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Demography of the over-exploited Mediterranean red coral (*Corallium rubrum* L. 1758)*

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SUMMARY: The precious octocoral, *Corallium rubrum,* endemic to the Mediterranean, has long been overexploited. A demographic approach to the conservation and management of this species would therefore be highly valuable. To this end, a coastal population of red coral was studied in detail. The population represents a true "genetic unit", as it is mainly "self-seeding". It is moreover gonocoric, and the sex ratio is significantly biased toward females. For this study, 4408 colonies, collected from 28, 300-cm^2 samples, were divided into 10 size (age) classes. Recruits represent about half the population. The frequency of colonies in each class decreases exponentially with colony size. On these bases, an "*ad hoc*" life history table has been updated to include the mortality and reproduction coefficients actually measured in the population. The major reproductive output is due to the first 3 reproductive classes (79%), while larger colonies, although having higher reproductive coefficients, are sparse and only account for a small portion of the population overall reproductive output. The ratio of larval survival to adult density found indicates that some density-dependent limitation of population growth is likely at play in the population under study. Such results will be important for understanding dynamics of red coral disturbed or exploited populations.

Key words: Octocorallia, red coral, Mediterranean Sea, population structure, population dynamics, life tables.

RESUMEN: DEMOGRAFÍA DEL SOBREEXPLOTADO CORAL ROJO (*CORALLIUM RUBRUM* L. 1758) DEL MEDITERRÁNEO. – El coral rojo o precioso, *Corallium rubrum*, endémico del Mediterráneo, hace tiempo que está sobreexplotado. Por ello, una aproximación demográfica a la conservación y gestión de esta especie sería muy valiosa. Con este fin, se estudió en detalle una población costera de coral rojo. La población representa una verdadera "unidad genética", pues es principalmente de "autosiembra". Además es gonocórica, y la proporción sexual está sesgada de manera significativa hacia las hembras. Para este estudio se utilizaron 4408 colonias, que fueron recolectadas de 28 muestras de 300 cm^2 y divididas en 10 clases de tamaño (edad). Los reclutas representan aproximadamente la mitad de la población. La frecuencia de colonias en cada clase se reduce exponencialmente con el tamaño de la colonia. Sobre estas bases se ha puesto al día una tabla de vida *"ad hoc"* para incluir los coeficientes de mortalidad y reproducción que se midieron realmente en la población. La principal producción reproductiva se debe a las tres primeras clases reproductoras (79%), mientras que las colonias mayores, aunque poseen coeficientes de reproducción superiores, son raras y explican sólo una pequeña porción de la reproducción total de la población. La relación de supervivencia larvaria a densidad de adultos que se encontró indica que es probable que haya alguna limitación dependiente de la densidad en el crecimiento poblacional en la población estudiada. Dichos resultados serán importantes para comprender la dinámica de poblaciones perturbadas o explotadas de coral rojo.

Palabras clave: octocorales, coral rojo, mar Mediterráneo, estructura de la población, dinámica de la población, tablas de vida.

INTRODUCTION

The continuing loss of many animal habitats and current high rates of species rarefaction have led ecologists to adopt demographic approaches to conservation. Life history tables, which summarize the mortality and reproduction of individuals within a population, are suitable for demographic studies of long-lived species with complex life cycles and closed populations, and should also prove to be

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invaluable instruments for the conservation of over-exploited species in marine habitats as well (Gotelli, 1991; Ebert, 1999; Fujiwara and Caswell, 2001). Life tables moreover represent indispensable tools for compiling transition matrices (non-linear Leslie matrices of population growth), which in turn provide reliable projections of population trends over time in stage-subdivided populations (Tuljapurkar and Caswell, 1997).

