

Population dynamics of the rare plant *Kosteletzkya pentacarpos* (Malvaceae): a nine-year study

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Received July 2005; accepted for publication October 2006

Rare plant species have extremely narrow distributions that can be reduced to a single or few populations. The rare long-lived plant *Kosteletzkya pentacarpos* is one such species because only two extant localities are known in the western Mediterranean. In this study, we analyse the population dynamics over nine years of the only population known in north-east Spain, which is located at the Llobregat delta (Barcelona). We collected basic demographic data to build a transition matrix model. We computed population growth rates λ and their confidence intervals for each year of study. We conducted elasticity and variance decomposition analyses to determine the relative importance of vital rates to overall population dynamics. On average, the *K. pentacarpos* population exhibited an increasing dynamics. Survivorship of adult plants contributed the most to each λ , whereas temporal variance in fecundity and juvenile fate explained the observed variation in λ . Despite the increasing dynamics of *K. pentacarpos*, important reductions in fecundity resulting from biotic agents and recruitment owing to habitat limitations are constraints for population growth. We conclude that the knowledge generated in this long-term study should be used to create new *K. pentacarpos* populations at the Llobregat delta in order to minimize the risk of extinction following catastrophic events that are nearly impossible to predict. © 2007 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2007, 153, 455–462.

ADDITIONAL KEYWORDS: elasticity analysis – long life-span – matrix models – narrow distributions – variance decomposition analysis – vital rates.

INTRODUCTION

Habitat loss and fragmentation resulting from changes in climate and land use represent a major threat to biodiversity because extant populations tend to decrease in size and increase their degree of isolation (Young & Clarke, 2000). In the case of rare plants with restricted distributions that occur only in small and isolated populations, the risk of extinction is expected to be high owing to higher demographic, environmental and/or genetic stochasticity (Goodman, 1987; Menges, 1991; Fischer & Matthies, 1998). The extreme case of isolation can be found in plant species from which only one population is known in a given

area. There are some well-documented studies on these plant species in the Mediterranean Basin. For example, in the Prepyrenean mountain ranges of Huesca (Central Prepyrenees), the rare *Borderea chouardii* (Gaussen) Heslot (Dioscoreaceae) is known from a single population occupying about 1000 m², including approximately 2000 individuals from which only one third are females (García, Guzmán & Goñi, 2002). In Murcia and Valencia (south-eastern and eastern Spain, respectively), just a few individuals of *Cistus carthaginensis* Pau (Cistaceae) are known to exist (Boscaiu & Güemes, 2001). Severe limitations in fecundity and recruitment were reported for demographic (e.g. *B. chouardii*) and genetic (e.g. *C. carthaginensis*) reasons that ultimately constrained population growth. Hence, populations of

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these particular plant species tend to merely survive or even slightly decrease at their respective sites.

In this study, we focus on *Kosteletzkya pentacarpos* (L.) Ledeb. (Malvaceae), another rare species in Spain from which only a few localities are known to exist in the western Mediterranean (Webb, 1964). All Spanish populations are concentrated in two isolated locations: the Llobregat delta (Barcelona, north-eastern Spain) and the Albufera (Valencia, eastern Spain). Such a narrow distribution was first reported several decades ago (Sennen, 1925; Bolòs & Bolòs, 1950). Apart from these sites in Spain, *K. pentacarpos* can be found small, isolated populations in seaside bogs and marshes in the Mediterranean, Black and Caspian Seas (Kikvidze & Ohsawa, 2001). High agricultural and urban pressures have caused the loss of many of these localities in the last few decades (Pignatti, 1982), leading to a particularly vulnerable species status in Europe. As a result, the species was catalogued as strictly protected in the Habitats Directive of the Council of the European Community (1992).

