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Population dynamics and conservation biology of the over-exploited Mediterranean red coral

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Abstract

The main goal of ecologists is nowadays to foster habitat and species conservation. Life-history tables and Leslie–Lewis transition matrices of population growth can be powerful tools suitable for the study of age-structured over harvested and/or endangered species dynamics. Red coral (*Corallium rubrum* L 1758) is a modular anthozoan endemic to the Mediterranean Sea. This slow growing, long lived species has been harvested since ancient times. In the last decades harvesting pressure increased and the overall Mediterranean yield reduced by $\frac{2}{3}$. Moreover, mass mortality (putatively-linked to global warming) recently affected some coastal populations of this species. Red coral populations are discrete genetic units, gonochoric, composed by several overlapping generations and provided of a discrete (annual) reproduction. A population of this precious octocoral was studied in detail and its static life table was compiled. In order to simulate the trends overtime of the population under different environmental conditions and fishing pressures, a discrete, non-linear model, based on Leslie–Lewis transition matrix, was applied to the demographic data. In this model a bell-shaped curve, based on experimental data, representing the dependence of recruitment on adult colonies density was included. On these bases the stability of the population under different density, reproduction and mortality figures was analysed and simulations of the population trends overtime were set out. Some simulations were also carried out applying to the studied population the mortality values measured during the anomalous mass mortality event which really affected some red coral populations in 1999. The population under study showed high stability and a strong resilience capability, surviving to a 61% reduction of density, to a 27.7% reduction of reproduction rate and to an unselective harvesting affecting 95% of the reproductive colonies.

Keywords: Red coral; Conservation biology; Global change; Age-structured discrete model; Population dynamics

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1. Introduction

Ecology can actually give a real contribution to biodiversity conservation (i.e. population, species, and habitat conservation) by means of methods and models suitable for this target (Dobson, 1998). Demography in particular, can supply useful tools for conservation and management of overexploited or endangered species (Dobson, 1998). A classic example is given by the demographic study on the bighorn (*Ovis dalli*; Bergher, 1990). Models based on life-history tables and Leslie–Lewis transition matrices of population growth can be powerful tools for the study of population trends overtime. Such models could help to assess population status, to examine the causes of poor performances, and to make predictions of population trends and viability overtime (Ebert, 1999; Beissinger and McCullough, 2002).

Demographic population models, based on life-history tables and Leslie–Lewis transition matrices have been widely applied by conservation biologists to the study of population dynamics (Caswell, 2001) of several marine species: e.g. the loggerhead sea turtle *Caretta caretta* (Crouse et al., 1987) and the Right whale *Eubalena glacialis* (Fujiwara and Caswell, 2001).

The precious red coral (*Corallium rubrum* L 1758) is a clear example of an over-harvested marine species which populations have been severely depleted (Santangelo and

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Abbiati, 2001). There is not the risk of an ecological extinction for this species but an economical extinction will be possible (i.e. a population of a slow growing species, with positive density dependence, can survive to over-fishing but cannot reach again a size/age structure and a density suitable for commercial harvesting).

Red coral is a colonial (modular) anthozoan endemic to the Mediterranean Sea and neighbouring Atlantic areas, living on rocky bottoms between 20 and 200 m depth (Zibrowius et al., 1984). Due to the high economic value of its axial, carbonate skeleton, this species has been harvested and traded world wide since ancient times. Nowadays a clear-cut, sharp reduction of overall fishing yield was recorded and in the last two decades the Mediterranean yield reduced by $\frac{2}{3}$ (Santangelo and Abbiati, 2001).

Red coral is a long-lived, gonochoric, brooder species, whose lecithotrophic larvae (planulae) do not travel very far from their parent colonies (Vighi, 1972; Weinberg, 1979). This species is structured in several genetically differentiated, self-seeding units (populations) (Abbiati et al., 1993) that are composed by several overlapping generations. Reproduction is discrete and occurs within a limited time interval in early summer (Santangelo et al., 2003). Such populations can only decrease in number (due to mortality) between two different reproductive cycles (Ricklefs and Miller, 1999).

As red coral has been harvested following a "bloom and burst" strategy in many countries, the main part of red coral populations have been now depleted. Moreover, a mass mortality event affected in late summer 1999, the benthic fauna in some areas of the Western Mediterranean Sea (Cerrano et al., 2000) and the red coral populations in the Provence region (France) suffered a wide mortality (Garrabou and Harmelin, 2002). Also a red coral population living in the Italian Ligurian Sea (Calafuria-Livorno), studied since several years, suffered in the same period a sharp reduction of the net recruitment rate (Bramanti et al., 2005). These events co-occurred with a thermal anomaly ($\Delta T > +4\,^{\circ}\mathrm{C}$) which affected the same geographic area in the same period. Such anomaly was thus considered to be the cause of these events. As over-fishing could now be coupled with mass mortality, the co-occurrence of these two mortality sources could dramatically depress population recovery. In this framework models suitable to project red coral population trends overtime could supply highly useful insights into population dynamics and suggestions for species conservation.