This paper focuses on the demography of red coral (*Corallium rubrum* L. 1758), the precious red coral *par excellence*. This modular anthozoan (Octocorallia, Gorgonacea) is endemic to the Mediterranean and neighbouring Atlantic rocky shores, where it occurs between 20 and 200 meter depth (Zibrowius *et al.,* 1984). This precious octocoral has long been severely over-harvested, and only recently have some efforts been aimed at rational management of its populations (Cicogna *et al.*, 1999). However, due to the depth of its habitat, its main population and life-history features are still largely unknown.

The research presented herein deals with a coastal red coral population under observation for a number of years. Its isolated geographic position and phylopatric larval behaviour, together with the genetic evidence available, indicate the population under study is (at least partially) reproductively isolated from other similar populations (Abbiati *et al.*, 1993; Santangelo and Abbiati, 2001). This population, having a ten-year life span, has revealed a typical demographic structure in which several half-overlapping generations co-occur. It is moreover gonocoric, the sex ratio being biased toward females, and reproduction takes place in a "discrete" period during the summertime (Santangelo *et al.*, 2003).

Population dynamics are strongly influenced by the population sexual structure, and even small differences in sex ratio or age at maturity could lead to huge differences in population trends over time (Fujiwara and Caswell, 2001). In this study we have made use of reliable population reproductive data on fertility, fecundity, size at maturity and sex ratio, actually measured in the population (Santangelo *et al.* 2003), which has allowed us to set out a faithful life history table. Moreover, the possibility of matching demographic and population reproductive data has enabled us to estimate the ratio between larval survival rate and colony density and thereby reveal whether any density-dependent limitation may be affecting recruitment rates. Such data and analyses will prove to be useful in developing suitable demographic models to study the dynamics of such populations.

As coastal red coral populations have recently suffered mass mortality in different Mediterranean areas (Garrabou *et al.*, 2001), better knowledge of their demographic features and renewal processes could foster rational harvesting and conservation of this important species.

MATERIAL AND METHODS

Sampling and population analysis

The population studied is located in the Eastern Ligurian Sea, just off the Calafuria shore, near Leghorn, Italy (43°30' N, 10°20" E). The colonies dwell in crevices along a vertical cliff between 25 and 40 m (Abbiati *et al.*,1992).

Twenty-eight quadrats, 300 cm^2 each, for an overall area of 8400 cm^2 , were sampled by chisel-scraping. Colonies (n = 4408) were collected during two different years (1992 and 1997) and assigned to a size class (i) on the basis of the diameter of their base, using the following relation between diameter, D, and number of growth rings, A (Abbiati *et al.*, 1992; Santangelo *et al.*, 1999):

$$D = 1.3738 \times A^{0.7505}$$

In brief, the number of growth rings was determined on a sample of colonies of this population by preparing thin sections of their bases and counting the number of growth rings (Grigg, 1974; García-Rodríguez and Massò, 1986). As a highly significant correlation was found between number of growth rings and size (diameter, in particular), it was inferred that all colonies can be classified simply, via the above relation, into different growth-ring classes on the basis of their diameters (Santangelo *et al.*, 1999) .

Demographic population features

The population sexual status is gonocoric (at both the polyp and colony levels); its sex ratio is significantly biased toward female colonies in the ratio 1.37:1. Sexual maturity was reached by the colonies in size class 2, of which 57% were sexually mature, a percentage that rises to 100% for colonies in class 6 (Table 1). The average fecundity of female polyps

TABLE 1. – Birth coefficient (b_i) estimates for each age-size class (i). q = average fecundity of female polyps; P_i = average number of polyps per colony in each size class; SR = sex ratio; F_i = percentage of colony fertile females in each size class.