Basic knowledge of the demography of plant species with narrow distributions is of high conservation concern given the fact that their populations are exposed to high probabilities of local extinction following catastrophic events. This could be the case for *K. pentacarpos* in the Llobregat delta where the single population is restricted to a small wetland of less than 50 ha facing high anthropogenic habitat pressure (Pino & de Roa, 2003). We collected basic demographic data of this population over nine years (from 1996 to 2004) in order to analyse its dynamics and demographic traits by means of a matrix population model. Population growth rates with their confidence intervals were computed for each year of study. Elasticity and variance decomposition analyses were conducted to determine the relative importance of demographic traits for population behaviour. We addressed the following questions: (1) What are the population dynamics of *K. pentacarpos* at the Llobregat delta over nine years? (2) What are the vital rates that contributed the most to the observed population dynamics? We finally discuss the relevance of our results for assessing the conservation status of the species in the western Mediterranean.

MATERIAL AND METHODS

PLANT SPECIES AND STUDY AREA

Kosteletzkya pentacarpos is a long-lived hemicryptophyte with height ≤ 1.5 m and basal diameter ≈ 1 m. The plant has a short rhizome from which aerial shoots (up to 100) arise in May–June, but the plant does not exhibit vegetative reproduction. *Kosteletzkya pentacarpos* flowers throughout the summer. Flowers

(up to 50 per shoot) are hermaphrodite, solitary and spaced along the shoots. The species has a self-compatible mating system (Palau, 1954). Fruits are capsules containing five seeds. Several biotic agents have been reported to attack the plant dramatically reducing the extent of sexual reproduction (Monés, 1998): larvae of the moth *Crociosema plebejana* grow inside the stems producing an anomalous development of the shoots resulting in the total loss of flowers; larvae of the heteropteran *Oxycarenus lavaterae* feed on undeveloped seeds; and different fungi (e.g. *Fusarium oxysporum*, *Alternaria* sp.) affect seed development as a whole.

It is noteworthy that *K. pentacarpos* is abundant at its western distribution limit: the Albufera of Valencia and several adjacent wetlands probably house thousands of individuals in an area of more than 2000 ha. In contrast, only ephemeral populations were reported in two localities in Cabrera and Menorca islands several decades ago (Palau, 1954) where they now seem to be extinct (L. Sáez, pers. comm.). The only population at the Llobregat delta has been known since the first half of the 20th century (Sennen, 1925; Bolòs & Bolòs, 1950). The population occurs in a 50 ha marshland around the Ricarda lagoon, colonized by *Phragmites communis*, *Juncus maritimus*, *J. acutus* and *Spartina versicolor* (Pino & de Roa, 2003). The population is divided into ten patches totaling 700 adult plants and distributed across an area of 250×250 m in the marshland (central coordinates: $2^{\circ}6'46''E$, $41^{\circ}17'40''N$). Drainage of the surrounding cropping areas determines the flooding periodicity of the lagoon, which only occurs for short periods of time throughout the year. Occasional flooding does not seem to affect *K. pentacarpos* in terms of survival, growth or fecundity. Mean annual precipitation at Llobregat delta ranges between 500 and 550 mm.

POPULATION SAMPLING

Demographic data were obtained from a total of 145–268 individual plants monitored each year over nine years (1996–2004). All censuses were conducted in September–October in three patches separated 200 m apart and containing 181, 46 and 41 individuals, respectively, at the end of the study in 2004. All initial individuals within patches, as well as those appearing throughout the study, were tagged and monitored to obtain the demographic attributes of the population. We pooled all data from the three patches to analyse the species population dynamics because the number of individuals per patch was insufficient to conduct proper demographic analyses.

Each year, we recorded plant basal diameter, total number of shoots, number of fruiting shoots and number of fruits per shoot. A random sample of 100 fruits

was collected to determine the mean number of seeds per fruit. Individual seed production was estimated by multiplying the number of fruiting shoots per plant by the mean number of fruits per shoot by the mean number of seeds per fruit.