In this paper we resume data for the red coral population of Calafuria, collected through the years, and formulate a Leslie-type model based on the specific measures. In Section 2 we present these data and in Section 3 we set up the model. Finally, in Section 4 we run various simulations of the model in order to discuss some questions concerning conservation of the red coral population.

2. Population features and data

For several years now, our research has been addressing the genetic (Abbiati et al., 1993), demographic (Santangelo and Abbiati, 2001; Bramanti et al., 2003; Santangelo et al., 2004) and reproductive structure (Santangelo et al., 2003) of a red coral coastal population in the Western Ligurian Sea (Calafuria, Livorno, Italy, $43^0\ 30'$ N, $10^0\ 20'$ E). Red coral patches dwell onto the vault of small crevices between 20 and 45 m depth. This population is made up of small, young, crowded colonies, $\frac{1}{3}$ of which are reproductive and reach early sexual maturity (Santangelo et al., 2003). The reproductive isolation of this population (Abbiati et al., 1993) allows us to set out realistic dynamic models in which larval output and recruitment occur locally and are coupled (Caley et al., 1996). In this population a clear-cut positive correlation between recruit and adult colony density has been also found (Santangelo et al., 2004). In the following we present the dataset of the studied population.

2.1. Demographic data

Data on population demographic structure have been collected using two different sampling techniques. In a first sampling all the colonies (1802), living in 20 squares, 180 cm^2 each were collected. Colonies were scraped with a chisel by scuba diving from the vault of randomly selected crevices in which red coral settled. As scraping does not allow the identification of all recruits (they measure 0.62 mm in diameter) a micro-photographic (non-destructive) sampling, was also performed on 28 squares, 180 cm^2 each. On these last samples the relation between recruits density and estimated number of planulae produced in the same area (the control function in Section 2.3) was calculated.

There are several different estimates of red coral growth rates (Garcia-Rodriguez and Massò, 1986; Abbiati et al., 1992; Cicogna et al., 1999; Garrabou and Harmelin, 2002; Marschall et al., 2004). Such variability could be due to the different environments in which the populations dwell (caves, crevices, overhangs, cliffs). Also variable, all these estimates indicate red coral is a slow growing long-lived species (the annual growth of colony diameter ranges between 1.32–0.24 mm/y and the estimated life span ranges between 15 and >50 years).

In order to obtain a reliable classification of the colonies into size–age classes, we measured the growth rate of colonies settled on long-term artificial substrates (Bramanti et al., 2005). After four years we found that the colonies exhibited an average diameter of 2.49 ± 0.48 mm (±SD), corresponding to an average annual growth of 0.62 ± 0.19 mm/y. These findings allowed us to share all the colonies into 13 different size/age classes on the basis of their diameters, as reported in Table 1. In Fig. 1 we present the population distribution that show a decreasing pattern, typical of populations in a steady state.

Table 1
Static life-table of the red coral population

Size–age class i (year)	Diameter (mm)	Number of colonies X_i	Survival $S_i = X_{i+1}/X_i$
1	$<0,62$	822	0,889
2	0,62-1,24	731	0,633
3	1,24-1,86	463	0,697
4	1,86-2,48	323	0,517
5	2,48-3,1	167	0,437
6	3,1-3,72	73	0,287
7	3,72-4,34	21	0,571
8	4,34-4,96	12	0,333
9	5,58-6,2	4	0,75
10	6,2-6,82	3	1
11	6,82-7,44	3	0,333
12	7,44-8,06	1	1
13	$>8,06$	1	

Colonies were shared into 13 age–size classes.

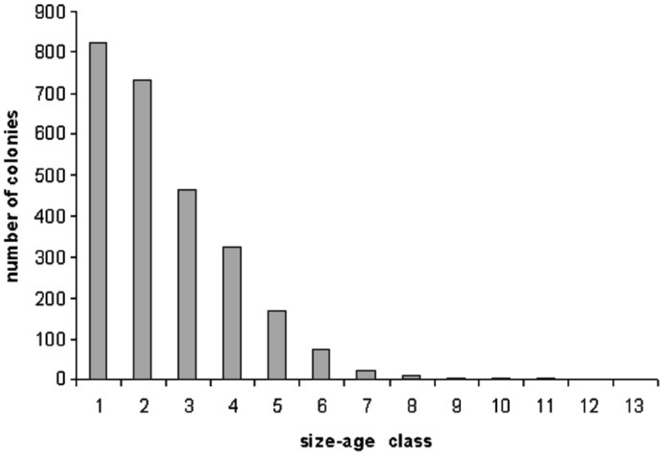

Fig. 1. Size/age structure of the red coral population.

