Demography, Reproductive Biology and Trophic Ecology
of Red Coral (*Corallium rubrum* L.) at the Costa Brava
(NW Mediterranean):
Ecological Data as a Tool for Management

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Ernährungsökologie der Roten Koralle (*Corallium rubrum* L.)
an der Costa Brava (NW Mittelmeer):
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IMPRESSUM

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To my Parents, who always had faith in me,
and to all who believe in their dream

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1 SUMMARY

The Mediterranean red coral (*Corallium rubrum*, L. 1758) is a characteristical gorgonian living in semidark habitats in the coralligenous zone of sublittoral hard bottoms. Despite being harvested commercially for the use of its red calcium carbonate skeleton in the jewelery industry, its ecology is still little understood. Thus the objective of this study was to increase knowledge on the population structure, reproduction and feeding ecology of red coral and to use these data to evaluate the efficiency of current management strategies of this species.

The size/age structure of a population records valuable information, summarising the effects of mortality, recruitment and growth of past years. The six studied populations at the Costa Brava (NE Spain) consisted mainly of small/young colonies, as larger colonies are commercially exploited. Average size and age were estimated at 3 cm height and 7.5 years, whereas the species is capable of reaching 50 cm and 100 years. Furthermore, these young populations consist of colonies that have developed only few branches, offering considerably less three dimensional structure to the ecosystem than unharvested populations. One of the studied populations is located in a protected area, the Medas Islands Marine Park, and consisted of significantly larger/older colonies, thus allowing to distinguish harvesting effects from environmental ones.

The reproductive output of red coral was found to significantly depend on colony size, having important implications for its management. Another aspect of potential importance for optimal harvesting is mesoscale variation of reproductive output. In a comparison of eight stations, however, we did not find significant differences, indicatig a homogenous reproduction. Colonies in deep water were found to spawn slightly earlier than shallow water ones. However, this phenomenon was observed only when temperature stratification in summer was particularly pronounced. Yet depth was not found to affect reproductive output itself, again in contrast to the demographic features.

The trophic ecology is one of the key aspects of the biology of an organism, helping to understand its demography and reproductive biology. The main proportion of the diet of *Corallium rubrum* was found to be particulate organic matter, while crustaceans such as copepods played a smaller role due to the irregular capture. Red coral appear to be able to meet their energy requirements by constant access of resuspended detritic material, while taking advantage of occasional capture of large zooplankters. Prey capture rate per polyp is higher in small colonies, and also in colonies situated in deep water. We did not find a clear seasonal pattern in red coral feeding, as observed in some gorgonians, which indicates that changes in water movement have a stronger effect on the prey capture rate than the seasonal

succession of the plankton. The grazing impact of red coral populations was estimated to be lower than that by other gorgonians, which is a result of its population structure being dominated by small colonies.

Ecological data like those presented in this study are the base for ecosystem management, as they allow to calculate the secondary production of a population. We therefore used the demography and reproduction data to provide management recommendations for red coral, by using the Beverton-Holt fishery management model to calculate maximum sustainable yield. The results show that the red coral fishery at the Costa Brava would reach its maximum yield only at a considerable age of first capture, whereas the colonies are harvested at a much younger age. This results in an estimated annual catch that is only a fraction of what could be harvested using an optimised management strategy. Furthermore, harvesting at this age provides a short reproductive period before capture, compared for example to the sustainable fishery of black coral in Hawaii. The comparison of calculated and declared harvests indicates considerable poaching activities and undeclared harvest. Finally, a recent rise in mortality confirms a non-sustainable level of harvesting.

Concluding, the results confirm the paramount importance of data on the reproductive biology and population structure of a species for its management. In this study we investigated the effects of harvesting, spacial mesoscale variability and depth on the population structure, reproduction and feeding ecology of red coral. The data show that red coral populations at the Costa Brava are very young and have a diminished reproductive potential due to overharvesting, yet show a considerable impact on the seston. Protecting young colonies is proposed as the central management measure.

ZUSAMMENFASSUNG

Die Rote Koralle des Mittelmeeres (*Corallium rubrum*, L. 1758) ist eine charakteristische Gorgonarie, welche in halbdunklen Habitaten der coralligenen Zone von sublitoralen Hartböden lebt. Trotz kommerzieller Befischung für die Verwendung ihres roten Kalkskeletts in der Schmuckindustrie ist nur wenig über ihre Ökologie bekannt. Daher war die Zielsetzung dieser Studie, das Wissen über die Populationsstruktur, Fortpflanzungsbiologie und Ernährungsökologie roter Korallen zu erweitern und die Daten dazu zu benutzen, die Effizienz der aktuellen Managementstrategien zu beurteilen.

Die Größen-/Alters-Struktur einer Population speichert wertvolle Informationen, indem sie die Effekte von Mortalität, Rekrutierung und Wachstum vergangener Jahre zusammenfasst. Die sechs untersuchten Populationen an der Costa Brava (NO Spanien) bestehen hauptsächlich aus kleinen/jungen Kolonien, da größere Kolonien kommerziell gesammelt werden. Durchschnitts-Größe und -Alter wurden auf 3 cm Höhe und 7,5 Jahre geschätzt, obwohl die Spezies in der Lage ist, 50 cm und 100 Jahre zu erreichen. Überdies bestehen diese jungen Populationen aus Kolonien, die nur wenige Zweige entwickelt haben und damit ihrem Ökosystem erheblich weniger dreidimensionale Struktur bieten, als unbefischte Populationen. Eine der untersuchten Populationen befindet sich in einem geschützem Gebiet, dem Islas Medas-Naturpark, und besteht aus signifikant grösseren/ älteren Kolonien. Dies erlaubt, fischereibedingte von umweltbedingten Faktoren zu unterscheiden.

Das Reproduktionspotential Roter Korallen hing signifikant von der Koloniegröße ab, was wichtige Implikationen für das Management hat. Ein anderer Aspekt von potenzieller Wichtigkeit für optimale Befischung ist die Variabilität des reproduktiven Potentials auf mittleren geographischen Skalen. Im Vergleich von acht Stationen fanden sich jedoch keine signifikanten Unterschiede, was auf eine homogene Fortpflanzung hinweist. Kolonien in tieferem Wasser geben ihre Larven früher ab, als Kolonien in flachem Wasser. Dieses Phänomen wurde jedoch nur beobachtet, wenn die sommerliche Temperatur-Schichtung besonders ausgeprägt war. Ein Einfluss der Tiefe auf das reproduktive Potential wurde dennoch nicht festgestellt, was erneut im Gegensatz zu den demographischen Charakteristiken steht.

Die Ernährungsökologie ist einer der Schlüsselaspekte der Biologie eines Organismus, da sie dessen Demographie und Fortpflanzungsbiologie zu verstehen hilft. Der Hauptbestandteil der Nahrung von *Corallium rubrum* war partikuläres organisches Material, während Crustaceen, wie etwa Copepoden, aufgrund ihres unregelmässigen Vorkommens eine geringere Rolle spielten. Rote Korallen scheinen ihren Energiebedarf

durch die konstante Aufnahme resuspendierten organischen Materials zu decken, wobei sie zusätzlich auf größere Zooplankter zurückgreifen.

Ökologische Daten, wie sie in dieser Studie präsentiert werden, sind die Basis für das Management eines Ökosystems, da sie es ermöglichen, die Sekundäreproduktion einer Population zu bestimmen. Daher verwendeten wir die Demographie- und Reproduktionsdaten, um Managementempfehlungen für rote Korallen zu entwickeln. Dazu benutzten wir das Beverton-Holt-Modell, um den Maximalertrag einer nachhaltigen Fischerei zu berechnen. Die Resultate zeigen, daß die Rote Korallen-Fischerei an der Costa Brava ihren Maximalertrag erst bei beträchtlichem Mindestalter der Kolonien erreicht, wobei aber derzeit schon sehr junge Kolonien gefischt werden. Das hat zur Folge, daß der berechnete Jahresertrag nur einen Bruchteil dessen ausmacht, was mit optimalem Management gefischt werden könnte. Darüberhinaus gestattet eine Befischung junger Kolonien nur eine kürzere reproduktive Phase vor dem Fang, verglichen zum Beispiel mit der nachhaltigen Fischerei von schwarzen Korallen in Hawaii. Der Vergleich von berechnetem und angegebenem Ertrag deutet auf erhebliche Schwarzfischerei und nicht-deklarierte Erträge hin. Darüberhinaus bestätigt der Anstieg der Mortalität während der letzten Jahrzehnte ein nicht-nachhaltiges Niveau der Befischung.

Zusammengeffaßt bestätigen die Resultate dieser Arbeit die enorme Wichtigkeit von Daten über die Fortpflanzungsbiologie und Populationsstruktur für das Management einer Spezies. In dieser Studie wurden die Effekte von Befischung, geograpischer Variabilität auf mittleren Skalen und Tiefe auf die Populationsstruktur, Fortpflanzung und Ernährungsökologie Roter Korallen untersucht. Die Daten zeigen, daß Rote Korallen-Populationen an der Costa Brava aufgrund von Überfischung sehr jung sind und ein reduziertes Reproduktionspotential besitzen. Trotzdem üben sie einen bedeutenden Einfluss auf das Seston aus. Der Schutz junger Kolonien wird als zentrale Management-Massnahme empfohlen.

RESUMEN

El coral rojo (*Corallium rubrum*, L. 1758) es un gorgonáceo característico del Mediterráneo que vive en hábitats semi-oscuros en la zona coralígena de los fondos duros sublitorales. A pesar de tratarse de una especie comercialmente explotada por el uso de su exoesqueleto rojo de carbonato de calcio en la industria de joyas, su ecología es poco conocida. El objetivo de este estudio consiste en mejorar el conocimiento acerca de la estructura de poblaciones, la reproducción y la alimentación del coral rojo, para usar finalmente estos datos en la evaluación de la eficiencia de las estrategias actuales de gestión de esta especie.

La estructura de talla / edad de una población memoriza información útil, resumiendo los efectos de mortalidad, reclutamiento y crecimiento de los años pasados. Las seis poblaciones estudiadas en la Costa Brava (NE de España) están principalmente constituidas por colonias pequeñas/ jóvenes, siendo las colonias más grandes explotadas para el comercio. La estima de su talla media es de 3 cm de altura y 7.5 años de longevidad, aunque la especie sea capaz de llegar a los 50 cm de altura y 100 años de edad. Además, estas poblaciones jóvenes consisten en colonias que desarrollan pocas ramas, ofreciendo una estructura tridimensional considerablemente menor de lo esperable respecto a las poblaciones no explotadas. Una de las poblaciones estudiadas se halla en un área protegida de la Reserva Natural de las Islas Medas, observándose de modo significativo colonias más altas, de mayor calibre (grosor de la columna) y más ramificadas, permitiendo así distinguir los efectos de la explotación de los efectos naturales.

El esfuerzo reproductor del coral rojo depende de forma significativa de la talla de la colonia, lo que tiene implicaciones importantes para su gestión. Otro aspecto potencialmente importante para una explotación optima es el estudio de la variación a mesoescala horizontal del esfuerzo reproductor. No se han encontrado, comparando ocho estaciones, diferencias significativas, indicando una reproducción relativamente homogénea. Se observa que las colonias situadas en la zona más profunda liberan sus larvas antes que las colonias situadas a menor profundidad, observándose este fenómeno cuando la estratificación de temperatura en verano era particularmente pronunciada. A pesar de esto, la profundidad no parece afectar el esfuerzo reproductor.

La ecología de la alimentación es uno de los aspectos claves de la biología de un organismo, pues ayuda a entender su demografía y biología reproductora. La dieta de *Corallium rubrum* esta constituida fundamentalmente por partículas de materia orgánica, mientras que crustáceos, como los copépodos tienen menos importancia por ser capturados de forma irregular. El coral rojo parece ser capaz de completar sus requerimientos

energéticos a través de la ingesta de material orgánico resuspendido, aprovechando la captura ocasional de zooplancton de mediano tamaño como copépodos y nauplios de copépodo. La tasa de captura por pólipo es mas alta en colonias pequeñas y también en colonias situadas en aguas profundas. No hemos encontrado un ciclo estacional claro en la alimentación del coral rojo, como se observó en otras gorgonias, indicando que la actividad es menos dependiente de las corrientes principales y de las pautas dominadas por la termoclina. El impacto en el seston de poblaciones de coral rojo se estimó más bajo que el de otras gorgonias; eso es un resultado de la predominancia de pequeñas colonias en la estructura de sus poblaciones.

Datos ecológicos como los que se presentan en este estudio constituyen una base para la gestión de ecosistemas, porque permiten calcular la producción secundaria de una población. Por eso hemos usado los datos de demografía y reproducción, proponiendo recomendaciones para la gestión de esta especie, usando el modelo de Beverton-Hold para calcular la máxima captura sostenible. Los resultados demuestran que la pesca de coral rojo en la Costa Brava llega a su carga máxima solo cuando la edad de la primera captura es considerablemente alta. Sin embargo, las colonias se pescan a una edad mucho más joven. Esto resulta en una pesca anual estimada que es solo una fracción de lo que se podría pescar con una gestión optimizada. Además la captura en esta edad joven deja un periodo reproductor muy corto comparado por ejemplo con la pesca sostenible de coral negro en Hawai. La comparación de la pesca declarada y capturada indica un porcentaje muy alto de fraude y pesca sin declarar. Finalmente, una subida reciente de la mortalidad confirma un nivel no sostenible de explotación.

En conclusión, los resultados confirman la importancia de los datos de la biología reproductora y estructura de población de una especie para su gestión. En este estudio hemos investigado los efectos de explotación, la variabilidad a media escala espacial y la profundidad en la estructura de población, la reproducción y la ecología de alimentación del coral rojo del Mediterráneo. Los datos demuestran que las poblaciones Mediterráneas de coral rojo son muy jóvenes y tienen un potencial reproductor reducido a causa de la sobre-explotación, pero pueden tener un impacto considerable en el seston. Se propone la protección de colonias jóvenes como principal medio de gestión de este recurso renovable.

2 INTRODUCTION

Ecologic features of octocorals

Benthic suspension feeders capture seston particles from the water column and thus play an important role in pelago-benthic energy transfer processes (Cloern 1982; Officer et al. 1982; Fréchette et al. 1989; Kimmerer et al. 1994; Riisgård et al. 1998; Arntz et al. 1999). The most efficient filter feeders are active ones, such as sponges, bivalves and ascidians which have long been the focus of attention as they can significantly deplete the seston in the water column in shallow coastal ecosystems (Fréchette and Bourget 1985; Petersen and Riisgård 1992; Pile et al. 1996; Ribes et al. 1999a). However, the impact of passive suspension feeders, especially of cnidarians on the seston has recently come to light (Gili and Coma 1998; Fabricius 1998; Arntz et al. 1999).

Among these, gorgonians are the most conspicuous and play an important role in many ecosystems (True 1970; Kinzie 1973; Brazeau an Lasker 1989; Coma et al. 1995; Orejas et al. 2001). They structure and stabilise the ecosystem (Hiscock and Mitchell 1980; Mitchell et al. 1993) by providing three-dimensional complexity and increasing diversity (Dayton et al. 1974; Jones et al. 1994).

Gorgonians are longevous cnidarians, with low growth and reproductive rates, and are typically characterised as K-strategists (Grigg 1989). They are usually gonochoric, brood their larvae internally or externally and feature seasonal gamete production and synchronized spawning. The diet and reproduction of several species has been described, but the biology of most gorgonians is still little understood although data on the population structure, growth, trophic ecology and the reproductive cycle are the key to understand environmental and anthropogenic influences on any community (Dayton 2003).

Red coral biology

The Mediterranean red coral (*Corallium rubrum* L. 1758, Gorgonacea, Octocorallia) is a sessile colonial cnidarian (Fig. 1) with an arborescent growth form (Fig. 2) that can reach a size of 50 cm (Garrabou and Harmelin 2002), and belongs to the longest living inhabitants of the coralligenous, living for may be more

Figure 1: *Corallium rubrum* branch with polyps in various stages of expansion. From Lacaze-Duthiers 1987

than 100 years (Riedl 1984; García-Rodríguez and Massó 1986b). It is a sciaphilic species that can be found in depths of 5 – 300 m, though more commonly at 30 – 200 m (Carpine and Grasshoff 1975; Weinberg 1978; Riedl 1984), and is distributed throughout the Mediterranean, though mainly in the western part, and at the neighbouring Atlantic coasts (Marchetti 1965, Zibrowius et al. 1984; Chintiroglou and Dounas-Koukouras 1989).
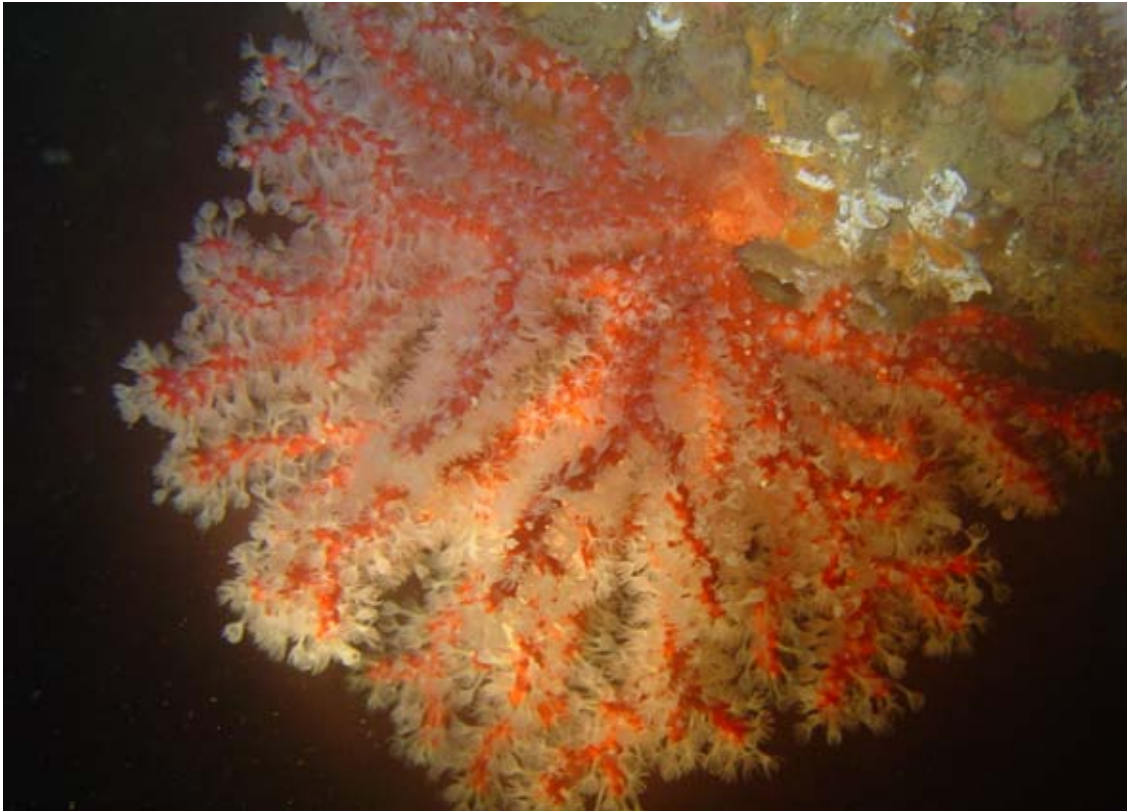

Figure 2: Red Coral colony in the Medas Islands Park. Highly branched colonies such as this 12 cm high specimen were rarely observed during the study

Red coral has long been of interest to marine science (see Lacasse-Duthiers 1864), and being a commercially exploited species, the interest in its population dynamics and reproductive biology has increased in recent years (Garrabou and Harmelin 2002; Santangelo et al. 2003). Gorgonians are useful study objects for population dynamics, as establishing the age structure of a population, estimating abundance and setting up recruitment experiments provide reliable data on these sessile longevous organisms. However, despite the commercial and scientific interest in studying red coral, it is not yet clear how the main environmental factors influence its biology.

The next paragraphs describe more closely how some factors are hypothesised to affect population structure, reproductive output, and prey capture, three key components of an organism's biology. Understanding how these relate to environmental factors allows to assess the human and environmental impact on red coral populations.

Demography

The size/age structure of a population reflects the combined effects of mortality, recruitment, growth and other processes that affect the population and thus records its history especially in longevous species (Santangelo et al. 1993). Thus demographic studies have been a valuable tool to determine the state of octocoral populations (Grigg 1976; Weinbauer and Velimirov 1996; Bak and Meesters 1998).

In red coral and other commercially harvested precious corals the size/age structure has been found to be shifted towards small/young individuals by lacking older and larger ones. (Gárcia-Rodríguez and Massó 1986a; Grigg 2001; Santangelo et al. 2003). This type of demographic structure has also been observed in a natural black coral population in a New Zealand fjord where destructive landslides are common (Grange and Singleton 1988). Consequently, shifts towards small and young individuals indicate an increase in mortality or recruitment limitation (Grigg 1989).

The comparison of the size/age structure of a protected red coral population within a Marine Protected Area at the Spanish coast with nearby commercially exploited areas enabled this study to distinguish between harvesting effects and environmental inter-habitat differences.

Population density and the spatial distribution pattern further reveal the influence of environmental factors on a species. As *Corallium rubrum* populations at the Costa Brava grow in much shallower water than they do in France and Italy, this study investigated the influence of depth on the abundance and population structure of red coral. This may help to better understand the significant differences in the vertical distribution of red coral in different regions of the Mediterranean.

Reproduction

Studying the variation of the reproductive output as a function of various parameters is crucial for our understanding of population dynamics. The survival of any population depends on a sufficiently high reproductive potential and on the success of the recruits. Thus, it is important to determine the proportion of sexually mature individuals in the population and quantify the contribution of various size classes. Colony size affects energy allocation and thus reproduction in octocorals, as small colonies suffer higher mortality and poorer food capture ability than large colonies (Szmant 1985; Hall and Hughes 1996; Beiring and Lasker 2000). Large individuals thus produce up to 40 – 98 % of the gonads, although making up only 3 – 50 % of the population (Babcock 1984; Coma et al. 1995; Beiring and Lasker 2000). This fact is of special importance in exploited species like red coral, as harvesting is size selective and may significantly diminish the reproductive potential of a population. The relatively young reproductive age of red coral, compared to other gorgonians, seems to have ensured its recoverability (Grigg 1989). It has been pointed out, however, that full reproductive potential is not reached until several

years after the age at first reproduction (Santangelo et al. 2003; Torrents et al., submitted). The starting point for this study was to establish the reproductive cycle of the studied population. This made it possible to compare the reproductive output of the most common size class at the Costa Brava with the output of a larger class in a Marine Protected Area.

The vertical distribution of red coral extends above the thermocline, and deeper habitats differ in light intensity, hydrodynamism and mean annual temperature from shallow ones. Earlier studies have attempted to elucidate the role of depth in the reproduction of red coral (Vighi 1972; Santangelo et al. 2003), but a difference in reproductive output has not been confirmed to date. The shallow limit of the coralligenous is much more accessible at the Costa Brava (18 – 40 m) than in other parts of the Meditterranean (60 – 80 m) (Margalef 1985). This provided the opportunity to study the effect of depth on red coral reproduction within a representative range where notable environmental changes can be observed.

Figure 3: This engraving from the 16th century illustrates the early coral harvesting in Sicily. using goggles imported from Japan to pick up large colonies by breath hold diving. From Cicogna and Cattaneo-Vietti 1993

Trophic ecology

The quantification of the energy uptake of a species allows to determine its role in energetic fluxes of the ecosystem, and helps to explain patterns of environmental adaptation observed (Harland et al. 1992; Kim and Lasker 1997). Studies on Mediterranean gorgonians contributed to our understanding of the annual variation of the impact of suspension feeder communities on the seston, as well as to our understanding of their life cycle (Coma et al. 1994; Ribes et al. 1999b; Ribes et al. 2003; Rossi et al. 2004). As the plankton abundance in the Mediterranean follows a distinct seasonality (Siokou-Frangou 1996; Calbet et al. 2003), feeding conditions for suspension feeders vary during the year (Coma et al. 2000). Colony size has also been shown to affect prey capture rates in gorgonians (Kim and Lasker 1997) and depth has been suggested to influence prey capture (Lasker et al. 1983). This first *in situ* study on feeding of *Corallium rubrum* examined the seasonal feeding cycle in red coral and examined the effect of depth and colony size on prey capture rate.

A short overview of red coral fishery

In order to obtain a complete view on the ecology of red coral it is necessary to consider its long history of exploitation. The calcium carbonate skeleton of precious corals has been used for rituals and ornament in the earliest civilizations, dating back 30,000 years (Tescione 1973). At least fifteen centuries before Christ coral was one of the most sought after exchange products on the oriental markets. Mediterranean red coral was first collected in form of fragments and even bigger branches (Fig. 3) as they washed up on the shore (Tescione 1973). Reports about first fishing efforts of red coral in the Ionian Islands (Greece) by means of pointed iron devices (the *"kouralió"*, hence the name "coral"), nets, and breath hold diving (Tescione 1973), indicate that originally red coral grew to

Figure 4: Fishing with the St. Jordi Cross, a wooden cross with nets attached, that is twisted on the bottom and then hauled up to obtain the coral branches. In the year 1830 the Kingdom of Naples employed 1800 coral fishing boats manned by 17,000 sailors. From Cicogna and Cattaneo-Vietti 1993

Figure 5: Coral diver Tony Recco with his harvest from more than 100m depth. From Diolé and Falco 1976

impressive size in quite shallow water.

Fishing on an industrial scale began as early as in the Neolithic age, ca. 7000 years ago (Grigg 1976). In the year 1830 the Kingdom of Naples employed 1800 coral fishing boats manned by 17,000 sailors. Coral was then dredged and netted by simple devices such as the Sant-Andrew Cross or the "Barra Italiana" (Cicogna and Cattaneo-Vietti 1993)

(Fig. 4). In the 1950s the advent of SCUBA diving brought greater efficiency and selectivity to coral fishing (Fig. 5), and today the Mediterranean red coral is still regarded as the precious coral par excellence in the jewellery industry.

However, like in most fisheries, stocks declined during the industrialisation period, and the catches dropped dramatically in 1976 – 1984 (Fig. 6) (FAO 1984, FAO 1988). Expert meetings and consultations set up a number of recommendations to optimize management of the red coral fishery that were only partially adopted, and the known stocks, once exploited, never recovered (FAO 1984, FAO 1988). In recent years the overall Mediterranean coral yield dropped to about 25 – 30 t per year, of which 4 – 5 t originated from the Spanish Mediterranean coast, and ca. 1 t from the Costa Brava (Fig. 6). However, unlike many other cases of exploitation of longevous species (e.g. whales, see Fujiwara and Caswell 2001), red coral is still successfully fished today and does not appear to be threatened by extinction (FAO 1988). In 1998 the government of Catalonia (Spain) committed to a stepwise ban of coral fishing at the Costa Brava, that was subsequently taken back, which is reflected in a drop of number of licences and catch (Fig. 6).

Valuable lessons about how to successfully manage a precious coral fishery can be learned from the Hawaiian black coral fishery (Grigg 1976). The study of its population structure and abundance, growth rate and reproductive cycle represented a useful holistic approach. Applying these data in the Beverton-Holt fisheries management model allowed useful recommendations, that, thanks to the compliance of fishermen with these recommendations, resulted in a sustainable fishery of Hawaiian black coral (Grigg 2001). The General Fisheries Council for the Mediterranean in 1988 stressed that more precise data on basic biological parameters such as mortality and growth were necessary to confirm red coral fishery models (FAO 1988). This study, using estimates for red coral abundance and reproduction on the Costa Brava population, as well as new data on red coral mortality and growth, presents an updated model for sustainable fishery.
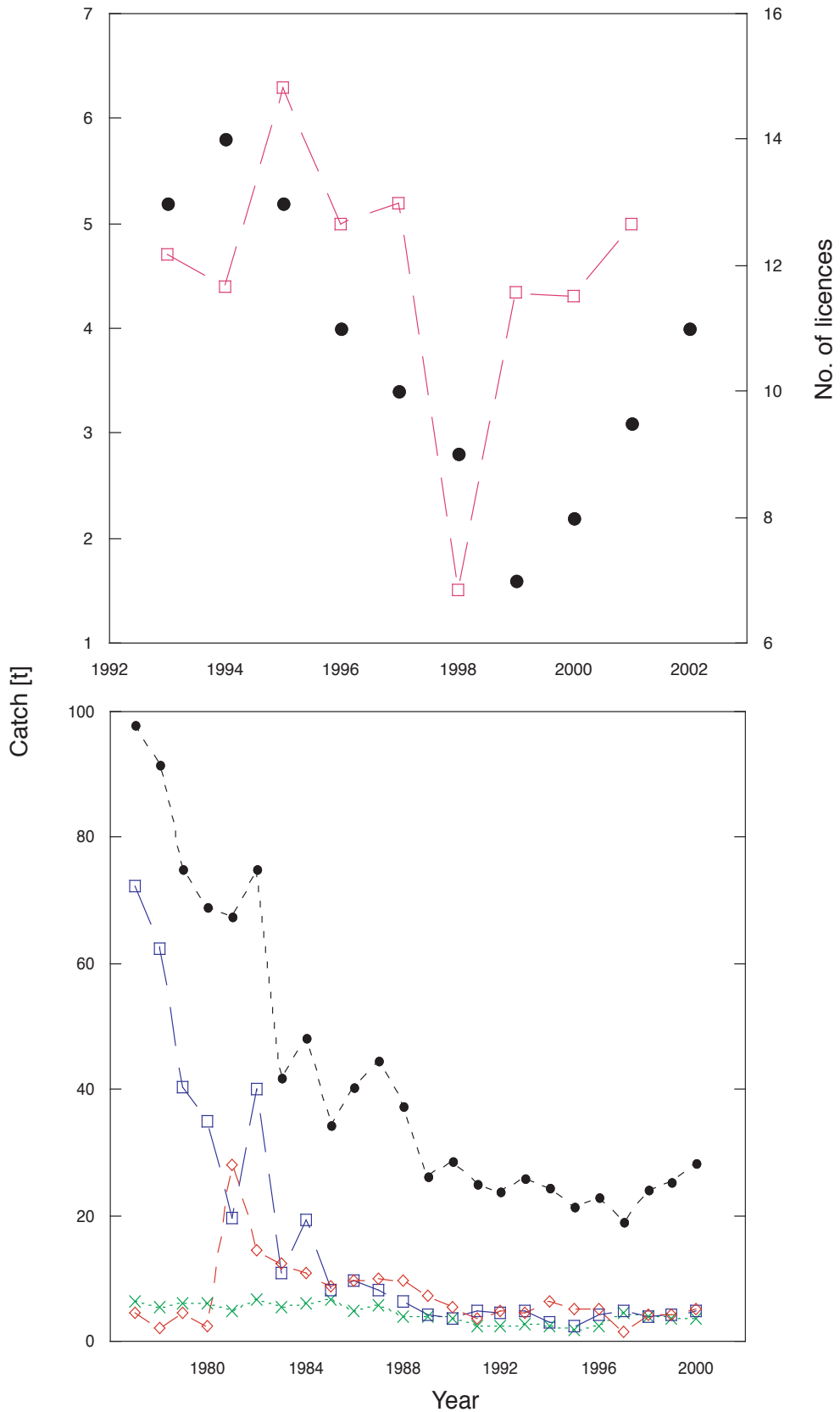
Figure 6: Above: Red coral catch (●) and number of fishing licences at the Costa Brava (—□—). Data from the Government of Catalonia (Spain) Below red coral harvest in the French (····×···), Italian (—□—) and Spanish Mediterranean (—◇—) compared to the sum of harvest (– – ● – –). Data from FAO

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AIMS OF THIS STUDY

Demography

1) To quantify the abundance of red coral in the coralligenous.

