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Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvest for a tropical palm tree

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Summary

1. Structured population models are used in a range of forms to predict the long-term behaviour of populations of economic or conservation interest. Such models rarely include density-dependence and do not account explicitly for the ordering of events within a generation.

2. We analysed a model for the harvesting of adults of the edible palm *Euterpe edulis* in which the role of density-dependence had been clearly defined. We modified the timing of harvesting in relation to the point in the life cycle at which populations were censused.

3. It is shown that the timing, form and intensity of harvesting are all important in determining asymptotic population behaviour. If harvesting affects only those individuals that were recorded as being adults at the start of a year, then the model predicts that all adults may be harvested without population eradication. In contrast, if harvesting also affects individuals moving from the next smaller size class during the course of a year then populations can, under some forms of harvesting, tolerate much lower levels of harvesting.

4. If density-dependence is not taken into consideration, predictions of population responses to harvesting may be erroneous. A review of transition matrices for woody plants indicates that many of these may have been derived from populations subject to strong population regulation.

5. *Synthesis and applications.* In the specific case of *E. edulis* our model shows that, although populations appear to be robust to very high levels of harvesting, when modelled as affecting only reproductive adults, this conclusion may be sensitive to varying the timing and form of harvest, and to the assumption that only reproductive individuals are removed. Structure population models used to determine levels of harvesting should account for the existence of density-dependence as well as its timing.

Key-words: Atlantic forest, *Euterpe edulis*, matrix model, population regulation, size structure, sustainable harvesting.

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Introduction

Structured population models are widely employed in applied ecology as a tool for predicting the fate of populations of economic and conservation concern under different forms of management or intervention (Crouse, Crowder & Caswell 1987; Boot & Gullison 1995; Olmsted & Alvarez-Buylla 1995; Frederiksen, Lebreton & Bregnballe 2001; Hunt 2001; Kaye *et al.* 2001). The most commonly employed form of model is a matrix population model, whereby the population is divided into discrete classes based on age or stage (Ebert 1999; Caswell 2001). The population growth rate derived from such a model predicts the tendency of populations to increase or decrease over time, while

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elasticity analysis of this matrix can be used to investigate the relative effect on population growth rate (λ)of changes to model parameters representing different transitions in the life cycle (de Kroon *et al*. 1986; Silvertown *et al*. 1993; Silvertown, Franco & Menges 1996).

The majority of matrix models incorporate a number of basic assumptions: (i) the elements are time invariant; (ii) the elements do not vary with density; (iii) the fate of individuals is independent of their past; and (iv) the elements are constrained by being measured relative to a single census point. All of these assumptions may be readily relaxed (Alvarez-Buylla 1994; Olmsted & Alvarez-Buylla 1995; Caswell 2001; Fieberg & Ellner 2001) but there are formidable difficulties in collecting the appropriate data. Of these four assumptions, most attention has focused on the consequences of variability through time of the matrix elements (Fieberg & Ellner 2001; Lennartsson & Oostermeijer 2001) or variability in the estimates of these elements (Zuidema & Franco 2001).

Within structured population models the rates of birth, death, growth and stasis are measured in relation to a single census date, or with respect to a fixed interval, typically a year. However, the dynamics of a population may be sensitive to when mortality occurs in relation to other events within the life cycle (Morris 1965; Watkinson 1982; Crawley 1983; Getz & Haight 1989) and the consequences of this for harvesting can be easily overlooked (Boot & Gullison 1995). While Olmsted & Alvarez-Buylla (1995) found little impact of varying the timing of harvest (either pre- or post-reproduction) on the model predictions for two species of palm, this need not generally be the case. For example, Watkinson (1982) found that 50% mortality within populations of the annual *Vulpia fasciculata* could either have no impact on the numbers of adult plants or reduce numbers by more than 50% depending on when that mortality occurred.

In this study, we explored the consequences for harvesting of two of the assumptions outlined above, namely the impacts of density-dependence and the time of harvesting within the life cycle relative to the census date. The analysis was carried out with specific reference to the tropical palm *Euterpe edulis* Mart. Despite the large number of studies that have produced matrix models for structured plant populations (Silvertown *et al*. 1993), it is only relatively recently that models incorporating density-dependence have begun to appear (Alvarez-Buylla 1994; Silva Matos, Freckleton & Watkinson 1999). In addition there is wider acceptance that systematic changes in vital rates with density are likely to be common in populations of woody plants (Wills *et al*. 1997; Harms *et al*. 2000). The net consequence of such processes is that the births and deaths in a transition matrix are not fixed but may vary with density. The implications of the incorporation of density-dependence within structured models for harvesting, however, have not been explored.

The aims of this study were to (i) determine the impact of density-dependence on the harvest that can be taken from populations; (ii) determine the impact of the timing of harvests on the optimal harvesting schedule; and (iii) explore the impacts of harvesting on size structures of populations of a tropical palm for which the role of density-dependence has been clearly documented.

Methods

STUDY SPECIES

The edible palm *E. edulis* is a single stemmed palm that occurs in forests along the Atlantic coast of Brazil (Henderson, Galeano & Bernal 1995). It typically occurs in swampy areas where, although potentially locally abundant, intensive harvesting of the high-quality heart of palm that it yields has led to a decline over much of its range (Galetti & Fernandez 1998). The heart of palm, or palmito, corresponds to the apical meristem of the plant together with the developing new leaves, and is harvested by cutting stems. *Euterpe edulis* has a single apical meristem and removal of the heart of palm results in the death of the plant. A detailed description of the trade in palm hearts is provided by Galetti & Fernandez (1998).

Previous studies of *E. edulis* indicate that flower production may begin when the plants are between 6 and 8 years old (Bovi, Goody Junior & Saes 1988) and that the palm takes from 8 to 10 years to grow to a stage at which it can be harvested commercially (Carvalho & Martins 1994). The peak of flowering occurs at the beginning of the wet season (Silva Matos & Watkinson 1998) and individual plants may produce between 1500 and 4800 fruits (Reis 1995; Silva Matos & Watkinson 1998), each fruit containing a single seed. The seeds are able to germinate immediately if the pericarp is removed (Bovi & Cardoso 1975), otherwise most seeds die within 3 months of shedding (Silva Matos & Watkinson 1998). The life cycle of the palm is conducive to harvesting because regeneration is rapid. However, it is also argued that sustainable exploitation is unlikely because plants have to be killed at harvest in order to remove the heart of palm (Cunningham 2001).

Overexploitation of *E. edulis* has led to the movement of the centre of the palm heart industry from the Atlantic forest to the estuaries of the River Amazon, where the multi-stemmed *E. oleracea* is exploited (Galetti & Fernandez 1998). The harvesting of *E. edulis* nevertheless continues. *Euterpe edulis* may be harvested legally under license but there is also substantial illegal harvesting. Galetti & Fernandez (1998) have estimated that approximately 58 000 palms are harvested illegally each year in the Seta Barras region alone. This represents an area of about 227 ha, implying an exploitation rate of 255 plants ha^{-1} year^{-1}. Most of the palm hearts sold in markets are still from natural stands, despite efforts to promote plantations and the management of palms.