2.2. Population reproductive structure

The structure of red coral populations is complex. Each colony is a modular animal composed by several genetically identical modules (polyps). Each female and fertile polyp can brood and release lecitothrophic larvae (planulae) which settle near their parent colonies producing a new individual (recruit) (Vighi, 1972; Weinberg, 1979). Thus, to calculate the average number of planulae produced by a colony (b) in a certain size–age class, the following parameters have been estimated (Santangelo et al., 2004)

- q is the fecundity (number of larvae produced by each colony),
- F the fertility (percentage of fertile female colonies),
- sr the sex ratio,
- P the number of polyps in each colony

so that b is calculated as the product of all parameters above

$$b = q \times F \times sr \times P.$$

Table 2
Fecundity table of the red coral population

Age i	F_i	q_i	sr_i	P_i	b_i
1	0	0,87	0,58	0	0,00
2	0	0,87	0,58	6,20	0,00
3	0,36	0,87	0,58	15,91	2,89
4	0,64	0,87	0,58	31,07	10,03
5	0,82	0,87	0,58	52,18	21,59
6	0,97	0,87	0,58	79,72	39,02
7	0,98	0,87	0,58	114,07	56,41
8	0,99	0,87	0,58	155,58	77,72
9	1	0,87	0,58	204,57	103,23
10	1	0,87	0,58	261,33	131,87
11	1	0,87	0,58	326,14	164,57
12	1	0,87	0,58	399,24	201,46
13	1	0,87	0,58	480,87	242,65

Here F_i is the fertility, q_i the fecundity, P_i the number of polypos, $b_i = q_i \times F_i \times sr_i \times P_i$ the average number of planulae produced by one colony.

All these reproductive parameters are summarized in a fecundity table of the population under study (Table 2).

2.3. The control function

After their release planulae have a limited time interval within which they must settle or die (Weinberg, 1979). We estimated the larval survival, that is the ratio between the number of recruits found in the sampled area and the estimated number of planulae produced within the same area (see Section 2.1). We note that the recruitment process resulted density dependent (Santangelo, 2004), according to the well-known mechanisms for which populations cannot grow exponentially for a long time, since density, regulating recruitment, maintains them around their carrying capacity (Levin, 1986; Caley et al., 1996). In many cases negative intra-specific interactions (negative density dependence) can be effective; in some cases, also a positive density dependence may occur (e.g. Allee effect; Stephens and Sutherland, 1999).

Data reported in Fig. 2 show that the reproductive process of our coral population is really regulated by both mechanisms. They have been obtained from the analysis of the photographic samples and have been fitted by the following bell-shaped parameterized curve,

$$S_0(u) = \frac{2.94}{u + 520e^{-0.14u}}, \tag{1}$$

where u is the adult density and is measured in colonies/dm^2. According to this function, adult density has a two-fold effect on population reproductive success (recruits/planulae): a positive effect until a threshold density value and a negative effect above this value.

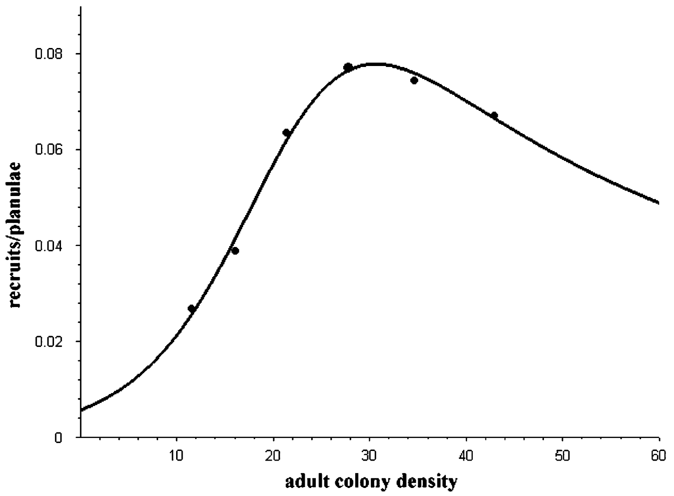

Fig. 2. Experimental fitting of the larval survival (recruitment to larval-output ratio) according with the parameterized function (1). The adult density u is measured in colonies/dm^2.