Size class (i)	q	P_i	SR	F_i	b_i
1	/	/	/	/	0
2	0.87	27.24	0.58	0.57	7.8
3	0.87	57.45	0.58	0.82	23.5
4	0.87	93.89	0.58	0.97	45.7
5	0.87	135.53	0.58	0.98	67.2
6	0.87	181.67	0.58	1	91.7

within this population was 0.87 planulae per polyp (Santangelo *et al.*, 2003). The average number of polyps per colony in each size class was determined by counting, through the stereomicroscope (20x), the polyps of 146 colonies belonging to all classes found in the population. Our observational data set is thus composed of: 1) *biometrical descriptors* of each colony: size (age) class (i), average number of polyps in the colonies of each age class (P_i), and fecundity (q_i), i.e. the number of planulae produced by each fertile female polyp (Table 1); 2) *basic demographic rates*: mortality of each age class (m_i), average reproductive output of one colony in each class (b_i); 3) *population descriptors*: colony density (n° dm^{-2}), number of colonies in each class (X_i, where i ranges between 1 and 6), population sex ratio (SR) and percentage of fertile colonies in each class (F_i; Santangelo *et al.*, 2003).

Recruitment density and adult colony density, measured in the same samples (n =28), were plotted one against the other, and the ratio between the estimated colony larval output ($\Sigma\ b_i X_i$) and the number of recruits (r) was calculated. As this population was found to be a self-seeder genetic unit, in which recruitment is mainly local (Abbiati et *al.*, 1993), this ratio yields an estimate of the local survival rate of planulae. Finally, larval survival rate was plotted against the density of adult colonies. Data were fitted using the Curve Expert program (v.1.1).

RESULTS

The population structure

The population structure, in terms of size classes, was fitted by a curve with negative exponent, as described by the following exponential function:

$$X_i = (46.3 \pm 2.7)\ e^{-(0.79 \pm 0.03)\ (i-0.5)}\ ;\ (n = 4408;\ \text{Fig. 1}).$$

FIG. 1. – Population size structure of *Corallium rubrum*: the distribution of colonies (X_a dm^{-2}) into size classes (a) is reported. Points have been fitted by the following power curve: $X_i = (46.3 \pm 2.7)\ e^{-(0.79 \pm 0.03)\ (i-0.5)}$

This curve exhibited a decreasing "monotonic" pattern (each age class is invariably greater than the next) typical of populations in a "steady state" (showing constant mortality and reproduction rates; Chadwick-Furman *et al.*, 2000). The overall size class structure of the population is also reported in the life table (Table 2). As few colonies within this population fell into the largest classes (6-10), they were grouped into a new class 6 that includes all colonies having a diameter greater than the upper limit for class 5 (4.59 mm). More than 50% of the colonies are in class 1 (recruits), while only few colonies fall into the two biggest classes, 5 and 6.

The birth coefficients

The larval production of modular organisms like anthozoans is a function of both module (polyp) fecundity (number of planulae produced by each fertile female polyp) and fertility (% fertile polyps per

TABLE 2. – "Life table" constructed for the *Corallium rubrum* population. X_i = Density of colonies (n° col dm^{-2}), m_i = mortality ($1 - X_{i+1}/X_i$), b_i = birth coefficient and b_iX_i = number of planulae produced by each size class i. Data refer to a 1 dm^2 area.

Size class (i)	X_i	m_i	b_i	b_iX_i
1	27.27	0.48	0	0
2	14.14	0.53	7.8	110.3
3	6.65	0.54	23.5	156.3
4	3.05	0.75	45.7	139.4
5	0.77	0.23	67.2	51.7
6	0.59	-	91.69	54.1
			Total:	511.8

female colony; Sakai, 1998). The average number of polyps in each size class was fitted using the following relation:

$$P_i = 15.07 \cdot i^{1.46}\ ;\ (n=146).$$

As the average fecundity and fertility, as well as the average number of polyps per female colony were known for each size class, we were able to calculate reliable estimates of the birth coefficients of our colonies in each class (b_I in Table 1). The birth coefficients integrate the fecundity, average number of polyps, sex ratio and fertility of the colonies in each class. Such estimates were arrived at by multiplying the average fecundity of female polyps (q), times the average number of polyps of colonies in each class (P_i), times the sex ratio (SR), times the percentage fertile female colonies in each class (F_i in Table 1), all actually measured in the population. Class 1 colonies were always sterile, while more than half the colonies in class 2 were already mature, a percentage that rises to 100% for colonies in the last class.

