Original article

Evolutionary optimization of life-history traits in the sea beet *Beta vulgaris* subsp. *maritima*: Comparing model to data

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ABSTRACT

At evolutionary equilibrium, ecological factors will determine the optimal combination of life-history trait values of an organism. This optimum can be assessed by assuming that the species maximizes some criterion of fitness such as the Malthusian coefficient or lifetime reproductive success depending on the degree of density-dependence. We investigated the impact of the amount of resources and habitat stability on a plant's age at maturity and life span by using an evolutionary optimization model in combination with empirical data. We conducted this study on sea beet, *Beta vulgaris* subsp. *maritima*, because of its large variation in life span and age at first reproduction along a latitudinal gradient including considerable ecological variation. We also compared the consequence in our evolutionary model of maximizing either the Malthusian coefficient or the lifetime reproductive success. Both the data analysis and the results of evolutionary modeling pointed to habitat disturbance and resources like length of the growing season as factors negatively related to life span and age at maturity in sea beet. Resource availability had a negative theoretical influence with the Malthusian coefficient as the chosen optimality criterion, while there was no influence in the case of lifetime reproductive success. As suggested by previous theoretical work the final conclusion on what criterion is more adequate depends on the assumptions of how in reality density-dependence restrains population growth. In our case of sea beet data R_0 seems to be less appropriate than λ.

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1. Introduction

Organisms, in order to maximize their fitness, have to optimize many intrinsic traits related to reproduction and survival, i.e. life-history traits. Reproductive and survival depend on the same limiting resources (e.g. food, water, light, etc.), and are interrelated by trade-offs (Stearns, 1992). At evolutionary equilibrium, the particular set of external factors corresponding to the biotic and abiotic environment of the organism will determine its optimal strategy, i.e. the optimal

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combination of values of life-history traits in this specific context (Stearns, 1976). Many studies, like ours, try to assess the consequences of these different ecological factors on the evolution of life-history traits.

Among the ecological factors influencing life-history strategies, mortality due to external causes (predation, disturbance, drought, etc.) is certainly the most studied. High adult mortality due to external causes is often thought to favor shorter life span, intense and precocious reproduction, with annuality as the extreme possibility (Gadgil and Bossert, 1970; Charnov and Schaffer, 1973; Michod, 1979; Charlesworth, 1980; Young, 1981; Reznick et al., 1990, 1996; Hautekèete et al., 2001), although the opposite is also possible (Reznick et al., 2004) when extrinsic mortality decreases population growth rate or can be limited by greater body maintenance (e.g. prey/predator system). It is noticeable that the mortality regime has an impact on which criterion of optimality should be used in models. One criterion, λ (population growth rate), is adequate in the situation of unlimited exponential population growth, and in the situation where a population is stabilized by environmental stress acting uniformly on all age groups. Another commonly used criterion, the lifetime reproductive success of an individual, R_0, is more adequate in situations of differential mortality rates between age classes (Mylius and Diekmann, 1995; Brommer, 2000; Williams and Day, 2003; Teriokhin and Budilova, 2008).

A second ecological factor potentially able to modify the optimal life-history tactic is the quantity of available resources, which can be light, water, nutrients or else. Length of the growing season affects indirectly the amount of available resources in plant species by allowing photosynthesis and nutrient acquisition during this period. Gadgil and Bossert (1970) suggested that increasing resources should favor precocious reproduction and higher reproductive effort. However, Ronce and Olivieri (1997) argued that the opposite prediction holds for metapopulations. Effects of resources have also been included in other models through growth rate or length of the growing season (e.g. Stearns and Koella, 1986; Iwasa and Cohen, 1989; Berrigan and Koella, 1994), apparently without any agreement on the consequences for age at maturity, reproductive effort or life span.

It is obvious that numerous external factors are potentially influencing the same life-history trait, and, as a consequence, discriminating experimentally between the various factors might appear complicated. Many empirical studies are set up to evaluate the relationship between environmental variability and the diversity of life-history strategies (e.g. Law et al., 1977; Reinartz, 1984; Till-Bottraud et al., 1990; Young, 1990). In plants, age at maturity (age at first reproduction, in years) has proved to be positively related to latitude (Smith, 1927; Cooper, 1963; Reinartz, 1984; Lacey, 1988; Wesselingh et al., 1994) or altitude (short review in Reinartz, 1984). Numerous factors, such as length of the growing season or light and water availability, are related with latitude and altitude and may plausibly act on life histories (Cooper, 1963; Harper, 1977). Drought obviously may change optimal life histories through adult extrinsic mortality (Reinartz, 1984; Young, 1990) but water can act as a resource too (Harper, 1977). Length of the growing season is tightly related to the quantity of resources acquired during the season and at high latitudes

or altitudes plants may therefore achieve less vegetative growth. Flowering in their first climatically favorable season would then weaken survival and future reproduction without compensation by sufficient current reproduction. A shorter growing season might consequently favor later age at maturity and longer life span (which are highly interrelated; see Charnov and Berrigan, 1990). Vernalization requirement for flowering, i.e. induction of flowering by exposure to low temperature during winter (Napp-Zinn, 1987), imposes a later age at maturity in higher latitudes in many plant species.

The sea beet *B. vulgaris* subsp. *maritima* (L.) shows a particularly high variability in life-history strategies. It occurs along the Atlantic coasts of Western Europe and of western North Africa, from Sweden to the Azores, as well as along the coasts of the Mediterranean (Letschert, 1993). Inland wild beets are also known in the south-western part of France (Desplanque et al., 1999). Mean life span (estimated per population) increases with latitude from about two years in the inland habitats of south-western France to over 10 years in North Brittany, then it decreases to about five years in the northernmost populations (Hautekèete et al., 2002). Life span's heritability has been estimated in sea beet to 0.48 among French populations (greenhouse conditions, Van Dijk unpublished data). Noteworthy heritable variability has also been described in *B. v. maritima* for the vernalization requirement for flowering (Boudry, 1994; Van Dijk et al., 1997; Boudry et al., 2002). In Mediterranean populations, most individuals flower without vernalization requirement (genotypes BB and Bb), whereas in northern populations all individuals require vernalization to bolt and flower (genotype bb). Between these areas, both genotypes coexist at various rates in the same population (Van Dijk et al., 1997). If germination does not occur very early in the season vernalization requirement delays first flowering until the second year, so in the present study we will consider the percentage of vernalization requirement as equivalent to the percentage of first flowering in second year (late age at maturity).