2) The comparison of the frequency distribution, colony height, basal diameter and branching pattern across a wide range of the Costa Brava (NE Spain), including a protected marine park, thus revealing harvesting effects on population structure.

Reproduction

3) To determine the annual reproductive cycle of the Costa Brava population, comparing two colony size classes and two depth strata.

4) Comparing the reproductive output of different communities across the Costa Brava in order to investigate mesoscale variations in the recoverability of red coral populations.

5) Determining the size at first reproduction of red coral at the Costa Brava.

Trophic ecology

6) To study the annual variability of the diet and prey capture rate in red coral, and compare feeding of two size classes and of colonies situated in two depths.

Management

7) The application of new data on mortality, population structure at the Costa Brava and growth to produce an updated model on the maximum sustainable yield for the red coral fishery.

8) To use the data on reproduction and population structure at the Costa Brava to recommend an age at first capture and compare this age, as well as the calculated sustainable yield, with current practice in the Costa Brava fishery, considering older data, fisheries statistics and indications of new trends in the fishery to evaluate the state of the stock and the sustainability of the fishery.

STUDY AREA

Location and environmental features

The study presented here was carried out in the northern part of the Costa Brava (NE Spain) in the northwestern Mediterranean. The Mediterranean is an oligotrophic sea of high salinity, as evaporation is higher than the input of freshwater by rivers, and nutrient rich deep water emanates into the Atlantic, whereas nutrient poor Atlantic surface water enters through the Strait of Gibraltar (Margalef 1985). Due to its small size there are virtually no tidal waves. It is a warm temperate sea showing a distinct seasonality of rainfall, winds, water movement, temperature and seasonality. This results in warm (26° C), calm surface water in summer, that is depleted of nutrients and has low planktonic primary productivity, whereas in winter temperature drops to 13° C and frequent storms mix the water at the Costa Brava (Pasqual and Flos 1984). Spring conditions are characterised by plankton blooms (Siokou-Frangou 1996; Calbet et al. 2003) that are an important energy input to suspension feeder communities such as the ones studied (Coma et al. 2000). The western Mediterranean is more eutrophic than other parts of the Mediterranean and the coralligenous begins to form as shallow as 18 – 40 m, as opposed to 60 – 80 m (Ros et al. 1985). Strong wind driven currents are present in the study area throughout the year
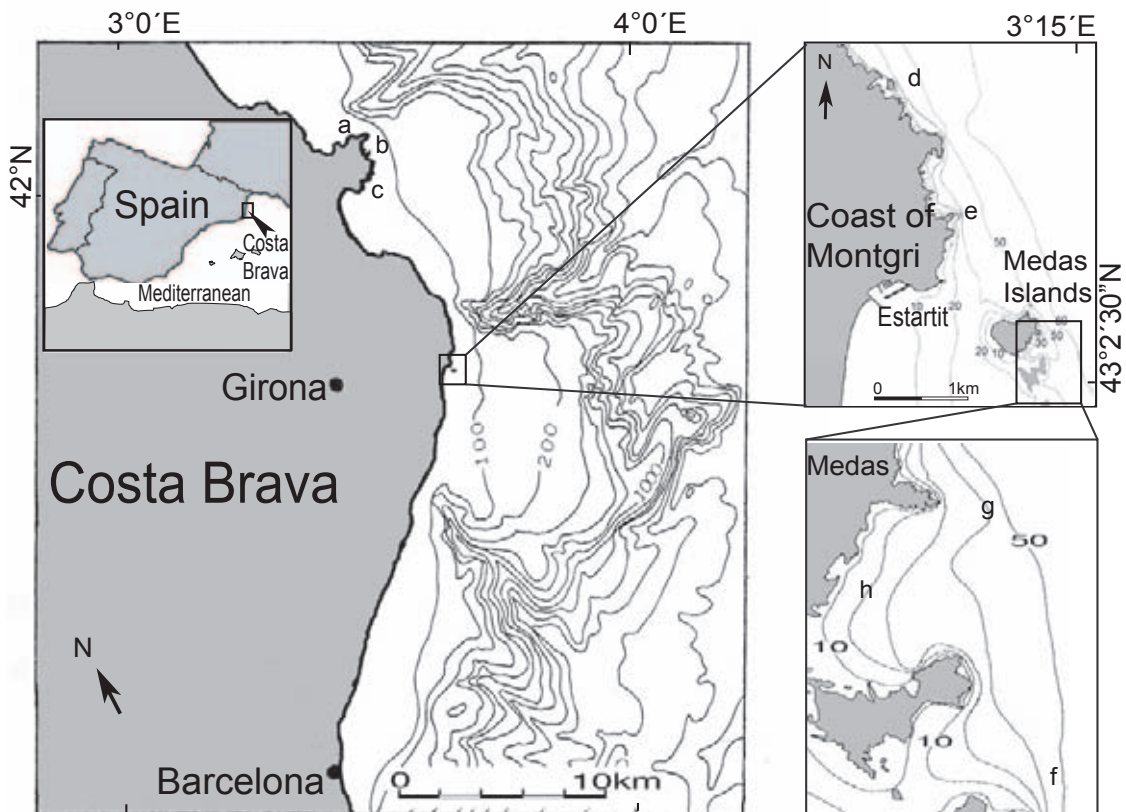

Figure 7: Study area and sampling arrangement. a: Punta Falconera (36 m depth), b: Punta de sa Oliguera (40 m), c: Ses Ielles (30 m), d: Illa de Düi (25 m), e: Punta Salina (20 m), f: Serra Ventosa (18 m), g: Barda del Sastre (40 m), h: Cova de la Reina (18 m). a – f: Study of spacial variation of reproductive output. g – h: Monthly sampling for reproductive and trophic study (15-month period).

(Pasqual and Flos 1984).

The sampling stations are situated between the Cap de Creus area (42°20'1"N, 3°16'30"E) in the north to the Coast of Begur (42°1'N 3°14'55"E) in the south (Fig. 7). The geographical range studied along the coast spanned 7 km. The annual cycles and experimental work were carried out at the Medas Islands and the adjacent coast. The Medas Islands consist of seven islets (emerged area: 21.92 ha), situated 1 km from the Coast (43°2'30"N, 3°13'30"E, Fig. 7). The Islands show an asymmetric underwater topography, with deep reaching cliffs on the northern side and gentle slopes on the southern side (Ros et al. 1984). The sampling stations are located on the northern, off-shore side, where currents and waves are stronger, and the influence of the nearby river "Ter" is low. The study of these islets proved advantageous as its bionomy has been studied (Ros et al. 1984) and the declaration of the Medas Islands as a Marine Protected Area (MPA) in 1991 offered the opportunity to study unfished red coral populations.

In general, all studied habitats consist of weather-exposed hard bottom substrate at 18 – 48 m depth, characterised by its coralligenous community.

The Mediterranean coralligenous community

The Mediterranean is a temperate oligotrophic sea where some benthic communities show a diversity and complexity that is comparable to coral reefs (Margalef 1985). The most structured and species rich community of the Mediterranean benthos is the coralligenous (Fig. 8), which is situated in the semi dark sublittoral (Ros et al. 1985; Laubier 1966). It extends from the lower level of photophilic algae and sea grasses to 100 m depth and more, where multicellular plants can survive. Although plants are no longer the main contributors to the biomass, they do play a key role in this dimly lit zone: calcareous algae growing on coarse gravelly substrates coalesce the calcareous sediments to form a continuous, organogenous substrate on which the coralligenous community develops. This habitat is characterised by steady and sometimes strong currents and constantly cool water, which create beneficial conditions for suspension feeders (Coma and Gili 1998). They occupy the upper stratum of the habitat, which is usually composed of large gorgonians and sponges. The intermediate stratum consists of large bryozoan colonies, sponges, ascidians and polychaetes. A lower stratum that consists of small animals and an under stratum with endobionts and borrowing fauna further increases the complexity of this community. The hard bottom coralligenous constitutes a stable environment and permits the existence of longevous sessile organisms. Some of them dominate various coralligenous communities, like facies of large sponges with bryozoans and madreporarians, or communities dominated by various octocoral species (Gili and Ros 1985). Horizontal substrates exposed to waves and currents are commonly dominated by *Eunicella* sp., whereas another common Mediterranean gorgonian, *Paramuricea clavata*, is found on vertical dark substrates that are swept by strong currents. Even darker

transition zones such as cave entrances, dark overhangs, vertical cliffs and crevices are occupied by sciaphilic species (Laborel 1961). The most conspicuous in these semi dark boundary zones is red coral, a commercially important precious coral that is endemic to the Mediterranean. The name "coralligenous" originates from findings of debris of red coral branches and calcareous organisms in trawling hauls of semi dark sublittoral bottoms with coarse gravel, which were thought to be `generators of coral´ (Ros et al. 1985). Red coral, however, does not belong to the community forming the coralligenous, but to the semi dark transition community (Margalef 1985).

Figure 8: Typical corralligenous habitat. Note gorgonians (a) at exposed locations and red coral (b) in semi dark crevices. Drawing by M. Zabala in: Ros et al. 1984

MATERIAL AND METHODS

Studies on population structure

Red coral population density at the Costa Brava was estimated by laying a horizontal transect line and counting coral patches within 2 m on either side of a 50 m measuring tape (2660 m^2 in total). The patch sizes were measured, and the colony density within patches was determined by the use of either 20 x 20 cm or 1 x 1 m quadrates, depending on the population density (see publication 1).

Figure 9: Measurement of colony height and basal diameter by photographic sampling. Note the size of the colonies, which is the most common size class found at the Costa Brava (NE Spain). Photo: S. Rossi

Size frequency at 44 stations, focusing on six areas of the Costa Brava, was estimated by photographing 7600 colonies with a small ruler attached next to the colonies in the same axis as the colony (Fig. 9). This allowed to measure the basal diameter of the colony (which was later used to convert the data into age frequency), the maximum height of the colony, and to count the branches and classify the branching pattern of each colony. The resolution of the digital camera used allowed a precision of 1 mm, which constitutes an error of age estimate of less than a year.

The Medas Island populations served as a reference that allowed to compare the population structure of a protected population with harvested ones along six stations at the Costa Brava.

Trophic and reproductive cycles

In order to contribute to the understanding of the ecology of red coral this study established the trophic and reproductive annual cycle of two populations (following the definition of Lincoln et al. 1998) located at different depths. This allowed to compare the reproductive and feeding annual cycle and created a reference for the spatial comparison of the reproductive output. The sampling for both cycles took place at the Medas Islands Marine Park in monthly intervals during a 15-month period (Fig. 7). In the deep population small
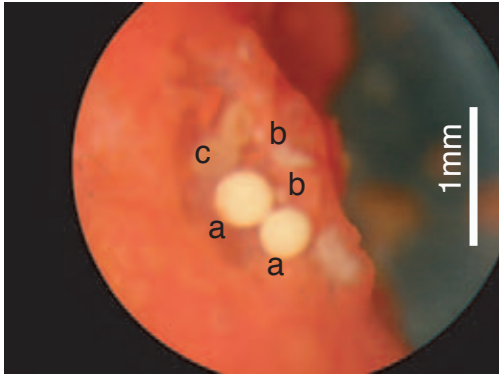
Figure 10: Red coral branch showing two mature oocytes (a) and two immature ones (b), as well as two possible remains of planulas (c)

colonies and large ones were sampled, in order to study effects of colony size. The samples from the shallow population, and the six coastal stations sampled for the spatial comparison of reproductive output, consisted of small colonies only (Fig. 7). The next two paragraphs describe the methods of each aspect closer.

Reproduction

The reproductive cycle of red coral was investigated at two depths and two colony size classes by sampling a 2 cm branch from 20 colonies each month during a 15-month period. The samples were processed by dissecting polyps under a binocular microscope (50x magnification) in order to count the gonads and measure their size (Fig. 10). A set of 20 branches were sampled from each of eight size classes of 0 – 2 cm high colonies to 10 – 12 cm high ones, in order to examine the size at first reproduction. A spatial comparison of the reproductive output at 8 stations was carried out in June, prior to spawning.

Figure 11: *In situ* incubation chambers connected to pumps (right hand side) to recirculate the water.The chambers are closed systems allowing to obtain water samples before and after the incubation of the red coral colonies. Note the third chamber is used as control.

Trophic ecology

The seasonal variation in prey capture rate was studied by sampling a red coral population in monthly intervals during a 15 month period. Each sample consisted of 2 cm long branches from 20 colonies, that were fixed in Formalin and later processed by dissecting five polyps per branch and classifying and counting prey items as well as measuring their size. In line with the reproductive study, two populations situated at different depths (18 m and 40 m), as well as two colony size classes within the 40 m population were sampled.

In order to quantify very small food items, *in situ* incubation experiments were carried out with transplanted red coral colonies. The colonies were transplanted on PVC posts and acclimated for several weeks. For each experiment two colonies were positioned in an acrylic dome chamber (Fig. 11) that was connected to a recirculating pump that created a closed circuit turbulent water flow, keeping particles in suspension. Water samples were taken before and after an incubation time of ca. 3 h and filtered through precombusted GF/F filters that were analysed for particulate organic carbon.

Fishery management

This part of the present study applied the data obtained in the earlier parts, and additional data from other studies, to make recommendations for management. Maximum production, determined for the Cap de Creus stock, and age at first reproduction were compared to catch statistics in order to evaluate the state of the fishery.

In order to determine the age of the studied population, a series of settlement experiments was begun, that, however, can not be used until they are at least ten years old. Instead, recent data on a productive population in Italy (Bramanti et al. 2003), were used to transform basal diameter into age. Growth ring analysis has proven unreliable (Garrabou and Harmelin 2002; Santangelo, pers. comm.), so that long time experiments are necessary. Being able to age the population, and knowing the relationship between colony size and weight in the studied population (García-Rodriguez and Massó 1986b) makes it possible to apply the data to estimate the productivity of the Costa Brava stock.

The use of the Beverton-Holt fishery model allowed to estimate the maximum sustainable yield. The model is based on the premise of constant recruitment, which, judging from its demographic structure (Tsounis et al., submitted), appears to be the case in red coral and is common as well in other precious corals (Grigg 1976). Assuming a stock in equilibrium with constant recruitment, the fate of a cohort over a period of years is equivalent to the fate of all cohorts in a single year (Royce 1996). Maximum yield is the product of maximum production (yield per recruit) and the number of recruits in that cohort. Harvesting a population at this level of production yields the maximum biomass per year while being sustainable. Yield per recruit consists of two factors, the first of which describes the weight gain (see García-Rodríguez & Massó 1986a), and the second describes the mortality losses (see Grigg 1976).

The Beverton-Holt model relies on precise estimates for growth and mortality. A reliable value for natural mortality is the most critical parameter, and can be estimated using the population structure of a natural population (Grigg 1976). Given steady state recruitment, the mortality of a population can be considered as the decrease in individual numbers between age classes of a population (Grigg 1976).

Thus, by evaluating the slope of the regression of the natural logarithm of N versus time, m can be calculated:

Ln $N_t = a - m*t$

(Grigg 1976)

Where: N_t = number of individuals at time t; N_0 = number of individuals at time 0; t = time in years; m = instantaneous annual rate of mortality. As no natural population could be found for this purpose, the decrease of survivors in a colonisation experiment (Garrabou and Harmelin 2002) was used.

SUMMARY OF RESULTS

The following section summarizes and discusses the results of the four publications. A more detailed discussion can be found in the respective publications.

Demography of red coral at the Costa Brava

Red coral was found to be ubiquitous in coralligenous habitats, and showed a very patchy distribution pattern. Its abundance averaged 3.42 ± 4.39 colonies m^{-2}. Colony density measured within patches showed a moderate correlation to depth. Depth was also found to have a significantly positive effect on maximum height. Thus depth appears to affect the distribution pattern and demographic structure of red coral. It is possible that further differences (as in basal diameter) may have been masked by the high variance. Being a sciophilic species, red coral prefers dimly lit crevices and cave entrances. In deeper water however, it can grow on more exposed structures (Riedl 1984; Hofrichter 2002), and thus has more space to grow less densely and to expand its branches wider. The colony density in other areas of the Mediterranean has been found to be much higher, demonstrating regional differences in population structure.

Comparing the population structure of six stations along the Costa Brava revealed significant differences between harvested areas and the protected Medas Islands: Basal diameter, maximum height (Fig. 12), and branch numbers were significantly higher in the protected population. Despite its slow growth rate, only 13 years of protection of the Medas Islands have been sufficient to result in a different population structure (however still not a natural one). This indicates a very high harvesting pressure outside the marine

park. *Corallium rubrum* can reach a size of up to 50 cm (Tescione 1973; Garrabou and Harmelin 2002) yet the largest colonies found hardly exceeded 20 cm height and the average height was 3 cm (Fig. 12). The average basal diameter of 4.8 mm corresponds to the average age of 7.5 years. Furthermore, the arborescent branching pattern typical in this species is not yet developed in the young colonies consisting of only one or few branches. The similarity of the harvested populations in their demography indicates a homogenisation due to harvesting.

Similar population structures, although with a less severe shift towards young colonies, have been observed in a harvested black coral (*Antipathes* sp.) population off Hawaii (Grigg 2001) and in an unharvested black coral population in a New Zealand fjord, where land slides are common. Most other octocorals, including unharvested Mediterranean ones, have been found to be characterised by a higher proportion of old colonies (*Paramuricea clavata*, Coma et al. 1995; *Lophogorgia ceratophyta*, Mistri 1995).

Figure 12: *Corallium rubrum* colony height distribution at the Costa Brava (■) and the Medas Islands Marine Park (▨)

Harvesting has resulted in a distorted population structure of *Corallium rubrum* at the Costa Brava, as small colonies dominate the population.

Reproduction of red coral at the Costa Brava

Corallium rubrum was found to be gonochoric at colony and polyp level. The population sex ratio of 1:1 differed from a population studied in Italy (Santangelo et al. 2003), in line with differences in the population structure (Santangelo et al. 1993; see publication 1). Spermiogenesis takes one year and oogenesis considerably longer. Thus, as spawning occurs in July, two size classes of oocytes are present in female colonies. A high temperature gradient between shallow water and below the thermocline resulted in depth staggered spawning in summer 2002 (Fig. 13), as observed earlier in red coral (Vighi 1972) and in Californian octocorals (Grigg 1977).
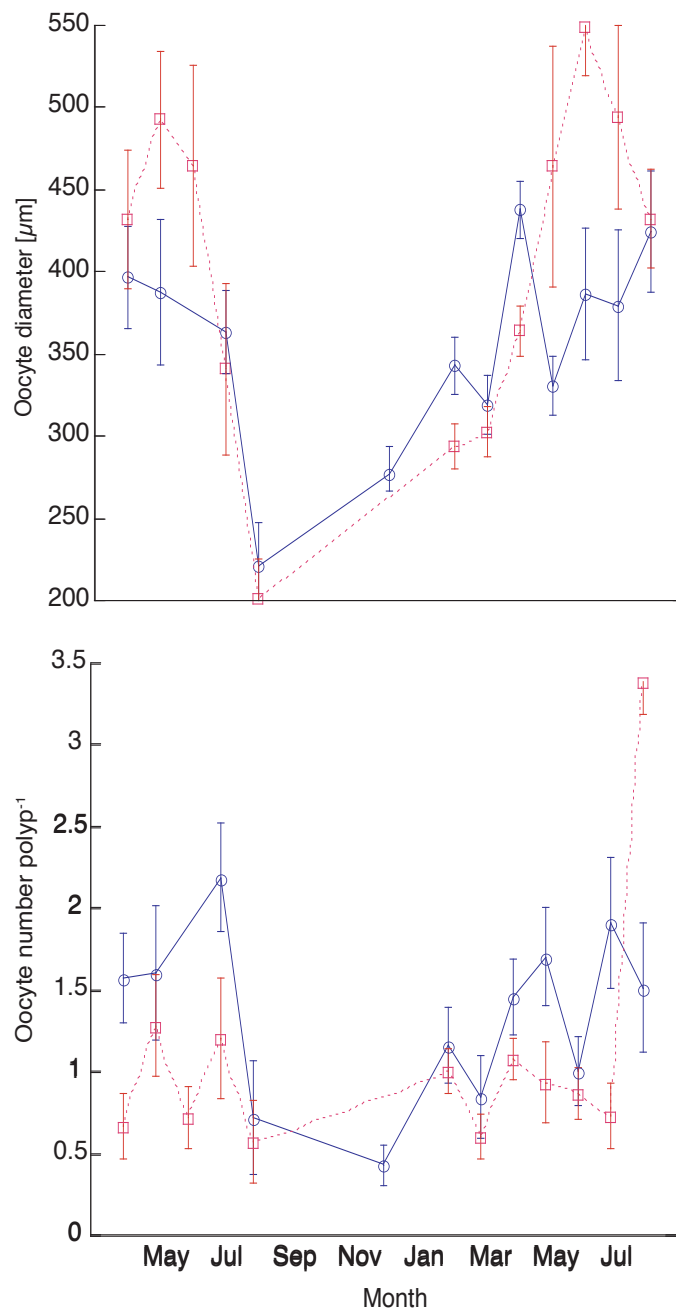

Figure 13: Red coral oocyte diameters (above) and numbers (below) in colonies at 40 m depth (–○–) and 20 m depth (··□··) in 2002 / 2003. (Mean ± SE)

Effects of depth on the reproductive output (Gonad number and size), however, were not found, also in line with other studies. This study sampled a wider depth range than previous studies (18 – 40 m) which, however, is still small compared to the distribution range of red coral (5 – 300 m, Zibrowius et al. 1984). No difference in reproductive output was found between the 8 stations, thus demonstrating that mesoscale inter-habitat differences may influence population structure (publication 1), but apparently not reproductive output. Recent large scale comparisons of red coral recruitment, however, found significant differences between red coral populations from Italy and Spain (Bramanti et al. 2004), probably due to demographic differences.

Reproductive output significantly increases with colony size. In line with other studies, already 2 cm high colonies were found to reproduce (FAO 1988;

Santangelo et al. 2003). However, 100 % fertility is reached at 6 cm height, which is important when estimating the reproductive potential of the present populations.

> **Pronounced water stratification in summer can lead to depth staggered spawning, however reproductive output has not been found to depend on depth.**
>
> **No mesoscale variation was detected in reproductive output.**
>
> **Colony size positively affected gonad number and size. Relatively young and small coloniesof 2 cm height were found to be reproductive. However, 100 % fertility is reached only at 6 cm colony height.**

Prey capture rate and annual feeding variation in Mediterranean red coral

The main proportion of the diet of red coral was found to be detritic particulate organic matter (POM) (25 – 44 %, depending on the sampled population). Copepods and crustacean fragments (14 – 46 %) constituted the second major part of the diet, and invertebrate eggs (9 – 15 %) and phytoplankton (8 – 11 %) were captured less frequently.
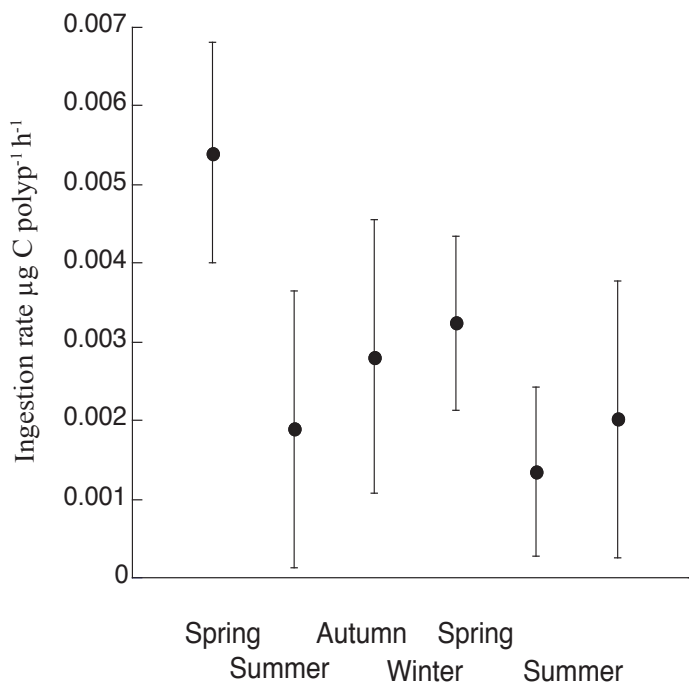
Although ingestion was found to be highest in spring, there was a lack of a typical seasonal pattern (Fig. 14) known from other Mediterranean gorgonians, such as *Paramuricea clavata* (Coma et al. 1995). This result is, however, in line with data on *Leptogorgia sarmentosa* (Rossi et al. 2003), and indicates that in species capturing large amounts of POM, water movement plays a greater role than the seasonal succession of the plankton. Apparently, living in crevices and cave entrances allows *Corallium rubrum* to constantly access detritic particles. Zooplankton on the

Figure 14: *Corallium rubrum*: ingestion rate (µg C polyp-1 h-1) during an annual cycle (2002 / 2003), estimated from stomach contents of 100 polyps. The colonies ranged from 6–10 cm in height and were located at 40 m depth, representing the majority of the population. (Mean ± SD)

other hand, while being an energy rich food source, was caught very irregularly, arriving in rare pulses, probably due to its clumped distribution (Parsons et al. 1984).

Small colonies captured more prey per polyp than large ones, although size has been found to have a positive effect on prey capture in other gorgonians (Kim and Lasker 1997). Colonies situated at 40 m captured more prey per polyp than colonies at 18 m, again contradicting the general pattern in gorgonians (Lasker et al. 1983). These differences are probably linked to the high proportion of POM in the diet, as its availability

Table 1: Population grazing impact* of various gorgonian species *(from *in situ* studies)

Species	Grazing rate $(mg\ C\ m^{-2}\ d^{-1})$	Location	Source
Dendronepthya hemprichi	451	Caribbean	Fabricius et al. 1998
Plexaura flexuosa	0.15	Caribbean	Ribes et al. 1998
Paramuricea clavata	< 170	Mediteranean	Coma et al. 1995b; Ribes et al. 1999
Leptogorgia sarmentosa	2.3 – 16.8	Mediteranean	Rossi et al. 2003
Corallium rubrum	0.091 – 0.15	Mediteranean	This study

differs from the zooplankton availability, a food source most other gorgonians exploit. In situ incubation experiments measured a grazing rate of $0.07 \pm 0.05\ \mu g\ C\ polyp^{-1}\ h^{-1}$ (mean ± SD) which was slightly higher than the estimates with gut content analysis, being able to detect very small prey items. The overall grazing impact of a red coral population considering the colony abundance and population structure (see publication 1) at the Costa Brava is $0.4 – 9.6\ mg\ C\ m^{-2}\ d^{-1}$. This is less than in some other gorgonians (Table 1), but considering the current population structure it suggests that the impact of unharvested red coral populations on the seston community is comparable to other gorgonian species.

Particulate organic matter constitutes the major part of the diet of *Corallium rubrum*, followed by copepods and other crustaceans that are captured irregularly, whereas in other gorgonians crustaceans constitute the main part of the prey.

A typical seasonal pattern in prey capture rate, as common in some suspension feeders of temperate seas, has not been found in *Corallium rubrum*, indicating that resuspension may be the main factor influencing prey capture.

Small colonies captured more prey than large ones, and deep water colonies captured more prey than shallow ones, contradicting studies on other gorgonians.

The grazing impact of most red coral populations at the Costa Brava is lower than that of other Mediterranean gorgonian populations. This is in part due to the population structure that is changed towards small/young colonies by harvesting.