MODEL FOR POPULATION DYNAMICS

The harvesting model we analyse here is derived from the matrix model presented by Silva Matos, Freckleton & Watkinson (1999), which was based on data from a population that had recovered substantially from harvesting. As described in Silva Matos, Freckleton & Watkinson (1999), the model was parameterized by tracking the sizes and fates of marked individuals within permanent 5 × 5-m plots over a period of 4 years. This allowed size-specific rates of growth, mortality and fecundity to be estimated. Using these estimates, a model for population dynamics was constructed. This model is a size-based matrix model with seven size/stage classes based on the morphology of the plants, the diameter of the plants at soil level and reproductive state: size class 1 (0–3 leaves), 2 (4 leaves–10·1 mm), 3 (10·1–20 mm), 4 (20·1–30 mm), 5 (30·1–60 mm), 6 (60·1–120 mm) and 7 (120·1 + mm). Only the plants in size class 7 are reproductive. The transition matrix **A** describing the flux of individuals from one year to the next was of the form:

$$\mathbf{A} = \begin{bmatrix} P_1 & 0 & 0 & 0 & 0 & 0 & F_7 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{bmatrix} \qquad \text{eqn 1}$$

where P_i is the annual probability of surviving and remaining in the same size class, G_i is the probability of survival and growth to the next size class and F_7 is the number of offspring produced per reproductive palm per year expressed in terms of the mean number of plants in size class 1 (seedling with less than 3 leaves) produced per plant of size class 7 (> 120 mm diameter).

If population dynamics are density-independent then the entries of equation 1 are fixed and do not change as populations size changes. The long-term behaviour of the population is then determined by λ, the dominant eigenvalue of **A**. If $\lambda > 1$ then the population is viable and increases, if $\lambda < 1$ the population is inviable and declines, and if $\lambda = 0$ the population remains at a constant equilibrium density.

If population dynamics are density-dependent then one or more entries of **A** vary as population numbers change, and λ also changes with density. In the case of *E. edulis*, density-dependence was found to affect **A** through two effects on G_1, the probability of individuals surviving and moving from class 1 to class 2 (Silva Matos, Freckleton & Watkinson 1999). First, G_1 was a function of the number of seedlings in class 1, specifically (where density of seedlings, N_1, is measured per 5 × 5-m plot, the size of plots in the original study):

$$G_1 = 0{\cdot}496(1 + 0{\cdot}012N_1)^{-1} \qquad \text{eqn 2}$$

This response is likely to reflect competition between seedlings for light and resources. Secondly, recruitment of seedlings from class 1 to class 2 is greatly reduced in the presence of an adult canopy, presumably owing to the effects of shading. This was modelled by further modifying G_1 to:

$$G_1 = 0{\cdot}496(1 + 0{\cdot}012N_1)^{-1} \exp[-0{\cdot}28N_7] \qquad \text{eqn 3}$$

Increasing the density of adults (N_7) leads to an exponential decline in the rate of recruitment of seedlings from size class 1 to size class 2. By using the variable function in equation 3 rather than a fixed value for G_1 (i.e. by iterating the model numerically, updating the value of G_1 each generation as densities change), we can predict population dynamics including density-dependence. We assume that this density-dependence acts at the same time as reproduction occurs.

Alternatively equation 3 can be used to predict the growth of populations from low densities, for example as they recover from intense harvesting. We set $G_1 = 0{\cdot}496$, which is the asymptotic value of G_1 as N_1 and N_7 in equation 3 tend to zero. By employing this fixed value and analysing population dynamics based on a density-independent version of **A** we can predict the tendency of populations to grow or decline from low densities. In the context of predicting the impacts of harvesting, analysis of the model in this form allows the sustainability of different harvesting strategies to be modelled.

The model assumes that populations of *E. edulis* are continuous. In reality *E. edulis* exists within a matrix of other vegetation and may therefore represent a variable component of the total canopy. The predictions of numbers from our model therefore have to be weighted by this proportion. For this reason the unit of density employed is the number of plants in a small 5 × 5-m patch, corresponding to the scale at which individuals were monitored.

MODELLING HARVESTING

Palms are typically not harvested until they reach size class 7. We model the harvest of plants by modification of the transition matrix such that between time t and $t + 1$ a fraction $1 - p(t)$ of the adults are removed by harvesting per annum, i.e. a fraction $p(t)$ survives. In doing so, however, it is necessary to account for when this mortality occurs in relation to other processes within the life cycle. Consider first the dynamics of the seedling class in the absence of harvesting:

$$N_1(t + 1) = P_1N_1(t) + FN_7(t) \qquad \text{eqn 4}$$

All adults present at time t are assumed to reproduce and hence contribute to the number of seedlings present at time $t + 1$. If reproduction takes place prior to harvesting then the dynamics of class 1 are correctly modelled by equation 4, as all adults alive at time t are able to reproduce. If, however, reproduction follows harvesting then the dynamics of the seedlings are given by:

$$N_1(t+1) = P_1 N_1(t) + p(t) F N_7(t) \qquad \text{eqn 5}$$

if it is assumed that only the $p(t)N_7(t)$ surviving adults reproduce. In the case of adults, in the absence of harvesting:

$$N_7(t+1) = G_6 N_6(t) + P_7 N_7(t) \qquad \text{eqn 6}$$

The number of adults present at time $t + 1$ is a function of the survival of individuals within the adult size class for a year, as well as the growth of individuals from size class 6 to class 7. In this case, therefore, the effects of harvesting depend on whether this occurs before or after growth from class 6 to class 7. If σ_6 and σ_7 are the survival of trees within classes 6 and 7, respectively, then $\sigma_{6\to7}$, the survival of plants making the transition to class 7 when harvesting of adults occurs, is:

$$G_{6\to7} = G_6^{\tau} G_7(p(t))^{1-\tau} \qquad \text{eqn 7}$$

where τ is the fraction of the year that trees remain in class 6 before entering class 7. Because in the absence of harvesting $\sigma_6 = 0{\cdot}97$–$0{\cdot}98$, compared with a value of $\sigma_7 = 0{\cdot}99$, we can set $\sigma_6 \approx \sigma_7$ in equation 7, yielding:

$$\sigma_{6\to7} \approx \sigma_6(p(t))^{1-\tau} \qquad \text{eqn 8}$$

Since $G_i = \sigma_i\gamma_i$, where γ_i is the probability of transition from class i to class $i + 1$:

$$G_{6\to7} \approx G_6(p(t))^{1-\tau} \qquad \text{eqn 9}$$

In the case of *E. edulis*, Silva Matos & Watkinson (1998) found that plants produce fruits over the period from October to January, with no plants bearing fruits before October or after January. The census data on which the model is based were collected between late January and early April (Silva Matos, Freckleton & Watkinson 1999). Hence the census point assumed by the model is in the period following reproduction. In the modelling below, therefore, pre-reproductive harvesting occurs from April to October while post-reproductive harvesting occurs between January and April. Unfortunately no comparable data on the phenology of plant growth are available. We therefore varied the timing of harvest and τ between possible extremes in order to generate a range of predictions of population behaviour (see below). We have assumed that transitions from class 6 to 7 occur at a discrete point (tau) since these plants live in a seasonal environment.