The presence of a persistent soil seed bank for the species was discounted after conducting two experiments of seed burial in 1994 and 1996. Sets of 100 seeds were sowed at the Ricarda marsh in areas without adult populations of *K. pentacarpus*. Seeds were spaced 2 cm apart in plastic pots that were buried in the marsh. The experiments started in November, coinciding with the natural seed-shedding period. A subsample of these pots was collected after one year of burial and the remaining seeds were counted. We found that about 95% of these seeds disappeared during this period, concluding that *K. pentacarpus* has no persistent seed bank.

Recruitment of new plants into the population was estimated by conducting seed sowing experiments at the study marsh in four different years (1995, 1997, 1999 and 2000). Seeds used in the experiments were obtained from plants raised in a greenhouse during the reproductive period prior to each experiment. Given the endangered status of the species, we preferred to obtain seeds from greenhouse stock rather than wild plants. A total of 18–24 plots (50 × 50 cm) were laid out across the study site. We sowed 200 seeds per plot and their fate was monitored during two years. Seed germination, seedling survival and subsequent establishment as flowering plants were monitored during two years after the beginning of the experiments. Mean values for these parameters were used for the years in which we did not conduct seed-sowing experiments. There are other standard methods to estimate recruitment rates from field data, such as the ratio between the number of reproductive plants per plot at time t and the number of recruits observed in the same plot at time $t + 1$ (Horvitz & Schemske, 1995; Picó & Riba, 2002). However, this was not possible in the case of *K. pentacarpus* as it was difficult to find seedlings in the plots because of the dense vegetation dominating the marsh.

MATRIX MODELS AND ANALYSES

Basic demographic data were used to construct size-based Lefkovitch matrices (Lefkovitch, 1965; Caswell, 2001). The projection matrix model used has the form: $n_{(t+1)} = \mathbf{A} n_{(t)}$, where $n_{(t)}$ and $n_{(t+1)}$ are vectors whose elements, a_i , are the number of individuals that belong to the i -th category at time t and $t + 1$, respectively. \mathbf{A} is the population projection matrix, whose elements, a_{ij} , represent the transitions or contributions from individuals in the j -th category to the i -th category over one time step. The dominant eigenvalue of the matrix

gives the population growth rate λ . The associated right and left eigenvectors w and v give the stable-stage distribution and the reproductive values of each stage class, respectively.

Size categories were determined using a biological approach (Horvitz & Schemske, 1995; Picó & Riba, 2002; Sampaio Picó & Scarano, 2005). *Kosteletzkya pentacarpus* plants with a basal diameter below 15 cm exhibited an increasing probability of sexual reproduction (on average from 0 to 50%) with increasing plant size, whereas above 15 cm, all plants had the same probability of reproducing sexually (on average 75%). In addition, most of the casualties recorded during the nine years of study (72%) took place among plants with a basal diameter below 15 cm. For these two reasons, we used a plant diameter of 15 cm as a threshold size to create two adult categories, adult 1 and adult 2. Given that *K. pentacarpus* does not form a persistent seed bank, fecundity was estimated directly as juvenile production. For each adult plant and year, juvenile production was calculated as the product between seed production, seed germination probability, and seedling survival probability during the first year. The number of juveniles produced per adult size category was obtained by averaging the number of juveniles among fertile plants. Probabilities of juvenile survival and growth to the first adult category were estimated directly from the seed-sowing experiments (see above). Hence, the *K. pentacarpus* life cycle included three categories: juvenile, adult 1 and adult 2 (Fig. 1).