Proposals for red coral fishery management at the Costa Brava

The results show that the fishery of a slow growing longevous species such as red coral reaches maximum yield at 98 years (Fig. 15). Harvesting at an age of first capture of 98 years yields 68 gr per recruit, which results in a yield of 64 t annually for the stock off Cap de Creus, where 90 % of all red coral at the Costa Brava coral is harvested. The current practice of harvesting at 11 years (7 mm of basal diameter) is estimated to yield only 4.5 t annually. Declared harvests of recent years, however, are even lower with ca. 1 t (Fig. 6), indicating undeclared harvest and poaching in order to approximate 4.5 t, or indicating an even lower age at first capture. In fact, recent patrols found frequent harvests of illegally small coral by poachers and licensed fishermen at an increasing rate (Zabala et al. 2003; Pluja, pers. com.). A 7 mm size limit for the harvest of red coral originates from the inability to process thin branches in early days, and may have been sufficient to preserve a minimum reproductive potential of the populations. Advances in technology, however, now make the harvest of illegally small coral profitable. Compared to the black coral fishery of Hawaii, the current age at first capture of 11 years leaves an unsatisfactorily small reproductive period before corals are harvested, as 100 % fertility
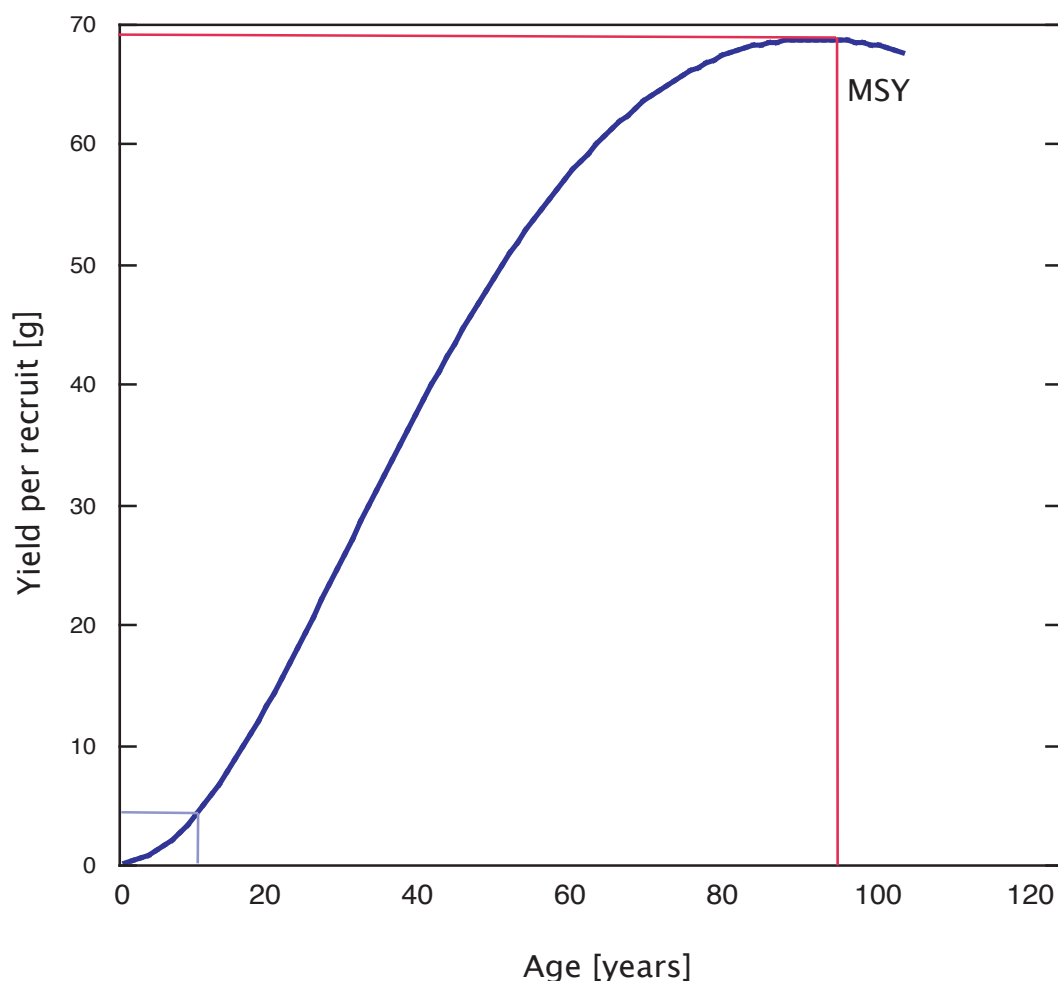

Figure 15: Yield per recruit in red coral. The red lines indicate the maximum sustainable yield estimated by the Beverton-Holt (1986) method. Current fishing regulations harvest at an age of ca. 11 years, resulting in a lower yield per recruit (blue lines).

is reached at 6 – 9 years (Santagelo et al. 2003; publication 2). Studies on other octocorals demonstrate that a small number of old colonies contribute the majority of larvae. Thus, judging from the present demographic structure, the reproductive potential of *Corallium rubrum* at the Costa Brava is severely diminished.

Finally, mortality has risen in the last 18 years, clearly indicating that harvesting is at an unsustainable level. Colonies more than 30 years old, still young for this species that is capable of reaching 100 years, have virtually vanished from unprotected areas.

Maximum sustainable yield in red coral is reached at an age of first capture of 98 years;

however, it is harvested at an age of 11 years, and illegal harvest of small colonies appears to have become more frequent.

The calculated maximum yield at an age of first capture of 11 year old colonies at Cap de Creus is with 4.5 t four times higher than the declared yield, indicating poaching and undeclared harvest.

Mortality has risen in the last 18 years, indicating a non sustainable level of harvesting.

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8 PUBLICATIONS

Although the four chapters of the here presented doctoral thesis act as parts contributing to the same main objective, each chapter has been structured following the format of publication in a scientific journal. This allows to focus on each aspect within the overall context, and facilitates the presentation of the results to the scientific community. Below, the contribution of each author to the respective publication is indicated:

Publication I
Tsounis G, Rossi S, Gili JM, Arntz WE
Demography of an exploited benthic cnidarian: The case study of red coral (*Corallium rubrum* L.)
Vie et Milieu, submitted

The initial idea and concept of this publication were developed by the first three authors. Practical work and data processing was carried out by the first two authors. The data analysis was conducted by the first author and the concept of the first version of the manuscript was developed by the first author and improved in cooperation with the co-authors.

Publication II
Tsounis G, Rossi S, Aranguren M, Gili JM, Arntz WE
Effects of spatial variability and colony size on the reproductive output and gonadal development cycle of the Mediterranean red coral (*Corallium rubrum* L.)
Marine Biology, submitted

The original idea and concept of this publication were developed by the first, second and fourth author. Practical work was conducted by the first three authors. The data analysis was conducted by the first author. The concept of the first version of the manuscript was developed by the first author and improved in cooperation with the second, third and fourth co-author.

Publication III

Tsounis G, Rossi S, Laudien J, Bramanti L, Fernández N, Gili JM, Arntz WE

Seasonal Variation in the prey capture rate of the Mediterranean red coral (*Corallium rubrum* L.)

Marine Biology, submitterd

The original concept of this publication was developed by the first author in cooperation with the second and sixth author. The experimental design was developed by the first author in cooperation with the third author. Field work was carried out by the first author in collaboration with the fourth and fifth author. Sample processing was carried out by the first author in collaboration with the fifth author. The data analysis was conducted by the first author. The concept of the first version of the manuscript was developed by the first author and improved in cooperation with the second, third, sixth and seventh co-author.

Publication IV

Tsounis G, Rossi S, Gili JM, Arntz WE

Red coral (*Corallium rubrum* L.) harvesting at the Costa Brava (NW Mediterranean): Strategies for management and conservation.

Conservation Biology, manuscript

The original idea and concept were developed by the first three authors. The data analysis was conducted by the first author. The concept of the first version of the manuscript was developed by the first author and improved in cooperation with the co-authors.

PUBLICATION I

DEMOGRAPHY OF AN EXPLOITED BENTHIC CNIDARIAN: THE CASE STUDY OF RED CORAL (*Corallium rubrum* L.)

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ABSTRACT

Octocorals are an important part of many ecosystems as they add three-dimensional complexity to the benthos and thereby increase biodiversity. Mediterranean red coral (*Corallium rubrum*, L. 1758) is a longevous octocoral that is harvested commercially, yet natural and anthropogenic influences on population age structure are little understood. This study found that the population structure of harvested red coral populations had a significantly different size structure when compared to populations at the nearby Marine Protected Area of Medas Islands at the Spanish Costa Brava (NW Mediterranean). 89 % of the red coral in the harvested Costa Brava area are less than 10 years old and 96 % of all colonies have not yet grown more than 2nd order branches. The size/age-distribution of the harvested population is notably skewed towards younger and smaller colonies. Thus, although red coral is still abundant, its population structure is strongly distorted by harvesting. The results confirm that Marine Protected Areas are useful to distinguish between anthropogenic and natural influences on population structure. However, 14 years of protection appears to be an insufficient recovery time for a longevous octocoral population such as red coral. This study confirms that the demography of a population is a useful indicator for its state, especially in the case of longevous sessile species.

KEYWORDS: Red coral, population structure, age structure, overharvesting, longevous species, mortality, Mediterranean, marine protected area (MPA)

INTRODUCTION

Gorgonian octocorals are characteristic and conspicious members of many benthic communities in tropical, temperate and polar ecosystems (e.g. Kinzie 1973; Coma et al. 1995; Arntz et al. 1999). They play an important role in marine ecosystems as they add three-dimensional complexity to the habitat and consequently increase biodiversity (Dayton et al. 1974; Jones, Lawton and Shachak 1994).

Previous demographic studies have been a valuable tool to determine the state of octocoral populations (e.g. Grigg 1977; Weinbauer and Velimirov 1996; García-Rodríguez and Massó 1986a; Bak and Meesters 1998). As age distribution reflects the combined effects of mortality, recruitment, growth and other processes that affect the population, it records the history of a population, especially in the case of sessile longevous species such as red coral (Santangelo et al. 1993a). The age structure of a healthy population in steady state recruitment is structured by a monotonic curve with a negative exponent. A severe lack of old individuals is an indicator of high mortality, either due to natural causes (Grange and Singleton 1988) or due to harvesting (Grigg 1976). These factors manifest themselves as a shift of the age distribution towards young colonies, deviating from a steady state distribution, as commonly observed in harvested species (Santangelo et al. 2004).

The Mediterranean red coral (*Corallium rubrum* L. 1758) (Gorgonacea, Octocorallia) is a sessile cnidarian whose polyps form arborescent colonies, which can reach a height of 50 cm (Garrabou and Harmelin 2002). Red coral is a slow growing species (García-Rodríguez and Massó 1986a; Santangelo et al. 1993a; Garabou and Harmelin 2001; Bramanti 2003), with a life span of up to 100 years (Riedl 1984). However, red coral populations all over the Mediterranean are dominated by young, small colonies (García-Rodríguez and Massó 1986a; Abiati et al. 1991, 1992; Cattaneo-Vietti et al. 1993; Santangelo et al. 2003). Red coral has a long history of exploitation (Tescione 1973), and during the last decades it has become evident that it is now an overexploited natural resource (FAO 1984; FAO 1988; Santangelo and Abbiati 2001). In order to examine the effect of harvesting, this study compared the age structure of several populations at the Costa Brava, including one in a protected marine park in the same area (Fig. 1). A problematic aspect in such comparisons is that red coral populations in other parts of the Mediterranean have been shown to differ in structure (Cattaneo-Vietti et al. 1993). However, by comparing nearby populations, it can be expected that environmental differences are kept small, resulting in minor interhabitat differences of population structure (Desbryéres et al. 1973; Grémare et al. 1998). We hypothesize that differences in height, basal diameter and branch number between protected and harvested populations must be significantly higher than differences between harvested populations. The analyzed factors are expected to show a homogeneous population structure due to

harvesting pressure, as interhabitat environmental and biological differences should be masked by the considerable fishery pressure.

Table 1: No. of sampling stations in the six sampling areas

Sampling areas	Coordinates	No. of sampling stations	Depth Range [m]
Northern Cap de Creus	42°20`1"N 3°16´30" E	14	15 – 48
Eastern Cap de Creus	42°16'5"N 3°16'50"E	27	7 – 40
Southern Cap de Creus	42°13'45"N 3°13'1"E	17	11 – 45
Medas Islands	43°2´30``N  13`30``E	13	15 – 48
Coast of Montgri	42°5'56"N 3°12'51"E	9	13 – 33
Coast of Begur	42°1´N 3°14´55"E	9	18 – 30

MATERIAL AND METHODS

Study area

The study was carried out at the Spanish Costa Brava where 44 stations, divided into six areas (Table 1), were surveyed between January 2002 and September 2003. The areas are situated in the coralligenous hard-bottom sublittoral (Sará 1969; Gili and Ros 1984)
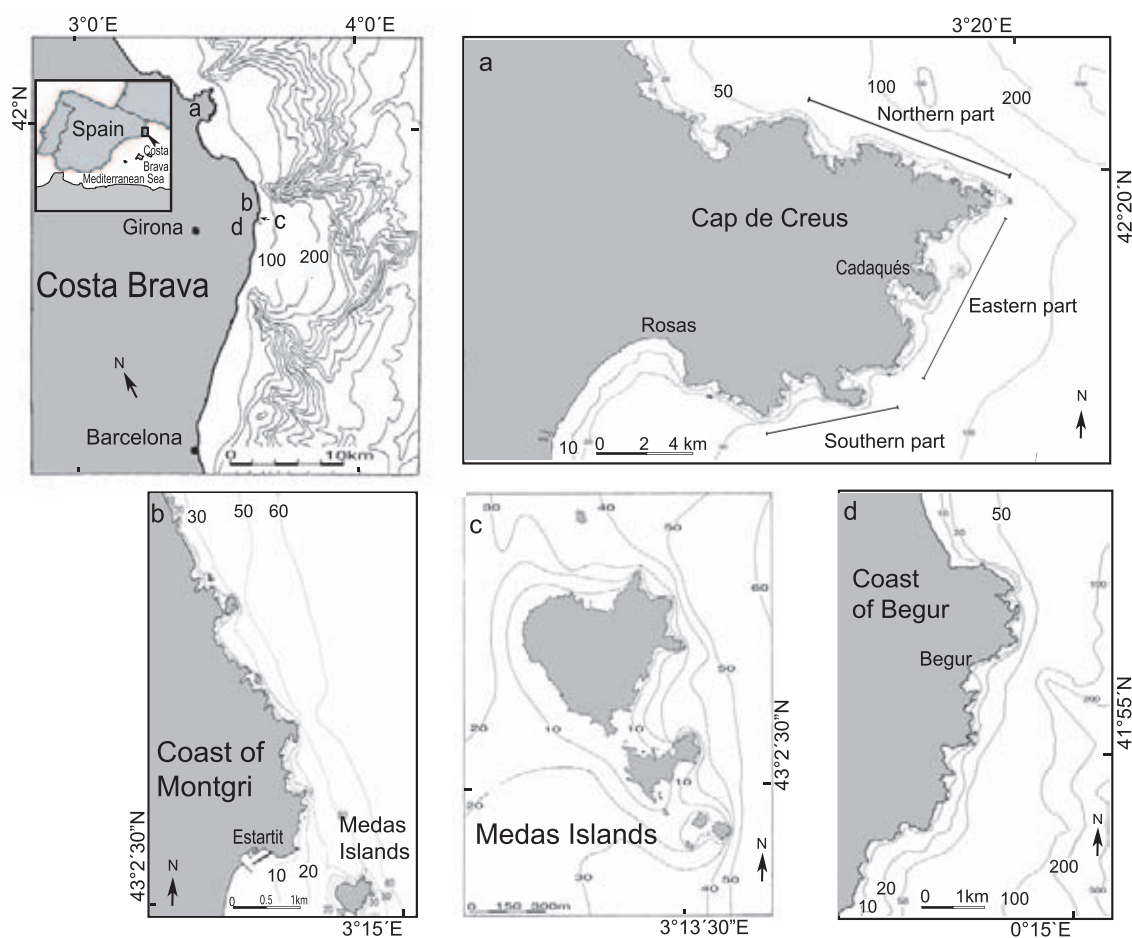
Figure 1: Map of the study area at the Costa Brava (NE Spain), indicating the Medas Islands Marine Protected Area

and were sampled during 89 survey dives using SCUBA. In all areas except the Marine Protected Area (MPA) of the Medas Islands (Fig. 1) the populations are subject to commercial exploitation.

Colony density and distribution

Coral density was estimated at the Coast of Begur and Montgri, as well as the Medas Islands, by laying a 50 m long measuring tape along the selected isobath, using it as a transect line. A zone of 2 m on each side of the transect line was surveyed by SCUBA diving, resulting in 200 m² per 50 m transect. Coral patches within the survey area were counted and measured. Red coral patches usually consist of a number of densely growing colonies that inhabit a suitable microhabitat like a crevice or an overhanging wall (True 1970; Gili and Ros 1984; Riedl 1984).

Colony density and patchiness varied across a wide range (shallow and deep patches typically differed markedly), requiring two different methods to estimate colony density reliably. In shallow water (depths less than 30 m) red coral competes with fast growing organisms (e.g. algae, bryozoans, hydrozoans) and grows on semidark overhangs or in crevices forming small and disperse patches with high colony densities, thus requiring a 20 cm x 20 cm quadrat to count colonies efficiently. This size has successfully been used in other studies (Weinberg 1979; Santangelo et al. 1993a), and in preliminary tests for this study it was found to be a good balance between an efficient working pace and minimum error (Benedetti-Cecchi et al. 1996). 20 cm x 20 cm quadrats were placed at random within a patch.

At some sites colony density was extremely low (typically below 30 m depth), while patches extended over huge banks. Those populations could not be sampled with a 20 cm x 20 cm quadrat, thus a 1 m x 1 m quadrat was used which was positioned in 1 m increments on the transect line, which was placed across the largest distance through the bank. This dual approach was necessary to estimate the coral abundance with optimal precision and efficiency in either case of distribution pattern. The total area surveyed was 2660 m².

A regression analysis of colony density, total patch area per survey area, and total colony abundance against the independent factor depth was done. Where the data distribution allowed, an ANCOVA was used to test effects of populations and depth.

Demographic comparison between the six population

The biometry of red coral was studied by photographic sampling. This method allowed to obtain an extensive set of data in a non-destructive way. Colonies were photographed at random within patches encountered. As the photo sampling is not a quantitative method and in order to obtain a maximum number of photographs from each patch, the photo sampling was not restricted to the survey area along the survey line. This allowed to

obtain a representative number of samples, measuring a total of 7600 colonies at the Costa Brava. A 3.1 megapixel digital camera (Sony Cybershot DSC S75) was used in a waterproof plastic housing (Mangrove 2000, Aditech) with illumination provided by a 12 Volt 35 Watt divers light. For each photo a small ruler was placed for size reference next to the coral, in a way that it was oriented parallel to its axis.

The photos were processed with Adobe Photoshop™ software. In each photo the scale was calibrated using the ruler as a size reference, which allowed a precision of 1 mm. This way the basal diameter and height of coral colonies could be measured in each photo. A colony was defined by its stem, and the basal diameter of a colony as the diameter of the stem 5 mm above the substrate. Colony height was defined as the maximum distance between the base of the stem and the tips of the farthest branches. The branches were counted after they were classified into a branching order (1st, 2nd, 3rd and 4th order) following the classification system used to describe branching patterns in gorgonians (Brazeau and Lasker 1988, Mitchell et al. 1993, Coma et al. 1995), as this system allows a comparison of the quantity of newly grown apical branches.

The hypothesis that the population at the Medas Islands is structured differently was tested by comparing the basal diameter and colony height within the sampled populations (following the definition of Lincoln et al. 1998). This was done using an ANCOVA with `populations´ as one

Figure 2: Red coral colony density (within patches) as a function of depth

factor and `depth´ as the second factor. If significant, and if no interactions between the factors were found, the ANCOVA was followed by a Tukey post hoc test (Zar 1996) in order to compare single groups. The basal diameter data showed comparable variances (O´Brien´s test), but showed normal distribution (Shapiro-Wilk test, P = 0.1), only after logarithmic transformation. As the variances of the colony height data were not homogenous (O´Brien´s test), they were transformed using the following equation:

$$X´ = \log 10 (X + 3/8) \hspace{3cm} \text{(Zar 1996)}$$

After transformation the data met the assumptions for parametric testing as described above and the data were tested in the same way as the diameter data. Additional to the ANCOVA and the Tukey test, a Kolmogorov-Smirnov test was utilized to compare the
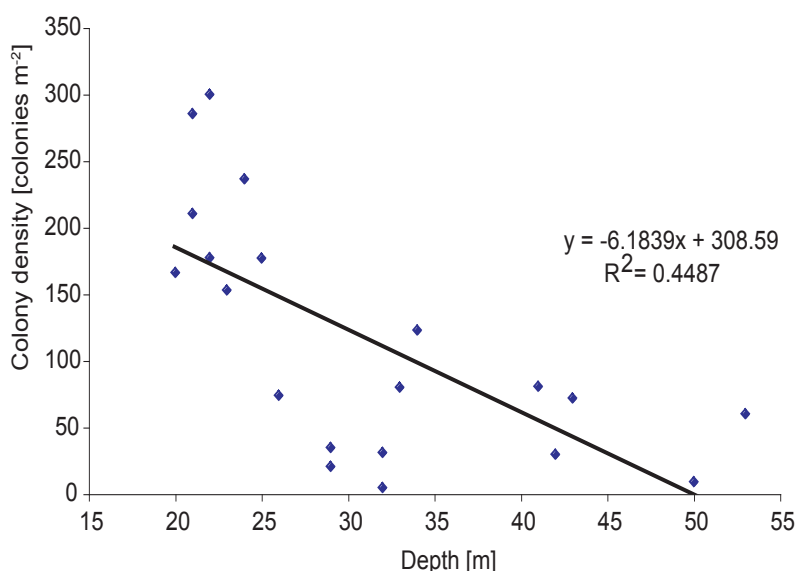
Table 2 :Tukey test results comparing single populations for differences in basal diameter: Stations not connected by "X" are significantly different (ANCOVA, F = 59,2; P = 0.001)

| | Cap de Creus | | | Medas | Montgri | Begur |
	Northern	Eastern	Southern	Islands	Coast	Coast
Northern Cap de Creus			X			
Eastern Cap de Creus					X	X
Southern Cap de Creus	X					
Medas Islands						
Coast of Montgri		X				X
Coast of Begur		X	X		X	

basal diameter and colony height frequency distribution of the six populations.

The six populations were tested as well for differences in quantity of branches of various orders. In cases where the data transformation did not result in comparable variances, a Kruskal-Wallis test was applied by doing a *chi* square approximation (Zar 1996, JMP Synergy software), as non parametric testing is of adequate power, if a large data set is used (Zar 1996).

Table 3: Red coral basal diameter and colony height at the Costa Brava

Area	Basal diameter [mm] (avg ± SD)	Colony height [mm] (avg ± SD)
Northern Cap de Creus	5.7 ± 2.4	36.6 ± 20.3
Eastern Cap de Creus	4.6 ± 1.7	32.1 ± 16.9
Southern Cap de Creus	5.3 ± 2.1	26.8 ± 15.2
Medas Islands	6.9 ± 2.4	41.9 ± 25.6
Coast of Montgri	4.9 ± 2.1	25.5 ± 14.2
Coast of Begur	4.9 ± 1.5	29.5 ± 16.5

Biometry

The ratio of colony height to basal diameter of the various populations was compared as a measure of the developmental stage of the colonies. Additionally, the correlation between colony height and basal diameter was analysed.

Table 4: Chi square test showing differences in branch numbers of different orders among red coral populations

| Population | Mean branch number ± SD | | | |
	Primary	Secondary	Tertiary	Quartiary
Northern Cap de Creus	2.6 ± 2.4	0.8 ± 1.0	0.2 ± 0.5	0.021 + 0.15
Eastern Cap de Creus	2.9 ± 3.1	0.8 ± 1.0	0.1 ± 0.4	0.001 + 0.03
Southern Cap de Creus	2.0 ± 1.6	0.6 ± 0.7	0.1 ± 0.3	0.004 ± 0.06
Medas Islands	3.4 ± 3.6	1.1 ± 135	0.3 ± 0.6	0.03 ± 0.18
Coast of Montgri	2.5 ± 1.9	0.8 ± 0.8	0.2 ± 0.7	0.02 ± 0.26
Coast of Begur	2.4 ± 2.2	0.7 ± 0.9	0.1 ± 0.4	0.011 ± 0.10
Chi square Test Results	χ^2 = 68.9; DF = 5; P < 0.001	χ^2 = 108.3; DF = 5; P < 0.001	χ^2 = 106.7; DF = 5; P < 0.001	χ^2 = 75.7; DF = 5; P < 0.001
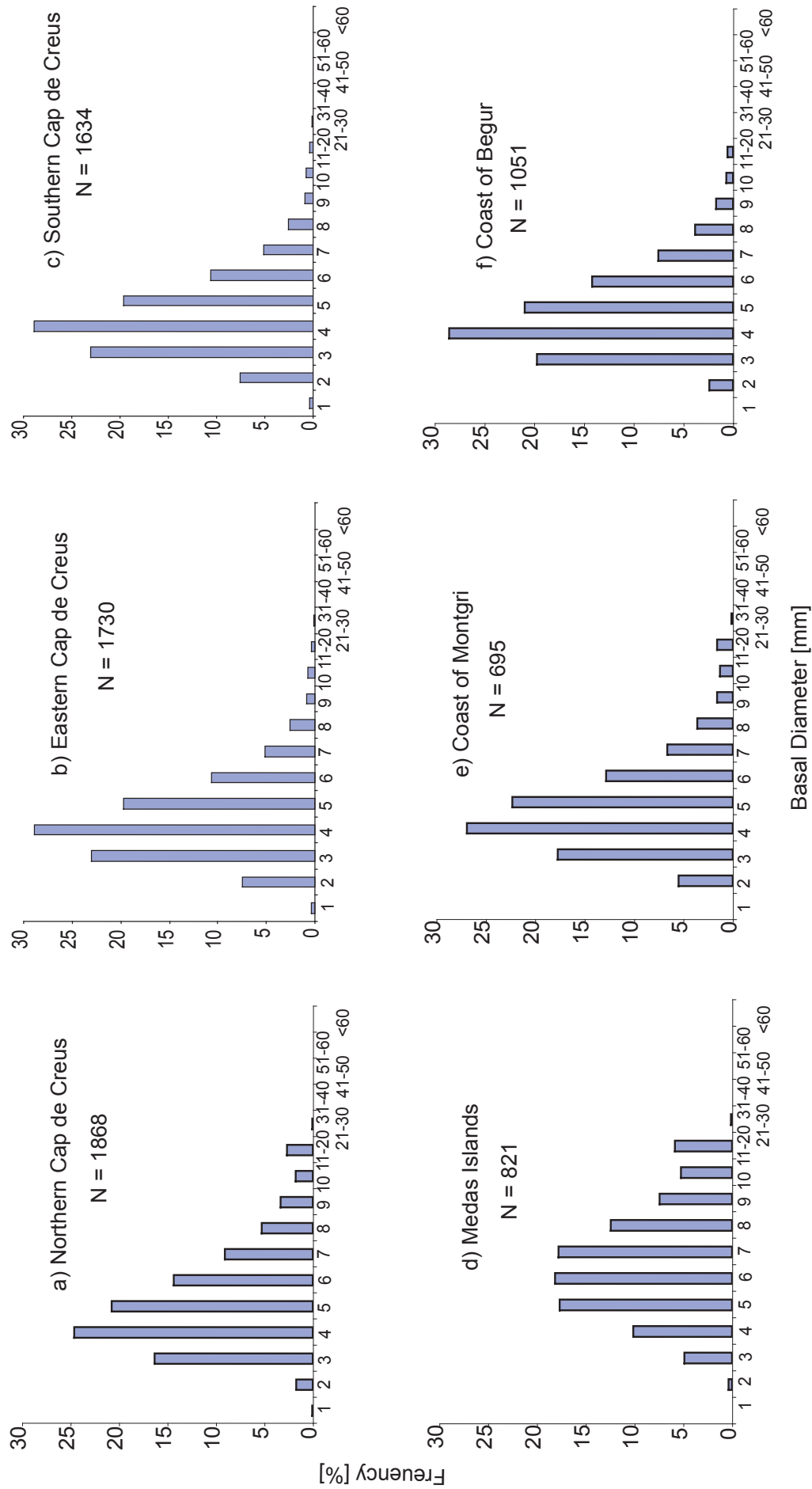
Figure 3: Relative frequency distribution of the basal diameter of red coral colonies at the Costa Brava (NE Spain)
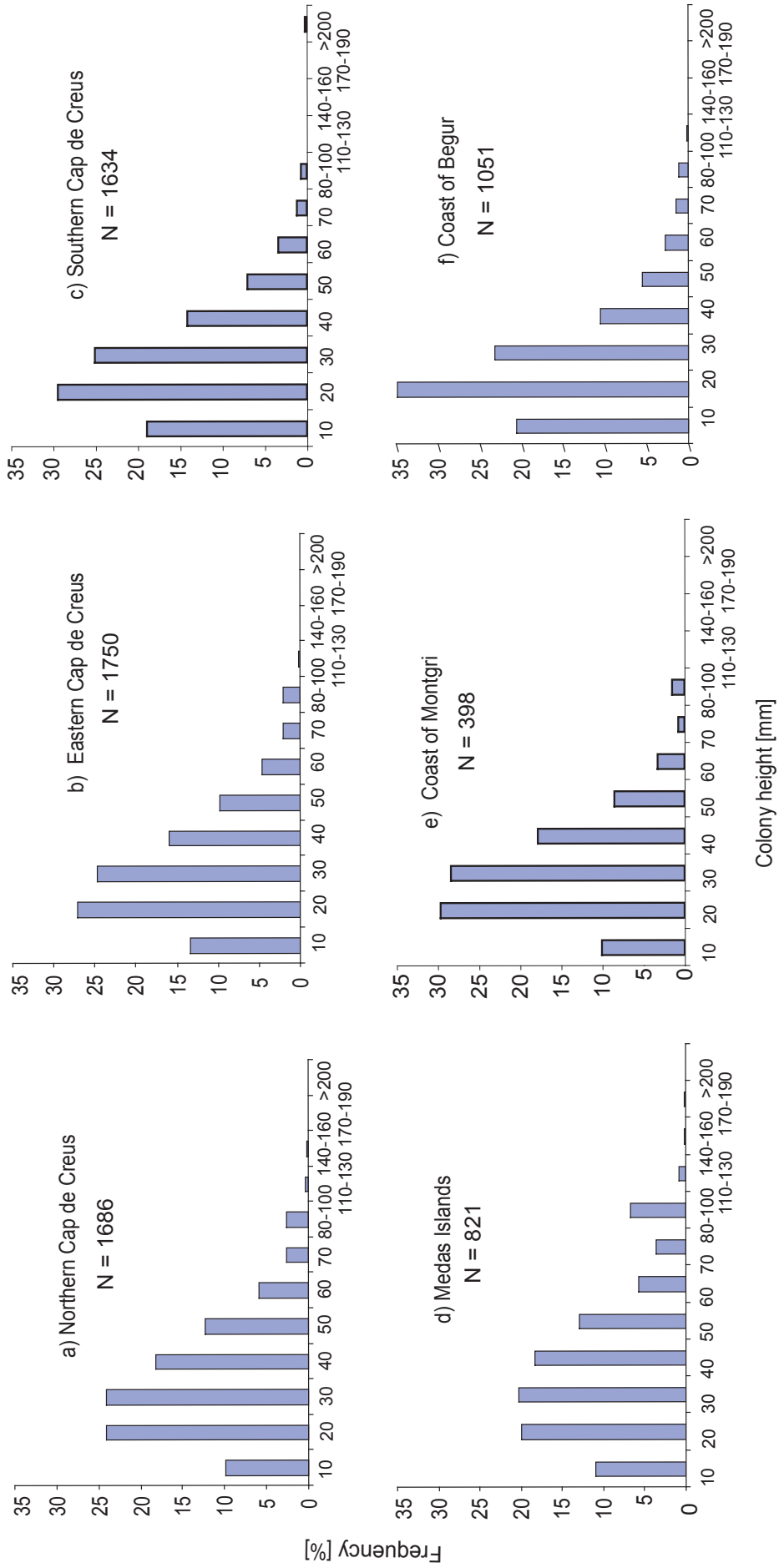
Figure 4: Relative frequency distribution of the colony height of red coral colonies at the Costa Brava (NE Spain)
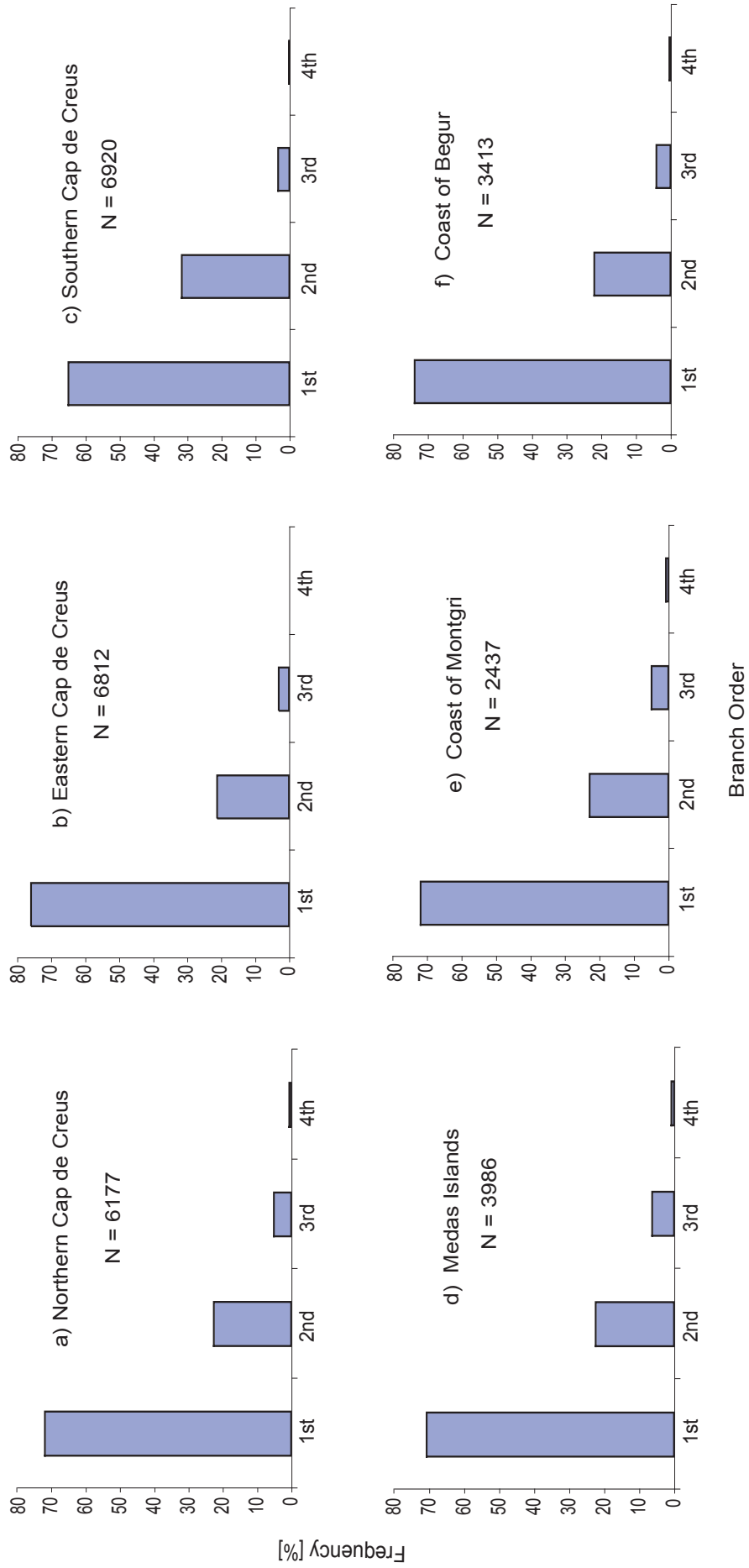
Figure 5: Relative frequency distribution of the number of branches of red coral colonies at the Costa Brava (NE Spain)