For the purposes of the modelling, we assume that the life cycle begins in March (i.e. the fixed census point). The period March–October represents the pre-reproductive period of the life cycle. Reproduction begins in October, with the period October–February representing the period following the onset of reproduction. In reality of course the timing of reproduction will vary from year to year, for example as a result of weather variations, and will be spread out rather than occurring as a discrete event. However, the intention of the modelling is to explore how varying assumptions regarding the timing of mortality relative to reproduction affects model predictions, and this formulation allows us to compare directly the extremes of the timing of harvest.

In the simulations we explore the impacts of harvesting on the population growth rates (λ) of *E. edulis* utilizing the baseline model (Table 1) (i) in the absence of harvesting and density-dependence (i.e. $G_1 = 0{\cdot}496$), where we are able to explore the consequences of harvesting only through analysing the effects on λ, the finite rate of increase; (ii) modified to incorporate

Table 1. Parameters in the transition matrix (equation 1) for modelling the population dynamics of *Euterpe edulis*: the baseline model with or without density-dependence and the parameters for describing variation in the timing and intensity of harvesting. Varying the timing and intensity of mortality ($1 - p$) in the pre- and post-reproductive harvest matrices only affects the elements G_6, P_7 and F_7 as it is only reproductive plants that are harvested (see text for details)

	Baseline	Pre-reproductive harvest	Post-reproductive harvest
Survival and growth			
G_1	0·496 or equation 3	0·496 or equation 3	0·496 or equation 3
G_2	0·11	0·11	0·11
G_3	0·20	0·20	0·20
G_4	0·39	0·39	0·39
G_5	0·18	0·18	0·18
G_6	0·19	0·19	$0{\cdot}19\ p^{1-\tau}$
Survival and stasis			
P_1	0·51	0·51	0·51
P_2	0·76	0·76	0·76
P_3	0·74	0·74	0·74
P_4	0·61	0·61	0·61
P_5	0·80	0·80	0·80
P_6	0·78	0·78	0·78
P_7	0·99	$0{\cdot}99\ p$	$0{\cdot}99\ p$
Reproduction			
F_7	98·00	$98\ p$	98

harvesting assuming that harvesting occurs in the part of the year before reproduction and growth of plants from class 6 to class 7; and (iii) modified to incorporate harvesting in the part of the year following the onset of reproduction, allowing for the harvest of a proportion of the plants that make the transition from size class 6 to 7 depending on the time of harvest, by varying τ. These two timings of harvest should represent the extremes of the possible range of variation we would expect to observe. A range of further modifications are of course possible; these three forms have been chosen to yield a range of behaviour.

MODELLING THE FORM OF HARVESTING

We explored several contrasting forms of harvesting. The first form of harvesting (constant proportion harvesting) assumes that a constant proportion of individuals is removed each year. Thus, the harvested proportion $p(t)$ is constant and does not vary through time. This is one of the most common forms of harvest included in structured population models (Caswell 2001).

The second form of harvest assumes that populations are harvested down to a minimum threshold density, T, each year, and not harvested if populations are lower than this density. The rationale for modelling this form of harvest is that it has been suggested that sustainable harvesting of *E. edulis* may be achieved by adhering to such a threshold (Reis *et al.* 2000). This form of harvesting was modelled in the following way: if the density of adult palms, N_A, exceeded the critical threshold T then the harvested proportion is:

$$p(t) = \frac{(N_A(t) - H)}{N_A(t)} \qquad \text{eqn 10}$$

In the case of the pre-reproductive harvest the density of adult palms is simply N_7, the density of class 7. In the case of the post-reproductive harvest the calculation is more complex. If plants make the transition from class 6 to class 7 at relative time τ, then the density of adult palms is given by:

$$N_A(t) = \sigma_6^{\tau}\gamma_6 N_6(t) + N_7(t) \qquad \text{eqn 11}$$

The proportion harvested is then given by substituting equation 11 into equation 10. It is assumed that palms are harvested at random. Consequently no distinction is made between palms that made the transition to class 7 between t and $t + 1$ and those already in class 7 at time t; these are therefore assumed to be harvested in proportion to their abundance.

The third and final form of harvest assumes that harvesting occurs periodically. This reflects the current recommended practice of allowing *Euterpe* populations to recover following harvesting (Reis *et al.* 2000; Zuidema 2000). Specifically we assumed (i) populations remain undisturbed for $K - 1$ years; (ii) when harvesting occurred in year K it was of the threshold form outlined above. Note that, in the second two forms of harvesting the fraction surviving harvest, $p(t)$, is not constant but varies from year to year.

FIELD DATA FROM HARVESTED POPULATIONS

Data on recently harvested populations were collected from five populations in remnant forest areas in the Vale do Ribeira, São Paulo, Brazil (23°33′S, 46°38′W). The five forest fragments were located in and around the Campinas Agronomic Institute in an area where illegal harvesting occurred regularly. Three plots of 10 × 10 m were set up at random locations within each of the forest fragments. Within each plot the size structure of all palms was recorded according to the diameter of the stems at soil level (except for the seedlings where the number of leaves was used), following the size classification for *E. edulis* of Silva Matos, Freckleton & Watkinson (1999) but in which the two smallest size classes were combined: size class 1 and 2 (0–3 leaves, 4 leaves–10·1 mm), 3 (10·1–20 mm), 4 (20·1–30 mm), 5 (30·1–60 mm), 6 (60·1–120 mm) and 7 (120·1+ mm).

Results

PRE-REPRODUCTIVE HARVEST, PROPORTIONAL AND THRESHOLD REMOVAL

Figure 1 shows the predictions of the model with pre-reproductive harvesting where either a constant proportion of the population is harvested each year (Fig. 1a–c) or only those individuals above a threshold number (Fig. 1d–f). The difference between these two forms of harvest is that the threshold form of harvest is basically a density-dependent form of harvesting. This is because harvesting ceases at low densities, allowing low density populations to recover in numbers. In contrast, where a constant proportion of individuals is harvested, the same fraction of individuals is removed irrespective of population size. Consequently, although the constant proportion form of harvesting may lead to population eradication at high levels of harvesting (i.e. λ in Fig. 1a is reduced below unity), under the threshold number form of harvest population eradication occurs only when the threshold for harvesting is set at zero (Fig. 1d).