We conducted a full demographic analysis using the eight resulting transition matrices obtained for the *K. pentacarpus* study population (from 1996 to 2004). First of all, we calculated the λ -value of each matrix. We applied Monte Carlo simulations to compute confidence intervals for each λ value following the method developed by Alvarez-Buylla and Slatkin (1993). This method assumes that estimated demographic parameters are the sum of the actual value plus an error term that represents the error made in estimating

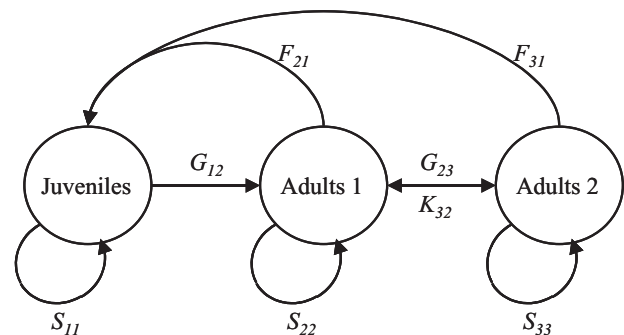


Figure 1. Life-cycle graph indicating growth (G_{ij}), retrogression (K_{ij}), survival (S_{ij}) and fecundity (F_{ij}) of *Kosteletzkya pentacarpus* plants.

demographic parameters. The error term was included in the simulations by taking into account the observed variance estimates for seed production. Sampling variances in fecundity were estimated according to a log-normal distribution whereas those for transition probabilities were estimated according to a binomial distribution. The method also accounts for the effects of truncating the distribution of matrix errors so that only biologically possible values occur. For each one of the eight transition matrices, we conducted 500 simulations obtaining 500 new simulated matrices. As a result, 500 new λ -values were produced from which the standard error (σ) was used to calculate approximate 95% confidence intervals (i.e. $\lambda \pm 2\sigma$). Confidence intervals are very useful in plant demography because they provide a means to test whether λ -values differ significantly from unity (i.e. stability). When unity falls within the estimated confidence intervals of an λ -value, it can be assumed that a given λ does not significantly differ from unity (Alvarez-Buylla & Slatkin, 1993).

An estimate for plant longevity was computed using the algorithm reported in Cochran & Ellner (1992) as the mean age at death conditional on reaching the largest adult category. Longevity was calculated on the mean matrix computed over years.

Given that a matrix entry is a function of more than one vital rate (e.g. recruitment is a function of survival of adult plants and their fecundity; Franco & Silvertown, 2004), we conducted elasticity analyses on underlying vital rates to determine their relative contribution to λ (de Kroon *et al.*, 1986; Caswell, 2001). We applied formulae for calculating vital rate elasticity published elsewhere (Franco & Silvertown, 2004). Elasticity values are presented as percentage standardized contributions (as in Franco & Silvertown, 2004).

A variance decomposition analysis of random effects (Brault & Caswell, 1993; Caswell, 2001) was conducted to decompose the observed variance in λ into contributions from the variance in, and covariance amongst, vital rates. The variance contribution of each vital rate χ_{ij} was computed as the sum of two elements: first, the product between the variance in a_{ij} and the sensitivity s_{ij} evaluated at the mean matrix, and second, the half of the sum of the product between the covariance of a_{ij} with each a_{kl} and the product of their sensitivities s_{ij} and s_{kl} evaluated at the mean matrix. Variance decomposition results were presented as percent contributions. Negative values can be obtained as a result of negative covariances between demographic transitions.

The routines to compute population growth rates, confidence intervals, sensitivities, elasticities and variance contributions of vital rates were all generated using MATLAB (MathWorks, 2001).

RESULTS

The *Kosteletzkya pentacarpos* study population yielded a mean estimate of longevity of 92 years and exhibited high survival rates of adult plants and low recruitment values (Table 1). The proportion of flowering individuals per year ranged between 58.0 and 73.2%.

Population growth rates λ for each of the eight periods of study ranged from a low of 0.988 ± 0.02 in 1998–99 to a high of 1.247 ± 0.41 in 2002–03 (Fig. 2). The mean population growth of the *K. pentacarpos* population was 1.115 ± 0.01 , indicating that on average it

Table 1. Average (\pm SE) transitions computed over nine years for the *Kosteletzkya pentacarpos* study population. The diagonal corresponds to survival, below diagonal to growth and above diagonal to retrogression values of each life-cycle stage. Fecundity values from the two adult categories are shown in italics. Nonexistent transitions are indicated by dashes. The underlying vital rates were computed from matrix transitions following Franco and Silvertown (2004)