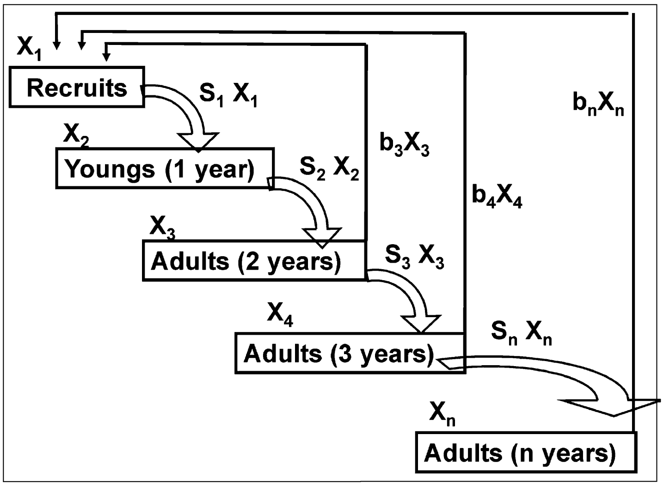

Fig. 3. Model sketch: life cycle graph of the coral population. X_i is the number of colonies in the class i, S_i the survival from class i to class $i+1$, b_i the average number of planulae produced by one colony.

3. The mathematical model

Here we propose a discrete dynamical model to describe the growth of the coral population, with the purpose of calibrating the model on the basis of experimental data and realistic situations. We adopt a discrete age-structured model because red coral has a discrete yearly reproduction in summer. Thus, we may use a discrete time (and age) unit of one year and denote by

$$X_i^n = \textit{the number of colonies in the age class i at time n},$$

where $i = 1, \ldots, A$. Moreover, we denote by

b_i = *the (average) number of planulae produced by each colony in the age class i at each (yearly) reproduction event*,

S_i = *the probability for a colony in the age class i, to survive and enter the class* $i+1$,

$S_0(u)$ = *the larval survival, i.e. the fraction of planulae that survive and settle when the density of the population is u.*

Where the density u is the number of colonies per unit of surface. Note that, since the recruits (class $i = 1$) are not considered as "colonies", the density at time t is given by

$$u^n = \sum_{i=2}^{i=A} X_i^n/\Sigma, \tag{2}$$

where Σ is the surface of the site occupied by the population.

With these definitions, the model follows the scheme sketched in Fig. 3, and is formulated by the following difference equations:

$$\text{(i)}\quad X_1^{n+1} = S_0(u^n)\sum_{i=1}^{i=A} b_i X_i^n,$$

$$\text{(ii)}\quad X_{i+1}^{n+1} = S_i X_i^n, \quad i = 1, \ldots, A, \tag{3}$$

where u^n is given by (2).

The search for equilibria of the model leads to the following equations on the set $(X_1, \ldots, X_A)$:

$$\text{(i)}\quad X_1 = S_0(u)\sum_{i=1}^{i=A} b_i X_i,$$

$$\text{(ii)}\quad X_{i+1} = S_i X_i, \quad i = 1, \ldots, A, \tag{4}$$

that of course is satisfied by the trivial equilibrium $X_i = 0$, $(i = 1, \ldots, A)$. The search for non-trivial equilibria can actually be reduced to a single equation on X_1. In fact 4(ii) yields

$$X_i = S_{i-1}S_{i-2}\cdots S_1 X_1 = \Pi_i X_1 \quad (i = 2, \ldots, A), \tag{5}$$

where $\Pi_i = S_{i-1}S_{i-2}\cdots S_1$ is the probability for a single recruit to survive to the age-class i. Plugging (5) into 4(i), we get

$$1 = \mathscr{R}_0 S_0(\theta X_1), \tag{6}$$

where

$$\mathscr{R}_0 = \sum_{i=1}^{i=A} b_i \Pi_i, \quad \theta = \sum_{i=2}^{i=A} \Pi_i/\Sigma.$$

$\mathscr{R}_0$ is the average number of planulae produced by a single colony during the whole life-span, while $U = \theta X_1$ is the average density of the population. Thus, for any non-trivial solution of (6) we get a non-trivial solution through formula (5). Of course, solutions to (6) exist according with the shape of the function $S_0(x)$ and the values of the parameters involved. Our aim is now to calibrate the previous model on the specific situation arising from the data presented in the previous sections.