Disturbance has been suggested as an important factor in life span evolution of *B. v. maritima*, selecting for shorter life spans by lowering adult survival probability. In sea beet life span indeed appears to be highly associated with habitat type, which is in its turn associated with mortality regime (Hautekèete et al., 2002). This supports the earlier cited existing theoretical work (Gadgil and Bossert, 1970; Charnov and Schaffer, 1973; Michod, 1979; Charlesworth, 1980; Young, 1981; Reznick et al., 1990, 1996). Shorter growing seasons in higher latitudes were suggested to reduce growth, thus favoring a higher age at maturity (Van Dijk et al., 1997). A complication is that factors favoring a high age at maturity might also favor a long life span by allowing reproduction when the plant is more vigorous. In corollary, a long life span may also favor a high age at maturity: more time can then be spent on juvenile growth which is advantageous because larger individuals can produce more offspring. As a consequence factors suspected to influence the evolution of one life-history trait might also influence the other. It is thus difficult to determine which factors are directly implicated into life span and age at maturity evolution in the sea beet.

Our first aim was to assess specific theoretical expectations on life span and age at maturity evolution depending on

mortality regimes and resources (length of the growing season, which can be considered as equivalent) as well as to evaluate the importance of demographic hypotheses, i.e. of the chosen criterion of optimality λ or R_0, on the impact of both factors. Many models of life-history evolution as a function of environmental parameters have been described in the literature, but none of them is appropriate for our purpose. First, no models combine mortality and resource supply and second, they rarely use both possible fitness criteria (as for example, Berrigan and Koella, 1994; de Jong et al., 2000). Therefore we developed a realistic model (evolutionary optimization) that describes the evolution of both life-history traits (life span and age at maturity), under the two categories of factors that are suspected to act on the evolution of these traits (mortality regime and resources), using the pre-cited optimization criteria (λ and R_0).

Then, using empirical data in the sea beet, we assessed the respective influences of disturbance (a major source of mortality) and several climatic factors (which define the length of the growing season and therefore the level of available resources, as well as some aspects of extrinsic mortality) on life span and age at maturity. This was done by multivariate analyses conducted on disturbance estimators in the sea beet populations described in Hautekèete et al. (2002) and meteorological data.

Finally, empirical data and results of the evolutionary optimization model were confronted and discussed.

2.   Materials and methods

2.1.   Model

We supposed that the population dynamics can be adequately described by a classic Leslie transition matrix with elements m_x, the fertility at x-th age group, and p_x, the probability to survive from age x to age $x + 1$. For the species we model, x was expressed in years. In our simulations, where we model individual life histories from "birth" to death (without any interaction between individuals), we substituted age x by time (in years) t. A year was actually simulated over a shorter period: the growing season. Mortality was supposed to happen between the growing seasons. Technically, mortality during the growing season was ascribed to the previous inter-seasonal period (i.e. we considered individuals not having survived the current season as not having survived the previous winter) and in the same way mortality in the first year (the year of germination) was implicitly taken into account as reduced fertility.

The dominant eigenvalue λ of the transition matrix is commonly used as a quantitative measure of Darwinian fitness (Sibly, 1989; Metz et al., 1992; Kozlowski, 1993). It can be shown, that λ is an adequate criterion of optimality in, at least, two situations: first, in the situation of unlimited exponential population growth, and second, in the situation where a population is stabilized by uniform density-dependence on all age groups (Mylius and Diekmann, 1995). Evolutionary optimization in these situations consists therefore in searching for values of p_x and m_x that maximize λ. In other situations other criteria can be adequate (or a simple criterion of evolutionary

optimality in the above sense may not even be found). In particular, when density-dependence acts only on juveniles, or, to the contrary, only on adults, an adequate criterion is the lifetime reproductive success of an individual, R_0 (Mylius and Diekmann, 1995). Maximization of λ in the first case and maximization of R_0 in the second case are necessary and sufficient in order that the obtained strategies be ESS (Mylius and Diekmann, 1995). As in many applications it is not clear how the environment acts but the preference is often given to R_0 because of less computations needed (Kozlowski, 1993; Charnov, 1997).

The elements p_x and m_x are interrelated by trade-offs, described either by trade-off curves, which link p_x and m_x explicitly (Williams, 1966; Calow, 1979; Sibly and Calow, 1986) or through the allocation of common resources among different needs of the individual such as growth, reproduction, repair, maintenance, etc. (Kozlowski, 1991; Perrin and Sibly, 1993). An advantage of this approach, which we will use here, is that it allows modeling in more detail of the hypothetical physiological mechanisms underlying the trade-offs.

We supposed as it is usually done (Roff, 1983; Ziolko and Kozlowski, 1983; Day and Taylor, 1997) that the amount of biomass produced during one unit of time, B, is proportional, with a coefficient D, to some power E, $0 < E < 1$, of an individual's biomass W

$$B = DW^E \tag{1}$$

This equation is widely accepted for describing the basic metabolism of an organism (West et al., 1999) with $E = 0.67$ (Rubner's law) or $E = 0.75$ (Kleiber's law). We tried both values in computations and obtained similar results, so only results for $E = 0.67$ are presented. We only considered the biomass used for growth, reproduction, and inter-seasonal survival. So we implicitly assumed that these expenses constituted a roughly fixed proportion of the total biomass produced by the individual at each moment. We considered the parameter D as reflecting the nutritional quality of the environment through the duration of the productive part of the season.

D also depends on the unit in which B and W are expressed.

The biomass produced by an individual was divided among several needs. A fraction s_t was invested in inter-seasonal survival; the residual, $(1 - s_t)$ between growth and reproduction. The year (the growing season) was divided into two periods of duration g_t and $1 - g_t$. In the first period the residual biomass was invested in growth and instead of the linear approximation equation for W_t

$$W_t = W_{t-1} + g_t(1 - s_t)DW_{t-1}^E \tag{2}$$

we used a more precise equation obtained by integrating the differential equation

$$\frac{dW}{dt} = (1 - s_t)DW^E$$

over the period $t - 1$ to $t - 1 + g_t$:

$$W_t = W_{t-1+g_t} = \left[W_{t-1}^{1-E} + (1 - s_t)D(1 - E)g_t \right]^{1/(1-E)} \tag{3}$$

(W_0, the individual's size at birth, $t = 0$, is one of the parameters of the model).

In the remaining period, $1 - g_t$, the size remained constant and the residual biomass was allocated to reproduction,

whether immediately or in the form of biomass accumulated to be used for future reproduction. The total season investment in reproduction, u_t, is given by the equation

$$u_t = (1 - g_t)(1 - s_t)DW_t^E \qquad (4)$$

One additional variable, we denoted f_t, must be added to indicate whether the individual saves reproductive investment for the next year ($f_t = 0$) or liberates all ($f_t = 1$). We did not consider intermediate values.

We supposed that s_t was constant over the entire growing season but could differ among years, the latter also being the case for g_t and f_t. We therefore had to optimize s_t, g_t and f_t in each year. Before presenting the way in which the optimization is done, the link has to be made between the variables s_t, g_t and f_t and the transition matrix elements p_t and m_t.