RESULTS

Distribution of colony density

The regression analysis showed a moderate relationship between depth and colony density within patches (Fig. 2). Total patch area per survey area (y = 0.0008x + 0.0047, where y = colony density (colonies m^{-2}) and x = depth (m); R^2 = 0.0968) and overall colony density (y = 0.0003x + 0.002; R^2 = 0.0968) showed weaker relationships with depth. The average colony density within patches was 127.1 ± 118.6 colonies m^{-2} (mean ± SD), the patch size was 0.428 ± 0.741 m^2, and the patch abundance was 0.063 ± 0.05 patches m^{-2}. Total red coral abundance (m^{-2}) of coralligenous hard substrate was estimated at 3.42 ± 4.39 colonies m^{-2}. Patch size did not significantly differ between populations and depths.

Demographic comparison of the six populations

The populations differed significantly in their basal diameter (ANCOVA: N = 4170; F = 59.2; P = 0.001). Since no effect of the factor depth was found (and consequently no interaction of the two factors), a Tukey test was employed showing that basal diameters are significantly larger at the Medas Islands than at the other populations (Table 2). Northern and southern Cap de Creus, eastern Cap de Creus and the coast of Begur, as well as southern Cap de Creus and the coast of Begur were also significantly different from each other (Table 2). However, there is a significantly higher difference in mean diameter between the Medas Islands (6.9 ± 2.4 mm) and the other populations (Table 3).

The populations did also differ significantly in colony height (ANOVA: F = 30.5; P = 0.001). As there was a significant interaction of the factor `depth´ with the factor `populations´ (ANCOVA: F = 12.3; P = 0.001), no post hoc test could be used to compare the populations. However, the colony height of the population at the Medas Islands is notably higher than in all other populations (Table 4).

Depth had a significant effect on colony height (ANCOVA: F = 37.7; P = 0.001). However, no significant effect of depth on the basal diameter, and no interaction of depth and populations was found.

The frequency distributions of the basal diameter and colony height are similar in the three populations at Cap de Creus and the two coastal populations at Montgri and Begur, all showing a positively skewed curve (Fig. 3 – 4). The Medas Islands population shows a strikingly different frequency distribution for basal diameter, being bell shaped, with an elevated number of the larger colonies (Fig. 3).

The sampled populations differed significantly in number of primary, secondary, tertiary and quartiary branches (χ^2: P = 0.001, see Table 4). The distribution of branch orders shows a higher percentage of 4th order branches off northern Cap de Creus and the Medas Islands, whereas in the other populations colonies lack the characteristic arborescent morphology, consisting of only one or two branches (Table 4).

Table 5: Comparison of shallow water gorgonian abundance and maximum size

Species	Density[a] [Ind./ m^2]	N[b]	Area[c] [m^2]	Depth[d] [m]	Max. Size[e] [cm]	Location	Source
Pseudopterogorgia acerosa	0.52	33	64	0.5 – 2	100	Florida	Opresco 1973
Pseudopterogorgia americana	0.02	1	64	0.5 – 2	86	Florida	Opresco 1973
Pterogorgia citrina	4.1	262	64	0.5 – 2	46	Florida	Opresco 1973
Pterogorgia anceps	0.08	5	64	0.5 – 2	47	Florida	Opresco 1973
Paramuricea meandrina	0.18– 1.43	-	-	42 – 54	>200	Hawaii	Grigg 1965
Muricea californica	1.8 – 5.9	-	-	15 – 17	60	California	Grigg 1975
Muricea californica	0.45 – 7.9	-	210	12 – 20	60	California	Grigg 1977
Muricea fructicosa	0.1 – 2.35	-	210	12 – 20	40	California	Grigg 1977
Muricea californica	0.0005 – 0.1	-	6050[f]	12 – 20	60	California	Grigg 1977
Muricea fructicosa	0 – 0.01	-	6050[f]	12 – 20	40	California	Grigg 1977
Antipathes aperta	25	2988	-	15 – 25	400	New Zealand	Grange and Singleton 1988
Antipatharians	0.02 – 1.5	-	200	17 – 27	-	Caribean	Sànchez 1999
Lophogorgia ceratophyta	6.8 ± 3.0	123	40	19 – 22	100	Ligurian Sea	Mistri 1995
Paramuricea clavata	56 ± 23	-	-	17 – 29	150	Costa Brava	Coma et al. 1994
Eunicella cavolini	162 ± 15	-	625	25	50	Corsica (Channel)	Weinbauer and Velimirov 1996
Eunicella cavolini	51 ± 23	-	625	16 – 28	50	Corsica (Wall)	Weinbauer and Velimirov 1996
Eunicella cavolini	68 ± 21	-	some m^2	10 – 15	50	Corsica (Boulders)	Weinbauer and Velimirov 1996
Corallium rubrum	30	-	0.04	31 – 36	50	Ligurian Sea	Santangelo et al. 1993a
Corallium rubrum	200 –1300	-	-	-	50	Portofino	Cattaneo-Vietti et al. 1993
Corallium rubrum	5247	4408	0.84	25 – 40	50	Ligurian Sea	Santangelo et al. 2003
Corallium rubrum	127 ± 118	2451	2660	18 – 48	50	Costa Brava	This study

[a]Density is colony density per square meter within patches; [b]N states the number of colonies counted; [c]Area refers to the area sampled in the respective study; [d]Depth refers to the depth at which the studied population was situated; [e]Maximal size is the largest size that individuals of a given species reach; [f]Density was estimated by dividing the number of colonies counted by the area covered during a dive.

The fact that 71 % of all colonies sampled have only first order branches, and 96 % have not yet grown tertiary branches (Fig. 5), represents a very young developmental stage.

The comparison of the basal diameter frequency distribution by the Kolmogorov-Smirnov test revealed that the distribution off the Medas Islands is significantly different ($\alpha = 0.05$) from all other populations, except off eastern Cap de Creus. All other populations

did not differ significantly from each other. The distribution of colony height was different between all populations except at the Medas Islands and at the opposing coast of Montgri. No similarities in distribution of branch orders were found between any population.

Biometry

A linear correlation analysis showed a moderately high correlation between colony height and basal diameter at the coast of Begur (N = 1015; P = 0.001; r = 0.631) and off northern Cap de Creus (N = 1685; P = 0.001; r = 0.676). Northern Cap de Creus is also the only population in which a notable correlation between primary and quartiary branches was found; a result of being the only population at which a notable amount of colonies with quartiary branches was found. The highest correlations were found between secondary and primary branches, with the Medas Islands and northern Cap de Creus showing the highest correlations among the populations. The ratio of colony height to basal diameter is lowest for the coast of Begur and the Medas Islands, indicating a relative large basal diameter for the colony size.

DISCUSSION

Distribution of colony density

Although the distribution of red coral depends on depth and depth was also found to have an effect on the colony height, only a weak correlation of depth and population density was found. This may be due to natural small-scale variation in environmental conditions, resulting in the considerable patchiness, and thus variance in population density, observed. Among several factors contributing to a suitable micro-habitat, space competition with other fast growing organisms that may produce a trophic shadow (Kim and Lasker 1997) could be the explanation for the more discontinuous distribution of red coral patches in shallower zones.

Table 6: Comparison of *Corallium rubrum* population structures in various geographic regions

Area	Author, Year	Growth Rate[a] [mm / a^{-1}]	Mean Basal Diameter [mm]	Colony Height [mm]	Comments on Size Structure[b]
Marseille, France	Garrabou and Harmellin 2002	0.24 ± 0.05	6.4 ± 0.5	69.3 ± 12	95 % are < 7 mm
Livorno, Italy	Santangelo et al. 1993a	0.91	3.9	40	95 % are < 3.6mm
Cap de Creus, Spain	García-Rodríguez and Massó 1986a	1.32	7.2	61.8	99 % are < 15 mm
Costa Brava, Spain	This study	-	4.8 ± 2.1	27 ± 17.1	98 % are < 7 mm 43 % are < 4 mm

[a]Growth rate refers to the annual increase of the colony´s basal stem in mm; [b]Comments on age structure state the proportion of a given basal diameter in the respective population.

An opposite depth gradient in colony density has been found in a population in the Ligurian Sea, Italy, where red coral grows in extremely dense patches (200 – 1300 colonies m^{-2}), with an increasing density from 25 m to 35 m (Cattaneo-Vietti et al. 1993; Santangelo et al. 1993a). Although the studied depth range was not very large and the number of patches tested small, it demonstrates a significant difference between the NW Italian and the NE Spanish populations. Other data from the western Mediterranean are similar to the results of this study: 55 colonies m^{-2} at a depth of 40 m in Palma de Mallorca and 20 colonies m^{-2} at a depth of 60 m along the Costa Brava (FAO 1984). In Corsica 90 – 100 colonies m^{-2} have been recorded (FAO 1984). Different techniques and different spatial scales contribute to the observed variation and make a comparison difficult. The scraping technique, for example, detects smallest recruits more reliably than other methods (Santangelo et al. 1993a). Nevertheless, colony density is higher in the Ligurian Sea compared to other regions (Table 5). This leads to the conclusion that red coral population structure can vary in different geographic areas, depending on environmental conditions (Table 5). Coral abundance is relatively great in all regions, even if harvested, which is the result of the relatively high recruitment rate of red coral (Grigg 1989; Santangelo and Abbiati 2001; Bramanti et al. 2003).

To better understand red coral demographic features it is essential to have more data on settlement and recruitment that may indicate the population dynamics (Bramanti et al. 2003). It has recently been demonstrated that the red coral recruitment patterns in Calafuria and Isola d'Elba (Italy) differ from those at the Medas Islands (Spain), as recruitment in the Calafuria population was higher and juvenile mortality lower (Bramanti et al. in press). Reproductive features and population density may be the key to understand the recent development of the red coral populations in these places: Another recently analyzed factor that may affect the demographic structure of red coral populations are mass mortality events. Bramanti et al. (2003) showed that the recruitment and mortality patterns of shallow red coral populations were affected by the mass mortality event detected off the French and Italian NW Mediterranean coasts in 2003 (Garrabou et al. 2001). In red coral populations of the Provence (France) shallow and smallest colonies were affected by partial or total colony mortality (Garrabou et al. 2001), which may shape the future demographic structure in that area.

Demographic comparison of the six populations

Sampling arrangement across a wide geographic dimension (the stations spanning across 12 km from north to south) may significantly help to understand how the harvesting pressure affects red coral: The small differences in diameter and height between the five legally harvested sites along Costa Brava (Begur, Montgrí, Cap de Creus South, East and North) indicate a high homogeneity of the Costa Brava population. In fact, throughout the Mediterranean, population structure and encountered diameters in red coral are similar

(Table 6). Red coral appears to be ubiquitous, but with a relative homogeneous demographic pattern. The observed small differences among the exploited populations may be explained by differences in growth rates or natural mortality, due to interhabitat differences.

The interactive effects of the factors depth and population on maximum height, as found by the ANCOVA, suggest the colonies in the deep part of the Medas Islands are larger than those in shallow water and than in all other populations. This is confirmed by the higher standard deviation of the Medas Islands data, and can be explained by the fact that some of the deeper banks in the Medas Islands are particularly protected from human impact, because they are situated at weather-exposed, remote and deep sites, which are not easily accessible neither to recreational divers nor poachers. The easier accessible zones, on the other hand, are exposed to a considerable human impact, as it can be assumed that a fraction of the 70.000 recreational divers that frequent the islands each season (Hereu et al. 2002) do collect a coral souvenir, or damage colonies by poor diving technique. This also explains why a previous study of red coral at the Medas Islands found almost no colonies with basal diameters > 7 mm between 18 – 40 m depth (Linares et al. 2000).

Figure 6: 12 cm high red coral colony with well developed branching pattern

These first mesoscale data on red coral demography allow the comparison of six populations along the northwestern Spanish coast. The positively skewed size distribution shows a dominance of small colonies within all populations, which indicates a high mortality of larger size classes (Grigg 1976; Bak and Meesters 1998). In all populations there are virtually no colonies present that exceed a basal diameter of 30 mm. However, in the Medas Islands population there is a higher percentage of medium sized colonies, which are the result of its protection during the last 14 years. Interhabitat differences in trophic conditions may explain minor differences in size distribution: Rich food supply can lead to higher growth rates in gorgonians that enable young colonies to escape into larger size classes where survival is higher due to a better recovery from partial predation, thus lowering mortality. Conversely, in old colonies, a better food supply only affects the growth rate (Yoshioka 1994). Differences in trophic conditions thus may explain some of the differences in the population structure between the populations. However, as the difference between the Medas Islands and the other populations are one order higher than differences among the other populations, it is concluded that differences in size distribution are the result of a lower mortality due to the lack of harvesting pressure on the population, and not the result of trophic advantages. Furthermore, although a noteworthy

environmental characteristic at the Medas Islands is the organic material input by the nearby river "Ter", the thriving red coral populations are situated on the pelagic side of the Medas Islands, where sedimentation induced by the river is lowest (Rossi et al. 2003).

Natural mortality in *Corallium rubrum* is low, as it is a longevous species with life spans of up to 100 years (Riedl 1984; García and Massó 1986b). Recent data confirm that red coral has a low mortality, as 60% of the recruits on experimental settling panels survived more than 22 years (Garrabou and Harmelin 2002). Natural mortality is associated to competition but also base detachment due to a variety of causes, such as damage due to waves (Grigg 1965), mechanical failure of weak substrate, or parasite induced weakness of the base (Branch 1984, Yoshioka and Yoshioka 1991, Cattaneo-Vietti et al. 1993, Corriero et al. 1997), combining to a low value compared to harvesting (G. Tsounis, unpublished data).

Size/Age structure

Historic data about coral height document the former existence of enormous colonies of more than 50 cm height (Tescione 1973; Garrabou and Harmelin 2002). Despite this growth potential, this study shows that 91% of the colonies in the Costa Brava population are smaller than 5 cm in height, and none are larger than about 20 cm. This illustrates not only the level of harvesting pressure, but also its selectivity towards larger colonies. Furthermore, only 19 years ago the population structure in the same zone was less skewed towards a basal diameter of 7 mm than today, showing a harvested but heterogenous population off Cap de Creus (García-Rodríguez and Massó 1986a). 19 years ago only 15 % of the population showed a basal diameter < 5 mm, whereas now it is 65 %. Even accounting for the sampling bias towards larger colonies, due to subsampling from professional harvests in the original study, the population structure was significantly different from the actual data in the present study. The study of García-Rodríguez and Massó (1986b) pointed out the importance of a different red coral fishery managment at the Costa Brava, but the harvesting pressure continued with little changes till today.

Size is the major determinant of first reproduction, reproductive output and survival in shallow water gorgonians (Yoshioka 1994; Coma et al. 1995). Colony height frequency distributions are useful as they can easily be compared with historical records or observations from fishermen and divers. However, due to its larger variability, height is not the best suited parameter for determining the age of a colony (Santangelo et al. 1993a). Nevertheless it is important to stress that colonies of a mean height of 2 – 3 cm, consisting of just one or two branches, cannot ensure the reproductive potential needed for the survival of a population (Santangelo et al. 2003; Bramanti 2003). Future work may confirm first indications that the reproductive potential of such distorted populations appears to be severely diminished. The variable relationship between height and age may be partially related to the fact that red coral is an exploited species: A coral colony can be deprived

of a large part of its height, e.g. by partial harvesting, whereas its basal diameter is much less prone to mechanical influences. The basal diameter of red coral colonies, on the other hand, is highly correlated with age and has been used in several studies to calculate age of gorgonians (García-Rodríguez and Massó 1986c; Grigg 1976; Santangelo et al. 1993; Bramanti et al. 2003).

In order to establish precise age distributions it will be necessary to incorporate growth studies on the same populations, which was not attempted in this study. Recent longtime experimental studies using recruitment panels found lower increases in basal diameter of 0.24 ± 0.05 mm per year (Garrabou and Harmelin 2002) and 0.64 mm per year (Bramanti 2003), indicating that the higher values estimated by growth ring analysis in the past overestimated growth due to non-validated sclerochronology methods (Garrabou and Harmelin 2002; Santangelo pers. com.). Further differences stem from interhabitat differences, which affect growth rate, as hydrodynamic conditions influence food availability to suspension feeders (Sebens et al. 1997). Thus it is likely that 0.24 mm describe growth in habitats of reduced water movement (Garrabou and Harmelin 2002). The Costa Brava, however, is a relatively eutrophic and weather-exposed part of the Mediterranean and coral divers in this region estimate diametral growth to be up to 1 mm per year (A. Pluja pers. com.). Thus a growth rate of 0.64 mm per year (Bramanti 2003) was used to convert basal diameter into age.

This conversion shows that the mean age of the colonies is 7.5 ± 3.2 years, and the most frequent age class is 6.6 years old. However, compared to earlier data of the same area they show a much younger average age now (García-Rodríguez and Massó 1986a). This change is partially due to a bias towards older colonies as the initial study subsampled colonies from professional harvests (Table 6). However, given the legal minimum harvest size of 7 mm, an average diameter of 7.8 mm in a professional harvest appears extremely low and indicates nearly depleted stocks.

The present branch morphology of the Costa Brava population also leads to the conclusion that the populations are extremely young, as the vast majority (98 %) of the observed colonies lack the arborescent growth form that is characteristic in older colonies (Fig. 6). It appears that no other example of such a situation has been recorded for other octocorals, leaving overharvesting as the only explanation.

Comparison with other species

The absence of natural red coral populations makes it difficult to distinguish human impact. Thus a comparison with other species serves to obtain a more reliable view of the biology of octocorals when interpreting size distributions (Table 5):

Colony abundance of the octocoral *Leptogorgia sarmentosa* in the Ligurian Sea, Italy (6.8 ± 3 colonies m^{-2}) is much lower compared to red coral (Mistri 1995). This difference can be explained by the fact that *L. sarmentosa* occupies a different ecological

niche: the soft bottom plains characterised by gravel and small boulders (Mistri 1995). Furthermore, it is a fast growing species compared to red coral, with a soft gorgonine skeleton unlike the calcareous one in *Corallium rubrum*. Thus, as abrasion due to wave movement may increase mortality (Grigg 1976), dense populations are disadvantageous for *L. sarmentosa*.

The age distribution in *L. sarmentosa* differs markedly from red coral populations, as extremely old individuals were found: The most frequent age recorded was 9 years, with a considerable part of the population reaching 30 years (Mistri 1995). This age distribution shows that the studied *L. sarmentosa* population has a lower mortality than any studied red coral population. Low mortality is expected for unharvested species as *L. ceratophyta,* but a black coral (*Antipathes aperta*) population studied in a New Zealand fjord showed that even an unharvested octocoral population may consist of mainly young colonies: 90 % were smaller than 50 cm, while the largest colonies reach 4 m (Grange and Singleton 1988). The authors explain this size structure with a high mortality, possibly due to landslides common in the area.

Another octocoral living in the Mediterranean coralligenous community is the aposymbiotic gorgonian *Paramuricea clavata*. Its colonies may reach 1 m in height and have a similar depth distribution as red coral (True 1970; Weinberg 1978). The density of this non-exploited cnidarian varies between 22 and 54 colonies m^{-2}, which is less dense than red coral colonies (Weinberg 1978, Coma et al. 1994). However, it is unlikely that a natural red coral population could maintain its colony density if it contained colonies of its maximum size of 50 cm in height, because the dominance of a few very large colonies may hinder the growth of newly settled ones, mainly due to the trophic shadow (Zabala and Ballesteros 1989).

In shallow populations (< 9.5 m) of *Pocillophora meandrina* in Oahu, Hawaii (Grigg 1976) and the Island of Hawaii (Grigg and Maragos 1974), large colonies are more abundant on the leeward than on the windward side. This indicates that the size frequency, distribution, and abundance of *P. meandrina* depend less on fishery mortality than on natural mortality (Grigg 1976). Thus, in shallow water gorgonians natural mortality from wave action plays a significant role, unlike in red coral which is a sciaphilic gorgonian with exceptionally low mortality (García and Massó 1986b; Garrabou and Harmelin 2002).

Conclusions

This study demonstrates that the three-dimensional structure created by red coral populations at the Costa Brava has degraded to a "grass-plain"- like structure, from the original "forest"- like structure, still observable 20 years ago (García-Rodríguez and Massó 1986a). The transformation of the population structure of this exploited benthic cnidarian may be even more dramatic if we consider the qualitative data gathered in Tescione (1973), and it seems that all over the western Mediterranean the situation is

similar (Santangelo et al. 1993b; Santangelo et al. 2004). The major part of *Corallium rubrum* populations off the Costa Brava consists of young, small colonies. The long history of exploitation has changed its population structure in all unprotected habitats. Size differences between harvested areas and the Medas Islands Marine Protected Area are in part due to deeper, less accessible areas. The relatively short time of protection of 14 years allowed the population to recover sufficiently to result in a significantly different population structure compared to exploited areas. Still, 14 years has not been a time long enough to allow the population to recover to a natural state: virtually no colonies larger than 20 cm were found, which is considerably less than the maximum size recorded for the species. Thoroughly protected marine reserves will undoubtedly prove useful for future work and are well worth the effort protecting them. Future work should employ long time experiments, as they are the most reliable way to contribute to our understanding of growth, mortality and recruitment.

Size structures like the ones described in this study are a useful descriptor for the state of a population, as shifts indicate changes in recruitment and mortality. In combination with knowledge about the biology of a species (especially growth rates, its reproductive cycle and feeding ecology), size structure is the key to detect species response to environmental and anthropogenic factors, and forms the basis for management decisions.

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PUBLICATION II

EFFECTS OF SPATIAL VARIABILITY AND COLONY SIZE ON THE REPRODUCTIVE OUTPUT AND GONADAL DEVELOPMENT CYCLE OF THE MEDITERRANEAN RED CORAL (*Corallium rubrum* L.)

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ABSTRACT

Red coral (*Corallium rubrum*, L. 1758) is an over-exploited Mediterranean gorgonian that might be managed better using data on its reproductive output, which would help in predicting variations in its recoverability potential both within and between populations. The gonadal development cycle of *C. rubrum* off the Costa Brava (NE Spain) area is examined for the first time. This study compares the gonad development and fertility in two colony size classes (colonies < 6 cm height, and > 10 cm height, both at 40 – 45 m depth), and two populations at different depths (16 – 18 m depth, and 40 – 45 m depth, both consisting of < 6 cm high colonies). The gonadal development of each population and size class was followed during a 15-month period in 2002 – 2003. The fertility of seven size classes (< 2 cm to > 12 cm high colonies, in 2 cm intervals) was examined in the deep population. Furthermore, reproductive output was compared in 8 patches (distributed along more than 70 km coastline) one month before spawning (June 2003).The sex ratio was 1:1, which differs from other NW Mediterranean populations. On the other hand, fertility of different size classes indicates that small colonies of 2 cm height already produce gonads, which is in line with previous studies. Female and male polyp fertility and sperm sac size increase significantly with colony size (sperm sac diameter: 476 ± 144 μm (mean $\pm$ SD) and 305 ± 150 μm in the > 10 cm high and < 6 cm high colonies, respectively), whereas no significant effect on oocyte diameter was found (oocyte diameter: 373.7 ± 18.7 μm). Depth staggered spawning, i.e. an earlier release of gonads in the shallow populations,

was observed in summer 2003, coinciding with the highest temperature gradient between shallow and deep water during the study period. The six studied populations at the Costa Brava showed a comparable reproductive potential, indicating small interhabitat variability of the reproductive output. Colonies of less than 6 cm height were significantly less fertile than colonies larger than 12 cm, thus the recommendation of this study is that a minimum height should be incorporated into fishing regulations.

KEYWORDS: Red coral, octocoral, fertility, gonadal development, reproductive cycle, spatial variability, NW Mediterranean

INTRODUCTION

The reproductive cycle of a species and factors affecting the reproductive potential of a population are the key to a better understanding of population dynamics (Dayton 2003). This kind of studies is especially relevant for key- and exploited species. Gorgonian octocoral populations are characteristic components that contribute significantly to biomass and energy flow of many ecosystems (e.g. Brazeau and Lasker 1989; Coma and Gili 1998; Arntz et al. 1999), yet little is known about the spatial variability of their reproductive output.

The Mediterranean red coral (*Corallium rubrum*, L. 1758) is a long lived species with slow growth, but an exception to the general K-selection pattern in gorgonians, as it has a low age at first reproduction (Vighi 1972; Grigg 1989; Santangelo et al. 2003a, b). Its age structure is generally dominated by young, small colonies (Santangelo and Abbiati 2001; Santangelo et al. 2003a), and the species may be at risk of local extinction in some places. Recent data demonstrate that this is the effect of red coral being commercially harvested for use in the jewellery industry since the 17th century (Tescione 1973; Santangelo and Abbiati 2001; Tsounis et al., submitted). Thus there is a need to better understand how colony size and environmental factors affect its reproductive potential, as this allows to develop optimal harvesting strategies and protective measures.

Colony size of modular organisms affects the allocation of energy into reproduction (Hall and Hughes 1996; Beiring and Lasker 2000) and the ability of an octocoral to feed (Kim and Lasker 1997). We hypothesize that polyp fertility and gonad diameter increases with colony size in red coral as it does in other gorgonians (Coma et al. 1995b, Beiring and Lasker 2000). Thus a better understanding of the effect of this factor allows an improved harvesting strategy, that does not harvest the stock down to colonies of lower fertility (Grigg 1976).

Population dynamics of modular organisms are frequently influenced by the depth they are living at, as depth affects the feeding capabilities of corals, and consequently their potential energy reserves (see Harland et al. 1992). This has a direct effect on larval recruitment, as a depth-dependent settlement of new recruits has been demonstrated in scleractinian corals (Mundy and Babcock 2000). Also, spawning has been found to occur earlier in shallow water colonies than in deep ones (Vighi 1972; Santangelo et al. 2003b).

A recent study demonstrated a wide small- and mesoscale variability in the red coral recruitment (Bramanti et al. in press, a), as larval settlement and mortality was different off the Costa Brava (NW Mediterranean Spanish coast) and Calafuria (NW Mediterranean Italian coast). Given the direct effect of reproductive output on larval viability in red coral populations (Bramanti et al. in press, b), the importance of spatial variability has to be taken into account when studying harvested populations. Studies restricted to a limited spatial scale may be insufficient in providing a tool for the management of the fishery of this benthic species.