The effects of either form of harvest on total population numbers can be large (Fig. 1b,e), although this is mainly a consequence of reductions in the number of smaller seedlings (see below). In terms of the effects of varying the proportion or threshold number for harvesting, the highest yields of palms are given by relatively intense forms of harvest. Under the constant proportion model the highest offtake (i.e. yield) is given by removal of *c.* 70% of individuals (Fig. 1c), whereas a threshold of only about one adult individual plot^{-1} (25 m^2) yields the largest offtake under the threshold model.

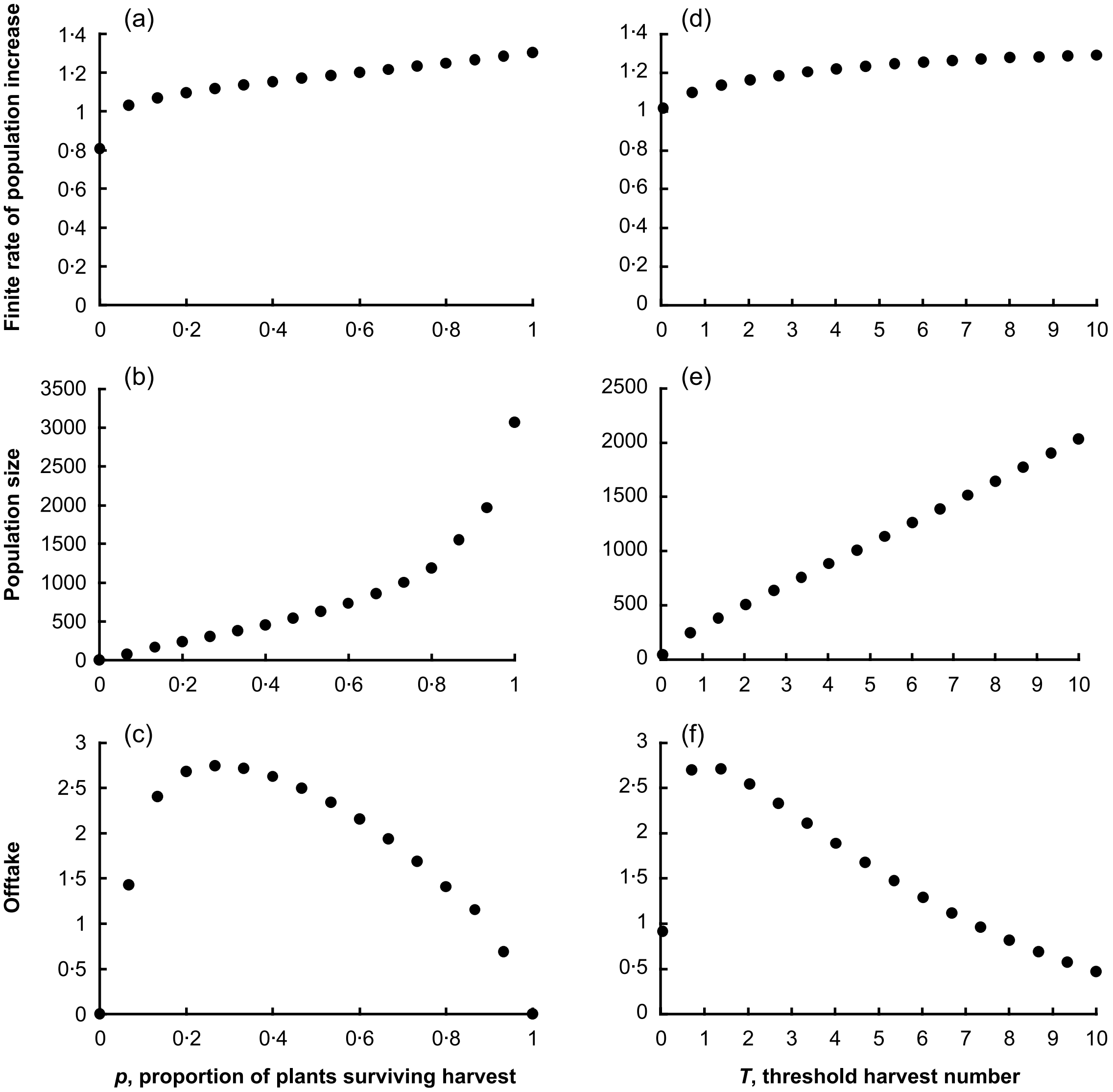

Fig. 1. Predictions of the model for the harvesting of *Euterpe edulis*. It is assumed that harvesting occurs before reproduction and the effects of density-dependence. Harvesting took one of two forms: (a–c) a constant proportion of individuals ($1 - p$) was removed from the population each year; (d–f) populations were harvested down to a threshold level each year (see text for further details). The graphs show the average value of the density-independent low-density value of the finite rate of increase (a, d), equilibrium population size (b, e) and average annual offtake (c, f).

POST-REPRODUCTIVE HARVEST: PROPORTIONAL AND THRESHOLD REMOVAL

Under post-reproductive harvesting reproduction can take place before harvesting occurs, so it might be expected that populations could withstand higher levels of exploitation. However, this may be offset by the removal of individuals that make the transition from the pre-reproductive class (class 6) to the reproductive adult class (class 7) before they are able to reproduce. As shown in Fig. 2, this is indeed the case under both forms of harvesting. Under post-reproductive harvest the finite rate of population increase is reduced by either increasing the level of harvest (through increasing the proportion harvested, Fig. 2a; or decreasing the threshold number, Fig. 2d) or decreasing τ, i.e. by increasing the proportion of class 6 individuals that are harvested.

From the point of view of using models to predict the impact of harvesting on populations of *E. edulis*, it is important to note that the largest impacts on the rate of population increase (Fig. 2a,d) and population size (Fig. 2b,e) of varying the timing of harvesting occur at the highest harvesting intensities (i.e. low values of p and low values of H). Analysis of the basic model (i.e. the pre-reproductive harvest model) indicated that populations would be robust to high intensities of harvesting (Fig. 1). The results in Fig. 2 indicate that this is only the case if harvesting occurs before reproduction and if individuals making a transition from class 6 to class 7 are not harvested.

