad (5)$$

where l and m are the survival rate and fecundity rate at age x . This equation provides the r that a population has with the same fertility, mortality and investment in diapause as the cohort. When applied to birth-flow organisms (as rotifers), this equation is a discrete approximation of the Lotka’s continuous model, and then using x as the midpoint between two consecutive cohort observations is advisable (Birch, 1948).

In dynamic life table experiments for rotifer cohorts, the type of reproduction of the females is unknown a priori. However, offspring inspection allows knowing if a female in the cohort is either asexual (producing daughters) or sexual (producing sons if not inseminated when young or alternatively diapausing eggs). As common experimental practice implies single-female culture of the cohort individuals, female insemination cannot occur. If the whole cohort (i.e., including both sexual and asexual mothers) and the produced daughters are used to estimate net age-specific fertility

– $l(x)m(x)$ –, then the Euler–Lotka equation gives r . Alternatively, if age-specific fertility is computed using only the sub-cohort of asexual females and the produced daughters are all regarded as asexual, then, Euler–Lotka equation gives r_{pot} .

Similarly, in the copepod case, when the whole cohort and the daughters produced subitaneously are taken into account to calculate net age-specific fertility, the Euler–Lotka equation gives r . However, a strategy to infer r_{pot} is based on the cost of producing a diapausing egg relative to the cost of producing a subitaneous egg for the females. As a simplifying assumption, it can be considered that the production of diapausing eggs is not more costly than that of subitaneous eggs, or alternatively, an approximate cost can be estimated (for instance, see Serra et al., 2005 for an example of this estimate in rotifers). Then, the development time, the egg survival proportion from laying to hatching, and the sex ratio observed in the subitaneous eggs could be applied to the number of diapausing eggs produced by the cohort, as if these eggs were subitaneous ones. This allows estimating the number of daughters that would hatch from the diapausing eggs under that assumption, and therefore the net age-specific fertility under the assumption that all the eggs are subitaneous. Using this net age-specific fertility the Euler–Lotka equation gives r_{pot} .

3.3. Data sources

To exemplify this methodology we used two different real datasets: a life table data set from Serra (1987) and a time series experiment Gabaldón et al. (in preparation).

The time series experiment (Gabaldón et al., in preparation) consisted in an experiment to study the combined effect of salinity (seven levels) and temperature (three levels) on the growth of two rotifer cryptic species (*Brachionus plicatilis* and *B. manjavacas*). Three replicates were performed for each combination; from acclimated cultures at the same experimental salinity and temperature, 20 individuals were transferred to flasks containing an excess of food and allowed to grow. Cultures were fixed after four days and the number of females and eggs counted. Intrinsic growth rate (r) was computed as $[\ln N(t) - \ln N(0)]/t$ where $N(t)$ is the density after four days and $N(0)$ the initial density and t the time interval. Proportion of sexual females (δ), E_{EP}/F_{EP} and b_{EP} were also computed. E_{EP}/F_{EP} was calculated as the total number of ameiotic eggs

(i.e., parthenogenetic eggs contributing to the current growth) per female (either sexual or asexual).

The life-table experiment (Serra, 1987) studied the combined effect of salinity (three levels) and temperature (three levels) on three genotypes of rotifers belonging to the *B. plicatilis* cryptic species complex. For each combination a cohort of 50 females was monitored every 12 or 24 h and survival and fertility schedules recorded. The females in the cohort were identified as sexual or asexual. From this data set (see Supplementary Data), both r and r_{pot} were computed. The 95% confidence intervals for both measures were obtained using bootstrap resampling and corrected following the bias-corrected percentile method (Efron and Tibshirani, 1986). The bootstrapping and its correction were implemented in R version 2.12.1 (R Core Team, 2010), and 10,000 randomizations were performed for each treatment and genotype.

4. Results

4.1. r_{pot} calculated from time series

Table 1 summarizes the results for a temperature (25 °C). *B. manjavacas* showed higher r than *B. plicatilis* at any salinity. However, *B. plicatilis* had higher r_{pot} than *B. manjavacas* in the lower range of the salinities tested, showing in this way its higher performance in such conditions. Gabaldón and her coworkers interpreted this result as a strategy of *B. plicatilis* to use its higher performance to produce diapausing stages, despite the cost of a lower current growth rate. This observation supports previous results that suggest that *B. plicatilis* is adapted to relatively low salinities if compared to *B. manjavacas* (Montero-Pau et al., 2011).