This work hypothesises: 1) that polyp fertility and gonad size increase with colony size, 2) that depth influences the reproductive output of red coral, and 3) that polyp fertility and gonad size of red coral varies between populations at various sites at the Costa Brava. The results are intended to provide tools for the local fishery management aimed at ensuring the recoverability of the stocks of this precious coral.

Table 1: Sampling stations at the Spanish Costa Brava

Station	Location	Coordinates	Depth	Type of Habitat	Facing
Punta Falconera	Southern Cap de Creus	42°13'45"N, 3°13'1"E	36 m	Wall	South
Punta de sa Oliguera	Eastern Cap de Creus	42°20'1"N, 3°16'30"E	40 m	Large boulders	South
Ses Ielles	Eastern Cap de Creus	42°18'40" N, 3°17'50"E	30 m	Large boulders	East
Punta Salinas	Coast of Montgri	42°05'56"N, 3°12'51"E	20 m	Wall	South
Illa del Düí	Coast of Montgri	42°06'11" N, 3°11'45"E	25 m	Wall	East
Serra Ventosa[a]	Medas Islands	43°2'30"N, 13°30"	35 m	Wall in a bay, open to east	North
Cova de la Reina[a]	Medas Islands	43°2'30"N, 13°30"E	20 m	Small overhang in bay	East
Barda del Sastre[a b]	Medas Islands	43°2'30"N, 13°30"E	40 m	Wall at exposed cape	East

[a]Monthly sampling during 15 months; [b]Two different size classes were sampled within the same population
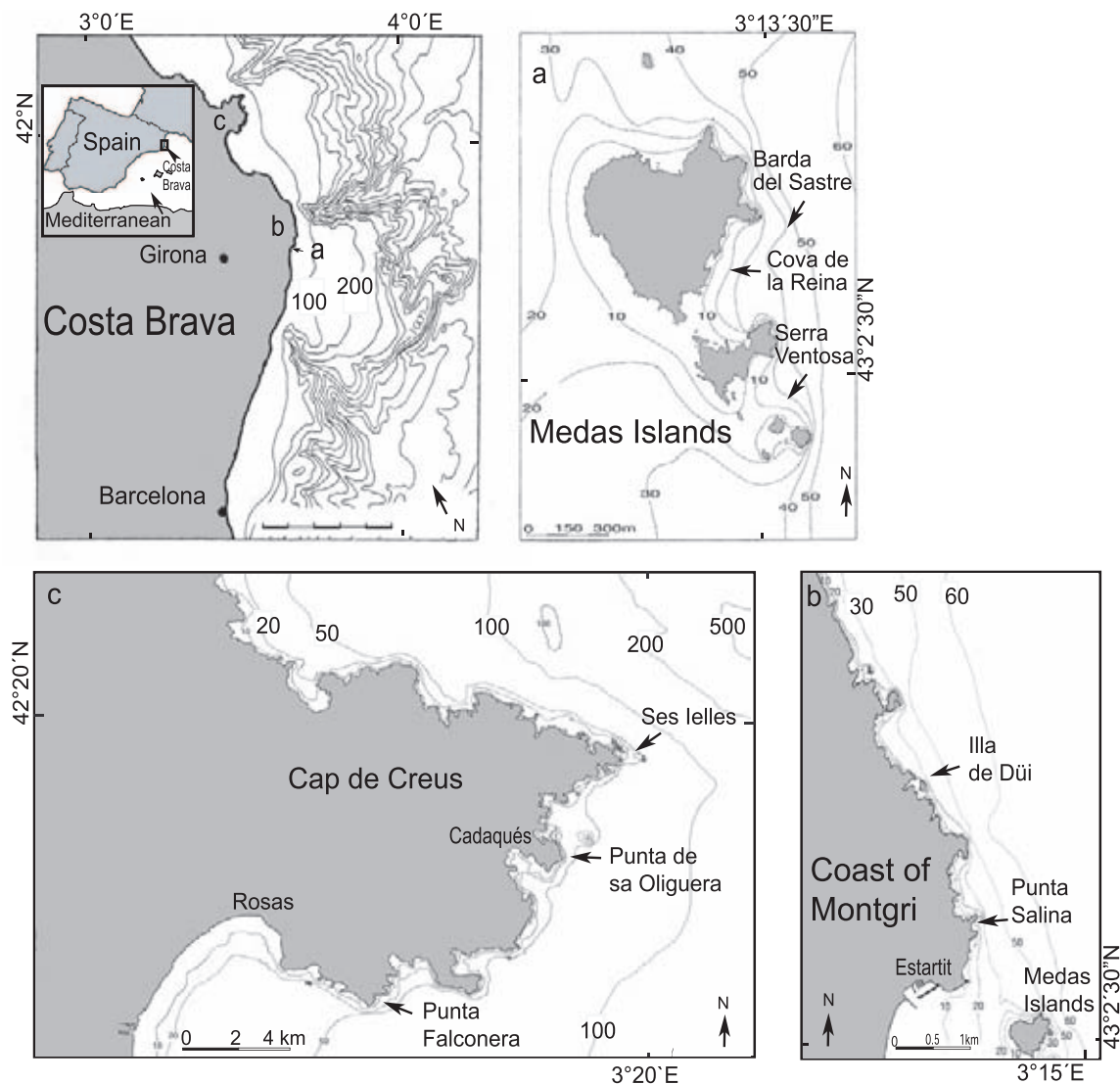
Figure 1: Map of the study area: The Costa Brava (NW Mediterranean)

MATERIAL AND METHODS

Sex ratio and size at first reproduction

In total 586 colonies were sampled in June 2002 in order to test the sex ratio of the Islas Medas population. In order to examine the size at first reproduction, 7 colony size classes were sampled, ranging from 0 – 2 cm colony height to 8 – 10 cm colony height. 20 branches from 20 different colonies were sampled per class on 11th July 2002 at 40 – 45 m depth. This was shortly before the release of the gonads, thus insuring that the sampling did not underestimate the fertility of the colonies.

Red coral samples were taken using cutting pliers extracting a 2 cm long apical coral branch from 20 different colonies < 6 cm in height (sampled at random) and placing it in a seawater filled PVC bottle that was kept in ice until fixation with 10 % Formalin (usually within 30 min). The sampled colonies measured 4 – 6 cm in height, representing

the most abundant size class in the Mediterranean (Santangelo et al. 2003a; Tsounis et al. submitted).

The coral samples were processed by opening coral polyps of the branches´ central part with fine tipped forceps under a binocular dissecting microscope (50x magnification) and counting oocytes and sperm sacs, as well as measuring their diameter with a calibrated eyepiece micrometer. Five polyps per branch were subsampled at random.

Gonadal development cycle and reproduction timing

Gonad development and number were studied in two populations at the Medas Islands Marine Protected Area in monthly sampling intervals between April 2002 and August 2003. One population (following the definition of Lincoln et al. 1998) is situated at an overhang at 16 – 18 m depth, while the other grows on a wall between 40 and 45 m. The distance between the two sites is 300 m, both being affected by the same main current (Pascual et al. 1995) (Fig. 1). As coral larvae survive for several days (Weinberg 1979) and can be swept considerable distances by currents, we must assume that there is a gene flow between the two populations at the Medas Islands and the opposite coast of Montgri. 600 colonies were sampled that measured 4 – 6 cm in colony height (the maximum distance from the base of the coral to the branch tips).

Differences between size classes

In order to examine the influence of colony size on gonad development, an addittional 300 samples from colonies larger than the 4 – 6 cm ones were taken from the population at 40 m, where enough large colonies could be found. These colonies measured han 10 – 12 cm and were taken in the same monthly intervals as the other samples. This allowed a comparison of gonadal develepoment and reproductive output of the two size classes.

Spatial comparison

Reproduction features of six red coral populations from different sites along the Costa Brava (see Fig. 1 and Table 1) have been sampled by SCUBA between 20th and 24th June 2003. 20 colonies were sampled from each population in the same manner as described above. All populations are characterised by a typical rocky shore sublitoral hardbottom community, the "coralligene" (eg. Sará 1969; Gili and Ros 1984).

Data analysis

The sex ratio was tested by applying a chi-square test. In order to test the hypothesis that the colony size classes varied in reproductive output, a one-factorial ANOVA was used to analyse differences in colony fertility and gonad size respectively between red coral colony size classes. Similarly, ANOVA was used to test for differences of reproductive
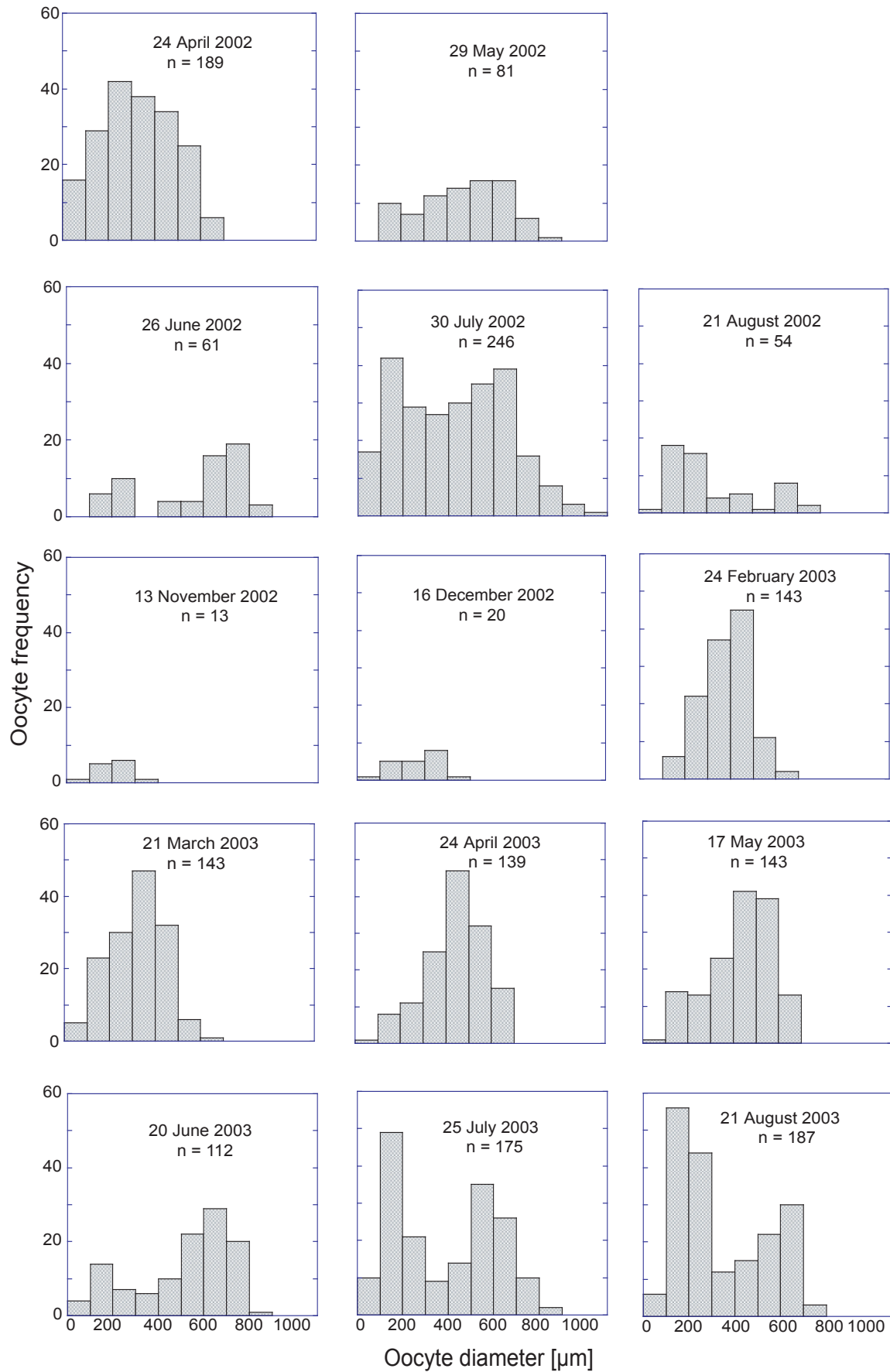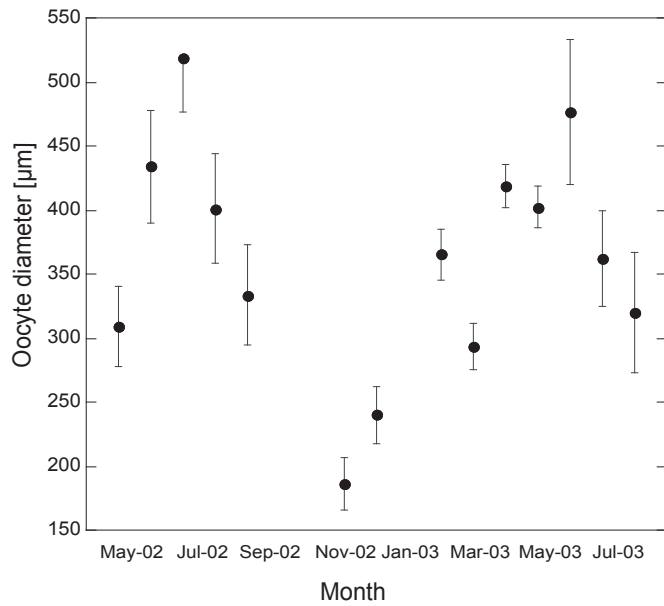
Oocyte diameter [µm]

Figure 3: Seasonal cycle of average (± SE) oocyte diameter in *Corallium rubrum*
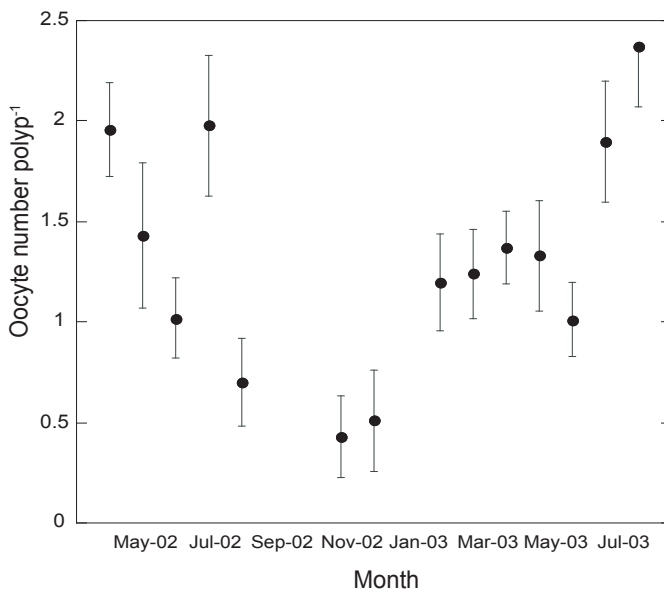
Figure 4: Seasonal cycle of average (± SE) oocyte number per polyp of *Corallium rubrum*

output between the two depth zones sampled, and likewise between the five populations.

Using the information from the gonad development cycle in order to compare gonad quantity and size allowed to exclude immature gonads by using only data from April to July. Colony fertility was defined as the number of gonads in five polyps per colony, using 20 replicate colonies per month. Conversely, gonad size was defined as the average gonad diameter of gonads encountered in five polyps per colony.

The data were not distributed normally and had different variances but met both of these criteria for parametric analysis after logarithmic transformation (Brown-Forsythe-test and Levene-test, P = 0.05; Shapiro Wilk-test, P = 0.1), thus permitting the use of an ANOVA. An exception were the oocyte number data comparing the two size classes, which had to be transformed using a modified square root transformation

Table 2: ANOVA results comparing gonad numbers polyp^{-1} and diameter for studied populations, or depth- and size classes respectivel

Factor	Oocyte number		Oocyte diameter		Sperm sac number		Sperm sac diameter	
	F	P	F	P	F	P	F	P
Area	0.9011	0.5055	2.609	0.05[a]	0.8099	0.5513	1.9512	0.0866
Depth	1.3374	0.2560	5.4741	0.05	1.3187	0.2530	31.5871	< 0.001
Size	4.2225	0.05	1.9951	0.1610	7.5981	0.01	50.2796	< 0.001

Bold: significantly different; [a]Welsh, nonparametric ANOVA
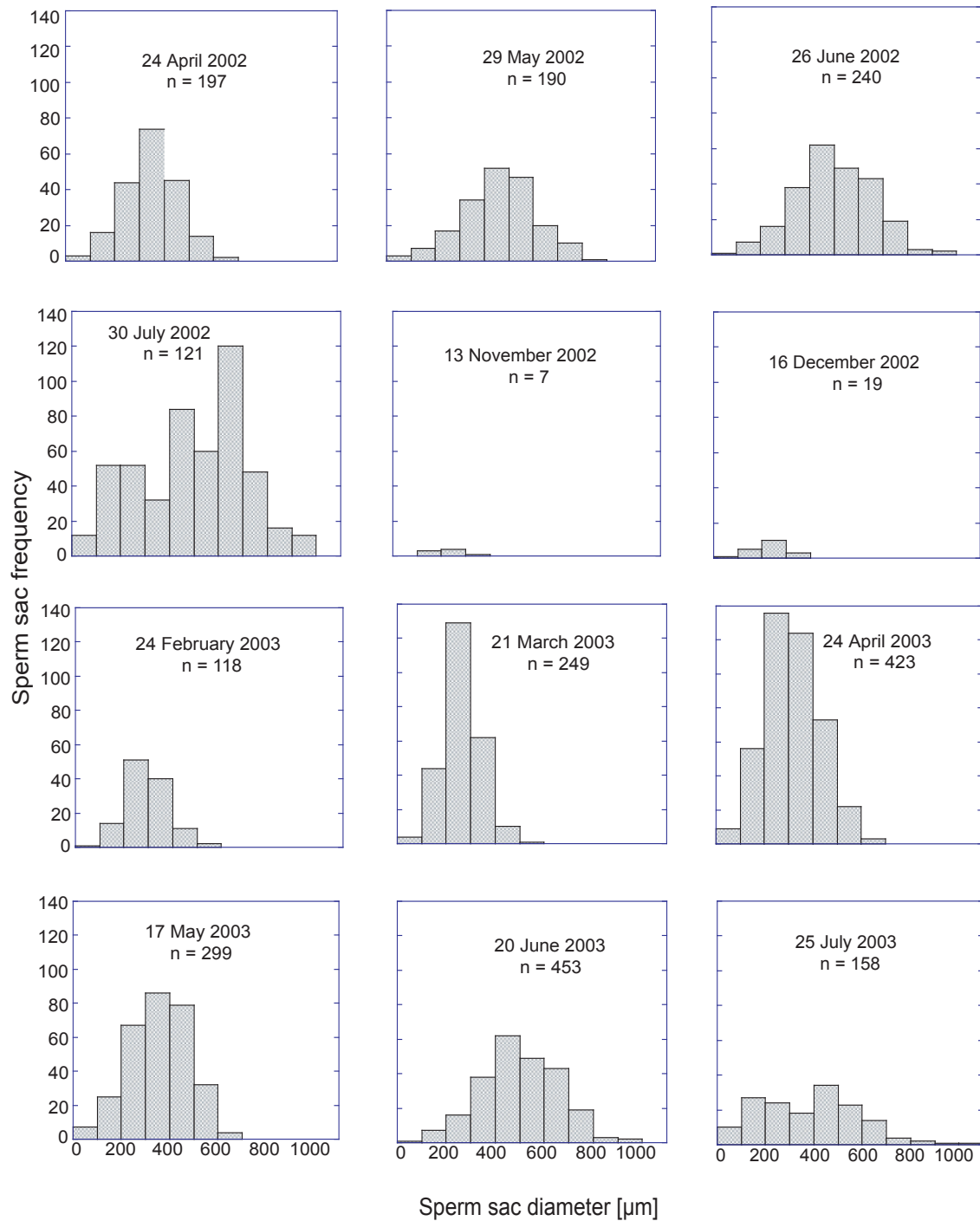
Figure 5: Seasonal frequency distribution in sperm sac diameter in *Corallium rubrum*
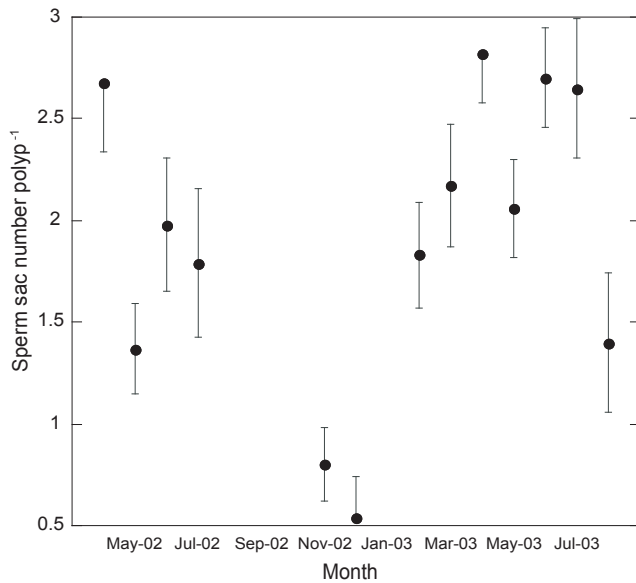
Figure 6: Seasonal cycle of average (± SE) oocyte number per polyp of *Corallium rubrum*
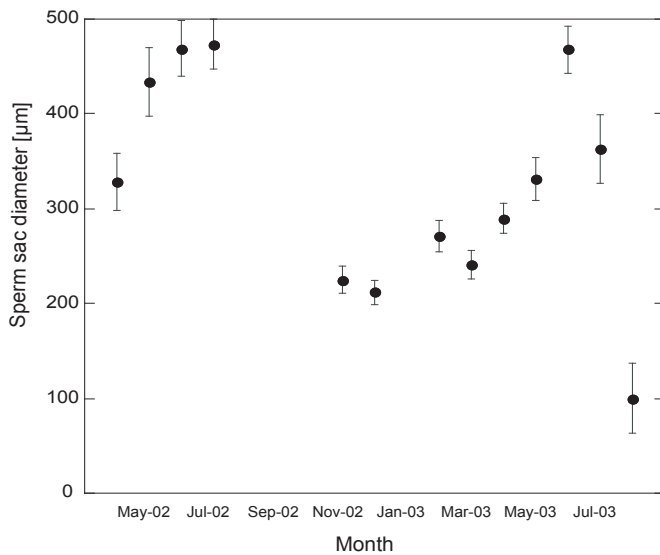
Figure 7: Seasonal cycle of average (± SE) sperm sac diameter in *Corallium rubrum*

(Zar 1996) in order to show comparable variances, and the oocyte diameter data comparing spatial differences had to be tested using a weighted, nonparametric (Welsh) ANOVA (JMP Synergy software), as data transformation did not result in comparable variances.

RESULTS

General reproductive features

Red coral was found to be dioecious and gonochoric both at colony and at polyp level. The overall sex structure of the Medas Islands population did not significantly deviate from 1:1 ($\chi^2 = 1.3$; P = 0.05). In total, 281 female and 305 male colonies were found.

Gonadal development cycle and reproduction timing

Gonad development in red coral followed an annual cycle with a

Figure 8: *Corallium rubrum* gonad number per polyp of various size classes (grey bars: females; black bars: males)

65
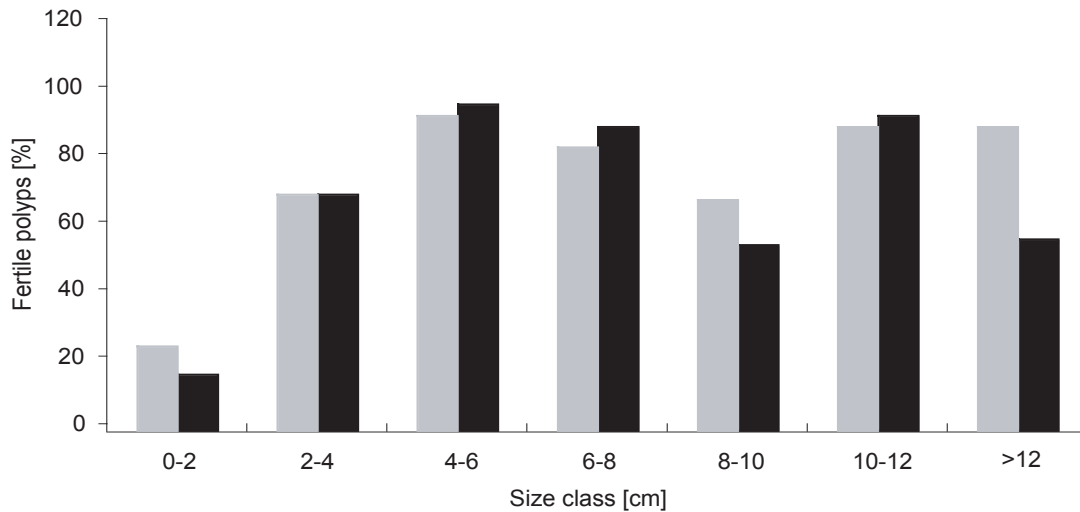
Figure 9: *Corallium rubrum* polyp fertility in the 7 studied
size classes (Grey bars: females; black bars: males)

synchronised release in summer. Oocyte development took more than 12 months, which manifested itself in the presence of two size classes of oocytes (Fig. 2). The ripe gonads measure 500 – 900 μm and were released in July/August, whereas the second, immatured cohort consisted of oocytes of 50 – 400 μm that continued to grow until their release in the following year (Fig. 3). Prior to the release in summer there was a reabsorbtion of oocytes, as oocyte numbers dropped between April and May (Fig. 4).

Sperm sac development followed an annual cycle with release of all sperm sacs in July (Fig. 5). Before release they reached a maximum size of 900 μm. No sperm sacs were found in August 2002 (Fig. 6), and polyps started containing newly formed sperm sacs of 50 – 300 μm diameter in November (Fig. 7).

Differences between size classes
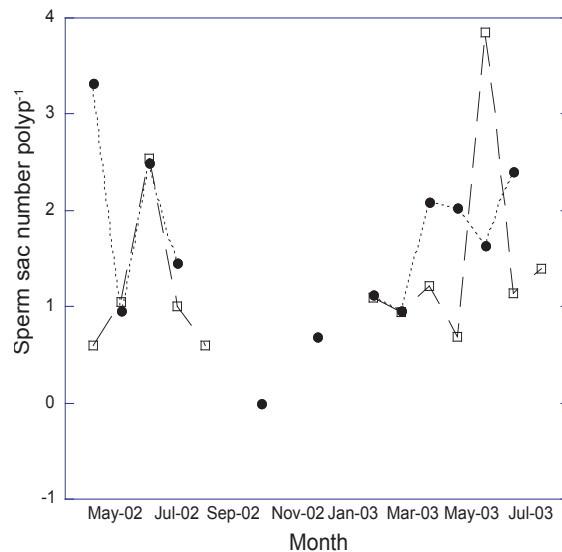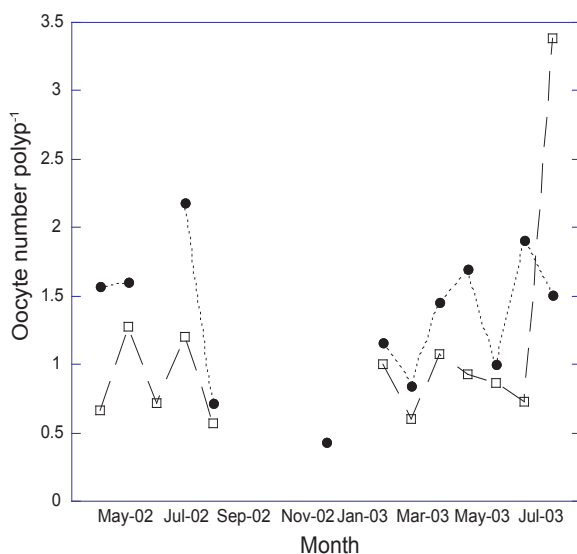
Figure 10: *Corallium rubrum*. Oocyte no. per polyp at 40 m depth (Circles) and 20 m (squares)

Figure 11: *Corallium rubrum*. Sperm sac no. per polyp at 40 m depth (circle) and 20 m (squares)

The sperm sac diameter was significantly larger in the large colonies (476 ± 144 μm) (mean ± SD) than in the small ones (305 ± 130 μm) (ANOVA: F = 50.3; P = < 0.001). No significant differences in oocyte diameter were found between the two size classes. The average gonad number was higher in the large colonies (0.66 oocytes polyp^{-1} ± 0.024 and 2.42 ± 0.166 sperm sacs polyp^{-1}) than in the small ones (0.58 ± 0.024 oocytes polyp^{-1} and 1.74 ± 0.18 sperm sacs polyp^{-1}) (oocytes: ANOVA: F = 4.2; P = 0.05; sperm sacs: ANOVA: F = 7.6; P = 0.05).