	Time t		
Time $t + 1$	Juvenile	Adult 1	Adult 2
Juvenile	0.207 ± 0.062	<i>0.368 ± 0.101</i>	<i>1.751 ± 0.506</i>
Adult 1	0.106 ± 0.026	0.721 ± 0.038	0.063 ± 0.013
Adult 2	–	0.242 ± 0.030	0.931 ± 0.014

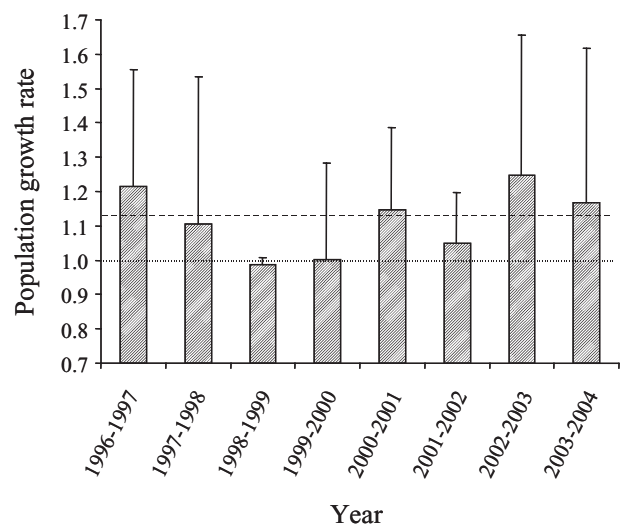


Figure 2. Population growth rates (\pm 95% CI) for each year of study of the *Kosteletzkya pentacarpos* study population. The mean population growth rate ($\lambda = 1.115$) is indicated by the dashed line and was computed by averaging annual population growth rates. Stability ($\lambda = 1$) is indicated by the dotted line.

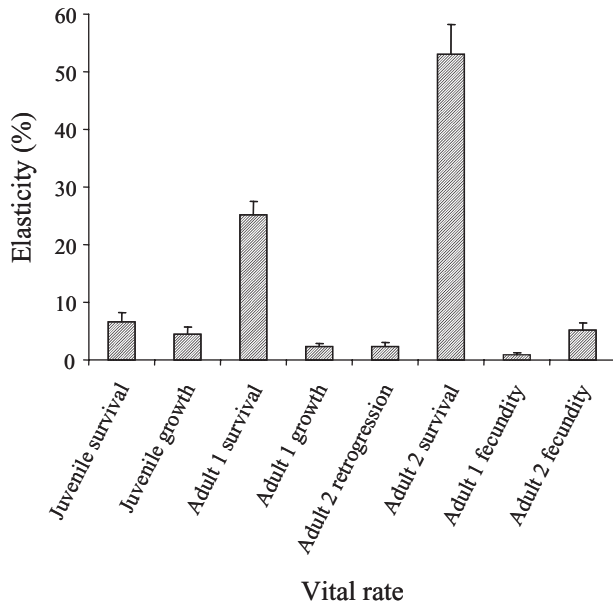


Figure 3. Average (\pm SE) elasticity values of vital rates for the *Kosteletzkya pentacarpos* study population.

increased during the entire study period. Nevertheless, confidence intervals indicated that none of the λ -values differed significantly from unity (Fig. 2), highlighting the stability of the system.

Survival rates of *K. pentacarpos* adult plants exhibited the highest elasticity values (Fig. 3). In other words, survivorship was by far the vital rate that contributed the most to annual λ . This means that small changes in survival rates would produce large changes in λ .