We supposed that there are two potential causes for an individual to die before the next season. The first cause is uncontrollable by the individual and due to the severity (instability) of the environment. In our simulations we considered a constant survival rate Q independent of the individual's age or state. The second cause of death was controllable by the individual, and survival rate here was taken as s_t^S, where the parameter S determines the efficiency of the relative investment in survival s_t: the lower the value of S, the higher the efficiency. We did not use the absolute value of investment in survival because larger individuals were supposed to need proportionally more repair (i.e. more energy to maintain the structures despite various causes of damage: UV radiation, sandy wind, salt, etc.).

We supposed that these two causes (they could be called environmental and physiological, or external and internal, or uncontrollable and controllable) acted independently and hence the overall probability to survive to the next season is

$$p_t = Qs_t^S \qquad (5)$$

A consequence is that $p_t = 0$ if there is no investment in survival (then the individual's life span is the value of t for which $p_t = 0$). The individual can thus deliberately prevent any investment in winter survival and use all economized resources for reproduction. This means that any of both possible strategies can be chosen in our model: determinate or indeterminate life span.

The model allowed the accumulation of reproductive investment during several years before liberating it in the form of offspring. The amount of reproductive investment accumulated at the end of t-th season, U_t, is equal to the sum of reproductive investment accumulated over the years with $f_t = 0$ since the last total release (the last year with $f_t = 1$).

$$U_t = U_{t-1} + u_t \qquad (6)$$

where $U_0 = 0$, and U_{t-1} was reset to 0 if the reproductive biomass was effectively used at the end of season ($t - 1$).

The evolutionary argument for the accumulation of reproductive investment instead of an immediate use was that reproductive output may not be a linear function of the allocation to reproduction. We assumed, as it seems biologically plausible, that the reproductive output m_t depends nonlinearly on the liberated reproductive investment

$$m_t = f_t U_t^C \qquad (7)$$

with $C > 1$. Such a relationship means that the gain in fecundity accelerates with investment and that it is disadvantageous to liberate small amounts.

We used the mathematical theory of optimal control (e.g. Bellman, 1957; Pontryagin et al., 1962) to find the optimal strategy of biomass allocation during the individual's lifetime. In the terms of this theory the time-dependent variables W_t and U_t are called the state variables of the system. A second set of variables, called control variables, was represented by s_t, g_t and f_t. The third basic notion in optimal control is formed by the state equations, i.e. equations which describe the dynamics of the state variables. The state equations for W_t and U_t were (3) and (6) respectively.

The question of choosing a suitable criterion of optimality is central to optimal control theory. In our case we used two criteria: the rate of population increase, λ, and the lifetime reproductive success, R_0.

The problem of optimization is formulated as searching for an optimal (i.e. maximizing the criterion of optimality) strategy of taking control decisions (i.e. of attributing values for control variables) knowing the individual's state (i.e. knowing the values of the state variables). In other words we should determine s_t, g_t and f_t as such functions

$$s_t = s_t(W_t, U_t, t), \quad g_t = g_t(W_t, U_t, t), \quad f_t = f_t(W_t, U_t, t)$$

of W_t, U_t, and t that λ or R_0 is maximized. One way to do this is to use the method of dynamic programming (Bellman, 1957; Mangel and Clark, 1988).

The central notion of dynamic programming is the so-called gain function $F(W_t, U_t, t)$. The value of this gain function should be given at $t = T$ (where T is somewhat higher than the maximum life span of the species modeled) for all values of the state variables (which are supposed, as well as t, to be discrete). At $t = T$ the individual is already dead so that $F(W_T, U_T, T) = 0$ for all values of the state variables. The values of the gain function at other time steps were calculated iteratively backwards from $t = T - 1$ to $t = 0$ in according with the so-called basic equation of dynamic programming. This equation allowed calculating the gain function for all values of the state variables at any time step t on the basis of knowing this function at time step $t + 1$. In our case the basic equation was as follows

$$F(W_t, U_t, t) = \max_{s_t, g_t, f_t}\{F(W_{t+1}, U_{t+1}, t+1)p_t + m_t\}\lambda^{-1}$$

(in the case of taking R_0 as criterion we simply set $\lambda = 1$).

Most important was to find at each iteration of age the optimal values of the control variables s_t, g_t and f_t for all sets of values of the state variables W_t and U_t, i.e. the sought optimal strategy. It can be shown (Taylor et al., 1974) that to find the maximum of λ it is sufficient to find the maximum of the left side of the Euler–Lotka equation for different values of λ and take as the result that value of λ which corresponds the maximum equal to 1. That means that we should solve the dynamic optimization problem for different values of λ and choose that value which satisfies the condition $F(W_0, U_0, 0) = 1$. This was realized by embedding the procedure of dynamic optimization on s_t, g_t and f_t into a procedure of solving equation in respect of λ by bisection method. The knowledge of the optimal strategy allowed thereafter finding the optimal dynamics of state variables W_t and U_t by iterating forward the state equations (3) and (6).

We tested the dependence of the optimal life-cycle strategies on the model parameters. Main attention was given to the influence of parameters D and Q which we associate with environmental resource supply and winter survival. The range of variation for the survival Q (probability to survive the winter considering external causes of death only) was investigated almost entirely. As regards the resource supply D, its range of variation was chosen in such a way as to obtain biologically plausible and interesting ranges of the life-history traits.

2.2. Data

2.2.1. Sea beet

In the Beta species-complex, the sea beet, B. vulgaris subsp. maritima (L.) Arcangeli, has a particularly variable life cycle (Letschert, 1993), from long-lived with vernalization requirement for flowering in the northern part of its distribution area (Atlantic coasts of France, Belgium, the Netherlands, Great-Britain and of the western Baltic sea) to short-lived semelparous without vernalization requirement for flowering in the Mediterranean area (Letschert, 1993) and in the inland populations of south-western France.

Sea beet overwinters as vegetative rosettes, which are produced at the end of the reproductive season. Except for the seeds, all other aerial parts (stems, leaves and flowers) dry out. Thick roots store resources, thus allowing overwintering and a quick growth in the following spring. Growth is indeterminate and although plant size variability over the distribution area has not been studied formally there is a relationship with life span. Except for the possible role of habitat disturbance on life span evolution (Hautekèete et al., 2002), to our knowledge few data are available on potential mortality sources, although we observed that sea beet, like cultivated beet, is attacked by many pathogens.

Seeds were collected in 1989 all over the French distribution area of B. v. maritima (see Van Dijk et al., 1997; Hautekèete et al., 2002). Plants were grown from seed in a glasshouse, in order to avoid external causes of mortality by controlling environmental conditions. Life span and the percentage of individuals requiring vernalization for flowering were estimated for each population. In this paper we restrict the data to the 94 populations for which we had homogeneous meteorological data: populations from the French Atlantic and Mediterranean coasts, Channel Islands (Jersey and Guernsey) and inland (south-western France).