4.2. r_{pot} calculated from life table data

Fig. 2 shows the values of r and r_{pot} for two of these genotypes. Genotype A is predicted to have faster growth than genotype B in all three salinity treatments, since the former has higher intrinsic rate of population increase. However, r_{pot} shows that the situation is reversed for the lower salinity treatment. This means that, if diapausing-stage production was inhibited, genotype B would grow faster than genotype A, implying that the former has higher capability to convert resources in growth (i.e., higher performance).

Table 1
Demographic response to salinity of populations of the rotifers *B. plicatilis* (Bp) and *B. manjavacas* (Bm), growing at 25 °C. The highest per capita growth rate at each salinity is in bold type. Values are averages over 3 replicates, with two exceptions^a. Time for egg development was assumed to be 0.462 days (Galkovskaja, 1987) when applied to estimate birth rate using Edmonson–Paloheimo method (b_{EP}).

Salinity (g/L)	Species	δ (%)	E_{EP}/F_{EP}	b_{EP} (d ⁻¹)	d (d ⁻¹)	r_{pot} (d ⁻¹)	r (d ⁻¹)
5	Bp	10.4	0.406	0.736	0.227	0.593	0.509
	Bm	7.1	0.496	0.871	0.258	0.613	0.613
10	Bp	25.3	0.535	0.925	0.202	1.043	0.723
	Bm	5.3	0.716	1.166	0.430	0.799	0.736
20	Bp	30.5	0.615	1.036	0.426	1.064	0.610
	Bm	6.2	0.763	1.225	0.568	0.738	0.658
30	Bp	1.8	0.816	1.289	0.726	0.587	0.563
	Bm	0.4	0.754	1.215	0.632	0.588	0.583
40	Bp	0.0	0.511	0.892	0.497	0.395	0.395
	Bm	3.9	0.537	0.925	0.448	0.512	0.477
50	Bp	0.0	0.591	0.997	0.800	0.198	0.198
	Bm	0.0	0.447	0.798	0.423	0.375	0.375
60	Bp	0.0	0.484	0.852	0.910	–0.058	–0.058
	Bm	0.0	0.361	0.663	0.605	0.058	0.058

b_{EP} estimation gave slightly negative mortality rates in one (Bp) and two (Bm) replicates at 5 g/L salinity, in those cases average, mortality of the other replicates was used.

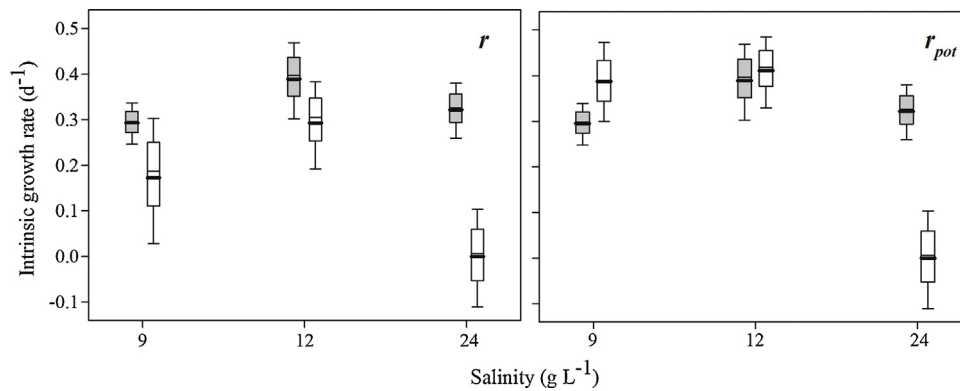


Fig. 2. Comparison between intrinsic rate of population increase (r) and potential intrinsic rate of population increase (r_{pot}) for two genotypes of rotifer *Brachionus plicatilis* at three different salinities (Genotype A, solid line; Genotype B, dotted line). This example shows how the inclusion of the diapause investment can lead to a different interpretation of the results. Data obtained from Serra (1987). Intrinsic growth rates were computed using a life table approach. Boxes represent 25th/75th percentile and black dots the 5th/95th percentile. Thin black lines and thick grey lines in each bar represent the median and the mean, respectively.

5. Discussion

Intrinsic rate of population increase is a common measure of performance in many ecological and evolutionary studies. However, investment in diapause entangles this use of the intrinsic growth rate, because the reproductive potential splits into investment in effective, current population growth and investment in future offspring. Here we have developed a simple method to integrate both growth components (current and future) into a single measure, the potential intrinsic growth rate (r_{pot}). As illustrated in the case studies shown above, comparisons of the performance of species or strains based on the effective and the potential growth rate may differ, and the discrepancies need to be analyzed after knowing what the different measurements mean. Failure to consider the potential for growing can yield misleading conclusions on relative performance when genotypes or environments are compared.