If harvesting occurs post-reproduction then very high intensities of harvesting can potentially be sustained by populations. Indeed, when a constant proportion of plants is removed the offtake may exceed 20 palms plot^{-1} year^{-1}, compared with 3 palms plot^{-1}

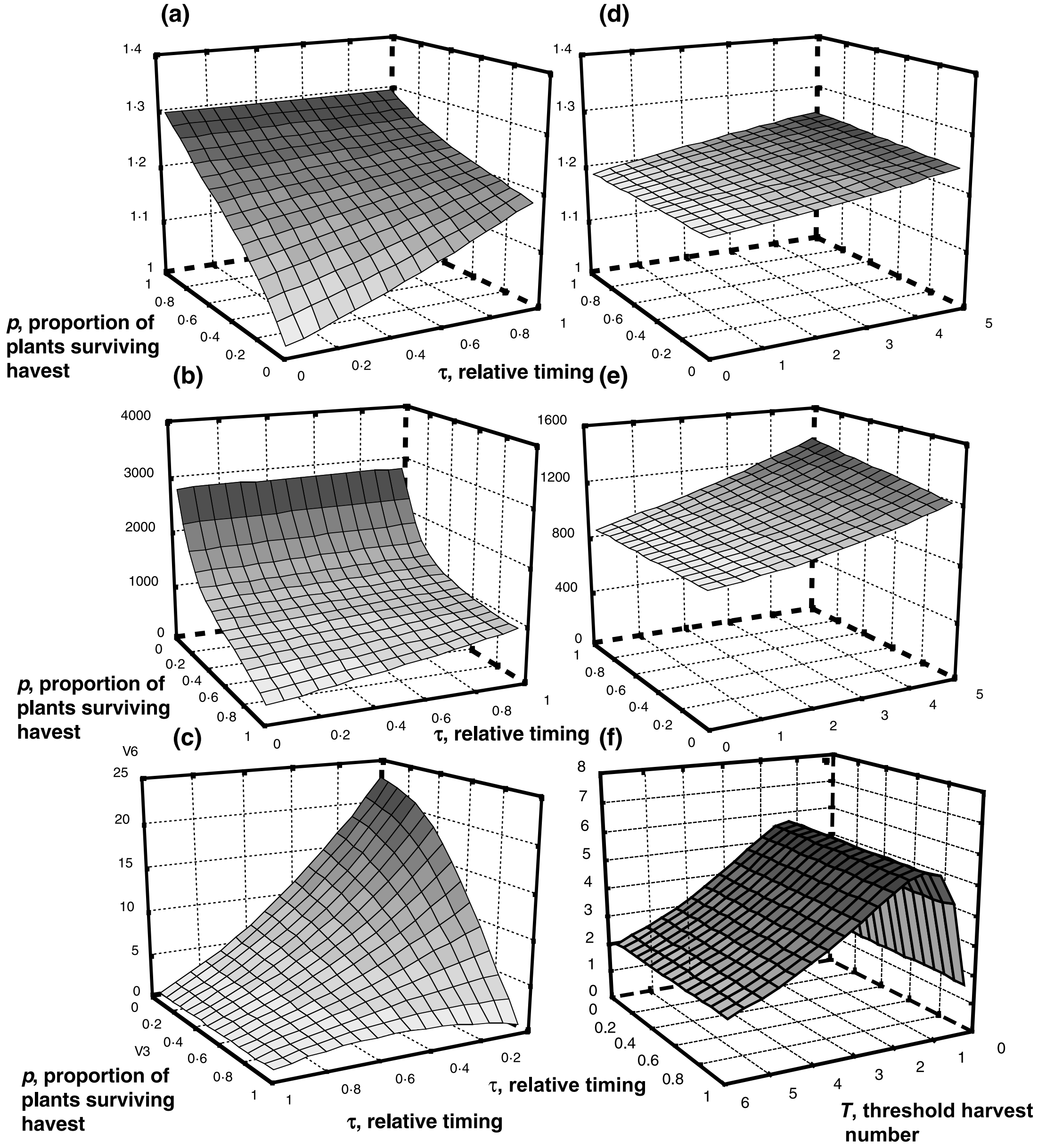

Fig. 2. Predictions of the model for the harvesting of *Euterpe edulis* in which harvesting occurs post-reproduction, with (a–c) a constant proportion of the population removed per year or (d–f) when harvesting is of the threshold form and individuals are harvested down to a threshold level each year. τ indicates the relative time during the life cycle at which harvesting of new adults (class 6 individuals making the transition to class 7) occurred. The graph shows the average value of the density-independent low-density value of the finite rate of increase (a, d), equilibrium population size (b, e) and average annual offtake (c, f).

year^{-1} under the pre-reproductive harvest regime (Fig. 1c) and 4 palms plot^{-1} year^{-1} under the post-reproductive harvest with threshold harvesting (Fig. 2f). The reason for this difference is that when harvesting occurs following reproduction, even if all reproductive adults are removed, recruitment from class 6 into class 7 yields some reproductive adults in the next year, whereas if harvesting occurs prior to reproduction only the reproductive adults that survive harvest are able to reproduce.

In reality, harvesting may occur at any time of the year and may take a range of forms. What the results presented above highlight is that the consequences of harvesting may not be simple to predict because variations in timing, intensity and form can dramatically impact on model predictions.

PERIODIC HARVESTING

Figure 3 summarizes the results from the model where harvesting occurs at periodic intervals. Figure 3a shows the results for the post-reproductive harvest model with τ set to zero (i.e. harvesting occurs after all individuals have moved from class 6–7); Fig. 3b shows the results for the post-reproductive harvest model with τ set to one (i.e. harvesting occurs before any individuals move from class 6–7); and Fig. 3c shows the results for the pre-reproductive harvest model. The