Meteorological data were used to describe the quality and/or the length of the growing season. We selected 29 locations along the French distribution of B. v. maritima for which meteorological data were available from 1961 to 1990 (MétéoFrance, 2000) to describe the climate in the study area. Sea beet populations were attributed to the nearest Météo-France locality. We chose synthetic parameters because they summarize meteorological conditions, which reduces the number of correlations between parameters and limits the risks of putting unintentionally too much weight on some aspects of the climate in the multivariate analyses.

We selected nine meteorological parameters: (1) the number of months between the first and last frosts over 30 years (FRO); (2) an estimate of the variability of temperatures over years (YVT, the difference between the values of the highest and the lowest quintiles for annual temperature); (3) an estimate of the variability of precipitation over years (YVP, same calculation). FRO gives the length of the period of potential mortality associated with winter. YVT reveals the variability of temperatures over years. These parameters are therefore mainly associated with mortality due to temperature, e.g. frost. YVP can be viewed as potentially associated with mortality due to lack or excess of water.

(4) The number of months with a minimum temperature higher than 8 °C (MIN8), during which we suppose that vernalization is negligible; (5) annual temperature (TEMP, in °C) and (6) annual precipitation (PPT, in mm). MIN8 might be an excellent estimate of the length of the growth season. TEMP (annual temperature) can be viewed as related with resources since a longer period of potential growth and a higher mean temperature allow a larger accumulation of resources and a higher metabolism. For similar reasons PPT (annual precipitation) can be considered as a resource too, as long as it varies between values that are high enough to allow survival but too low to fully meet plants' requirements.

(7) An estimate of the between-season variability of temperatures (SDT, the standard deviation of temperatures calculated from the 12 monthly mean temperatures), (8) an estimate of the between-season variability of precipitation (SDP, same calculation); (9) IPT follows the scale of ombrothermic diagrams. It is an index of water availability. This index might be interpreted as a resource when it is high, but might correspond to a climatic risk of mortality when it is very low, i.e. associated with high annual temperatures. SDP and SDT can be viewed as estimates of the amplitude of seasonality, and as such could be related with climatic mortality risks (a large SDT might correspond to very low temperatures during winter and/or to drought during summer, and a large SDP might be associated with summer drought) (Table 1).   Q2

To estimate disturbance, we established for each sea beet population a variable based on habitat type: habitat stability (STA; Hautekèete et al., 2002). We defined seven categories for STA: (1) margin of fields, (2) near-building area or roadside, (3) harbour or oyster basin, (4) beach or dune, (5) canal or estuary, (6) rocks or seawall and (7) cliff. The values correspond to probable disturbance rate, from the most disturbed (1, margins of fields, where beets are regularly mown or eliminated by hand or by herbicide treatments) to the least disturbed (7, natural cliffs) (Hautekèete et al., 2002). For each of the 29 localities we finally calculated from the surrounding populations (1) average stability index (STA) (2) mean life span (LSP) and (3) the number of individuals with or without vernalization requirement (bb vs B-) (Van Dijk et al., 1997; Hautekèete et al., 2002). We chose to pool populations rather than to attribute the climatic values of each MétéoFrance site to surrounding populations for two reasons. First this limited the risk of putting unequal weights on the climatic values of MétéoFrance sites depending on the number of surrounding populations. Second, life-history evolution in a population is the consequence of selection pressures on all populations that exchange genes regularly. As a consequence genotypes integrate selective pressures on a larger area than the population and thus pooling populations better reflects reality.

Table 1 – Abbreviations of the ecological parameters and life-history traits

Abbreviation	Description
IPT	Index of water availability, in mm/°C
MIN8	The number of months with a minimum temperature higher than 8 °C
FRO	The number of months between the first and last frosts
YVT	Between-year variability of temperatures
YVP	Between-year variability of precipitation
SDT	Between-season variability of temperatures
SDP	Between-season variability of precipitation
TEMP	Annual temperature, in °C
PPT	Annual precipitation in mm
STA	Habitat stability index
LSP	Mean life span of the populations
bb	Percentage of plants requiring vernalization (late maturity) in the populations

See text for details.

2.3. Data analysis

We first calculated the correlation matrix between all climatic and habitat variables, considering the 29 MétéoFrance sites, which revealed 19 significant ($\alpha = 0.05$) correlations among which 4 significant correlations between STA and the climatic factors. The latter correlations were mainly due to the localization of very unstable habitats (STA $\leq$ 3) in a restricted area from Agen to the Mediterranean (Hautekèete et al., 2002) with obvious climatic similarities that were confirmed by a Principal Component Analysis conducted on the 9 meteorological parameters for the 29 sites (not shown). Furthermore this large set of ecologically similar sites, compared with populations along the latitudinal gradient, might unbalance our analyses. Moreover, populations from Agen to the Mediterranean are phylogenetically separated from the other French populations (Desplanque et al., 1999). This led us to consider the data from this area with some caution. We then decided to restrict our analyses to data from Northern France to Biarritz (22 sites).

We conducted a Principal Component Analysis on the 9 meteorological factors (based on the correlation matrix). We only considered the Principal Components (PCs) with eigenvalues higher than 1. We checked that this arbitrary choice did not significantly affect the interpretation of the results. We then interpreted these significant PCs in order to identify the main factors possibly implicated in life span and vernalization requirement distribution in sea beet.

In order to assess which environmental characteristics explained the life span (LSP) or the percentage of plants

requiring vernalization (bb vs B-), we used stepwise regression analyses in which the life-history traits were the dependent variables whereas STA and the scores of the sites on PCs were the independent variables ($\alpha_{to-enter} = 0.05$; $\alpha_{to-exclude} = 0.05$). Among all variables, only the percentage of plants requiring vernalization departed significantly from normality (Ryan-joiner test). For that particular trait the stepwise analysis was consequently conducted on the binomial variable "number of individuals requiring vernalization for flowering" vs "number of individuals without vernalization requirement for flowering" (logistic regression, data described in Van Dijk et al., 1997, mean number of individuals = 56.23, s.d. = 69.12). Deviances were obtained by a regression analysis (logistic regression for vernalization requirement) that incorporated the significant factors from the stepwise analysis, ordered by decreasing deviances in the stepwise. The part of variance explained by each factor or axis was calculated as the ratio of its deviance on the null deviance of the model. PCA and regressions were conducted using Statistica 7.0 (StatSoft Inc., 2004) and $R_{2.6.1}$ (R Development Core Team, 2007) respectively.