In contrast, variance in λ across years was basically explained by contributions from fecundity of *K. pentacarpos* adult 2 plants and fate of juveniles (Fig. 4). This result means that fecundity and juvenile vital rates chiefly determined the observed variance in λ given their sensitivity and variance/covariance schedules. Although fecundity of adult 2 plants had low sensitivity values (results not shown), the high variance across years (1.53) accounted for its high variance contribution. Juvenile survival and growth had low/moderate sensitivity values (results not shown) and low variances across years (0.07 and 0.02 for juvenile survival and growth, respectively), but their strong positive covariance with fecundity of adults 2 (0.47 and 0.24 for juvenile survival and growth, respectively) also accounted for their important variance contributions. This means that a good year for recruitment was also a good year for the survival and growth of subsequent juvenile plants. Variance contributions from the rest of vital rates can be considered negligible.

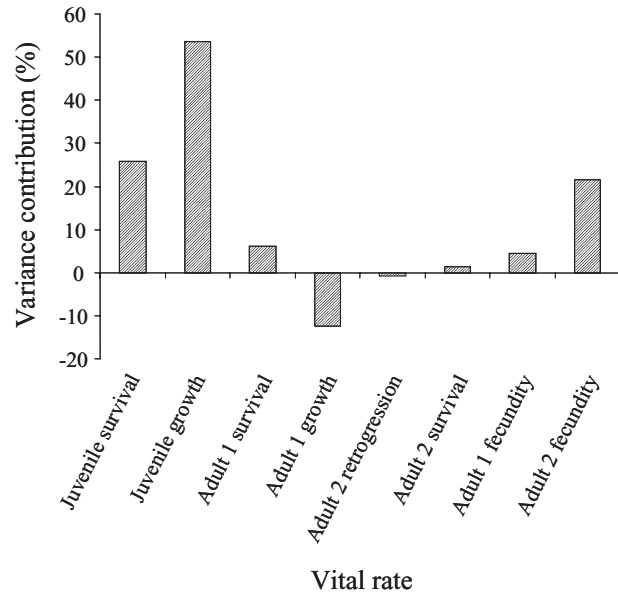


Figure 4. Contributions to the observed variance in population growth rate over years from vital rates of the *Kosteletzkya pentacarpos* study population.

DISCUSSION

The results showed that the *Kosteletzkya pentacarpos* population in north-east Spain had a trend for increasing dynamics over the nine years of study. In other words, *K. pentacarpos* is performing well at the Llobregat delta. Plant population biologists often differentiate between rare and 'new rare' plants (cf. Huenneke, 1991; Oostermeijer, Luijten & den Nijs, 2003). The so-called 'new rares' are plants that become rare because of recent human-induced habitat fragmentation. Given the fast transformation of their habitats and the dramatic reduction of their population sizes, 'new rares' often show genetic erosion and moderate/high inbreeding depression that ultimately affect population fitness and viability (Oostermeijer *et al.*, 2003). Stochastic processes also account for the increased extinction probability of small plant populations resulting from deteriorating habitat conditions (Matthies *et al.*, 2004). In contrast, rare plants, such as *K. pentacarpos* in Spain, have been rare for long time. Botanists reported in the 1920s that the species was restricted in the Llobregat delta at the Ricarda marshland (Sennen, 1925; Bolòs & Bolòs, 1950). Although rare plants often show lower levels of genetic diversity than widespread species (Falk & Holsinger, 1991; Hamrick & Godt, 1996), populations of rare plants might not be so seriously affected by reductions in population size (Gaudeul & Till-Bottraud, 2004) because of effective gene flow between extant populations and/or changes in the mating sys-

tem. In the case of *K. pentacarpos*, the combination of a long life span with a self-compatible system that ensures seed production can explain the observed dynamics of the population.