Our starting point is the assumption that the observed population (spread on a surface area $\Sigma = 36\,\text{dm}^2$ and partitioned into $A = 13$ size–age classes) is described by the previous model and has attained a non-trivial steady state so that the observed abundances reported in the first column of Table 1 provide the components X_i^* of this

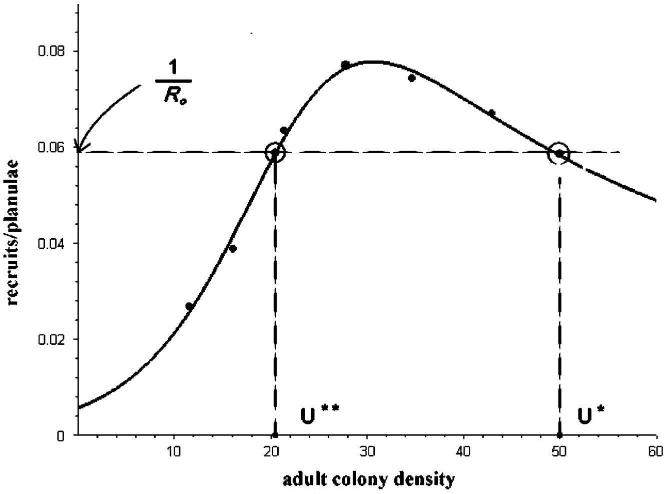

Fig. 4. Solution to Eq. (6), i.e. existence of two steady state with respective density U^* and U^{**}. The solution with density U^* corresponds to the observed population.

steady state and consequently allow to calculate the parameters S_i by

$$S_i = \frac{X^*_{i+1}}{X^*_i}.$$

Furthermore, the parameters b_i and the control function $S_0(x)$ are directly determined by the measures and, respectively, given by the last column in Table 2 and by the function (1). We note that with these choices we have

$$\mathscr{R}_0 = 18.12, \quad \theta = 0.061, \quad X^*_1 = 822.$$

so that

$$\mathscr{R}_0 S_0(\theta X^*_1) = 1.054 \approx 1$$

as expected, since the observed state $(X^*_1, X^*_2, \ldots, X^*_A)$ has been assumed to be a steady state. Furthermore, in Fig. 4 we note that, indeed, Eq. (6) has a second solution corresponding to another steady state, given by $X^{**}_1 = 328$ that we expect to be unstable.

4. Simulations

Six different sets of simulations, representing different reproduction, density and mortality conditions have been carried out as explained in the following:

(1) The reproductive coefficient $\mathscr{R}_0$ was reduced from its original value $\mathscr{R}_0 = 18.12$, to $\mathscr{R}_0 = 13$. With this value $1/\mathscr{R}_0 = 0{,}0769$ and is close to the maximum value attained by the function $S_0(u)$ over which Eq. (6) has no solution and the model does not admit any steady state but the trivial one. In Fig. 5 it is shown that for this value of $\mathscr{R}_0$ the model still has a non-trivial steady state (at a lower density) that attracts the solution. On the other hand, if $\mathscr{R}_0$ is further reduced to $\mathscr{R}_0 = 12.5$ the population falls down in 95 years (Fig. 5). Moreover, we have seen that if $\mathscr{R}_0$ is reduced to $\mathscr{R}_0 = 12$ and 10, the extinction time decreases to 60 and 20 years, respectively.

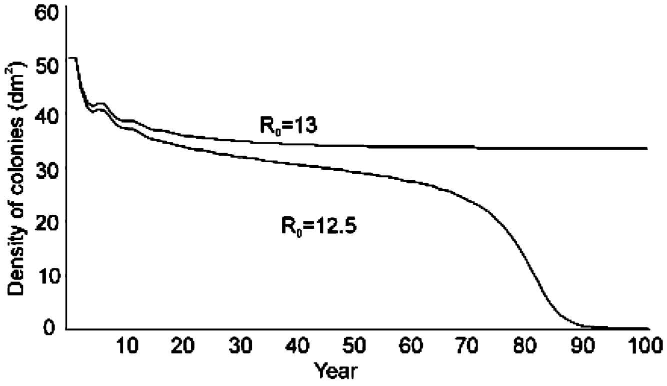

Fig. 5. Simulations of the model showing the extinction time for different values of $\mathscr{R}_0$.

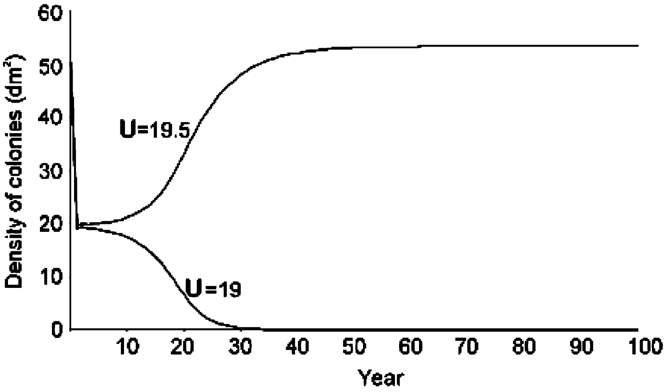

Fig. 6. Simulations of the model showing the extinction time for different values of U.