3. Results

3.1. Model

In Figs. 1–4 we present the optimal strategies obtained for D (resource supply) varying from 0.5 to 3 and Q (extrinsic survival) varying from 0.05 to 0.99. The parameters C and S were fixed: $C = 2$ and $S = 0.5$. The values of parameters C and S were chosen in such a way as to obtain a large range of life spans, from annuality to large values of 15–20 years, which fits well the sea beet maximum life span (over 15 years, Hautekèete et al., 2002 and unpublished data) and which approximates indeterminate life span (in our simulations, the strategies for life spans of 15–20 years did not differ much from those of indeterminate life spans). It was also taken into
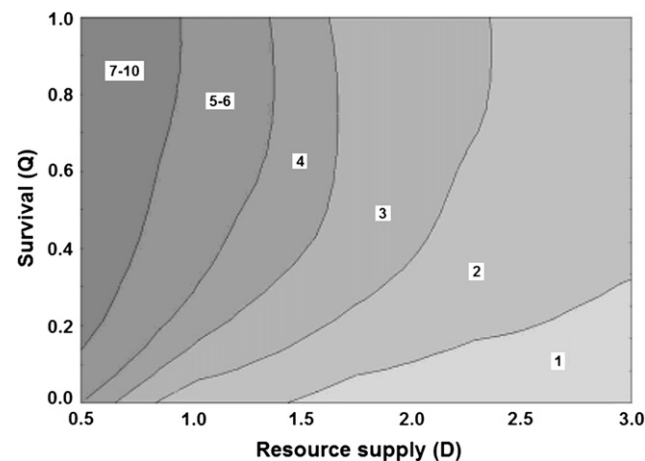

Fig. 1 – Dependence of the maturity age (white squares, in years) on resources (D; provisional units) and survival (Q; environment-related probability to survive the winter) for the case when λ is used as optimality criterion (C = 2, E = 0.67, S = 0.5).
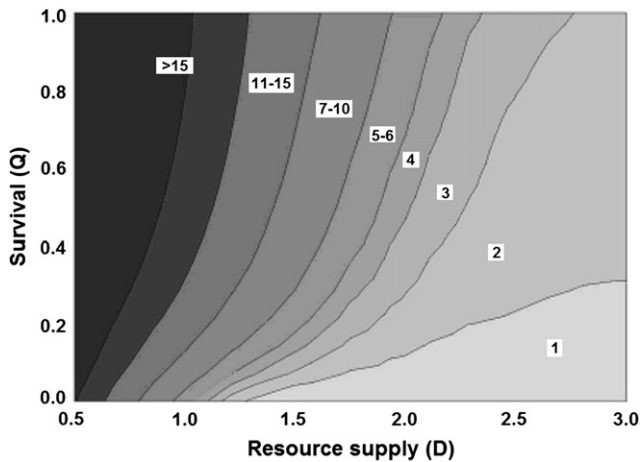
Fig. 2 – Dependence of the maximum life span (white squares, in years) on resources (D; provisional units) and survival (Q; environment-related probability to survive the winter) for the case when λ is used as optimality criterion (C = 2, E = 0.67, S = 0.5).

account that real values of λ should not differ greatly from 1, hence the ones obtained in modeling should not deviate much from 1 as well.

Fig. 1 shows how age at maturity depended on resources and survival when λ is used as optimality criterion. Fig. 2 illustrates the dependence of maximum life span on the same parameters for the same criterion. We may observe that both age at maturity and maximum life span increased when survival increased and/or resource supply decreased. The shortest maximum life span equal to 1 year was optimal when resources were abundant and/or survival was low. With less resources and higher survival, annual life cycles transformed firstly into biennial ones and then to life cycles of 3, 4, 5 and more years. For very low resource levels and sufficiently high survival the maximum life span became practically
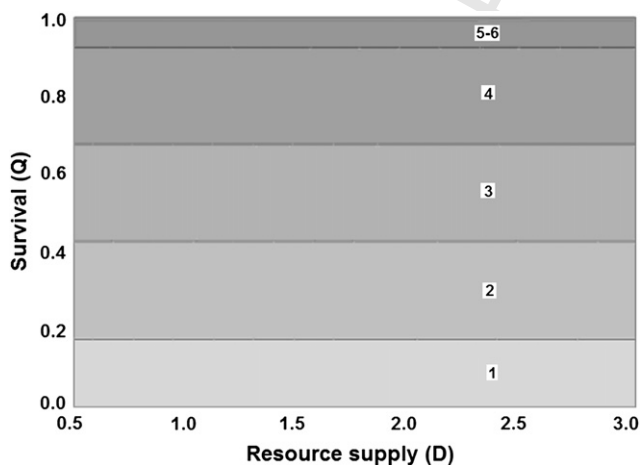

Fig. 3 – Dependence of the maturity age (white squares, in years) on resources (D; provisional units) and survival (Q; environment-related probability to survive the winter) for the case when R_0 is used as optimality criterion (C = 2, E = 0.67, S = 0.5).

indeterminate. Age at maturity in such situations and with the described values of the parameters reached 10 years.

Figs. 3 and 4 show the dependence of age at maturity and maximum life span on resources and survival when lifetime reproductive success R_0 was used as the criterion. We see, in particular, that neither age at maturity nor maximum life span depended on resource supply (for the analytical approach – see the Appendix). Growth became indeterminate for very rich resource supply (D > 2.5), reproduction occurred year after year following the first flowering.

3.2. Data

The correlation matrix conducted on 22 sites showed 13 significant correlations ($\alpha = 0.05$; Table 2). The PCA conducted on climatic factors gave 3 Principal Components (PCs) with eigenvalues higher than 1, explaining 86.12% of the total variance (Table 3). The most important variables (factor loading > 0.65) structuring PC1 were IPT, YVP, SDP, and PPT (all with negative coefficients on the axis). The most important ones for PC2 were FRO and YVT (positive values). The most important ones for PC3 were MIN8 and TEMP (positive values).

The stepwise regression conducted on LSP as a dependent variable with STA and scores of the sites on the 3 main PCs as independent variables gave the following regression: $LSP = 2.63^{**} - 0.55^{*} \, PC2 + 0.73^{***} \, STA + 0.33^{**} \, PC1 - 0.32^{*} \, PC3$ (p-values: $^{***}<0.001$; $^{**}<0.01$; $^{*}<0.05$). The overall regression explained 80.26% of the total variation. PC2, STA, PC1 and PC3 explained respectively 33.69%, 33.18%, 7.53% and 5.84% of the total variation for LSP.

The logistic stepwise regression conducted on the number of individuals with vs without vernalization requirement as a dependent variable with STA and scores of the sites on the 3 main PCs as independent variables gave the following regression: logit(bb frequency) $= 0.49^{ns} - 0.85^{***} \, PC2 + 0.95^{**} \, STA - 0.93^{*} \, PC3$ (p-values: $^{***}<0.001$; $^{**}<0.01$; $^{*}<0.05$; ^{ns}non-significant). The overall regression explained 77.95% of the total variation. PC2, STA and PC3 explained respectively 15.89%, 54.92% and 7.14% of the total variation for bb frequency.