The examination of six size classes revealed that all of them were fertile, including the class with colonies smaller than 2 cm height, however, colonies smaller than 2 cm contained less than 1 gonad polyp^{-1} (Fig. 8). Colonies of 2 – 4 cm height, which constituted the majority of population, showed 60 % fertility and colonies of 4 – 6 cm showed 100 %
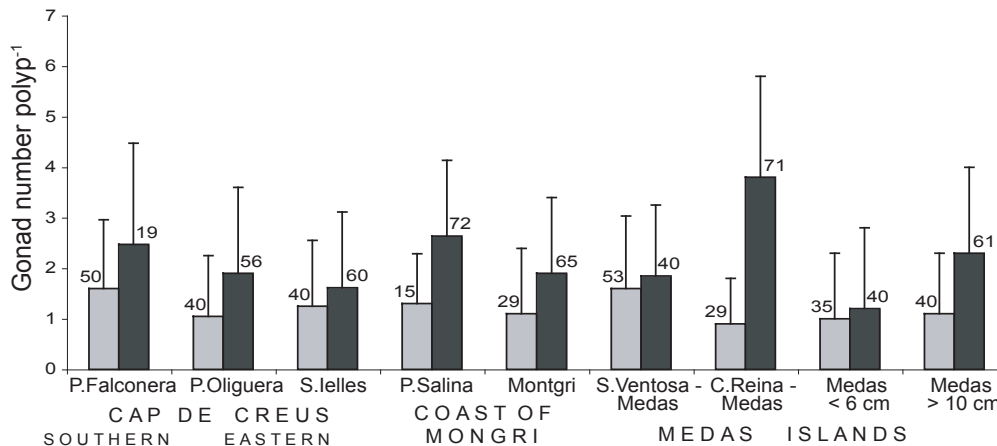
Figure 12: Gonad number per polyp in the studied *Corallium rubrum* populations sampled at the Costa Brava (Sample-N indicated above bars; grey bars: females, and black bars males)
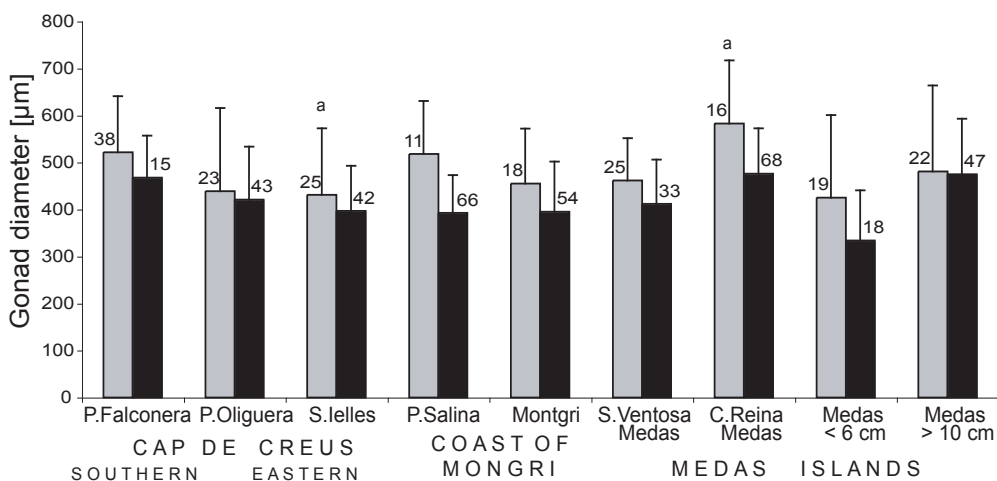
Figure 13: Gonad diameter in studied *Corallium rubrum* populations sampled at the Costa Brava (Sample-N indicated above bars; grey bars: females, and black bars: males; The two tations marked by "a" are significantly different from each other)

Table 3: Size/age at first reproduction in various gorgonians

Species	Location	First reproduction		Source
		Age (yr)	Height (cm)	
Antipathes dichotoma	Hawaii	10 – 12.5	64 – 80	Grigg 1977
Briareum asbestinum (branches)	Caribbean	2 – 3	10 – 20	Brazeau and Lasker 1990
Corallium rubrum	Mediterranean	-	2	This study
Corallium rubrum	Mediterranean	2	0.2	Santangelo et al. 2003b, Bramanti 2003
Monastrea annularis	Caribbean	4	-	Szmant-Froehlich 1985
Muricea californica	California	5	12	Grigg 1974, 1977
Muricea fructicosa	California	10	20	Grigg 1974, 1977
Paramuricea clavata	Mediterranean		50	Coma et al. 1995a
Parerythropodium fulvum fulvum	Red Sea	3 – 4	-	Benayahu and Loya 1984
Plexaura A	Caribbean	5	20	Brazaeu and Lasker 1989
Plexaura flexuosa	Caribbean	-	20 – 30	Beiring and Lasker 2000
Plexaura homomalla	Caribbean	-	20	Brazaeu Lasker 1989
Sarcophytum glaucum	Red Sea	7 – 10	-	Benayahu and Loya 1984
Stylophora pistillata	Red Sea	2	-	Rinkevich and Loya 1979
Xenia macrospiculata	Red Sea	2	1	Benayahu and Loya 1984

fertile polyps (Fig. 9).

Differences due to depth

Gonads were significantly larger at 20 m depth (oocytes: 404.6 μm ± 19.2; sperm sacs: 426.5 μm ± 17.1) than at 40 m depth (oocytes: 342.8 μm ± 18.1; sperm sacs: 287.3 μm ± 18) (oocytes: ANOVA: F = 5.5; P = 0.05; sperm sacs: ANOVA: F = 31.6; P = < 0.001). No significant differences between the two depths were found in oocyte and sperm sac numbers. The gonad number data reveal that in 2002 the release was synchronized between the two depths, whereas in 2003 the release was depth staggered, with the shallow colonies releasing earlier than the deep ones (Fig. 10 and 11).

Spatial comparison

The mean oocyte diameter differed significantly between populations (Table 3) (ANOVA: F: 2.6; P = 0.05), as diameters were larger at the shallow population at the Medas Islands than at Ses Ielles (eastern Cap de Creus, Fig. 1). However, no significant differences between the areas were found in oocyte and sperm sac numbers, and in sperm sac diameter (Fig. 12 and 13).

DISCUSSION

General reproductive features

All populations were found to be completely gonochoric at both the polyp and colony level, as previously found in other red coral and octocoral populations (Vighi 1972, Benayahu et al. 1989, Brazeau and Lasker 1990, Coma et al. 1995a, Santangelo et al. 2003b).

The sex ratio of *Corallium rubrum* of 1:1 at the Costa Brava differs from a recently studied population in Italy, where a bias towards females was found (Santangelo et al. 2003b). Other gorgonian species living in the same habitat as *C. rubrum* show the same sex ratio as *C. rubrum* (*Paramuricea clavata* sex ratio, Coma et al. 1995a; *Eunicella singularis,* Weinberg and Weinberg 1979), and other tropical and Antarctic gorgonians show the same trend (Kinzie 1974; Orejas et al. 2002). The difference of the sex ratio between the Italian and Spanish red coral populations can be explained by different population densities between the two sites (Santangelo et al. 1993; Tsounis et al., submitted), as well as different larval recruitment and mortality in both places (Bramanti et al. in press, a), as it has been demonstrated that population density in gorgonians affects the optimal fertilization strategy and thus sex ratio (Brazeau and Lasker 1990).

The results of the present study show that size at first reproduction in the *Corallium rubrum* population of the studied area is remarkably small, corresponding to a young age, as previously observed by Santangelo et al. (2003b). Unlike most octocorals that are typically characterised as K-selected species with long lifetimes, low mortality and low reproductive output (Grigg 1989; Gotelli 1991; Santangelo et al. 1993; Coma et al. 1995b), red coral appears to have a small size/age at first reproduction (Table 3) that enables it to sustain its populations despite intensive harvesting (Grigg 1989). However, the polyp fertility increases considerably with size, unlike the gorgonian *Paramuricea clavata* that shares a similar long lifespan and low mortality (Coma et al. 1995b). Thus the results of this study show that polyp fertility is significantly lower in colonies smaller than 6 cm height, requiring a minimum harvestable size limit well above the current average size of Costa Brava populations of 3 cm height (Tsounis et al., submitted).

Gonadal development cycle

The gonadal development cycle of red coral culminates in an annual summer spawning, a common phenomenon among octocorals in temperate seas (Weinberg and Weinberg 1979; Coma et al. 1995a; Santangelo et al. 2003b). Oocyte development in red coral takes longer than sperm development, which is a feature also shared with other octocorals (Benayahu and Loya 1984; Coma et al. 1995a) and scleractinians (Kojis and Quinn 1981; Szmant 1981). Oocyte development lasts longer than a year, so that immature oocytes are present in summer and are not released until they mature in the following year. Only the first cohort of ripe gonads is released. This has been observed earlier in a red coral population at the French coast (Vighi 1972), as also in the Mediterranean gorgonian *Paramuricea clavata* (Coma et al. 1995a). Production of sperm sacs begins in September and ends with their

release in July, and is thus much shorter than gonad production. Oocyte numbers dropped between April and May due to a reabsorption of gonad tissue. This little understood phenomenon has been observed in the Caribbean gorgonian *Plexaura* "A" (Brazaeu and Lasker 1989).

The larval release follows the sudden drop in oocyte number and diameter, as stated in a recent study made in the Medas Islands (Bramanti et al. in press, a). In fact, recruitment seems to follow the same trends in time, but not in number of larvae, in the Calafuria population (Italy) (Bramanti et al. 2003). In the same type of coralligenous habitat another octocoral (*Eunicella singularis*) also releases the larvae in July (Weinberg and Weinberg 1979). Stabilization of the thermocline has been suggested to be the main signal for larval expulsion in both octocorals (Weinberg 1979).

Differences between size classes

The results show a significant difference in reproductive output between the two size classes; large colonies contained significantly more oocytes and sperm sacs. Sperm sacs were also larger in the large colonies. The separate examination of colony fertility in the seven size classes revealed that even the small colonies of 2 cm height produce gonads, although in small numbers. Thus the data confirm the hypothesis that size has a positive effect on reproductive potential.

Small colonies produce less gonads as reproduction is of lesser priority during the young life phase. A greater resource allocation to growth at smaller size means a faster escape out of vulnerable size classes (Kojis Quinn 1981; Szmant 1985; Soong 1993; Ward 1995a; Hall and Hughes 1996; Beiring and Lasker 2000), improving their chances of survival, as small colonies suffer greater mortality (Connell 1973; Hughes and Jackson 1985; Jackson and Hughes 1985; Babcock 1991).

Colony size significantly affects the reproductive output (Ward 1995b), and has a direct relation to the number of released planulae (Tioho et al. 2001). The higher fertility of large colonies has a special implication in the case of red coral, as it is a harvested species with its population structure distorted towards young colonies (Santangelo and Abbiati 2001; Tsounis et al., submitted). In the Mediterranean gorgonian *Paramuricea clavata* large colonies constitute 3 % of the population but contribute 40 % of female gametes and 33 % of male gametes (Coma et al. 1995b). In the tropical blue coral *Heliopora coerulea,* colonies larger than 6 cm radius constitute less than 22 % of the population but produce 80 % of total annual gonad production (Babcock 1984).

However, not only is polyp fertility higher in large colonies, but the total number of reproductive modules increases exponentially with colony size of modular organisms, especially if they are highly branched (Stiller and Rivoire 1984; Sakai 1998; Santangelo et al. 2003b). Thus large colonies contribute disproportionately to gonad production, as in the case of *Plexaura flexuosa*, where large colonies (> 70 cm in height) produced on

average 6 times more gonads per polyp than small colonies, and 98 % of the gonads were produced by half of the colonies (Beiring and Lasker 2000). These studies demonstrate the importance of large colonies for the survival of an octocoral population. In red coral this is of even higher relevance due to the size selective harvesting.

Differences due to depth

The larger gonad diameters in the shallow population are the result of depth staggered spawning induced by seasonal differences in temperature stratification. Water temperature at 18 m rises above 22° C in summer, whereas at 40 m the water temperature did not rise above 16° C in summer 2003 (Cebrián et al. 1996). This increase in temperature shortens the time necessary to complete gametogenesis (Vighi 1972; Grigg 1977), thus the gonads in shallow colonies reach their terminal size earlier than deep ones. The same has been observed in the Californian gorgonians *Muricea californica* and *Muricea fructicosa* (Grigg 1977) and also in a nearby red coral population in France (Vighy 1972). A recent study on an Italian population also found shallow colonies to release gonads earlier than deep ones, and did not detect any differences in the gonad diameter nor in the number of gonads per polyp between depths (Santangelo et al. 2003b). The authors explain this finding with the fact that the studied depth range was narrow, compared to the range of red coral (20 – 200 m), and the modest temperature interval of $\Delta T = 0.5°C$ (Santangelo et al. 2003b). In the same Italian population, however, recruitment was found to be higher in the shallow colonies (Bramanti et al. 2003). The present study did not observe an asynchronous spawning in the studied depths in 2002; merely in summer 2003, which coincides with the strongest temperature differential during the study (own unpubl. obs.). Thus we conclude that depth staggered spawing in red coral can only occur during pronounced temperature differences. Finally, as gonad numbers were not different between the populations, we reject the hypothesis that depth influences reproductive potential. Future research on wider depth ranges, however, may help to confirm the hypothesis that gorgonian fecundity varies with depth due to phenotypic plasticity (West et al. 1993).

Spatial comparison

The data show a comparable reproductive potential in all sampled populations, as gonad numbers and sperm sac diameter were not significantly different between the sampling stations. This means that variation in factors such as exposition to different environmental conditions does not appear to introduce variance in reproduction. As red coral populations along the Costa Brava have very similar demographic features due to overharvesting, it can be concluded that reproductive features are equally homogeneous. Given the crucial importance of reproduction to the recoverability of the species, we recommend spatial comparisons of reproductive output as a tool for management plans (see: Lloret and Planes 2003). Although the results show a homogenous reproductive output of red coral along

the Costa Brava, which future research may find to be typical of healthy populations, we would like to stress the importance of this tool, especially since mass mortality events in red coral have been observed to affect populations with a remarkable meso- and small scale selectivity (Garrabou et al. 2001).

Conclusions

The reproductive output of red coral increases with increasing colony size, but was not found to be affected by spatial variation or depth. However, its release of larvae can be depth staggered when high temperature gradients occur in summer. The size at first reproduction is relatively low in red coral and has been suggested to be the reason for the resilience of its populations. However, this study confirms more recent results that show a lower fertility in small colonies. In fact, the present populations at the Costa Brava consist to a large part of colonies that have not yet reached a fertility of 100 %. Studies of the reproductive potential of exploited stocks are recommended to improve management strategies, as the exploitation is operating at the limit of the recoverability of this species. Future research should focus on red coral recruitment, which is the ultimate measure of reproductive efficiency.

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PUBLICATION III

SEASONAL VARIATION IN THE PREY CAPTURE RATE OF THE MEDITERRANEAN RED CORAL (*Corallium rubrum* L.)

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ABSTRACT

Gorgonians are passive suspension feeders, contributing significantly to the energy flow of littoral ecosystems. More than in active suspension feeders (e.g. bivalves, ascidians, sponges) their prey capture is affected by spatial and temporal prey distribution and water movement. *Corallium rubrum* is a characteristic gorgonian of Mediterranean sublittoral hard bottom communities. The aim of this study was to analyse its annual cycle of prey capture rate. Detrital particulate organic matter (POM) was found throughout the year in the polyp guts and constituted the main proportion of its diet (25 – 44 %). Crustacean fragments and copepods (14 – 46 %) accounted for the second major proportion, while invertebrate eggs (9 – 15 %) and phytoplankton (8 – 11 %) constituted the smallest part of the diet. To ratify the importance of detrital POM in the energy input of this precious octocoral species, *in situ* experiments were carried out during the winter-spring period. The results confirm the importance of detrital POM as the main source of food for *C. rubrum* (0.085 ± 0.089 μg C polyp^{-1} h^{-1} (mean $\pm$ SD)). This study also compares the seasonal prey capture rates of two colony size classes and two depth strata: Within the same patch, small colonies (< 6 cm height) captured significantly more prey per polyp (0.038 ± 0.09 prey polyp^{-1} h^{-1}) than larger colonies (> 10 cm high) (0.026 ± 0.097 prey polyp^{-1} h^{-1}) and showed a higher proportion of polyps containing prey (17 % compared to 10 %). Comparing colonies of similar size (< 6 cm height) revealed that the colonies situated at 40 m depth captured significantly more prey (0.038 ± 0.09 prey polyp^{-1} h^{-1}) than the ones at 20 m (0.025 ± 0.11 prey polyp^{-1} h^{-1}). One pulse of copepods was recorded

and constituted 16% of all captured prey during the 15-month period studied. The carbon ingestion averaged 0.003 ± 0.002 μg C polyp^{-1} h^{-1}, which combined with data on the density of the exploited population results in $0.4 - 9.6$ mg C m^{-2} d^{-1}. This value is in line with some other Mediterranean and tropical gorgonians. The grazing impact of present, heavily exploited and small-sized populations is comparable to that of larger Mediterranean gorgonians, suggesting that unexploited red coral populations may have a high impact compared with other passive suspension feeders.

KEYWORDS: *Corallium rubrum*, octocoral, passive suspension
feeders, benthic communities, trophic ecology, Mediterranean

INTRODUCTION

Suspension feeders significantly interact with the water column in littoral ecosystems by depleting food particles and transferring energy from the pelagial to the benthos (e.g. Cloern 1982; Officer et al. 1982; Fréchette et al. 1989; Kimmerer et al. 1994; Riisgård et al. 1998). Although bivalves, ascidians and sponges have been found to be among the most efficient filter feeders (Fréchette and Bourget 1985; Petersen and Riisgård 1992; Pile et al. 1996; Ribes et al. 1999a), octocorals have recently been recognised to play an important role in littoral ecosystems (Gili and Coma 1998; Arntz et al. 1999).

Prey capture rates of octocorals and other passive suspension feeders are strongly influenced by seasonal variation of water movement and seston composition (e.g. Graf et al. 1983; Clarke 1988; Coma et al. 2000). In warm temperate seas, such as the Mediterranean, the annual variation in seston abundance and hydrodynamic conditions is an important aspect for the understanding of ecosystem fluxes (Siokou-Frangou 1996; Calbet et al. 2003). Summer conditions are characterised by clear, stratified water, after the plankton-rich winter-spring bloom (Ribera d'Alcalá et al. 2004). In warm temperate seas, this results in a "trophic crisis" in summer and good feeding conditions in winter-spring for many benthic suspension feeders (Coma et al. 2000). Knowledge of the diet and temporal variability of prey capture rates (i.e. annual variations) in suspension feeders is essential to understand ecosystem energy fluxes. Yet there still is a lack of information about the diet of passive suspension feeders, and wide differences have been demonstrated between two warm temperate gorgonians from the same location (Coma et al. 1994, Ribes et al. 1999b, Ribes et al. 2003, Rossi et al. 2004).

Another factor which affects energy fluxes from the pelagic to the benthic system is the effect of three-dimensional biogenic structures: colony size and population density affect the water flow around colonies and alter the gravitational particle deposition, which in turn affects prey capture (Patterson 1984; LaBarbera 1984; Okamura 1985;

McFadden 1986; Coma et al. 1994; Kim and Lasker 1997). Studying differences in prey capture rates between two colony size classes within the same gorgonian population will improve our understanding of energy fluxes. Furthermore, a dependence of capture rates of passive suspension feeders on depth has been suggested (Lasker et al. 1983). The main hypothesis is that shallow passive suspension feeder populations could reach highest capture rates due to more constant food availability because of the more intense hydrodynamic processes.

This study examines the seasonal variability in prey capture rates of

red coral (*Corallium rubrum*, L. 1758). *C. rubrum* is a characteristic suspension feeder in western Mediterranean hard-bottom sublittoral habitats and forms dense patches in crevices, cave entrances and overhangs (e.g. Riedl 1984; Margalef 1985). Despite the fact that it is a commercially harvested species used in the jewellery industry

Figure 1: Study area at the Medas Islands (43°2' 30"N, 13°30'E), Costa Brava, Spain. The two *Corallium rubrum* patches at 18 – 20 m and 40 m depth are indicated.

(Cicogna et al. 1999, Santangelo et al. 2001) there are no *in situ* data on its nutrition. Red coral is distributed along a wide depth range of 7 – 200 m depth, but its vertical distribution varies between geographical regions (Marchetti 1965; Carpine and Grasshoff 1975; Weinberg 1979; Riedl 1984; Zibrowius et al. 1984; Chintiroglou and Dounas-Koukouras 1989). It is not clear whether differences in seasonal temperature stratification, harvesting, or trophic conditions limit the upper distribution zone of red coral in some areas. The importance to understand the biology of this species in order to allow a sustainable management of red coral has been stressed (Santangelo et al. 2003a). Therefore the objective of this work is to study the diet and the annual capture rates of *C. rubrum*, taking into account differences in colony size classes and depth of two patches situated in the same area. The final aim is to obtain more information on red coral about the biology and ecology for its future stock management.

MATERIALS AND METHODS

Differences of diet and capture rates between both depths and size classes

The two *Corallium rubrum* populations (following the definition of Lincoln et al. 1998) were studied in the Medas Islands Marine Protected Area (MPA) at the Costa Brava (NE Spain, see Fig. 1). Both are located at the off shore side of the island, one at 40 m depth and the other at 20 m, with a horizontal distance of 300 m in between.

Sampling was carried out monthly between April 2002 and August 2003 using SCUBA (15-month period). Two different size classes were sampled in the deep population: (1) colonies < 6 cm height (matching the size of the colonies at the shallow site) and (2) colonies > 10 cm height. Colony size was defined as the maximum distance between the colony base and the tips of the farthest branches.

Each sample consisted of 20 apical branches of 2 cm length taken from 20 different colonies, using cutting pliers. The samples were then stored in seawater filled PVC bottles and cooled with ice during a transport of about 30 min, until fixed in 5 % formalin. The colonies were processed by dissecting coral polyps under a binocular microscope (50x magnification). Prey items were counted and their size was

Figure 2: Two red coral colonies in an *in situ* incubation chamber which is connected to a portable submersible pump (not shown).

measured using a (calibrated eyepiece) micrometer. Five polyps per colony were chosen from the basal part of the branches, in order to avoid variability due to the age of the polyps sampled (Santangelo et al. 2003b).

Prey capture rate, expressed as the number of prey items captured per polyp and hour, was calculated using the following equation (Coma et al. 1994):

$$C = N \left[\sum_{t=0}^{D} 1 - (t/D) \right]^{-1}$$

where C is the number of prey items captured per polyp and hour, N is the number of prey items per polyp, t is the time (in hours) and D is digestion time (in hours).

Temperature affects digestion time and was incorporated using digestion times of *Leptogorgia sarmentosa* at various temperatures for red coral, as their diets are similar (Rossi et al. 2004). The ingestion rate was estimated by determining the from biovolume (Sebens and Koehl 1984) and converting it to wet weight using the specific weight of 1.025 g cm^{-3} (Hall et al. 1970). Dry weight was assumed to be 13 % of wet weight (Beers 1966), and

the carbon content was estimated at 45 % of dry weight (Biswas and Biswas 1979).

   In order to test the hypothesis that the factors `size´ and `depth´ affect the capture rate, prey size and ingestion rate of red coral, the two size classes and the two populations were tested for differences separately. The monthly data were pooled in order to test for differences between seasons. As the data could not be transformed successfully to meet the criterion of homogenous variance for parametric statistics (Levene´s test), a *Chi* square test was employed (Zar 1996).

In situ feeding experiments

While gastrovascular content analysis is a useful tool to study the seasonal variance of the natural spectrum of prey items, it may underestimate total carbon ingestion, if a significant part of the diet consists of quickly digestible soft bodied prey items (e.g. microplankton, fine POM; Ribes 1999b; 2003). Therefore *in situ* incubation chamber experiments were employed as a second approach in order to measure the ingestion rate including small food particles. 4 *in situ* incubation chamber experiments were run in March 2003, as the winter-spring period is the best time because prey particles are abundant and the thermocline, which strongly affects gorgonian polyp activity (Rossi 2002), is still not present (Ribes et al. 2003). Following the methodology of Ribes et al. (2000), whole colonies were
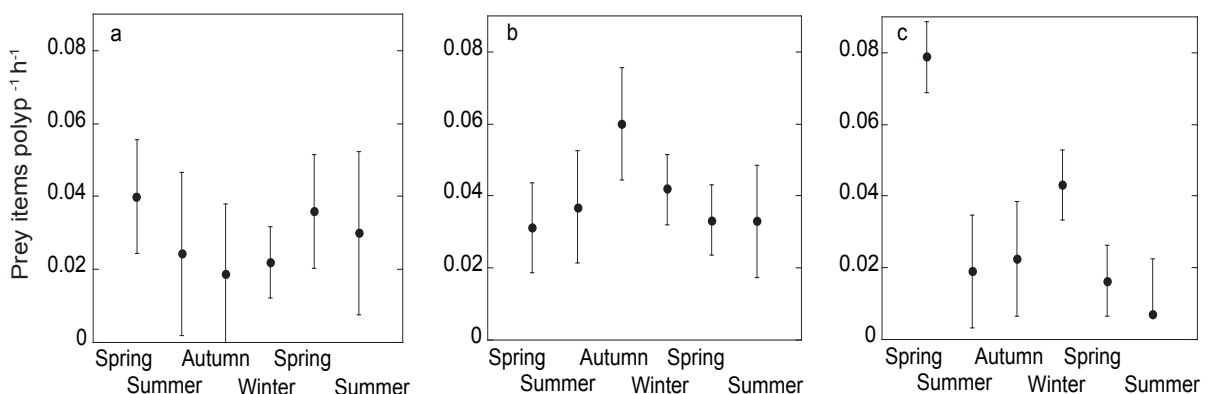
Figure 3: *C. rubrum*: Prey capture rate (prey polyp-1 h-1), estimated from stomach contents of 100 polyps; a: 20 m depth, colony height < 6 cm; b: 40 m , colony height < 6 cm; c: 40 m , > 10 cm
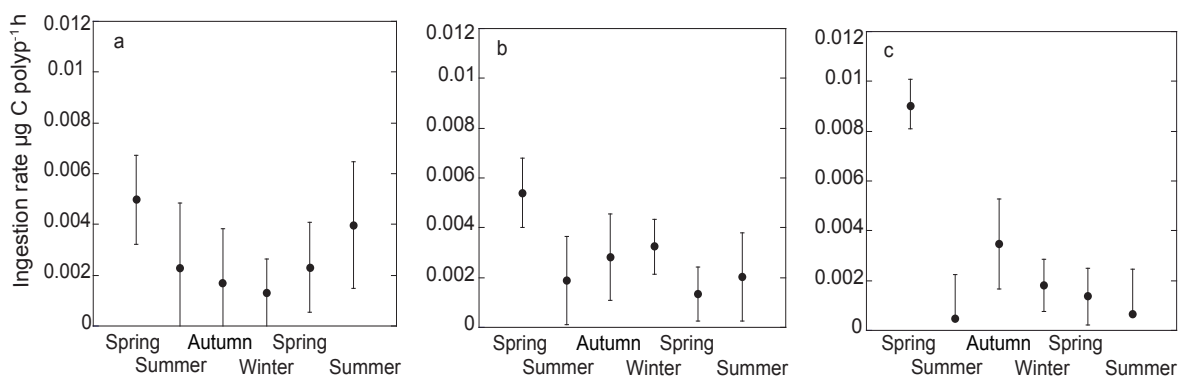
Figure 4: *C. rubrum*: Prey size (µm) during annual cycle, estimated from stomach contents of 100 polyps; a: 20 m depth, colony height < 6 cm; b: 40 m , colony height < 6 cm; c: 40 m , > 10 cm

incubated in submerged acrylic domes (volumes: 1175 – 1240 ml repectively) fitted with a recirculating pump that maintained a closed circuit of turbulent water flow (2.2 l min^{-1}), keeping food particles in suspension. In order to maximise the number of polyps vs. water volume, and thus minimise the incubation time, two small colonies of 3 – 5 cm height were placed into the experimental chamber (Fig. 2). Red coral colonies were transplanted to PVC posts and acclimated for 2 – 3 weeks in a semi dark cave entrance at 9 m depth (although very shallow for this species, natural *C. rubrum* colonies have been observed to grow at this depth only 300 m from the experimental site). Only colonies that had all polyps fully expanded were inserted into a chamber. Prior to each experiment the chamber was run 30 min in open flow mode in order to acclimate the colonies to the set up conditions. The inlet was fitted with a 500 *µ*m mesh to reduce contamination with sediment particles. Water samples were taken before and after the incubation time of ca. 200 min which allowed to calculate the grazing rate of the colony. The colonies were inspected every 30 min during the experiment, using SCUBA, and if one or both colonies started to contract their polyps, the experiment was terminated, which resulted in variable incubation times. Digital photos from various angles were taken during the inspections, to later quantify active polyps. Total POC was measured by taking three water samples of 200 ml from the chamber before and after incubation, and immediately pre-filtering
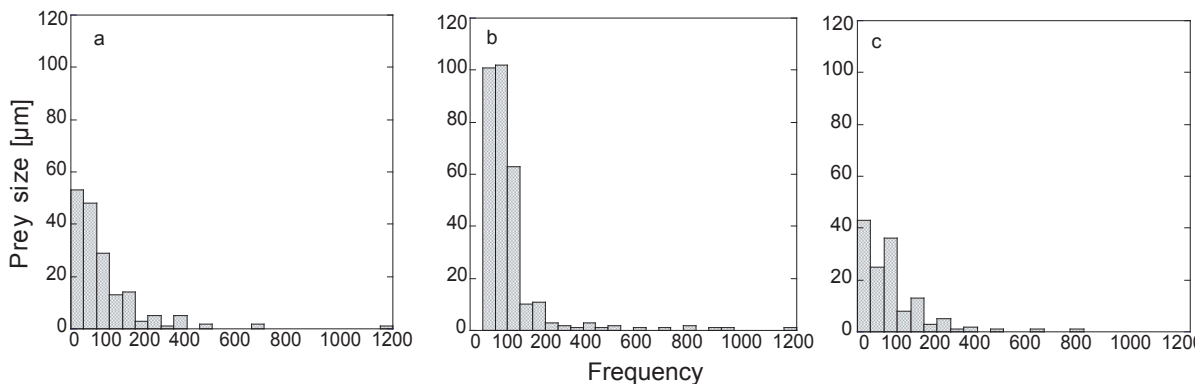
Figure 5: *C. rubrum*: Ingestion rate (µg C polyp-1 h-1) during annual cycle, estimated from stomach contents of 100 polyps; a: 20 m depth, colony height < 6 cm; b: 40 m , colony height < 6 cm; c: 40 m , > 10 cm
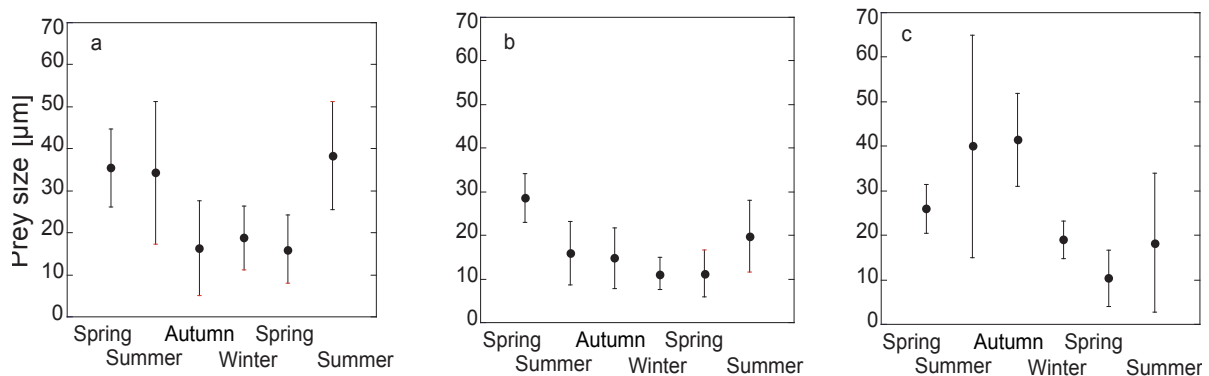
Figure 6: *C. rubrum*: Prey size (µm) frequency distribution, estimated from stomach contents of 100 polyps; a: 20 m depth, colony height < 6 cm; b: 40 m , colony height < 6 cm; 40 m height, > 10 cm