(2) In order to test the extinction time under different initial conditions, we have performed a few simulations with an initial datum corresponding to an overall colony density close to the value $U^{**} = 20$ of the second steady state, but keeping the same proportions through the size–age classes. We found that with an initial value $U = 19.5\,\text{col/dm}^2$ the population is still attracted by the stable non-trivial steady state (Fig. 6a), while at $U = 19$, it falls irremediably down to extinction in 35 years (Fig. 6 b).

Another set of simulations was performed to test the effect of selective mortality due to environmental changes like that which really affected some red coral populations in recent years (Garrabou et al., 2001).

(3) We call "Calafuria mortality" a mortality affecting 56% of recruits and 40% of 2 year old colonies, like that really observed at Calafuria in 1999 (putatively linked to an anomalous temperature increase; Bramanti et al., 2005). In Fig. 7A we see the population recovery after a single event of "Calafuria mortality". In this case the population, after a smooth weaving, reaches again the original density value. On the other hand, if repeated events of "Calafuria Mortality" occur with a periodicity of 4 years (Fig. 7B) the population, reaching lower density values, weaves indefinitively following the periodicity of the mortality

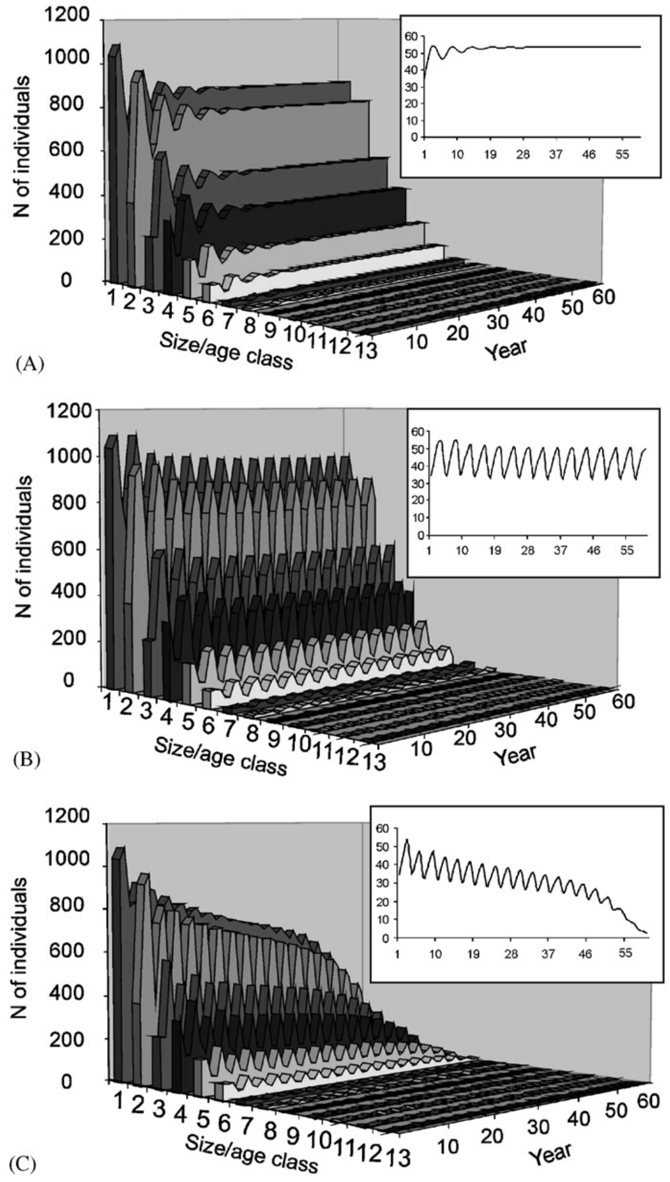

Fig. 7. Calafuria mortality: (A) single event; (B) repeated events 4 years spaced; (C) repeated events 3 years spaced. In the square at right overall colony densities are reported.

events. However, if such mortality occurs each 3 years, the population goes to extinction in 60 years (Fig. 7C).

(4) Another mortality event occurred at Marseille in 1999 (“Marseille mortality”) affecting the local red coral population and killing 15% of the colonies in the cohorts 1–4 and 8.5% of older colonies (Garrabou et al., 2001). We have also simulated such event with our model proceeding as in the previous set of simulations. In Fig. 8 results similar to those in Fig. 7 are shown. After one single event the population recovers in a few years (Fig. 8A), with a frequency of 10 years the population oscillates but it is still persistent (Fig. 8B), if the frequency of perturbation increases and the population is affected each 2 years, it goes to extinction in 60 years (Fig. 8C).