4. Discussion

The modeling (Figs. 1–4) of the dependence of the evolutionary optimal values of age of maturity and maximum life span on resources (parameter D) and on the safety of the environment (parameter Q) demonstrated roughly the same tendency. Long life span and later maturity are optimal for poorer and safer environments. This theoretical expectation is supported by sea beet in which long life span and later maturity correlate. However, in sea beet late-flowering genotypes flower at the latest in the second year (Boudry et al., 2002; Hautekèete et al., 2002). It is possible that the range of values for disturbance or resources encountered by sea beets effectively select for flowering in the first or second year. Another explanation would be that the evolution of later age at maturity simply is impossible in the sea beet due to a lack of the required genetic variation, physiological constraints, etc. (Antonovics and van Tienderen, 1991).
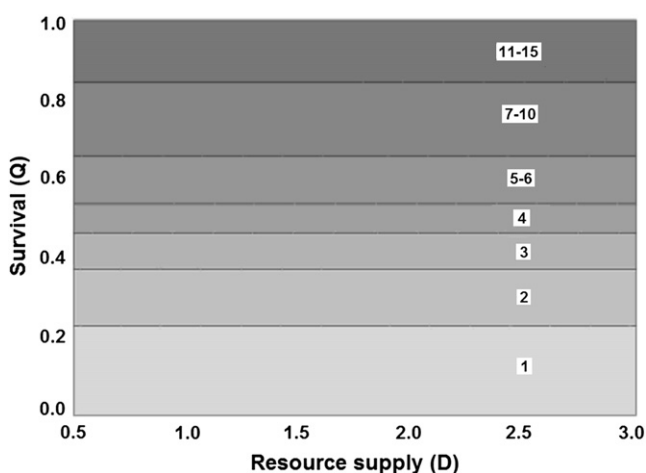
Fig. 4 – Dependence of the maximum life span (white squares, in years) on resources (D; provisional units) and survival (Q; environment-related probability to survive the winter) for the case when R_0 is used as optimality criterion (C = 2, E = 0.67, S = 0.5).

There are some interesting particularities in the results with respect to the optimality criterion used in computations. If lifetime reproductive success (R_0) is used as optimality criterion the effect of resource availability does not appear in modeling (Figs. 3 and 4). On the contrary, if we use the Malthusian parameter (λ) as a criterion of evolutionary optimality the effect of resources is similar to (and even more expressed than) the effect of environmental safety (Figs. 1 and 2). The problem of the choice of the criterion is an important one. Neither of these two fitness criteria would be perfectly adequate for many species. As noticed previously, λ is an adequate criterion of optimality when the exponential population growth is unlimited, or when the population is stable and this stability is kept by uniform density-dependence on all age groups. Exponential population growth is certainly not unlimited in non-pioneer plants, and purely uniform environmental pressure acting constantly on all age classes is not very probable. When density-dependence acts only on juveniles or on adults, the adequate criterion is R_0 but this seems also

unlikely. The use of R_0 would therefore not perfectly match reality either. It is probable that in many species environmental stresses act both on juveniles and adults but not uniformly: there could be a stronger pressure either on juveniles or on adults. Similarly, years without and years with age-dependent external mortality may alternate. Unfortunately empirical demographic data that are precise enough to be confronted to these hypotheses are not available for sea beet, nor, to our knowledge, for most species in general.

We presented results that were obtained with the apparently most realistic parameter values. Nevertheless, some details of the model, e.g. the abruptness of the sigmoid relationship between reproductive output and reproductive investment (results not shown), may modulate the resource effect on optimal life history (but never suppress it). Moreover, this model could be completed. Theoretical studies of the evolution of life histories often show that models based on a metapopulation give a prediction different from single-patch models (de Jong et al., 2000; Ronce and Olivieri, 1997). Due to lower density-dependence in the recently colonized populations of a metapopulation, generation time is expected to be lower. de Jong et al. (2000) observed earlier flowering of the monocarpic perennial *Carlina vulgaris* than expected in a single patch. Local extinction and colonization may also occur to a variable extent in sea beet, in particular in inland populations growing in man-disturbed habitats (Van Dijk and Desplanque, 1999). A logical further extension of our study would therefore be to develop a metapopulation model that could be compared to a single-patch model to test fitness measures which could be more adequate in that context (Metz and Gyllenberg, 2001). Finally, our model does not consider explicitly the accumulation of deleterious mutations with vanishing selection intensity (evolution of senescence). However since life-history optimization methods include trade-offs between investments into reproduction vs maintenance, our model is in complete agreement with the theories of antagonistic pleiotropy (Williams, 1957) and of the disposable soma (Shanley and Kirkwood, 2000). Q3

Empirical data suggest that sea beet life span may be explained by several climatic factors and by habitat stability. The Principal Component Analysis on 9 climatic factors for 22 localities along French coasts (from Northern France to southern Atlantic coast) gives 3 Principal Components (PCs)

Table 2 – Correlation matrix between ecological variables (climatic factors and habitat stability) in 22 MétéoFrance sites from Northern France to the southern Atlantic coast

	IPT	MIN8	FRO	YVT	YVP	SDT	SDP	TEMP	PPT
MIN8	−0.04 ns								
FRO	0.30 ns	−0.35 ns							
YVT	0.08 ns	−0.30 ns	0.81***						
YVP	0.54**	0.08 ns	0.14 ns	0.05 ns					
SDT	−0.20 ns	−0.03 ns	0.58**	0.68***	−0.04 ns				
SDP	0.67**	0.31 ns	−0.21 ns	−0.50*	0.57**	−0.60**			
TEMP	−0.01 ns	0.64**	−0.22 ns	−0.18 ns	0.41 ns	0.18 ns	0.32 ns		
PPT	0.90***	0.24 ns	0.16 ns	0.01 ns	0.70***	−0.14 ns	0.75***	0.42 ns	
STA	0.01 ns	−0.19 ns	−0.23 ns	−0.25 ns	−0.03 ns	−0.47*	0.04 ns	−0.29 ns	−0.08 ns

Values are Pearson correlations. See text for more details and Table 1 for abbreviations. ns = non-significant at $\alpha = 0.05$; *p-values ≤ 0.05; **p-values ≤ 0.01; ***p-values ≤ 0.001.

	PC1	PC2	PC3
Eigenvalue	3.52	2.59	1.64
% of the total variance	39.06	28.81	18.24
Cumulative %	39.06	67.87	86.12
IPT	**−0.68**	0.55	−0.36
MIN8	−0.44	−0.30	**0.68**
FRO	0.28	**0.89**	−0.05
YVT	0.46	**0.81**	0.13
YVP	**−0.68**	0.45	0.09
SDT	0.50	0.56	0.58
SDP	**−0.94**	−0.03	−0.20
TEMP	−0.50	−0.05	**0.80**
PPT	**−0.85**	0.48	0.01

Eigenvalues and percentage of the total variance explained by the Principal Components (PCs), and factor coordinates of the variables are based on correlations. See Table 1 for abbreviations of the ecological factors.

with eigenvalues higher than 1. The first retained Principal Component (PC1) is mainly structured by annual average precipitation (PPT), precipitation variability among (SDP) and over years (YVP), and water availability weighted by mean temperature (IPT), i.e. several aspects of water availability that can be associated either with resources or with mortality risks (see material and methods). PC2 is mainly structured by the length of the period of potential mortality associated with winter (FRO), and by temperature variability between years (YVT). YVT decreases with decreasing climatic stability and thus with increasing average mortality risk. Although YVT reflects climatic unpredictability for temperatures, it also increases average mortality. This axis is therefore mainly associated to mortality due to temperature, e.g. frost periods. Finally PC3 is structured by MIN8 and TEMP, i.e. the number of months with a minimum temperature higher than 8 °C and annual temperature. We can then consider that this axis is structured by resources (or length or the growth season as defined earlier) since (1) we took MIN8 as a good estimate of the length of the growth season and (2) a higher mean temperature during growth season might allow a higher metabolism and a larger accumulation of resources.