Although we have exemplified the computation of r_{pot} for two common life cycles, this method can be extended to other life cycles if appropriate assumptions are made. To do so, first, it is necessary to parameterize the population dynamics for exponential growth and to find the intrinsic rate of population increase (r) for the exponential model. In cases where systems of equations arise, convergence of the whole population to exponential growth has to be demonstrated. For instance, the model we have presented for obligate sexuals will be very similar to that of obligate parthenogenetic species with a switch to diapausing egg production. This kind of life cycle is characteristic of both many cladocerans (another major taxa of zooplankton) and some rotifer species.

Notice that some methods proposed here to estimate r_{pot} require simplifying assumptions (e.g., cost of a diapausing egg compared to the cost of a subitaneous one). If lack of robustness regarding assumption departure is suspected, then the method to estimation of r_{pot} should be refined by adding more realism, which would imply additional data on the life-history parameters (e.g., relative costs of diapausing eggs vs. subitaneous eggs in copepods). Despite this caveat, we propose that a rough estimation of r_{pot} is a better measurement of the demographic performance than intrinsic growth rate with no correction.

Additionally, some concerns associated to using egg-ratio methods may exist. Here we used Edmonson–Paloheimo's egg-ratio method (Paloheimo, 1974), which has been shown to be robust to departures from the underlying assumptions (Gabriel et al., 1987; Lynch, 1982), especially if the sampling interval chosen is close to the embryonic development duration (Gabriel et al., 1987). However, strong deviations from the exponential growth model, such a

non-continuous reproduction and the existence of cohorts, or deviations from the age-class stable composition make difficult using of egg-ratio methods. Those issues should be taken into consideration, especially when dealing with copepods which are more likely to depart from the assumptions. Future refining of the methodology presented here should consider the problems for the statistical inference of r_{pot} , especially how the errors in the demographic parameter estimates propagate to r_{pot} estimation from time series.

Besides a performance measure, the intrinsic growth rate is used as a fitness measure in some ecological scenarios. Using different approaches, Charlesworth (1980) and Lande (1982) showed that, if selection is density-, frequency-independent (plus additional, relatively minor assumptions), the intrinsic rate of population increase is the fitness measure. The relevance of this result for natural populations depends on how much the exponential growth phase lasts. In non-equilibrium populations, selection of high intrinsic rates of increase is expected to occur during long periods (Caswell, 2001), shaping life histories. However, this is not the case of temporary zooplankton populations, where the total number of diapausing eggs hatching at the beginning of the next growing season is considered the only between-year fitness measure (Campillo et al., 2011; Serra and King, 1999). Unfortunately, measuring the total production of diapausing eggs and their viability involves difficult and time-consuming experiments or field observations. Thus, fitness estimations based on short-term measurements like intrinsic rate of population increase or diapausing investment can be useful. However, if short-term intrinsic growth rate is used, then investment in the ultimate fitness component (i.e., diapausing stage production) is completely neglected. In contrast, if short-term production of diapausing stages is considered (i.e., production of diapausing stages is estimated for a period of time shorter than the growing season), then future return in diapausing stage production from current population growth is neglected. Therefore, investments in both diapause and current growth need to be combined, and in order to make comparisons, they should be expressed in a single metric; r_{pot} can work as such an integrated measure. An important point for using r_{pot} as a measure of fitness is that the resource allocation in diapausing stages is assumed to be optimal; in other words, this allocation should maximize the total production of diapausing stages for a given growing potential. Optimization of investment in diapause is a sound assumption because it only implies a mechanism to split the acquired resources, rather than a mechanism to acquire resources, which is likely more constrained. In fact, empirical evidence on rotifers suggests that this optimization evolves easily (Campillo et al., 2011; Carmona et al., 2009).

Our concern on using the effective intrinsic rate of population increase (r) to estimate population/genotype performance emerges from the fact that diapause investment inflicts a cost on current population growth. However, this same problem will arise when considering other trade-offs over population growth. For instance, it is well known that investment in sex leads to a cost for population growth (Maynard Smith, 1978). Thus, it may be interesting to generalize our approach to species of (1) obligate sexuals with a variable sex ratio or (2) cyclical parthenogens and facultative sexuals with a variable proportion of sexual offspring.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2013.09.020>.

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