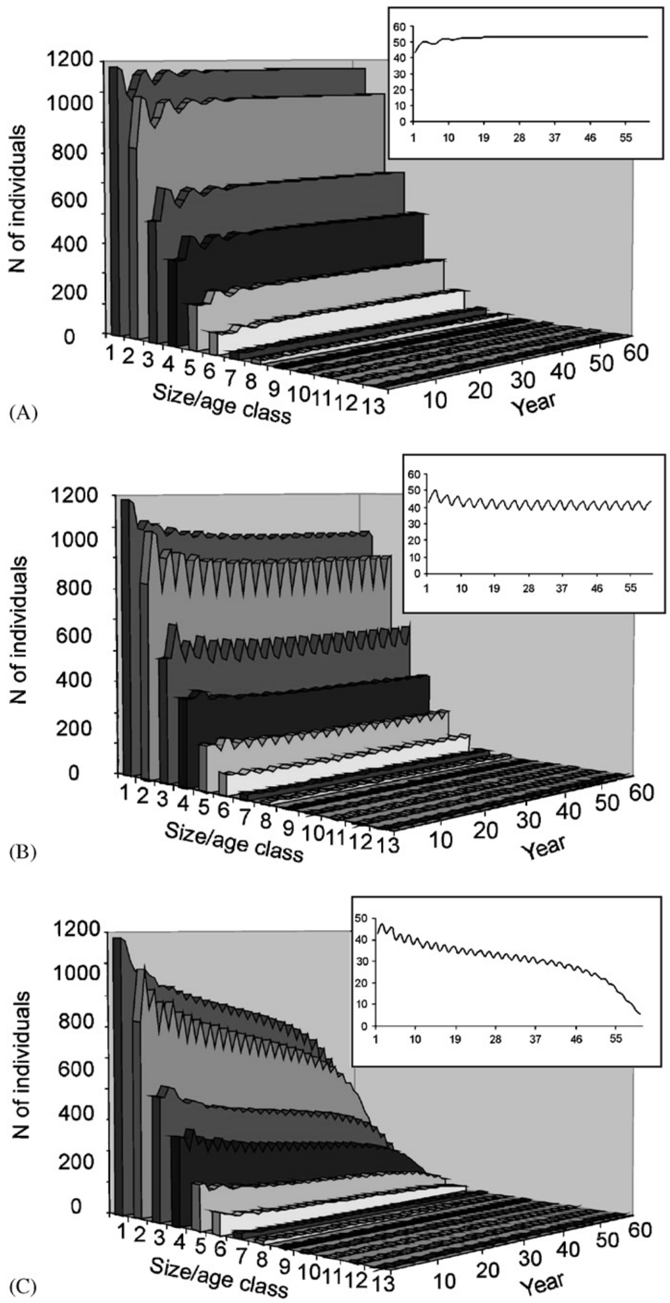

Fig. 8. Marseille mortality: (A) single event; (B) repeated events 10 years spaced; (C) repeated events 2 years spaced.

(5) In order to test the effect of enforcement on survival of older/bigger colonies that, being more valuable, are selectively affected by illegal harvesting, we have simulated the model taking $S_i = 0.6$ for the survival parameters of classes older than 5 years. Under these conditions the population reaches a stable structure and recruitment saturation in about 25 years (Fig. 9).

(6) Finally, we have simulated the action of overfishing. We assumed that all the colonies older than 4 years and part of the colonies in class 3 were harvested taking as initial datum (X_i = number of colonies in the i age class) $X_1^0 = 822$, $X_2^0 = 731$, $X_3^0 = 90$, $X_i^0 = 0$ for $i > 3$ (values for

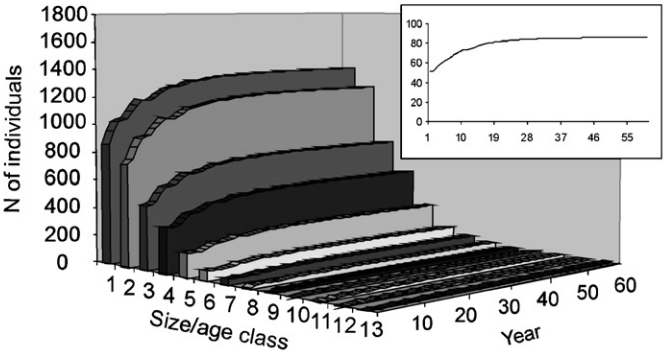

Fig. 9. Increase of survival (by enforcement) for classes 5–13. For these classes we set $S_i = 0.6$.