Sea beet life span along French Northern and Atlantic coasts is well explained by these three PCA axes and by STA. They indeed altogether describe 80.26% of its total variation. Temperature-related mortality risks (PC2, structured by FRO and YVT) explain 33.69% of life span variation along the French Atlantic coast in sea beet. FRO and YVT are negatively related to life span, suggesting that mortality due to extreme temperatures like frost might have selected for shorter life span in some sea beet populations. The estimate of habitat stability (STA) significantly explains 33.18% of life span variability in sea beet populations in this area. This supports the positive impact of habitat stability on life span evolution in sea beet, which has been described earlier in Hautekèete et al. (2002). PC1 explains 7.53% of the total life span variation. Its main structuring factors IPT, YVP, SDP and PPT, are negatively related with life span. On the one hand, PPT and IPT can be

viewed as water availability estimates. Their negative relation with life span would then suggest that life span might decrease with increasing water resource. On the other hand PC1 is also structured by YVP and SDP which mainly describe the amplitude of rainfall variations between years and between seasons. As such they describe the risk for a sea beet of encountering unfavorable watering conditions like drought. Since they are negatively related with life span, it can be interpreted as the selection of shorter life span with increasing drought risks. Therefore PC1 does not allow discriminating between mortality risks and resource effect associated with rainfall. Finally, PC3 and its two main parameters, namely MIN8 and TEMP, are negatively related with life span. Since this axis is mainly associated to the length of the growth season, this suggests that higher resource levels related with temperature and longer growth seasons might have selected for shorter life span in sea beet populations. Length of the growth season significantly explains about 5.84% of life span variation.

Our empirical data therefore suggest that (1) mortality due to climate, like extreme temperatures, or to habitat stability and (2) resource-related climatic factors such as the length of the growth season or mean annual temperature, apparently explain altogether a large part of the life span variability in sea beet from Northern France to Southern Atlantic coast. Rain-water availability explains a part of life span distribution too, although this is difficult to know from our data if this is due to resources or mortality risks.

These categories of ecological effects on life span evolution have already been documented in the literature. First, increasing life span with habitat stability has been shown in many species or systems. For example, annual species tend to be more represented in arable fields, while in human settlements their proportion is reduced at the expense of species with longer life spans – biennials and perennials, probably because arable land is disturbed every year due to agricultural management, whereas human settlements contain a mosaic of frequently disturbed sites and of sites that are occasionally left undisturbed for several years (Lososova et al., 2006). Hill et al. (2002) suggest that annuality in northern Europe is generally an indication of human disturbance but they recognize that it can also result from unfavorable seasons like summer drought, which is a climatic source of mortality. Moreover, Till-Bottraud et al. (1990) showed the evolution of shorter life span in *Poa annua* in dry sites compared with the regularly watered golf sites of the same area, which can be interpreted as the consequence of the climatic risk induced by drought. Finally van Kleunen (2007) showed that *Mimulus guttatus* is locally adapted to the permanent vs sporadic presence of water and is annual in populations suffering from annual drought inducing predictable plant death. All these results give interesting evidence of the influence of distur-bance and climatic risks on the evolution of life span and support the earlier cited existing theoretical literature and our data.

Data on the relationship between life span and resource-related climatic factors are less numerous in plants. von Arx et al. (2006) showed a positive correlation between altitude and life span in three forb species (two long-lived species *Penstemon venustus*, *Lupinus laxiflorus* and one short-lived

Rudbeckia occidentalis) along a 1000-m altitudinal gradient. They also found higher annual ring widths at higher altitude, suggesting that growth conditions were less favorable. This is in line with our results since climatic variations along altitudinal and latitudinal gradients are comparable. In these species longer life spans might be selected by the decreasing length of the growth season with altitude as suggested by our model.

The percentage of plants requiring vernalization for flowering per population, equivalent to age at maturity, was significantly explained by PC2, STA and PC3, which we previously interpreted as mortality risks due to temperature, habitat stability and length and quality of the growth season, respectively. These factors explain 77.95% of the total variation for vernalization requirement for flowering. 7.14% of the total variation in age at maturity is explained by PC3, mainly structured by the length of the growth season and mean annual temperature, which are negatively related with vernalization requirement. This supports the common hypothesis that late age at maturity (vernalization requirement) is selected by long winters. Long cold periods indeed (1) increase the reserves necessary to survive winter and (2) restrict the time for storage, flowering and seed maturation, thus necessitating early synchronous flowering within years (Van Dijk et al., 1997; Boudry et al., 2002). However our model suggests that later maturity might also be selected by the lower resource level consecutive to shorter and colder growth seasons. Since long winters are associated with short growth season and thus lower resources it is impossible to discriminate between both hypotheses in our study, and further studies including other types of resources might be interesting.

However the length of the growth season is not the main factor explaining age at maturity in our study. Habitat stability explains 54.92% of the total variation in age at maturity in sea beet along French Northern and Atlantic coasts. Moreover, age at maturity is also explained at 15.89% by PC2, i.e. mortality risks induced by frost or temperature variability. This supports the theoretical expectation that vernalization requirement should be highly counter-selected in disturbed or risky habitats where early reproduction is very important, since vernalization requirement postpones first reproduction to the subsequent year (Boudry et al., 2002). Finally, PC1 does not explain age at maturity significantly, which is surprising since life span and age at maturity are thought to be both selected by mortality and resources. This can be interpreted as a consequence of the very strong effect of disturbance on the distribution of this trait, which could lower the relative impact of rainwater as a resource or as a risk, and observing this effect would then be more difficult. It can also be hypothesized that, as in guppies (Reznick et al., 2004), one environmental factor has differential effect on life-history traits.

In the literature, age at maturity in plants is often shown to be positively related to latitude (Smith, 1927; Cooper, 1963; Reinartz, 1984; Lacey, 1988; Wesselingh et al., 1994) or altitude (Reinartz, 1984), which can be interpreted as a positive relation with the severity of the environment and a negative relation with the length of the growing season. On the contrary annual desert plants are known to advance their onset of flowering with the shortening of the growing period,

but in such situations aridity induces an extreme mortality risk. For example Volis (2007) showed in two annual grasses *Hordeum spontaneum* and *Avena sterilis* an advance in the onset of flowering with increasing aridity.