A common trait of many small, isolated populations is reduced fecundity, which also applies to the *K. pentacarpos* study population. Several factors may act in concert accounting for such a reduction in fecundity schedules. For example, pollen limitation and inbreeding effects have often been identified as the main factors responsible for fertility decline in animal-pollinated plants (Rathcke & Jules, 1993; Groom, 2001; Pflugshaupt *et al.*, 2002; Kéry & Matthies, 2004; Rasmussen & Kollmann, 2004). From a demographic point of view, it has been shown that rare plants can also exhibit recruitment limitation because of dispersal limitations or shortage of microhabitats for recruitment (Picó & Riba, 2002; García, 2003). Finally, other studies pointed out the detrimental effect of insects causing different damage in small populations of rare plants, but especially compromising seed production (Colling & Matthies, 2004; Johnson *et al.*, 2004). Although we do not totally exclude any of the factors outlined above, we believe that population growth of *K. pentacarpos* is limited mainly by reduced fecundity and recruitment. It must be emphasized, however, that the dynamics of the *K. pentacarpos* study population was increasing slightly despite the low success in fecundity, and that population increase would be higher if seed production in *K. pentacarpos* was not reduced by biotic agents.

Long-term demographic surveys are time-consuming and resulting data are usually subject to several model assumptions. In our case, it should be stressed that recruitment rates were estimated from an experimental design given the difficulties in detecting the juvenile population directly from field surveys. In contrast, adult plants of *K. pentacarpos* are clearly visible and population growth rate can be computed as the ratio between the number of plants at time $t + 1$ and the number of plants at time t simply by counting the number of plants in the same area over years. Using this method, on average over nine years, the *K. pentacarpos* study population exhibited a population growth rate of 1.03, whereas our estimate of average population growth rate over the same period using a matrix population model was 1.115. Although both estimates of population growth are consistent, we could be overestimating the actual growth rate of the *K. pentacarpos* population at the Llobregat delta. It must be noted, however, that the transition matrix model allowed us not only to obtain confidence intervals for annual λ -values, but also to identify the vital rates that contributed the most to the observed population dynamics of the species.

The effects of temporal variation in vital rates on dynamics of the *K. pentacarpos* study population were illustrated by results of the variance decomposition analysis. Variance/covariance patterns of fecundity and juvenile vital rates mostly explained the observed pattern of variation in population growth rate. In contrast, elasticity analysis clearly indicated that changes in adult survival rates would cause the largest impact on population growth rate. It is important to clearly differentiate these two different contributions of demographic traits to population behaviour. Retrospective analysis (i.e. variance decomposition analysis; Horvitz, Schemske & Caswell, 1997; Caswell, 2000) allows the identification and quantification of those demographic traits that explain the observed pattern of variation. In contrast, prospective analysis (i.e. elasticity analysis; Horvitz *et al.*, 1997; Caswell, 2000) permits forecast of the short-term effects of a given change in a demographic trait on population growth rate. For this reason, we can assert that reductions in the survival schedules of *K. pentacarpos* would produce a much more important decrease in population growth rate than reductions in fecundity. However, changes in fecundity partly contributed to the observed year-to-year fluctuations in population growth rate.

We conclude that the main threats to *K. pentacarpos* are catastrophic events that would eliminate plants and subsequently reduce population size. If fecundity was the only demographic trait affected, the population of such a long-lived plant would not grow but it would be able to persist over time given the long life span of the species (i.e. on average more than 90 years). This also applies to the rest of rare plants occurring in just a few or even one population at a given area (Boscaiu & Güemes, 2001; García *et al.*, 2002). Nevertheless, our study provides evidence that *K. pentacarpos* can maintain populations with increasing dynamics at the Llobregat delta. The knowledge generated by this long-term demographic study could be used to set up experiments to create new viable *K. pentacarpos* populations in other coastal lagoons at the Llobregat delta.

ACKNOWLEDGEMENTS

The study was partially funded by the Prat de Llobregat City Hall and AENA (Aeropuertos Españoles y Navegación Aérea). We would like to acknowledge the Director of Delta del Llobregat Nature Reserves and the proprietors (Inversiones EBYS) for permission to work at Ricarda marsh. The authors especially thank T. Contreras and E. Pino for their field assistance. Suggestions and comments from F. Lloret and M.B. García improved preliminary versions of the manuscript. We also thank two anonymous reviewers for

their comments. Finally we thank M.B. García for computing life spans.

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