Table 1a: *Corallium rubrum*. Sampled at 40m depth, colony height > 10 cm. Number and type of prey items captured over the sampling period (2002 to 2003), and total number of stomachs observed in 1450 polyps. At the bottom of the table is a breakdown of number of polyps with prey inside, and mean number of prey per polyp. POM: particulate organic matter; Other: juvenile bivalves and gastropods; appendicularians, sponge spicules

	24 Apr 2002	29 May 2002	26 Jun 2002	30 Jul 2002	29 Aug 2002	17 Oct 2002	13 Nov 2002	17 Dec 2002	24 Feb 2003	21 Mar 2003	24 Apr 2003	17 May 2003	15 Jun 2003	25 Jul 2003	21 Aug 2003	n	%
POM	3	1	3	0	0	0	1	2	2	37	9	4	10	2	3	77	25
Copepods	47	0	0	0	0	0	0	0	0	0	2	0	0	0	0	49	16
Crustacean fragments	62	4	1	0	0	1	1	5	0	8	5	0	3	1	0	91	30
Copepod eggs	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	5
Invertebrate eggs	0	0	2	0	0	0	5	5	0	0	0	0	0	0	0	12	4
Invertebrate larvae	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	4	1
Phytoplankton	20	0	0	2	2	0	0	0	0	4	1	0	0	0	0	29	10
Protozoa	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	8
Nidenoblasts	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tintinnids	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	1
Other	0	0	0	0	0	0	2	0	0	3	0	0	0	0	0	5	2
Total prey n	172	5	7	2	2	1	12	12	2	55	19	4	13	3	3	307	
Full polyps %	53	4	5	5	1	1	4	10	5	29	14	1	13	1	2	Mean =	
	57	4	5	5	1	2	5	10	5	29	16	1	13	1	2	10.4	
No. of prey polyp^{-1} Mean	1.7	0.05	0.07	0.02	0.02	0.02	0.1	0.1	0.02	0.6	0.2	0.04	0.1	0.03	0.03	Mean = 0.2	
SD	3.3	0.3	0.4	0.7	0.3	0.1	0.3	0.6	0.5	1.4	0.7	0.1	0.4	0.3	0.2	Mean= 0.6	

Table 1b: *Corallium rubrum*. Sampled at 40m depth, colony height < 6 cm. Number and type of prey items captured over the sampling period (2002 to 2003), and total number of stomachs observed in 1450 polyps. At the bottom of the table is a breakdown of number of polyps with prey inside, and mean number of prey per polyp. POM: particulate organic matter; Other: juvenile bivalves and gastropods; appendicularians, sponge spicules

	24 Apr 2002	29 May 2002	26 Jun 2002	30 Jul 2002	29 Aug 2002	17 Oct 2002	13 Nov 2002	17 Dec 2002	24 Feb 2003	21 Mar 2003	24 Apr 2003	17 May 2003	15 Jun 2003	25 Jul 2003	21 Aug 2003	n	%
POM	1	7	8	15	13	0	1	3	11	14	21	13	5	9	8	129	44
Copepods	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5	2
Crust. fragments	6	2	3	1	1	0	1	4	6	1	2	0	1	3	3	34	12
Copepod eggs	0	0	0	0	0	0	4	3	4	0	0	0	0	0	0	11	4
Invertebrate eggs	0	0	0	1	0	0	3	15	11	1	2	0	0	0	0	33	11
Invertebrate larvae	5	0	0	0	0	0	1	1	6	0	2	0	0	1	0	17	5
Phytoplankton	0	0	0	1	2	0	0	4	1	0	9	1	1	4	0	23	8
Protozoa	0	0	0	2	0	0	6	10	5	1	1	1	0	3	0	29	10
Nidenoblasts	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.4
Tintinnids	0	2	2	0	2	0	0	0	0	0	0	0	0	0	0	4	1
Other	0	0	2	0	0	0	0	2	5	1	1	0	0	0	0	11	3.7
Total prey n	16	11	13	20	18	0	16	44	49	18	38	15	7	20	11	296	
Full polyps %	7	26	18	17	11	0	12	30	47	15	20	19	4	16	10	Mean =	
	7	26	18	17	11	0	1	30	48	15	20	19	4	16	10	16.9	
No. of prey polyp^{-1}																	
Mean	0.2	0.1	0.1	0.2	0.2	0	0.2	0.4	0.5	0.2	0.4	0.2	0.07	0.2	0.2	Mean = 0.2	
SD	0.7	0.5	0.5	0.5	0.5	0	1	1	0.5	0.4	1	1.3	0.3	0.5	0.3	Mean = 0.5	

Table 1c: *Corallium rubrum*. Sampled at 20m depth, colony height > 6 cm. Number and type of prey items captured over the sampling period (2002 to 2003), and total number of stomachs observed in 1450 polyps. At the bottom of the table is a breakdown of number of polyps with prey inside, and mean number of prey per polyp. POM: particulate organic matter; Other: juvenile bivalves and gastropods; appendicularians, sponge spicules

	24 Apr 2002	29 May 2002	26 Jun 2002	30 Jul 2002	29 Aug 2002	13 Nov 2002	17 Dec 2002	24 Feb 2003	21 Mar 2003	24 Apr 2003	17 May 2003	15 Jun 2003	25 Jul 2003	21 Aug 2003	n	%
POM	11	1	4	1	2	5	1	1	2	13	1	2	4	12	60	36
Copepods Crustacean	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
fragments	1	3	6	1	3	1	2	0	3	4	1	2	2	2	31	18
Copepod eggs	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	1
Invertebrate eggs	2	1	0	0	3	0	0	0	0	1	7	0	0	0	14	8
Invertebrate larvae	3	0	3	2	2	0	2	1	0	0	1	0	2	0	15	9
Phytoplankton	0	1	4	0	2	1	4	0	0	1	5	0	1	1	19	11
Protozoa	1	0	0	0	0	0	0	0	0	7	0	2	1	1	12	7
Nidenoblasts	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	1
Tintinnids	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other	1	1	2	1	0	0	2	0	0	3	0	0	0	0	14	8.2
Total prey n	19	7	20	6	12	7	12	3	5	31	15	8	10	15	170	
Full polyps %	15	5	15	5	10	1	8	2	12	25	10	10	7	8		
No. of prey polyp^{-1}	15	5	15	5	10	2	8	4	12	25	10	10.1	7	8	Mean = 10	
Mean	0.2	0.07	0.2	0.06	0.1		0.07	0.1	0.03	0.05	0.3	0.2	0.08	0.1	Mean = 0.12	
SD	0.8	0.4	0.5	0.2	0.3	0.6	0.3	0.2	1.6	0.5	0.5	0.3	0.4	0.4	Mean = 0.5	

Table 2: *Corallium rubrum*. X^2-Test for the differences in prey size, no. of prey polyp^{-1}, and ingestion rate between the seasons (spring 2002 – summer 2003); bold = significant at 5 % level

	20m patch colony height < 6 cm	40m patch colony height < 6 cm	40m patch colony height > 10 cm	40m patch colony height < 6 cm
Prey size	$X^2 = 8.2$; df = 5; P = 0.15	$X^2 = 29.8$; df = 5; **P = 0.001**	$X^2 = 21.5$; df = 5; **P = 0.001**	
Number of prey polyp^{-1}	$X^2 = 12.8$; df = 5; **P = 0.02**	$X^2 = 80.6$; df = 5; **P = 0.001**	$X^2 = 28.2$; df = 5; **P = 0.001**	
Ingestion rate (µg C) polyp^{-1}	$X^2 = 13.4$; df = 5; **P = 0.02**	$X^2 = 241$; df = 5; **P = 0.001**	$X^2 = 23.9$; df = 5; **P = 0.001**	

through a 100 μm mesh to exclude faecal pellets that were deposited in the chamber. The first sample was taken *in situ*, without interruption of the acclimatisation, by connecting a PVC bag to the chamber outlet. The samples were cooled to 4° C during a 30 min transport until they were filtered through a pre-combusted GF/F glass fibre filter. Thereafter filters were immediately frozen in liquid nitrogen and stored at -80° C until analysis. The filters were prepared for the analysis by drying at 60° C for 24 h and exposure to HCl vapors for 48 h in order to remove inorganic material. Then they were dried again at 60° C for 24 h and analysed with a C:H:N autoanalyser (Model 2100 by CE Instruments (Thermo)).

Table 3: Results from the *in situ* grazing experiments with *Corallium rubrum*

day	hour	Incubation time (min)	No. of open polyps	Grazing rate (μg Carbon h^{-1} polyp^{-1})
11.3.2002	10:29 pm	200	149	-0.15
17.3.2002	10:11 pm	208	235	-0.04
17.3.2002	10:11 pm	208	100	0.17
17.3.2002	10:11 pm	208	141	0.10
17.3.2002	10:11 pm	208	146	0.12

Average (± SD): 0.085 ± 0.089

Population grazing impact

Taking into account the average red coral population density of 9.7 ± 137 colonies m^{-2} and population structure of the studied red coral population (Tsounis et al., submitted) allowed to calculate the grazing impact of the population: A mean number of 50 polyps per colony of 0 – 2 cm height (34 % of the population), 150 polyps per colony for colonies of 2 - 6 cm height (60 % of the population) and 400 polyps for colonies of 6 – 10 cm (6 % of the population) were estimated (own unpubl. obs.), resulting in 1270 polyps m^{-2}. The population impact is then estimated by multiplying this figure with the average capture rate per polyp.

RESULTS

General composition of the diet

Overall, detrital POM and crustaceans were the most important food items encountered in the polyp stomachs of both populations and both size classes: POM constituted 25 – 43 % of all prey items (20 – 43 % of all ingested carbon), and the proportion of crustacean fragments ranged between 11 – 30 %. Copepods were captured infrequently, although on one occasion a pulse of high numbers was captured (see below). Copepods and crustacean fragments accounted for 25 – 60 % of all ingested carbon. Phytoplankton and Protozoa were less frequent but still constituted a notable amount of prey (ca. 10 % each). The majority of prey items measured between 50 and 200 μm (Fig. 3), with a maximum prey size of 1200 μm (copepods).

Differences of diet and capture rates between both depths and size classes

The colonies situated in the deep zone captured more prey items per polyp than the shallow colonies (mean ± SD: deep: 0.2 – 0.6 prey polyp^{-1}; shallow: 0.12 – 0.5 prey polyp^{-1}). The two size classes show the same average, however, a high number of copepods captured by the > 10 cm high colonies in April 2002 represents a feeding pulse that constituted 16 % of all prey items captured during the 15 months (Table 1a), compared to 1.7 % in the small size class (Table 1b) and 0 % the shallow population (Table 1c). The capture of this pulse led to larger colonies showing a similar contribution of POM in their diet compared to the small ones (Table 1b). The small size class showed the overall highest proportion of polyps containing prey (17 %), whereas 10 % of the polyps contained prey in the large size class at 40 m (Table 1b) and in the 20 m patch (Table 1c).

The two patches at 40 m and 20 m differed significantly in number of prey items per polyp ($\chi^2 = 23.7$; P = 0.001) and prey size ($\chi^2 = 50.1$; P = 0.001) but not in ingestion rate ($\chi^2 = 2.7$; P = 0.098). The two size classes differed significantly in number of prey per polyp ($\chi^2 = 25.0$; P = 0.001), prey size ($\chi^2 = 6.2$; P = 0.05), and ingestion rate ($\chi^2 = 71$; P = 0.001).

The seasons differed significantly in number of prey items per polyp, prey size, and ingestion rate (Table 2) except in the shallow patch, where there were no significant seasonal differences in prey size. However, despite the statistical differences there is no uniform pattern visible in the two size classes and two patches (Fig. 3 – 5). In the > 10 cm high colonies, prey capture rate was highest in spring 2002 (0.08 prey items polyp $^{-1}$ h^{-1}), taking into account the April 2002 food pulse. Prey size was lowest in winter and spring (mean: 20 μm), and ingestion rate notably higher in spring (Fig. 6).

***In situ* feeding experiments**

Incubation experiments carried out in March and June 2003 revealed a grazing rate of 0.085 ± 0.089 μg C polyp^{-1} h^{-1} with a minimum of 0.1 and a maximum of 0.17 μg C polyp^{-1} h^{-1} (Table 3). Nearly all successful experiements were acomplished in March, as feeding activity lasted longer (up to 3 h) in March and was more frequent (often 100% of the colonies were feeding) than in June, where feeding rarely lasted longer than 1.5 h and where only a small proportion of the transplanted colonies was found to be feeding during daily inspections. This inactive feeding behaviour coincided with the build up of a thermocline that created clear, warm water conditions.

Population grazing impact

The average prey capture rate in the two populations and size classes was 0.026 ± 0.11 prey polyp^{-1} h^{-1} (20 m), 0.038 ± 0.09 prey polyp^{-1} h^{-1} (40 m, < 6 cm high colonies) and 0.026 ± 0.097 prey polyp^{-1} h^{-1} (40m, > 10 cm high colonies). Thus a typical young population at 40 m captures 50.8 ± 21.6 prey m^{-2} h^{-1}, and the average grazing impact

of a Costa Brava population is 1219.8 ± 518.5 prey m^{-2} d^{-1}. The ingestion rate ranges between 0.091 ± 0.043 mg C m^{-2} d^{-1} (gut content analysis) and 0.15 ± 1.5 mg C m^{-2} d^{-1} (incubation experiments).

DISCUSSION

***Corallium rubrum* diet and gut contents**

The diet of *Corallium rubrum* consists mainly of small prey (< 200 μm) with low motility (i.e. detrital POM, eggs and larvae). Other passive suspension feeders also feed on non-motile zooplankton of similar size (Lewis 1982; Sebens and Koehl 1984; Coma et al. 1994; Ribes et al. 1998, Rossi et al. 2004). Apart from the contribution of the copepod pulse observed in April 2002 (> 10 cm high colonies at 40 m depth, Table 1a), all observed cycles showed detrital POM as the main prey of red coral. The detrital POM proportion in the diet of *C. rubrum* (25 – 44 %, Table 1 a – c) is higher than the detrital POM proportion in the gorgonians *Leptogorgia sarmentosa* (14 %, Rossi et al. 2004) and *Paramuricea clavata* (1.6 %, Coma et al. 1994). Incubation chamber experiments with *P. clavata* showed that in winter detrital POM ingestion may reach 73 % of the ingestion contributed by zooplankton (Ribes et al. 1999b).

However, while *P. clavata* captures detrital POM mainly during turbulent winter conditions, it is a constant prey item in red coral. Resuspension of detritic sediment deposits observed in the study area (pers. obs.) may explain this constant availability of POM to red coral.

The proportion of crustacean fragments, especially of copepods, in the prey items captured by *C. rubrum* is generally low. This result is in line with data on *L. sarmentosa* (Rossi et al. 2004) and confirms the significance of POM for the diet in some Mediterranean gorgonians. In *L. sarmentosa*, bivalve larvae constitute a very important part of the incoming energy; the position of the colony (perpendicular to the seafloor) and the substrate (soft-gravel bottoms) are decisive factors to explain such a proportion of veligers (Rossi et al. 2004). The gorgonian *P. clavata* (Coma et al. 1994) and the hydrozoan *Eudendrium racemosum* (Barangé and Gili 1988) colonise hard substrates at different depths (15 – 60 m and 2 – 10 m, respectively, Gili and Ros 1985), and principal components in their diet are zooplankters (copepods, invertebrate eggs, nauplii, ostracods). Detrital POM is also part of their diet, but could only be detected with experimental incubation chambers (Ribes et al. 1999b). The high detrital POM proportion observed with the binocular microscope in red coral may be explained by its microhabitat preference, i.e. the characteristic of hanging in rocky cave roofs and crevices (Riedl 1984) where sediments that have accumulated above pass while falling down without being able to bury the colonies (pers. obs.).

It is problematic to estimate the nutritional value of the POM component in the

diet, as it is not possible to estimate the original size of POM parts in the guts. Being available throughout the year, POM constitutes up to 43 % of the ingested carbon in the large colonies. Thus it is an important part of the diet of *Corallium rubrum*. However, as energy rich prey like copepods is caught in pulses, the sampling rate may underestimate the total carbon ingested, and overemphasize the significance of constantly available prey items. The energetic significance of crustacean fragments, an important and frequently encountered prey item in this study, might be underestimated as well, as it is hard to tell the original size of the animals from the encountered fragments.

The mean gut content of 0.17 ± 0.53 prey polyp^{-1} is quite low compared to the gorgonians *L. sarmentosa* (0.7 ± 0.9 prey polyp^{-1}, Rossi et al. 2004) and *P. clavata* (0.6 ± 1.3 prey polyp^{-1}, Coma et al. 1994). It is more similar to tropical octocorals that usually show values below 0.3 prey polyp^{-1} (e.g. Lewis 1982; Fabricius et al. 1995). Consequently, the ingestion rates of *P. clavata* ($0.0038 - 0.026$ μg C polyp^{-1} h^{-1}, Coma et al. 1994) and *L. sarmentosa* (0.019 ± 0.002 μg C polyp^{-1} h^{-1}, Rossi et al. 2004) were also higher compared to *C. rubrum* (0.003 ± 0.002 μg C polyp^{-1} h^{-1}). These differences may be explained by the fact that *P. clavata* and *L. sarmentosa* colonies grow large (55-100 cm), compared to *C. rubrum*, where colonies exceeding 10 cm are rarely found outside marine protected areas (Tsounis et al., submitted). In consequence, its size (and microhabitat preference) prevents *C. rubrum* from reaching the water layer outside the benthic boundary layer with stronger currents. The present data show that *C. rubrum* colonies have to rely on water movement that causes enough turbulence to transport or resuspend food into crevices. The relatively high standard deviation in the prey capture rate indicates a high variation of food availability and further confirms the presence of prey pulses. The activity rhythms in red coral contribute to the variation, as they have been found to be unpredictable in contrast to other anthozoans (Rossi 2002). While activity rhythms in other passive suspension feeders seem to be affected by speed of the current, *C. rubrum* apparently reacts to the seston protein concentration in the water column and to the presence of particularly strong currents (Rossi 2002).

Food Pulses

In April 2002 a feeding pulse (mainly crustaceans, see Table 1a) was detected in the large colonies, whereas such a pulse was not detected in the small colonies settled within the same patch. Feeding pulses have also been described from other passive suspension feeders both in long term and short cycle studies and are likely to be an effect of patchy distribution of prey and variable water movement (Barangé and Gili 1988, Coma et al. 1994, Orejas et al. 2000, Rossi et al. 2004). In warm temperate seas, the pulses were more frequent during winter and spring, when capture rates are higher because the particles are more abundant and of higher nutritional value since they are linked to phytoplankton blooms (Grémare et al. 1997). The importance of such food pulses is still not well understood within the

context of the energy budget of passive suspension feeders, but it has been suggested that some species may rely entirely on this non-constant food income (Orejas et al. 2001). Future work should focus on explaining the role of such food pulses which may be the key to understand energy budgets and the plankton-benthos energy transfer, especially for filter feeding communities.

Effects of colony size and depth gradient on prey capture

Higher prey capture rates in colonies at deeper zones may be related to the lower density of red coral colonies (Tsounis et al., submitted). In line, Kim and Lasker (1997) described differences in prey capture related to density and height of gorgonians ("trophic shadow"). Although hydrodynamism is higher in shallow zones increasing prey capture (Sebens et al. 1997), the results of the present study show higher gut contents in deeper colonies of equal size (< 6 cm high). This seems to contradict the results of Lasker et al. (1983) describing higher feeding rates in shallow populations of two tropical gorgonians. Harland et al. (1992) also showed that shallow corals had higher lipid concentrations than deep ones, suggesting higher zooplankton availability in shallow zones. The occurrence of detrital POM in the red coral diet appears to be the explanation, as shallow *Corallium rubrum* colonies colonise areas in small patches where the resuspendable particles are less concentrated compared with deeper zones (Gili and Ros 1985). Thus the observed high capture rates in deep water are a result of the high POM proportion in the diet, whereas species depending on of zooplanktonic appear to capture more prey in shallow water (Lasker et al. 1983; Sebens et al. 1997; Harland et al. 1992).

In situ **feeding experiments**

The ingestion rate estimated from *in situ* feeding experiments varied between 0.1 and 0.17 μg C polyp^{-1} h^{-1} (0.085 ± 0.089 μg C polyp^{-1} h^{-1}), which is notably higher than the capture rate of 0.003 ± 0.002 μg C polyp^{-1} h^{-1} estimated from gut contents. This is related to the fact that fine particles such as microplankton and fine POM are only partially detectable in gut content analysis (Ribes et al. 1999b; Ribes et al. 2003). Thus the results confirm the microscopical observation that the detrital POC constitutes the main component of the diet. The average of 0.085 ± 0.089 μg C polyp^{-1} h^{-1} is close to the detrital carbon measured in the aposymbiotic gorgonian *L. sarmentosa* (0.06 μg C polyp^{-1} h^{-1}, Ribes et al. 2003) and higher than that measured in *P. clavata* (0.001 μg C polyp^{-1} h^{-1}, Ribes et al. 1999b). In both *L. sarmentosa* and *P. clavata*, detrital POC represents the most important part of the fine fraction (Ribes et al. 1999b; Ribes et al. 2003), which confirms the results for *C. rubrum*. Although detrital POC is a poor-quality food source in the Mediterranean sea (Grémare et al. 1997), it constitutes the most abundant source of nutrition in the water column throughout the year at the study site (Rossi et al. 2003). The applied methodology allows the detection of smallest components of the diet (diatoms,

dinoflagellates, ciliates, etc., Ribes et al. 2000); however, such components seem to be of minor importance in warm temperate octocorals compared to the detrital carbon (Ribes et al. 1999b, Ribes et al. 2003), thus this study did not focus on these groups.

Effect of red coral predation on seston abundance

The overall population grazing impact of $0.091 - 0.15$ mg C m^{-2} d^{-1} is considerably lower than those found in other octocorals (*Dendronepthya hemprichi*: 451 mg C m^{-2} d^{-1} Fabricius et al. 1998; *P. clavata*: < 170 mg C m^{-2} d^{-1} Coma et al. 1994, Ribes et al. 1999; *L. sarmentosa* 2.3 - 16.8 mg C m^{-2} d^{-1}, Rossi et al. 2003; *Plexaura flexuosa*: 0.15 mg C m^{-2} d^{-1}, Ribes et al. 1998).

However, this is still a high grazing impact taking into account the average size of red coral of only 3 cm (Tsounis et al., submitted), compared to most other gorgonians that average a height of 20 – 100 cm (Coma et al 1994; Weinbauer and Velimirov 1998; Rossi et al 2004). When evaluating the potential impact of the species, it must also be considered that *C. rubrum* populations are under an immense harvesting pressure and thus populations consist predominantly of younger and smaller colonies compared to colonies measured 20 years ago (García-Rodriguez and Massó 1986). Colonies of 20 cm have far more than 1000 polyps, ten times more than small colonies of 5 cm height (G. Tsounis, pers. obs.). Therefore, while the present, overexploited (Santangelo et al. 2001) red coral populations have a low impact on the seston, the potential impact of the populations under natural conditions would be magnitudes higher.

Seasonality

Unlike *P. clavata* (Coma et al. 1994) *C. rubrum* lacks a seasonal pattern in food capture. This diminished seasonality has also been observed in *L. sarmentosa* (Rossi et al. 2004), and indicates that not only the plankton composition of the water column, but especially water movement determines prey capture (Dai and Lin 1993; Sebens et al. 1997; Fabricius et al. 1995; but see Ribes et al. 1998). Unlike other passive suspension feeders, whose diet commonly reflects the composition and abundance of the plankton, *C. rubrum* and *L. Sarmentosa* employ a different feeding strategy: In addition to the ability to take advantage of large zooplankters when they become available in spring, those two gorgonians balance their energetic needs through the constant capture of detrital POM. A similar feeding strategy has been found in Antarctic suspension feeders that capture microbial plankton during the plankton-poor winter months (Orejas et al. 2001). Thus the constant availability of POM and the role of watermovement in prey capture explain the lack of a typical seasonality in the prey captire of *C. rubrum*.

Conclusions

This first study on the grazing impact of Mediterranean red coral populations found detrital POM and crustacean fragments to be the most important components of the diet. Prey pulses that are not easily detected by gut content studies may be a characteristic way of nutrition in passive suspension feeders, since the seasonal plankton composition of the water column influences prey capture rates less than water movement. Other factors that significantly affect prey capture rate were depth and colony size. The present grazing impact of *C. rubrum* populations on the seston community is comparable to other octocorals, and would hypothetically be much higher in unexploited populations.

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PUBLICATION IV

RED CORAL (*Corallium rubrum* L.) HARVESTING AT THE COSTA BRAVA (NW MEDITERRANEAN): STRATEGIES FOR MANAGEMENT AND CONSERVATION

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ABSTRACT

The Mediterranean red coral (*Corallium rubrum*, L. 1758) is an overexploited gorgonian with slow growth, low natural mortality and consequently a long lifespan. Commercial harvesting has significantly changed its population structure. 80 % of the present colonies are smaller than the legally harvestable size limit, and 98 % of all colonies show a rudimentary branching pattern, having only primary and secondary branches. This decline of red coral stocks has been observed throughout the Mediterranean during the last decades. This study used new data on red coral reproduction, growth and population structure in order to provide productivity estimates and recommendations for a sustainable fishing strategy at the Costa Brava (Catalan coast) in NW Spain. Maximum yield is reached at an age of first capture of 98 years. The yield per recruit corresponding to this age was estimated at 68 g, resulting in an annual maximum yield of 64 t for the Cap de Creus area, where 90 % of all red coral from the interior (nearshore) waters of the Costa Brava are harvested. However, current practise of harvesting at an age of first capture of approx. 11 years (corresponding to a basal colony diameter of 7 mm) was estimated to yield only 3.7 t anually, illustrating the fishery´s inefficiency compared to an optimal harvesting strategy. Declared annual yields are much lower at 0.8 – 1.7 t, which may indicate a significant amount of undeclared harvest and poaching. Mortality calculated for the commercial stocks has risen in the last 18 years, indicating overharvesting. The presented data show that current commercial fishing practises and poaching constitute a non-sustainable and suboptimal resource use. Recent trends in the illegal harvest of small colonies represent a further indication that the red coral stocks at the Costa Brava are overexploited.

KEYWORDS: *Corallium rubrum*, precious coral, fishery
management, maximum sustainable yield, poaching, Mediterranean

INTRODUCTION

The Mediterranean red coral (*Corallium rubrum*, L. 1758; Gorgonacea, Octocorallia) is a sessile cnidarian that forms arborescent colonies, whose calcium carbonate skeleton is highly regarded in the jewellery industry (Tescione 1973). *C. rubrum* colonies can reach a height of 50 cm (Garrabou and Harmelin 2002), yet due to over-exploitation the average colony height in the harvested zone off the Costa Brava is just 3 cm (Tsounis et al., submitted, a). The situation at the Costa Brava reflects harvesting effects that have been documented throughout the Mediterranean (Abiiati et al. 1992; Santangelo and Abbiati 2001). In Calafuria (Italy) for example, two thirds of the population are still not sexually mature (Santangelo et al. 2003a, b), although red coral is relatively young at first reproduction (Grigg 1989; Santangelo et al. 2003b; Tsounis et al., submitted, b). Other Mediterranean populations are likewise dominated by extremely young colonies (García-Rodríguez and Massó 1986a; Abiatti et al. 1991; Santangelo et al. 1993; Linares et al. 2003). A sustainable fishery management is needed, that maximises the yield while ensuring an adequate number of sexually mature individuals (Grigg 1976).

This study used recent data on the demography and reproduction of Costa Brava populations (Tsounis et al., submitted, a) to estimate the maximum production of this stock and compare it to declared yields and data on current fishing practises. The Beverton-Holt model for fisheries management (Beverton and Holt 1957) has been used to estimate the maximum sustainable yield as it has been successfully applied to the black coral fishery of Hawaii (Grigg 1976, Grigg 2001), and allowed recommendations for the red coral fishery (García-Rodríguez and Massó 1986b). This model is based on the principle that a stock gains in weight until that gain is overtaken by mortality losses, with the turning point defining the maximum sustainable yield for the fishery. The results help to estimate the optimal harvesting level for the Costa Brava population, which would allow a sustainable fishery while maximising its yield. Furthermore, by contrasting the data with recent industry trends, the study points out the problems and peculiarities of the red coral fishing industry at the Costa Brava.

MATERIAL AND METHODS

Study area
The present study was carried out at the Spanish NW Mediterranean coast, the Costa Brava (Fig. 1). The productivity and yield estimates focus on the Cap de Creus area since
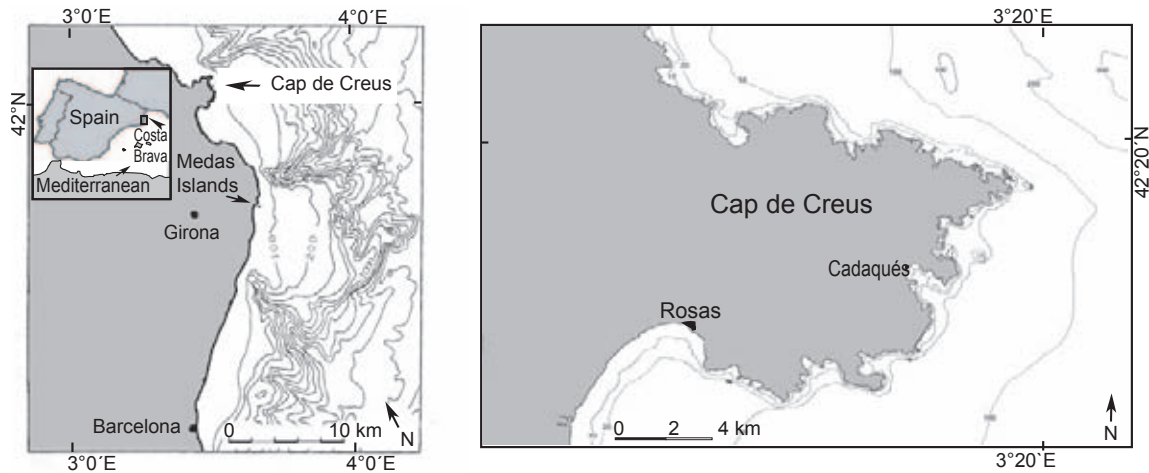
Figure 1: Map of the main red coral harvesting area:
Cap de Creus, located at the Costa Brava (Mediterranean)

this is where the main part of red coral is harvested. Furthermore, the Spanish fishery legislative (and thus fishery statistics) distinguish between interior waters, the coastal area from cape to cape, and exterior waters (outside the area enclosed by an imaginary line from cape to cape). In this study we focus our attention on interior waters, since 60 – 100 % of the Costa Brava coral is harvested here (A. Pluja, pers. com.).