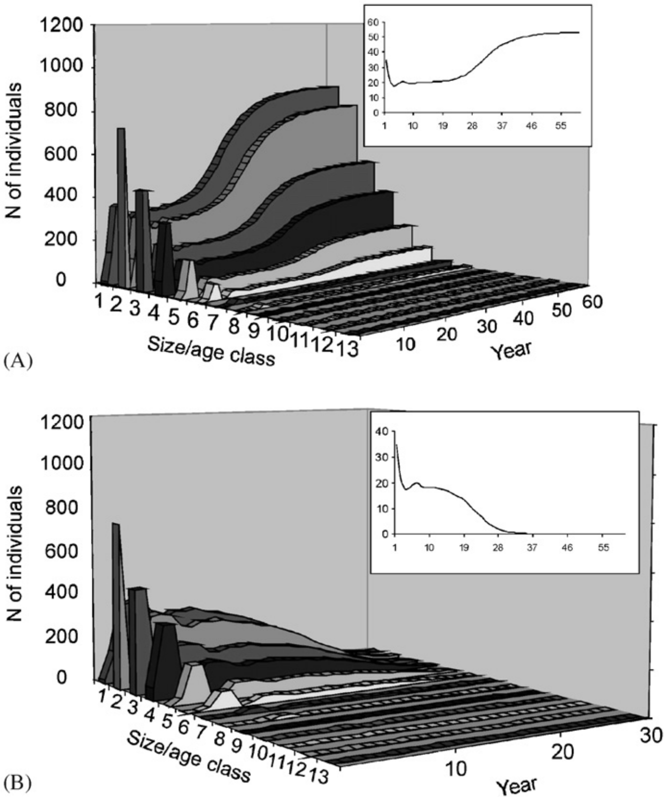

Fig. 10. The effect of overfishing selectively affecting all the colonies in older classes. (A) $X_1^0 = 822$, $X_2^0 = 731$, $X_3^0 = 90$, $X_i^0 = 0$ for $i > 3$; (B) $X_1^0 = 822$, $X_2^0 = 731$, $X_3^0 = 80$, $X_i^0 = 0$ for $i > 3$.

the first two classes are those of the original population in Table 1). The result is that the population survives and recovers in 60 years (Fig. 10A). If instead the class 3 is further harvested taking $X_3 = 80$, the population goes to extinction in 20 years (Fig. 10B).

5. Conclusions

Demographic approaches, based on Leslie–Lewis transition matrix, are widely applied to over-harvested or/and endangered species with complex life cycles and populations structured into several age classes with discrete reproduction and semi-overlapped generations (Tupuljanupur and Caswell, 1997; Caswell, 2001). Nevertheless, only a few such demographic analyses on marine, modular, slow growing, long lived species have been carried out. We tried to apply this approach to a population of the over-harvested, precious, Mediterranean red coral. The actual fishing and demographic patterns clearly indicate a regression for this species (Santangelo and Abbiati, 2001). The availability of reliable demographic data and of an exhaustive life-history table of one red coral population studied since several years, allowed us to set out a discrete, age-structured population model in which non-linearities occurs only in the first age class (recruitment) survival.

Our field data indicated that some density dependence regulation of recruitment actually occurs in the population under study (Santangelo et al., 2004). Such density dependence, indicated by the relationship between the estimated larval survival and adult colony density, is positive at low and negative at high adult densities (due presumably to the reduced availability of free space), such control of colony density on recruitment is included into the dynamic model.

The mathematical model that we have set up in order to describe red coral growth falls within a general class of non-linear discrete models that has received much attention in connection with population dynamics (Caswell, 2001). The specific features of our model are drawn from the experimental situation and the parameters are calibrated by the data. In particular, due to the particular cut-off function (1), the model exhibits backward bifurcation and existence of three steady states.

With this model we are able to have a new insight into the problems of conservation policies for the red coral. In fact we have used the model to make predictions under various different occurrences that are suggested by real events, simulating population trends over time and population responses to variation of density, reproduction and mortality. Some simulations were also carried out applying the mortality values measured on the same population, during the 1999 anomalous temperature increase (Bramanti et al., 2005), or on another red coral population affected by mass mortality at the same time (Garrabou et al., 2001). All this allowed us to analyse the stability of the population demographic parameters (survival and reproduction rates) and will allow us to set out suggestions for suitable management.

Red coral coastal populations, like that examined in this paper, showed a good resilience capability, to density and reproduction reduction and to mortality increase. This behaviour is typical of a species provided of an early sexual maturity, which is structured into several overlapping generations, slow growing and showing high reproduction rates. For such species a sporadic negative reproductive event (negative net recruitment rate or a mass mortality events) could have a limited effect on survival (Kwit et al., 2004) but, as our simulations showed, a clouded future for red coral could be forecasted if such mass mortality events will frequently occur.

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