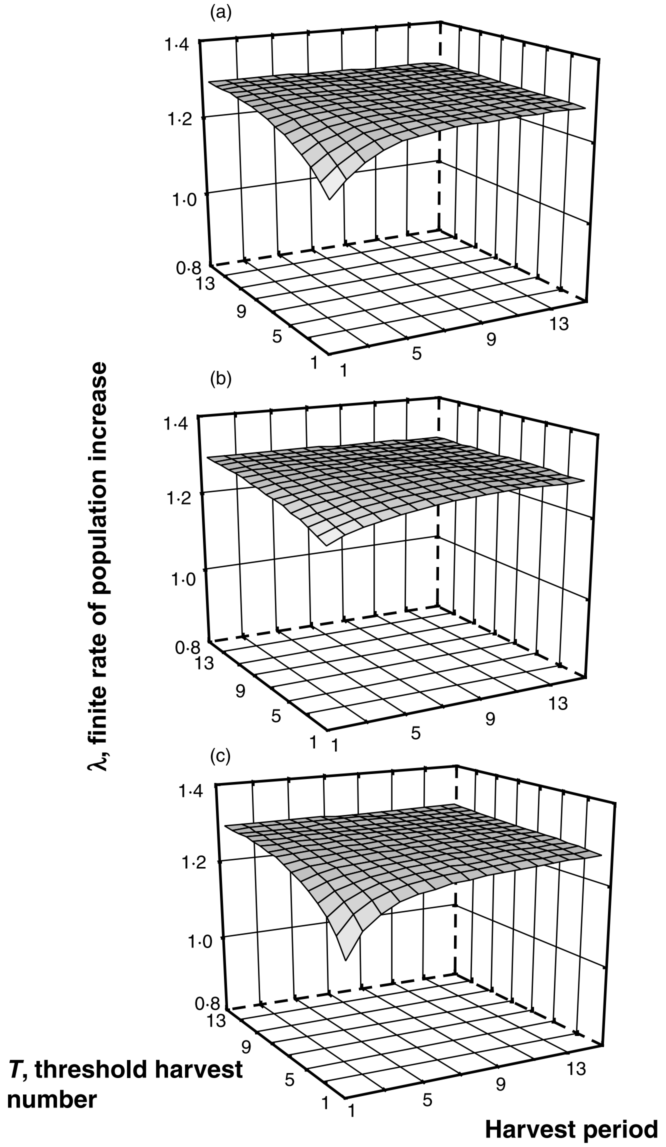

Fig. 3. Predictions of the finite rate of increase in models for the harvesting of *Euterpe edulis* with periodic harvesting: (a) predictions for the extreme of the post-reproductive harvest model when $\tau = 0$, (b) the extreme of the post-reproductive harvest model $\tau = 1$ and (c) the model for pre-reproductive harvest.

predictions of the models are generally very similar. The main differences occur at high harvesting intensities and frequencies, as was the case for the models explored above. In this case, the populations are never eradicated whilst a finite threshold is maintained. This is because the threshold always allows some adult plants to survive harvesting. All three models predict that populations can withstand high frequencies of harvesting, although there are considerable reductions in total population size at high harvesting intensities. The effect of increasing the harvest period is to minimize the difference between the model forms. This occurs because populations of *E. edulis* grow rapidly following harvesting, and this rapid growth in the non-harvest years offsets the differences in the details of the timing of harvesting in relation to reproduction. However, it should be noted that while the differences between the responses shown in Fig. 3a–c are generally slight, the largest differences occur in the region of parameter space where harvesting is intense and frequent, which is likely to be the case in reality.

IMPORTANCE OF CONTROLLING FOR DENSITY-DEPENDENCE

Many models for the effects of harvesting have been developed from static matrices in which density-dependence has been ignored. Figure 4 highlights the degree to which ignoring such processes can affect the predictions of models. The model incorporating density-dependence predicts an oscillatory approach to an equilibrium (Fig. 4a) and the value of G_1, the probability of survival and growth of seedlings to size class 2, varies inversely to density over this time period (Fig. 4b). The arrow in Fig. 4a represents a point in time when the population is close to its equilibrium and

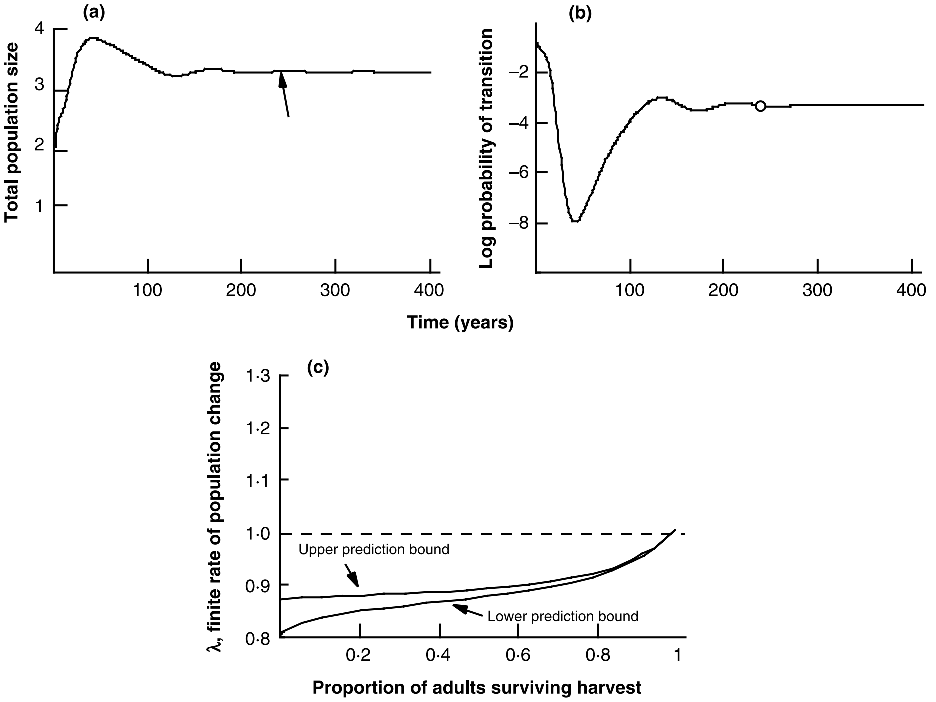

Fig. 4. An example of the importance of identifying and controlling for density-dependence in predicting the effects of harvesting. (a) Log total population size per patch (initial population vector $N(0) = [100, 1,1,1,1,1,1,1]$) over time, predicted from the density-dependent version of the model in the absence of harvesting (the 'baseline' model in Table 1). (b) The corresponding value of G_1, predicted using equation 3. (c) At the point indicated by the arrow in (a) the value of G_1 in the transition matrix is shown by the open symbol in (b). This value of G_1 was substituted into the baseline transition matrix and this modified model was treated as if it were the baseline model, and the effects of density-dependence were ignored. This model was used to generate predictions of the effects of harvesting on the finite rate of population increase, λ. The upper and lower bounds represent the extremes of the timing of harvest, either pre-reproduction (upper bound) or post-reproduction (lower bound).

at which the value of G_1 is recorded (the point in Fig. 4b). At this point, $G_1 = 5{\cdot}4 \times 10^{-4}$ and $\lambda = 1{\cdot}0011$.

We can use these values to mimic the situation whereby demographic rates are recorded within a population that is strongly regulated but incorrectly assumed to be density-independent. Assuming (incorrectly) that G_1 is static and independent of density, we can predict the effects of harvesting on population persistence (by removing a constant proportion of the population each year) for the low-density model. As shown in Fig. 4c, by employing this value of G_1 and not accounting for its dependence on density, the predictions of the model are very different from the appropriate low-density model (Fig. 1a). In particular, as λ is very close to unity, even small amounts of harvesting are predicted to lead to population eradication whereas the analyses in Figs 1–3 (that employ the appropriate value of G_1) predict that populations can potentially sustain high levels of harvesting before they are eradicated. The upper and lower bounds in Fig. 4 represent the extremes of pre- and post-reproductive harvest.

COMPARISON WITH FIELD DATA

We compared the predicted size structures of modelled populations in the presence and absence of harvesting with the observed size structure of harvested populations of *E. edulis* and an unexploited population in the Municipa Reserve of Santa Genebre, São Paulo. The data for the unexploited population come from Silva Matos, Freckleton & Watkinson (1999).