These examples show that the resource effect of a restricted length of the growing season should be separated, when possible, from the associated climatic risks, if any. It appears necessary in studies on the evolution of life-history traits in relation with climate or latitude/altitude to estimate the relative effects of climatic risks of death and of climatic resources, as well as to assess clearly which age classes are affected by the mortality causes, since this will change the predictions (Stearns, 1992).

Similar results are commonly found in animals (Blanck and Lamouroux, 2007), although the interpretation is more difficult than in plants. In animals high temperatures might induce more energetic expenditure due to an increased metabolism. Moreover, there is no real growing season in most animals, so temperature might not have a simple effect on resources acquisition.

Evolution of both life span and age at first reproduction (age at maturity) is possibly influenced by similar factors. Although our empirical data did not show any significant effect of rainwater on age at maturity, they suggest that life span is negatively influenced by climatic sources of mortality, by habitat disturbance and by climatic resources like length of the growth season or average temperature. It cannot be excluded that the evolution of these traits is influenced by other factors correlated with the tested environmental factors. Moreover the effect of habitat unpredictability on the evolution of life-history traits is possible in sea beet since this is one component of the between-year variability in climate, YVP and YVT. Unpredictability should select for bet-hedging strategies which could complete our model for further development. However, our empirical observations support the results of our model: it is highly plausible that life span and age at maturity in sea beet became shorter under the influences of resources and extrinsic mortality.

These are to our knowledge the first field data suggesting that life span and age at maturity might increase with less frequent disturbance, lower climatic risk and lower resource availability such as decreasing length of the growing season, and the first model suggesting that climatic effects on the evolution of these traits could be due to available resources and not only to mortality risks. Moreover, this model and its confrontation with experimental results suggest that in the sea beet R_0 might be less adequate than λ (which is plausible considering the metapopulational functioning of this species), since using R_0 the evolution of life span and age at maturity is not affected by resources contrary to our empirical results.

5. Conclusion

The model we used is particular in two aspects. First, we use two fitness criteria, lifetime reproductive success and intrinsic rate of population growth. Though it is largely recognized that these two criteria give different predictions (Mylius and Diekmann, 1995; Teriokhin and Budilova, 2008) usually only one of them is used (e.g. Stearns and Koella, 1986; Kozlowski

and Wiegert, 1987; Roff et al., 2005). Second, we study the joint impact of mortality and resource supply on life-history traits though usually only the effect of mortality is taken into account (a similar approach is used in Teriokhin et al., 2003).

Both the analysis of data on *B. v. maritima* and the results of evolutionary modeling point to the safety of the environment as the main factor, positively related with life span and age at maturity in sea beet. The influence of another important characteristic of the environment, resource availability, here, for example, the length of the growing season, on the same life-history traits also showed up. The theoretical support for this observation depended essentially on the assumptions on how density-dependence restrains population growth: either it acts on juveniles or adults or on both. The confrontation of our model with empirical data shows the importance of age-dependent effects and of the choice of the optimality criterion: as in sea beets, R_0 could be less appropriate in many species than λ. Choosing R_0 vs λ is definitely not "a matter of taste" (Pasztor et al., 1996). It also shows the importance of having precise demographic data in evolutionary ecology studies, since demography might change parameters used in models and, more concretely, factors influencing life histories in the studied populations. The present approach would be more appropriate if precise information about density-dependence was available. We therefore suggest that future ecological surveys, as well as future ecological models, should pay more attention to the mechanisms of density-dependence.

Uncited reference

Venable, 1984.

Acknowledgements

Appendix.

For the life span of one year Eq. (3) gives the following value of size

$$W_1 = \left[W_0^{1-E} + (1-s_1)D(1-E)g_1\right]^{1/(1-E)}$$

If we assume that W_0 is much smaller than W_1 (this assumption is not very restrictive because the weight of a seed is usually much less than the weight of a plant at the end of the season) then we obtain approximately

$$W_1 \approx \left[(1-s_1)D(1-E)g_1\right]^{1/(1-E)}$$

or

$$W_1 \approx \left[(1-s_1)g_1\right]^{1/(1-E)}[D(1-E)]^{1/(1-E)}$$

from where, in according with (6), the reproductive energy will be

$$U_1 \approx (1-g_1)\,(1-s_1)\left[(1-s_1)g_1\right]^{E/(1-E)}D[D(1-E)]^{E/(1-E)}$$

The last equation shows that optimizing U_1 in respect to s_1 and g_1 does not depend on D which enters into the right side of this equation as a constant multiplier. Similarly, for the life span of two years we have

$$W_2 = \left[W_1^{1-E} + (1-s_2)D(1-E)g_2\right]^{1/(1-E)}$$

After inserting W_1 we obtain

$$W_2 \approx \left[(1-s_1)g_1D(1-E) + (1-s_2)D(1-E)g_2\right]^{1/(1-E)}$$

or

$$W_2 \approx \left[(1-s_1)g_1 + (1-s_2)g_2\right]^{1/(1-E)}[D(1-E)]^{1/(1-E)}$$

Taking into account that

$$U_2 = U_1 + (1-g_2)\,(1-s_2)DW_2^E Qs_1^S$$

we find

$$U_2 \approx \Big\{(1-g_1)\,(1-s_1)\left[(1-s_1)g_1\right]^{E/(1-E)} + (1-g_2)\,(1-s_2)$$
$$\left[(1-s_1)g_1 + (1-s_2)g_2\right]^{E/(1-E)}Qs_1^S\Big\}D[D(1-E)]^{E/(1-E)}$$

so that again we see that optimizing U_2 in respect to s_1, s_2, g_1 and g_2 does not depend on D, and so on.

Note that it is not so in the case of maximizing λ. Indeed, for example, for the life span of two years we obtain from the 2×2 transition matrix the following quadratic equation for λ

$$\lambda^2 - m_1\lambda - p_1 m_2 = 0$$

from where

$$\lambda = \left(m_1 \pm \sqrt{m_1^2 - 4p_1 m_2}\right)\Big/2$$

Taking into account the equations

$$m_1 \approx (1-g_1)\,(1-s_1)\left[(1-s_1)g_1\right]^{E/(1-E)}D[D(1-E)]^{E/(1-E)}$$

$$m_2 \approx (1-g_2)\,(1-s_2)\left[(1-s_1)g_1\right.$$
$$\left. + (1-s_2)g_2\right]^{E/(1-E)}D[D(1-E)]^{E/(1-E)}$$

$$p_1 = Qs_1^S$$

we see that λ in a complex nonlinear way depends on D and hence the optimal values of s_1, g_1, s_2 and g_2 (those which maximize λ) will also depend on D.

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