The life table

A "static" life table, suitable for populations in the steady state (Caswell, 1982) was thus constructed (Table 2). It shows the population subdivided by size classes and provides the density (X = colonies dm^{-2}), mortality (m_i) and birth coefficients (b_i) for each class. As few colonies are >5 class, they were grouped into a sixth, open-ended class.

The overall, estimated larval output of the colonies (i.e. the overall number of planulae released during a reproductive season by this population) was 511.8 larvae dm^{-2}. This figure is given by the number of larvae released by each colony times the average number of colonies in each class found in the same area ($\Sigma\, b_i X_i$), where i ranges from 2 to 6. As can be seen in the life table (Table 2), most of the reproductive output is due to the first three reproductive classes (2, 3, 4), which, despite their being composed of smaller (younger) colonies with a smaller number of polyps, are more numerous. The other classes, on the other hand, though made up of larger colonies having higher reproductive coefficients, represent only a small portion of the overall reproductive population and thus contribute a smaller percentage (20.7%) of the total population reproductive output.

Mortality, about 50% for the first four classes, exhibits a sharp rise (up to 75%) between the fourth and fifth classes. The ratio between the estimated reproductive output and recruit density measured in the same area yielded a "local" larval mortality of 94.6%, on average.

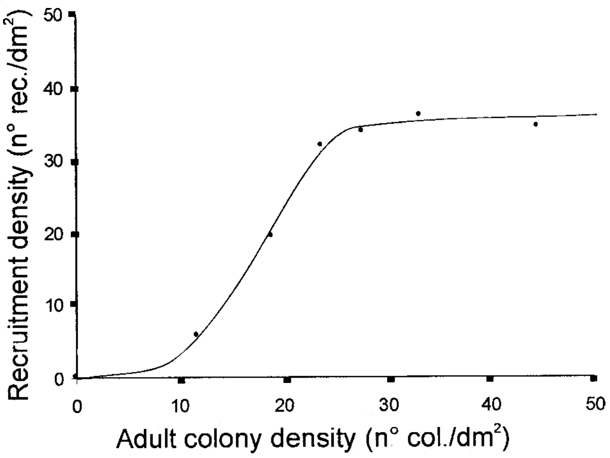

FIG. 2. – Regression curve between recruit and adult colony density (n° dm^{-2}): $y = 33.28x / (x + 1038.06\, e^{-0.2453\, x})$. $R^2 = 0.996$.

Relations between colony density and recruitment

The ratio of adult colony to recruit densities shows a good fit with the S-shaped curve:

$$y = 33.28x / (x + 1038.06\, e^{-0.2453\, x});$$

(n=28; Fig. 2). Recruitment density increases with colony density up to a certain threshold value (25-30 col dm^{-2}), above which recruitment increases no further. This trend suggests that some density-dependent limitation of population growth is at work in the population under study to limit recruitment above this adult density value.

The ratio between local adult density and the local larval survival, based on data collected in the same samples, was fitted by the curve

$$y = 1.84/(x+520.2\, e^{-0.14x})$$

(n=28) reported in Figure 3, which exhibits the following trends: at low adult colony density, the larval survival increases with increasing adult density, while at higher adult densities (>25-30 col dm^{-2}), larval survival reaches its maximum value and then decreases, albeit slowly.

All these findings indicates that both recruitment and larval survival decreases at higher colony densities.