The model predictions for size structure were obtained from the baseline matrix model outlined in Table 1 with G_1 set either at its maximum or by equation 3 with the population at equilibrium. This effectively allows for a 'low-density' prediction of the size structure on the basis of the density-independent population model, and a 'high-density' prediction based on the density-dependent form of the model at the population equilibrium.

Figure 5a shows the size structures of the populations in the five harvested fragments. The form of distribution is either linear or slightly 'L'-shaped when plotted on a logarithmic scale. This contrasts with the reverse-'J' shape of the unexploited population. The model predictions are for a reverse-'J' in high-density populations subject to density-dependence and for an almost linear size distribution (on the log scale) in the density-independent model (Fig. 5b); the latter closely resembles the pattern observed in the harvested populations. We would expect the harvested populations to resemble the low-density (density-independent) model as the fragments of forest surveyed were at low densities following recent exploitation and hence density-dependence should be weak. Similarly the size structure

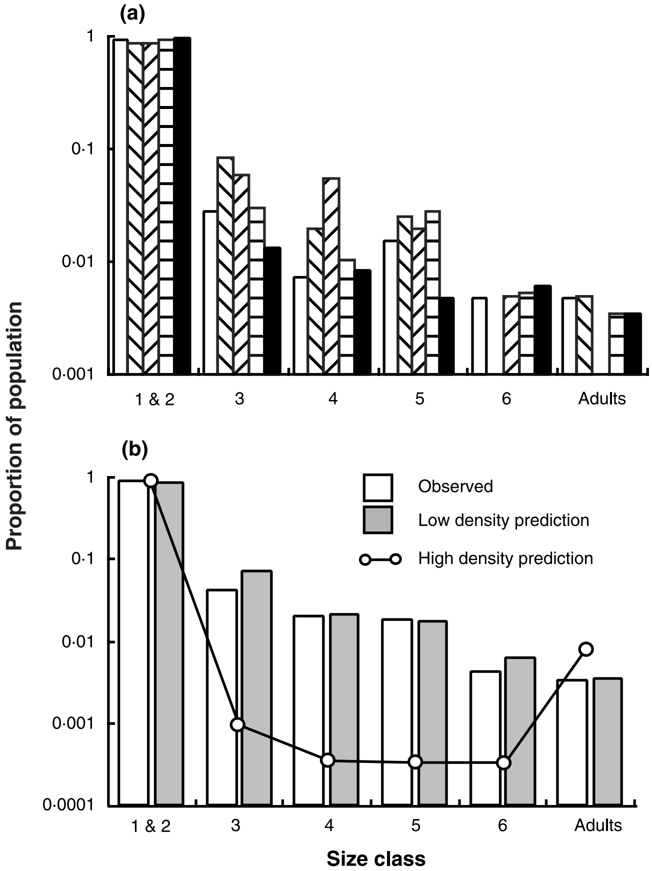

Fig. 5. Size structures of harvested and modelled populations (see text for details). (a) The size structure of *Euterpe edulis* in five forest fragments that had recently been harvested illegally. (b) The observed size structures compared with those predicted by the population model and those from an unexploited population. The observed size structure of the harvested populations is the average of the five populations presented in (a). The 'low-density' prediction is given by the low-density (density-independent) population model, while the 'high-density' prediction is the size structure predicted by the density-dependent form of the model at the population equilibrium (see Table 1 for details).

of the unexploited population closely resembles that of the modelled prediction at equilibrium.

Discussion

The model results presented above show how varying the timing of harvest can impact on the harvest and population size of an exploited population, and that consideration of density-dependence is essential if we are to make meaningful decisions on the extent of harvesting that populations can tolerate. In the particular case of *E. edulis*, we have demonstrated that if we model harvesting through simply changing the survival of existing adults (i.e. modifying P_7 alone) then we predict minimal impacts on populations even if all adults are harvested. In contrast, if we also include harvesting of adults earlier in the year, or harvesting of palms that enter the adult class during the course of a year, then the same level of harvesting is predicted to lead to population eradication. Similarly, while it is obvious that density-dependence should impact on population growth and structure, our analysis shows that the extent of this impact can potentially be so large that predictions based on measurements taken near equilibrium will be highly misrepresentative of the behaviour of populations at low density.

One of the important conclusions from this work is that the form of models may frequently be inappropriate for the system being studied. In this system it can matter whether a pulse of reproduction precedes or follows the removal of adult plants. If the interval over which dynamics are projected (in our model, a whole year) is too large, then details of dynamics within a season may be ignored, and this could impact on model predictions. Similarly, harvesting is assumed to affect one size class (class 7) in our model, whereas in reality a range of sizes may be harvested. To overcome this latter problem, integral projection models have been developed and applied to a range of problems (Easterling, Ellner & Dixon 2000; Rees & Rose 2002; Childs *et al.* 2003). These models yield more accurate model projections based on continuous rather than interval size distributions. Similarly, many systems analysed using discrete annual time intervals may be more suited to analysis at a finer temporal scale. One of the general conclusions from our results, therefore, is that it is not safe to assume that a single model formulation will be appropriate in all situations.

IMPORTANCE AND UNCERTAINTY OF THE TIMING OF HARVESTING

Euterpe edulis may be harvested for palmitos all year round (Silva Matos 1995). As a consequence removal of palms may occur at any time in relation to other events in the life cycle. It may not therefore be appropriate to model harvesting at a single fixed point in the life cycle. The range of model predictions represented in Figs 1–3 may realistically encompass a range of impacts that might occur. Given that anecdotal evidence from local people suggests a major contraction in range and abundance of this species over the past 30 years (Silva Matos 1995), the prediction that populations can sustain very high levels of harvesting without markedly affecting λ (Figs 1 and 2) is almost certainly misleading.

The major impacts of changing the timing of life-history events, as well as the inclusion of removal of individuals moving from class 6 to the adult class, occurred at very high levels of harvesting. This is because in the absence of density-dependence population growth is high, with a 30% increase in population size per annum, and recovery of populations is rapid following low and moderate harvesting.

For many species it may be the case that harvesting occurs as a discrete well-defined event at a specific time. This would include, for example, the harvesting of seeds or flowers (Bernal 1998; Velasquez Runk 1998). In these cases it is possible to be much more precise about the timing of harvesting in relation to other events in the life cycle. For other populations the details of timing could play a much more critical role in determining the outcome of model predictions. Olmsted & Alvarez-Buylla (1995) reported low impacts of varying the timing of harvesting on populations, although they did not explore the effects of removal of individuals from size classes other than the adult class. In their simulations they explored the effects of periodic harvesting, rather than removal of a constant proportion of individuals. Of these two forms of harvesting, our analysis indicated that the predictions of the model incorporating periodic harvesting was least sensitive to variation in the timing of harvesting (Fig. 3).