The Beverton-Holt model for fishery management

Maximum production of a fish stock is defined as the point where mortality losses outweigh the weight gain by growth (Beverton and Holt 1957). This point can be calculated by following a year class of recruits (cohort) as expressed by the following formula:

Yield/recruit = $0.086*(G*t)^{2.198} * N_0*e^{-m*t}$ (García-Rodríguez and Massó 1986b)

where G = growth rate; t = age; m = mortality. Maximum yield is the product of maximum production (yield per recruit) and the number of recruits in that cohort. Maximum yield was compared to declared yields in order to judge the efficiency of the fishery. Data on fishing practises were obtained from the FAO technical consultations, interviews with local red coral fishermen, and local fishery statistics provided by the Department of Agriculture and Fisheries of the Governement of Catalunya.
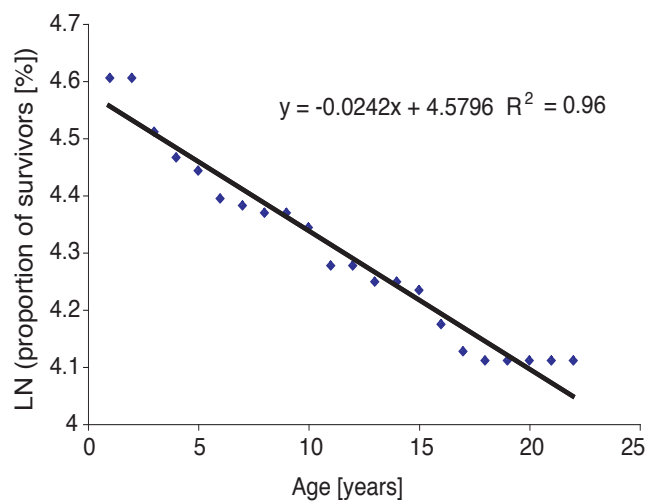
Figure 2: Natural mortality of *Corallium rubrum* in a colonisation experiment. Data from Garrabou & Harmelin (2002)

Mortality

A precise value for natural mortality is the most critical parameter in

the Beverton-Holt model, and can be derived from a natural population by applying the following equation:

$N_t = N_0 * e^{-mt}$
(see Grigg 1976)

Where: N_t = number of individuals at time t; N_0 = number of individuals at time 0; t = time in years; m = instantaneous annual rate of mortality.

However, estimating natural red coral mortality by using the population structure of natural populations is not possible, as no virgin populations are known. Thus the mortality value used in this study (m = 0.0242) was calculated in a similar way from the decrease of survivors in a 22 year settlement experiment by Garrabou and Harmelin (2002). Most recruits settled between 1976 and 1978 and recruitment was low and steady thereafter. This makes it possible to calculate the natural mortality of red coral (Fig. 2).

A maximum level of natural mortality of 0.066 was applied in the calculations (see FAO 1984), based on the observation that natural mortality of *Corallium secundum* in Hawaii is as high as 0.066 (Grigg 1976).

Table 1: Basal diameter growth rates of red coral

Location	Growth rate (mm yr^{-1})	Study method	Reference
Cap de Creus, Spain	1.32	Growth ring analysis	García-Rodríguez and Massó 1986
Calafuria, Italy	0.91	Growth ring analysis	Santangelo et al. 1993
Calafuria, Italy	0.64	Recruitment experiment	Bramanti et al. 2003
Marseille, France	0.24 ± 0.05	Recruitment experiment	Garrabou and Harmelin 2002

Total mortality at the Costa Brava was determined by the slope of the regression of the natural logarithm of the age frequency (Grigg 1976). The size structure obtained in a recent demographic study at the Costa Brava (Tsounis et al., submitted, a) was used for this purpose. As these data also provide a comparison between harvested populations and the Medas Islands Marine Protected Area (MPA), the present study could compare mortality in a harvested and a nonharvested population.

However, as those data underrepresent colonies younger than 6 years, these were excluded from the analysis. Only the middle part of the curves, from 6 years to 32 years, was used to calculate the slope, as this contained the most representative and reliable data. Finally, an additional estimate was made using the growth rate of 1.32 mm yr^{-1} in order to be able to compare the data to a study made in 1986 (García-Rodríguez and Massó 1986c).

Age conversion

The diametral growth rate of red coral was used to convert size classes into age classes, as age and the basal colony diameter show a high correlation (Santangelo et al. 1993).

Although it cannot be said whether the growth pattern is linear over the entire lifespan, it serves as a usable estimate. Growth rates used in this study were based on recent experimental studies measuring 0.24 mm yr^{-1} and 0.64 mm yr^{-1} (Table 1), depending on the environment. The higher growth rate of 0.64 mm yr^{-1} serves as the most probable approximation to coral growth at the Costa Brava, as it is an exposed coast with favourable trophic conditions and local fishermen state that diametral growth may be up to 1 mm yr^{-1} (Plujà 1999).

Weight-age relationship

Establishing a relationship between either colony size and weight, or ultimately age and weight, permits the calculation of the biomass increase of a single organism or a whole

Table 2: Maximum sustainable yield for various mortalities and growth rates of *Corallium rubrum*

Mortality	0.02307[a]	0.0242	0.02533[b]	0.0242	0.066	0.066
Growth rate (mm yr^{-1})	0.64	0.64	0.64	0.24	0.64	0.24
Maximum yield recruit[-1] (g)	62	68	76	7.9	7.6	0.87
Age at maximal production (yr)	85	98	93	98	33	33
Maximum yield (t)	58	64	71	7.5	7.1	0.82

[a]mean – std error; [b]mean + std error
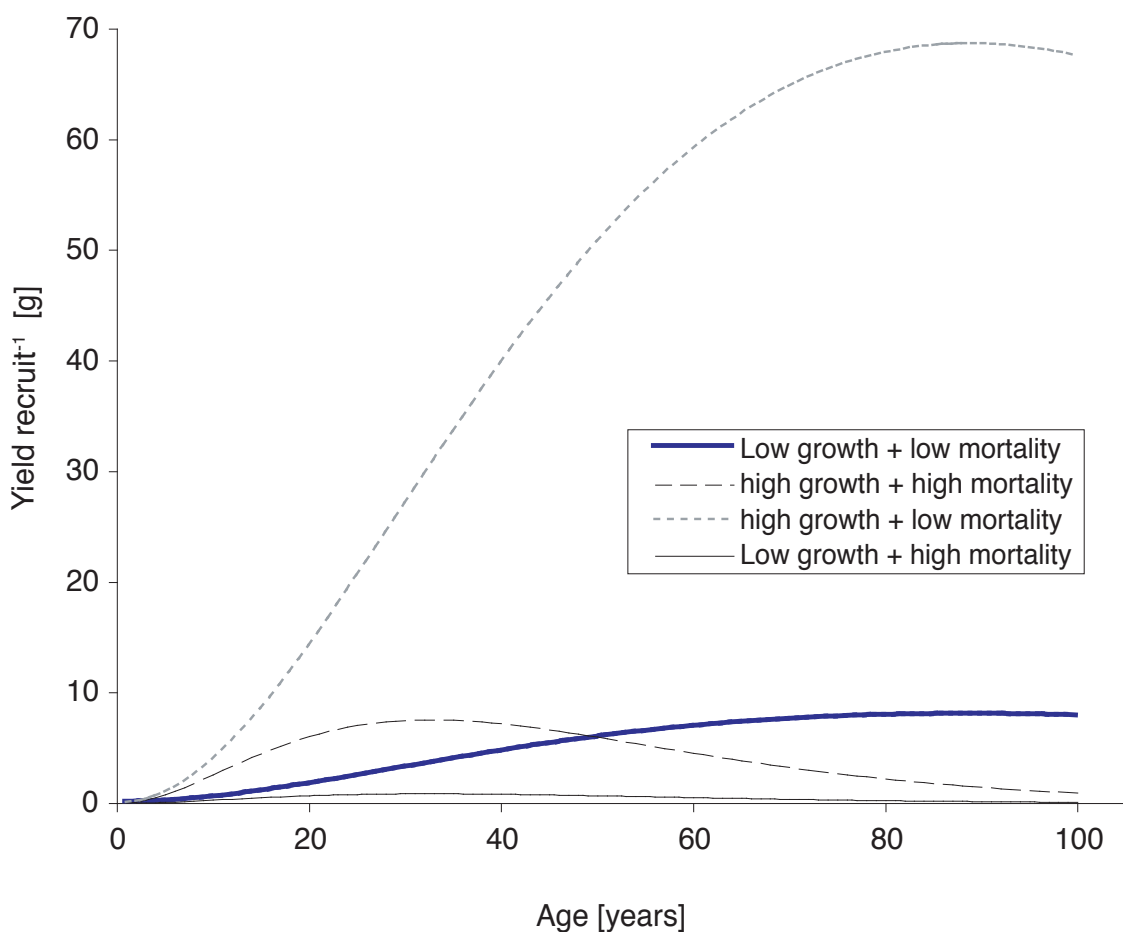
Figure 3: Yield per recruit curves for *Corallium rubrum* at various growth rates and mortalities

Table 3: Maximum yield of *Corallium rubrum* at various mortalities, at an age of first capture of 11 yr (7 mm basal diameter and at a growth rate of 0.64 mm yr⁻¹)

Mortality	0.0242	0.066
Yield recruit⁻¹ (g)	3.9	2.6
Yield (t)	3.7	2.4

Table 4: Total mortality of *Corallium rubrum* from the Mediterranean

		Growth rate of basal diameter (mm yr⁻¹)	
		1.32	0.64
Costa Brava	1986	0.5*	-
Costa Brava	2003	0.75	0.23
Medas Islands	2003	0.5	0.36

*García-Rodríguez and Massó 1986b
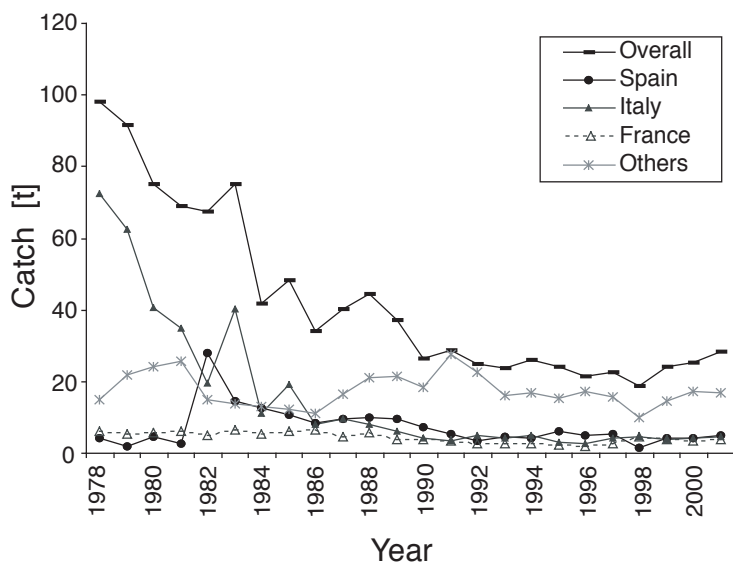
Figure 4: Red coral harvest in the Mediterranean. Data from FAO 1984

population, and is the key to estimate production. A weight-size relationship reported by García-Rodríguez and Massó (1986a), was used as it was established for the studied population:

$$W = 0.086 * G^{2.198}$$

(García-Rodríguez and Massó 1986a)

where: W = weight; G = basal diameter of the colony.

Stock size

An approximation for the proportion of length of coastline to coralligenous area has been obtained from a bionomical study of the Medas Islands at the Costa Brava (Ros et al. 1984) showing that 1 km of coastline corresponds to 0.01 km² of coralligenous substrate area. Increased surface area due to steep walls and boulders was not considered, as no
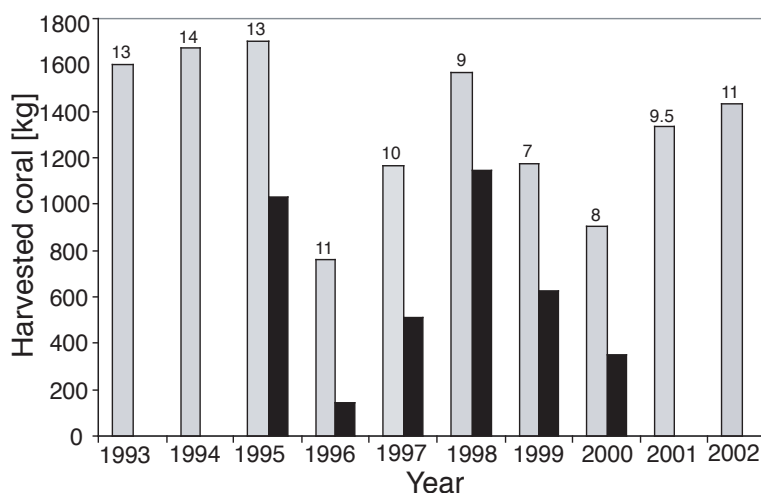
Figure 5: Red coral harvest in interior (grey) and exterior waters (black) of the Costa Brava (NE Spain). Interior (nearshore) waters are defined as areas inside capes. The numbers above the bars indicate the number of licenses

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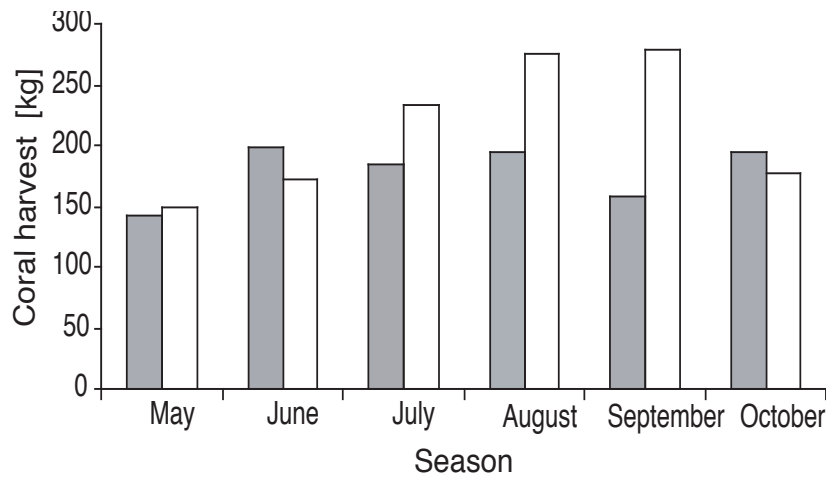
Figure 6: Monthly harvest of red coral in 2001 (grey) and 2002 (white)

quantitative data are available. This study considered only the Cap de Creus stock (Fig. 1), where 90% of all Costa Brava coral is harvested regarding interior (nearshore) waters. The surface area occupied by unsuitable habitats, such as shallow bays, was subtracted, and resulted in 275,000 m² of coralligenous area. Data on the red coral population density in coralligenous habitats at the Costa Brava (Tsounis et al., submitted, a) were used to calculate the stock size. Thus a *C. rubrum* abundance of 3.42 colonies m^{-2} results in a stock size of 940,500 colonies.

RESULTS

Yield estimates

The yield curve produced for this natural red coral population with low mortality and high growth rate results in a maximum yield recruit^{-1} of 68 g at an age of first capture of 98 years (Fig. 3). Using various combinations of growth rates and estimates for mortality results in an age at maximum production between 33 and 98 years and a maximum yield of 0.82 – 64 t (Table 2). A low growth rate as found by Garrabou and Harmelin (2002) in France results in a yield of 7.5 t which is 12 % of the yield obtained when assuming high growth rates as found in Italy (Bramanti 2003). However, the model demonstrates that the current practise of harvesting coral with a basal diameter of 7 mm (11 years old) results in a yield of only 6 % of what would
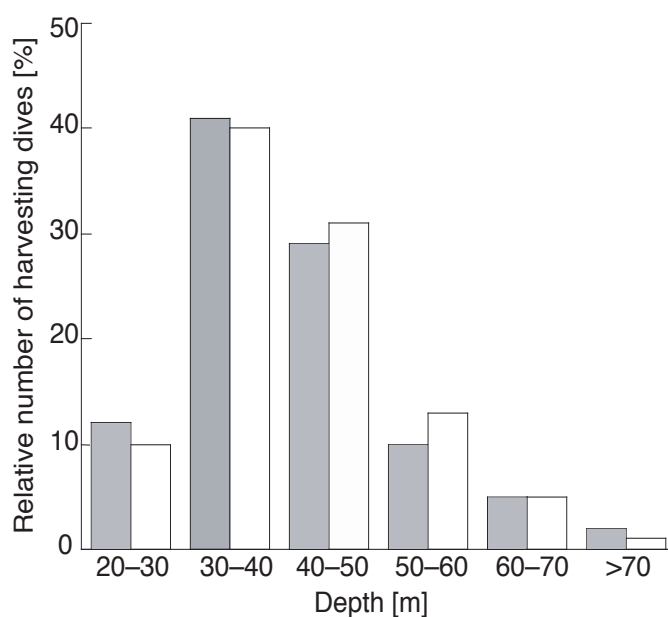
Figure 7: Bathymetric range of red coral fishing activities at the Costa Brava in 2001 (grey) and 2002 (white)

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be reached by harvesting coral colonies of 98 years. Even assuming a very high natural mortality of m = 0.066 results in an optimum age at first capture of 33 years, and harvesting 11 year old colonies yields only 34 % of the maximum value. Thus harvesting colonies of 7 mm in basal diameter results in a yield of 2.4 – 3.7 t (6 – 34 %), depending on the natural mortality (Table 3).

Mortality

Total mortality (the sum of natural and fishing mortality) is notably higher at the coast (m = 0.360) than in the Medas Islands Marine Protected Area (m = 0.230), although the mortality at the Medas Islands is not as low as the natural level (m = 0.0242 ± 0.00110 (mean ± SE)) (Table 4). Population structure models using these mortality values show a much higher number of old colonies than observed in reality. This indicates that mortality of large colonies must be infinitively high compared to young colonies due to selective fishery pressure.

Coral fishing data

In recent years the overal Mediterranean yield was about 25 – 30 t per year, 4 – 5 t of which were harvested in Spain (Fig. 4), of which 0.8 – 1.7 t were harvested off the Costa Brava (Fig. 5). The drop of number of licenses in 1996 – 98 (Fig. 5) reflects a political commitment to a stepwise ban of coral fishing at the Costa Brava, that was subsequently taken back. In recent years the number of fishing licences for interior waters of the Costa Brava was relatively constant at 7 – 11 licences, as has been the total yield in the Mediterranean and at the Costa Brava (Fig. 4 and Fig. 5). A moderate correlation between the number of licenses and total yield has been found ($W = 0.0041*N + 5.0867$, where W = harvested coral (kg yr^{-1}) and N = number of licences; $R^2 = 0.34$; p< 0.05). Local fishery statistics from the Costa Brava show that in 2001 and 2002 the yearly harvest was just above 1 t, most of which is fished in the Cap de Creus area.

The harvesting season begins in May when water temperature rises and the sea becomes calmer. Monthly harvest is highest in August and September when warm water temperature allows the longest working periods per day (Fig. 6). At Cap de Creus 70 % of all coral are harvested at depths of 30 – 50 m (Fig. 7). Only 2 % of 998 declared dives in 2001 were deeper than 70 m (in 2002: 1 % of 1024 declared dives). The harvest per dive and diver ranges between 0.5 and 2 kg. Interviews with red coral experts revealed that the Cap de Creus area is the most productive red coral stock known, i.e., where coral grows fastest and can be found at much shallower depths than elsewhere in the Mediterranean (see Plujà 1999).

DISCUSSION

Maximum sustainable yield in red coral

The Beverton-Holt model incorporates an exponential growth function combined with a logarithmic decline of mortality in time. Thus the resulting curves have a hyperbolic shape that marks at its turning point the age at first capture at which the maximum yield occurs. The curves illustrate that the fishery of a longevous species like red coral reaches its maximum yield only at a substantial age at first capture (33 – 98 years, depending on the natural mortality incorporated into the model: the lower is mortality, the later is maximum yield reached). Maximum yield in other precious corals such as *Anipathes dichotoma* and *Corallium secundum* has been estimated at 28 and 34 years, respectively (Grigg 1976). These Hawaiian gorgonian species reach the age at maximum yield earlier than *C. rubrum* as they have a higher natural mortality than red coral. The estimated maximum annual yield for the Cap de Creus stock of 64 t is far higher than the overall Mediterranean yield ever declared. When harvested at an age of 11 years (7 mm basal diameter of the colony), according to regulation by current laws, the yield drops to 4.5 t. Even then the declared yield is still several times lower. Although the population density estimates limit the precision of the results, it is unlikely that a yield that low has resulted in overexploited populations. Thus, even assuming a considerable overestimation of the yield, it appears that either a significant part of the yield is not declared, or colonies much younger than 11 years are harvested, thus further diminishing the yield.

Precision of the model

In line with other precious corals (Grigg 1976), the assumption of constant recruitment appears to be met in red coral, as the population´s demographic structure (Tsounis et al., submitted), shows no missing size classes.

Estimating the stock size is limiting the precision of the total yield predictions, however, due to the patchy distribution of red coral and the lack of bionomic maps of the Cap de Creus region this is the best approach possible at present. Furthermore, if errors in the model are small, it means that the estimated optimal age at first capture is correct regardless whether the absolute stock size is accurate. In fact errors in the model itself due to inprecise estimation of growth rate and mortality appear to be very small: Recent experimental studies tend towards low growth rates of 0.24 and 0.64 mm yr^{-1} growth in basal diameter, depending on the trophic conditions and geographic region (Table 1). Red coral experts regard the Cap de Creus as the most productive area in the Mediterranean (Plujà 1999), which makes the chosen growth rate of 0.64 mm yr^{-1} a conservative, but credible value.

Variations in the value of natural mortality of 0.01 can double or halve the yield (Grigg 1976). However, the similarity of the natural mortality value estimated in our study

from data by Garrabou and Harmelin (2002) with the one found by García Rodriguez-Massó (m = 0.028, 1986c) gives confidence in the value of this most critical parameter. García-Rodríguez and Massó (1986c) used an alternative method to calculate natural mortality on the basis of the observation that large colonies measure about 45 cm and must have survived for 90 – 145 years.

Figure 8: Left: rather rare red coral specimen with well developed branching pattern: right: specimen representing 71 % of the population that have not yet grown second order branches

The applied relationship of basal diameter and weight is supported by the fact that the calculated weight of a colony with an average age of 14 years (3 g of wet weight) coincides well with the average weight measured by Zabala et al. (2003), and the fact that a maximum weight of 2 kg (Garrabou and Harmelin 2002) is reached at 100 years (García-Rodríguez and Massó 1986c). The weight-size relationship of colonies with larger diameters in present overharvested stocks is better described by a different relationship, as the harvesting pressure causes a slight alteration of the biometry due to the lack of ramification in repeatedly harvested colonies (Zabala et al. 2003). However, these are not suitable to model a population in steady state, which is what the presented model tries to achieve.

Age at first capture

García-Rodríguez and Massó (1986c) proposed a minimum harvesting limit of a basal diameter of 8.6 mm on the basis of their modelling, which was not adopted by fishery policy makers. Instead, recent demographic data show that now there are even fewer colonies left that exceed a basal diameter of 7 mm than there were in 1986 (García-Rodríguez and Massó 1986a; Tsounis et al., submitted, a). The significance of this is stressed by studies decribing the larval production of various age classes of the population (Santangelo et al. 2003b; Bramanti 2003). In any red coral population a young colony produces only tens of planulae, while an old, large colony produces hundreds or even more than 2000 planulae (Stiller and Rivoire 1984; Santangelo et al. 2003b). This is due to the exponential relationship between the number of polyps and colony size/age in

modular organisms such as octocorals (Santangelo et al. 2003b).

Even a small percentage of colonies within the population is capable of producing the majority of the larvae (Babcock 1991; Coma et al. 1995).

Age at first capture for gorgonians should be substantially larger than age at first reproduction, to provide a sufficient time of reproduction before colonies are harvested (Grigg 1976). Ripe gonads can be found in colonies as young as 2 – 3 years (Santangelo et al. 2003b; Tsounis et al., submitted, b). However, contrary to the fast growing Italian and Spanish populations, a population with slow colony growth in a cave in southern France (Garrabou and Harmelin 2002) appears to reach the age at first reproduction at 9 years (Torrents et al. submitted). In any case, age at first capture should take into account, that 100 % fertility is not reached before 6 – 9 years (Santangelo et al. 2003b; Tsounis et al., submitted, b). Thus the harvesting limit of a minimum basal diameter of 7 mm (11 year old colonies) provides only a 3 – 6 year period of 100 % fertility before capture. It appears that this has been sufficient for the survival of many harvested populations. However, a reproductive period of 3 years is very short compared to the recommendations for the fishery of black coral (8 – 10 years of reproductive period, see Grigg 1976). We therefore conclude that red coral populations are harvested down to the limit of their recoverablity. It is uncertain if the current potential for recovery is sufficient to withstand the combined effects of harvesting and possible mass mortality events, as mass mortality has been found to affect especially young colonies (Garrabou et al. 2001). If the population structure is shifted towards young colonies by illegal harvesting, there is a risk that a mortality event finally diminishes the proportion of reproductive colonies below the threshold necessary for survival of the population.

Recent fishing trends and poaching

Data on fishing practises and fishery statistics help to explain why the harvesting pressure on red coral at the Costa Brava caused the observed changes in the population structure: The usual drop of total catch and, consequently, fishing effort observed in most fisheries around the world documents the exploitation of the red coral stocks. Number of licenses and total yield at the Costa Brava were relatively constant in recent years, which might easily be mistaken for a sustainable situation, as there are no data about the quality and age of coral harvested. It is possible to achieve the same yield by harvesting down the stock until mature colonies are diminished.

This is likely as recent cases of poachers as well as licenced fishermen harvesting illegaly small coral are reported with increasing frequency (Zabala et al. 2003; Pluja, pers. com.), which is a sure indication that the stocks are overexploited. A contributing reason is that in earlier days small colonies were rejected by the industry, whereas at some point technological advances enabled small fragments to be ground to powder in order to produce a formable paste (FAO 1984). While poachers have had no incentive to comply

with size limits since the introduction of the use of coral paste, it is worrying that now even licenced fishermen seem to frequently harvest immature colonies. Another indication that the stock is overexploited is the fact that mortality has risen since 1986 (García-Rodríguez and Massó 1986b), and the lack of a more developed branching pattern (Fig.8) than tertiary branches in 98 % of the population (Tsounis et al., submitted, a), confirming a deviation from steady-state equilibrium of the population.

The local fishery statistics show that 70 % of all red coral is harvested at depths of 30 – 50 m (Fig. 7). This is a characteristic of the Cap de Creus area as other red coral stocks are located below 80 m. Working shallow not only allows professional fishermen at Cap de Creus to maximise their working time underwater and thus economise their logistics; it enables poachers to work much swifter than if they were diving to greater depths, as shallow dives require only little decompression stops during ascent, making them less vulnerable to encounters with patrols.

Most professional operations at Cap de Creus yield 0.5 kg of declared harvest per dive and diver, sometimes up to 2 kg. The recent increase of the price for coral tips of 1 – 2 mm in diameter from 60 € kg^{-1} to 240 € kg^{-1} requires a daily catch of only 2 – 4 kg to be economically feasable (Pluja, pers. comm.). Thus making profit from harvesting immature colonies is possible. It is problematic that the commerce of immature coral can only be controlled by patrols on the water, as the small, traditional and personalised network of the industry provides numerous routes for illegal coral into the market.

Poaching occurs in an organised fashion, as well as in the form of souvenir-collecting by recreational divers. Among the regular poachers that work in a professional manner, there are selective ones that take only large colonies in deep areas or marine parks, and there are non selective poachers, that work shallow and leave the substratum bare of any coral. Discouraging poachers by fines has proven little effective due to the excentric manner in that these locals defend their practise and neglect to accept legislative. Even though many poachers are known in their region, they are not convicted, and violence against competitors and even prosecutors has occurred.

An additional characteristic of coral fishing that originates from diving practises is the coincidence of the reproductive season with the harvesting season. *C. rubrum* releases its larvae at the end of July, whereas the harvesting season begins in May, when the water temperature and sea conditions begin to facilitate diving work. While there is perhaps no reason yet to change this practise, given the current reproductive potential of the population, it serves as a good example of how little the coral fishery is adapted to its resource. It is, however, possible that delayed harvesting could increase production, and this factor should be incorporated in future, more complex, models. It also means that protection of endangered stocks is more critical in spring.

Summary and conclusions

The highest priority in red coral fishery management should be the protection of immature colonies. The increased pressure on shallow red coral populations and the harvest of immature colonies represents a worrying situation. A legal age at first capture corresponding to 7 mm basal diameter provides only a short time of full reproduction that, however, may have been sufficient in the past. If harvesting of immature colonies is becoming more frequent, as recent observations indicate, action must be taken now, as this can lead to local extinction (Dobson 1998; Santangelo et al. 2003b).

Maximum yield in red coral is obtained at an age of several decades, up to 98 years. This fact and its consequences for management are well accepted in other examples of long lived, slow growing exploited organisms with low natural mortality, such as trees. Current fishing operates at a suboptimal yield of 7 – 30% of the maximum potential, while actually overharvesting the stock, as mortality has risen in the last 18 years.

The results further demonstrate that declared fishing yields alone were not sufficient to overharvest the Cap de Creus stocks, and that poaching is high enough to cause serious economic damage by jeopardising the industry´s sustainability. Future work should concentrate on obtaining more precise values on growth using long-time experiments, and on comparing reproduction and demography in various habitats. Bionomic maps would likewise help to provide the basis for more complex models that will prove useful for management and our understanding of natural and anthropogenic influences on benthic populations.

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