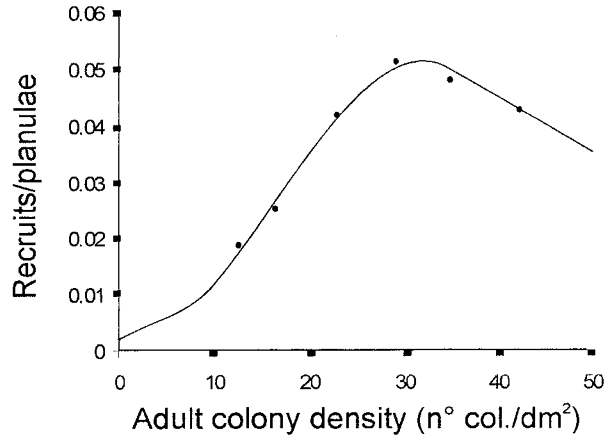

FIG. 3. – Regression curve between larval survival (recruitments-to-larval output ratio) and adult colony density (n° dm^{-2}): $y = 1.84 / (x + 520.18\, e^{-0.14\, x})$. $R^2 = 0.972$.

DISCUSSION

According to Dobson (1999), species conservation requires large demographic data sets, gathered on the whole population under study. Unfortunately, little population data is generally available for rare or endangered species. This is also true for benthic, deep-dwelling marine species. For several years now we have been collecting a large body of data on the structure of a red coral population, the ultimate aim being to develop suitable demographic models for reasonably reliable predictions of population trends over time. Such demographic studies now seem crucial for overexploited Mediterranean species, such as red coral, which have recently been affected by mass mortality (Garrabou *et al.*, 2001).

The decreasing monotonic pattern of the population size structure, without any cohort missing or overrepresented, indicates that no major disturbance had altered recruitment or mortality.

This finding, together with the availability of accurate estimates of population reproductive parameters (Santangelo *et al.*, 2003), has enabled us to construct a reliable static life history table, which summarises the main demographic parameters measured in the population. Mortality, roughly constant for the first classes, increases sharply between the fourth and fifth classes, a fact likely due to either harvesting by amateur divers (who selectively collect larger colonies), and/or attack by endobiont sponges (affecting mainly larger colonies) that cause their detachment (Corriero *et al.*, 1997). It is worth recalling that population persistence is more sensitive to variations in mortality than in fecundity (Dobson, 1999); this is especially true for long lived species like red coral. The main population reproductive output thus comes from colonies in the first 3 fertile classes (79%), while the other classes, although composed of larger colonies having more polyps and therefore higher individual reproductive coefficients, are too sparse to make a large contribution to reproduction, and therefore account only for a small portion of the population overall reproductive output. Under conditions of heavy mortality in older colonies, such reproductive population structure would foster population survival.

The ratio between larval output and recruit density, measured in the same samples, yielded a "local" larval mortality of about 95%. Clearly, we cannot know whether (or to what degree) larval migration might affect this local "mortality" estimate; nevertheless, this value is lower than those estimated for other octocorals (Grigg, 1997; Coma *et al.*, 1995).

The clear-cut S-shaped relation between recruitment and adult density exhibits a positive slope up to an average population density (25-30 col dm^{-2}) and then remains constant. This trend suggests that some density-dependent limitation of population growth (in terms of adult density limitation on recruitment) is likely operative in the population under study. A certain density-dependent limitation is also indicated by the curve fitting the relation between the estimated larval survival (recruitment-to-larval-output ratio) and the colony density. This curve shows a positive slope for low densities, peaks at average densities and then exhibits a negative trend at the highest densities, confirming that some density-dependent regulation of recruitment rates may actually occur in the population. Such density-dependence, due presumably to the reduced availability of free space, is to be included in a dynamic model, which will enable simulations of population trends over time. The model constructed in a previous work (Abbiati *et al.*, 1992) thus requires updating on the basis of such findings. The model includes an arbitrary feedback term representing the control exerted by adult density on population growth (Caswell, 1992). As some dependence of recruitment on adult colony density was actually found in field data, this trend will be represented in the enhanced model.

The density-dependent limitation found suggests that demographic factors (intrinsic to the population), more than environmental stochastic factors, could control the growth of crowded, coastal red coral populations. On the other hand, the mass mortality that has recently been reported in similar red coral populations (Garrabou *et al.,* 2001) indicates that stochastic, catastrophic events could also heavily influence stable, slow-growing, populations like the studied one, with the effect of limiting their growth more drastically than demographic factors.

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