The process we have explored here, in terms of the impact of the timing of harvest on population performance, is distinct from density-compensation that occurs when a reduction in the strength of density-dependence compensates for removal of individuals from the population. However, a variety of studies have shown that, for structured models, the timing of mortality relative to density-dependence affects the predictions of models for the effects of harvesting (Clark 1992; Kokko & Lindstrom 1998) and for many populations this phenomenon may be expected to operate in addition to the process we have explored.

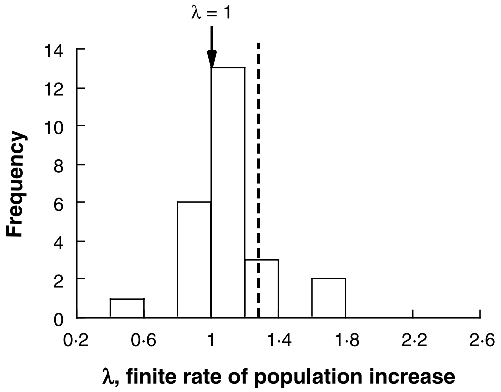

Fig. 6. Frequency distribution of estimates of λ, the finite rate of population increase, derived from the literature. The values are for trees and shrubs, taken from Silvertown *et al.* (1993), as well as the values reported by Alvarez-Buylla (1994), Silva Matos, Freckleton & Watkinson (1999), Olmsted & Alvarez-Buylla (1995) and Bernal (1998). The arrow indicates λ = 1, i.e. zero net population growth. The dashed line is the value reported for *Euterpe edulis* in the absence of the effects of density-dependence (λ = 1·28). The mean value of log λ is 0·040 (± SE = 0·24; not significantly different from zero, *t* = 1·64, d.f. = 25), the median value is 1·011.

CONTROLLING FOR DENSITY-DEPENDENCE

The lack of consideration of density-dependence in demographic models for tropical trees has been commented on in relation to understanding the factors that determine population abundance (Alvarez-Buylla 1994; Alvarez-Buylla *et al.* 1996; Silva Matos, Freckleton & Watkinson 1999). Boot & Gullison (1995), in reviewing approaches to modelling the sustainability of harvesting of tropical forests, argued that failure to include density-dependence was likely to compromise the predictive power and ultimate utility of demographic models based on census data and transition matrices. Our analysis shows that this is indeed the case. Moreover, models based on the analysis of populations taken near equilibrium may be highly misrepresentative of the behaviour of the same population at low density.

Many studies that ignore density-dependence report values of λ, the rate of population growth, close to unity. This is demonstrated in Fig. 6, which shows the frequency distribution of estimates of λ derived from the literature (see the figure legend for details). These are clustered around a value of λ = 1, i.e. zero net population growth. If populations are subject to strong density-dependence then we would expect this to be the case as populations should be regulated and hence near equilibrium. The value we report for the finite rate of increase of *E. edulis* from low densities is considerably higher than most estimates of λ. This would lead us to speculate that many studies are reporting demographic rates derived from strongly regulated populations and that these cannot be used to infer the behaviour of populations at low densities, such as when harvesting is imposed. Resolution of the debate over the role and strength of density-dependence in tropical trees is clearly critical, not only if we are to understand the dynamics of tropical trees but also if we are to make recommendations on sustainable harvesting. The analysis here, together with recent quantification of the strength and extent of density-dependence in tropical trees (Wills *et al*. 1997; Silva Matos, Freckleton & Watkinson 1999; Harms *et al*. 2000), points toward a greater awareness of density-dependence in tropical trees than previously argued (Hubbell & Foster 1986).

In the context of modelling harvesting, or predicting whether species of conservation concern are likely to become extinct, it is clearly very important to determine whether observed values of λ are influenced by density-dependence or not. For instance if the observed rate of population growth is low (i.e. $\lambda < 1$) then this could be because the population is non-viable and likely to become extinct, or alternatively populations could be at a high-density phase in which density-dependence is intense and pushing populations back to an equilibrium. This argues strongly for precisely determining the numerical value of λ and how it is influenced by density.

THE MANAGEMENT OF *E. EDULIS*

A sustainable management programme for *E. edulis* has been developed and incorporated into official state regulations (Reis *et al*. 2000). The management is based on population structure, growth rates and the number of reproductive trees per hectare. Essentially the approach involves the assumption of a steady-state size distribution, which when coupled with information on the growth rate of plants allows the length of the cutting cycle to be calculated and the offtake to be estimated. Recommended intervals between harvests are typically short (4–6 years) but longer intervals (< 15 years) are recognized as minimizing the risk of regeneration failure (Orlande, Laarman & Mortimer 1996; Reis *et al*. 2000). The maintenance of a minimum number of seed trees (50–60 ha^{-1}) is recommended to provide sufficient seedlings for the maintenance of the population.

The conclusions from this study reaffirm that high intensities of harvesting at frequent intervals are sustainable if a threshold level for harvesting is implemented. It is currently recommended that a minimum of 50 plants ha^{-1} is maintained in a forest for populations of *E. edulis* to support sustainable harvesting (Reis *et al*. 2000). Our analyses show that it is not possible to specify an exact threshold because the timing of harvesting is a key factor. If harvesting affects individuals growing from pre-reproductive to reproductive size classes, then much larger thresholds are required than if harvesting affects only mature plants. Moreover, thresholds required to maintain population persistence will be much lower than thresholds that maximize yields. Instead sustainable harvest programmes will need to consider a range of factors relating to timing and offtake.

CONCLUDING REMARKS

Our results suggest that the essentially static nature of most existing analyses of the impacts of harvesting on populations that employ structured population models can lead to misleading or uninformative predictions. In the case of the timing of harvest, our analyses allowed us to specify a likely range of population dynamics and an assessment of the potential impacts of varying the timing of mortality on offtake and the abundance of *E. edulis*. The role of density-dependence, however, can be assessed only when a density-dependent function has been fitted to census data. If this cannot be done then model predictions are unlikely to be reliable.

How general are our conclusions likely to be? The problems of the timing of events in the life cycle will depend on the system in question. In general, if events such as reproduction and harvesting occur discretely then the ordering of events is likely to be important. The role of density-dependence in the population dynamics of tropical trees is being increasingly recognized (Alvarez-Buylla 1994; Wills *et al*. 1997; Silva Matos, Freckleton & Watkinson 1999; Harms *et al*. 2000) and it seems likely that density-dependence is far more widespread than previously appreciated. Additionally, in the absence of an estimate of the strength of density-dependence, it is impossible to make predictions of population densities or to predict the finite rate of increase of populations from low densities, which is a severe limitation on the application of models. Therefore it seems likely that measuring density-dependence is going to be important for many species. To deal with this requires field studies and statistical and modelling techniques that recognize the importance of regulatory processes in population dynamics.

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