POPULATION DYNAMICS AND LIFE HISTORY TRAITS OF *CORALLIUM RUBRUM* POPULATIONS: IMPLICATIONS FOR SUSTAINABLE MANAGEMENT AND TRADE

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Abstract

Population demographics, especially density, abundance, size structure, and morphology (branching pattern), as well as certain life history traits (e.g. growth rates, reproductive strategy, and longevity), must be considered when developing fisheries management strategies for precious corals in the family Coralliidae, as these provide indicators of the status of these species and their vulnerability to harvest. All species of Coralliidae are sessile, modular (colonial) gorgonians characterized by slow-growth, low rates of natural mortality, and a long lifespan. They typically occur at low densities, but are capable of forming large, highly branched, tree-like structures in absence of disturbance. Most representatives in this family broadcast gametes into the water column on an annual cycle, relying on external fertilization and an extended planktonic development phase, while the endemic Mediterranean species, *C. rubrum*, is a brooder that releases well-developed, competent planula. This trait has allowed *C. rubum* to form dense assemblages in shallow water, where populations are dominated by small (< 5 cm tall), unbranched colonies. These populations exhibit high rates of early mortality, especially in environments frequently disturbed by natural stressors (e.g. temperature anomalies, bioerosion) and heavy collection pressure. However, this is not the normal situation: *C. rubrum* colonies are capable of achieving a much larger size (30-50 cm height) and more extensive ramifications, as reported historically, in deep water populations, and in shallow water when protected from fishing. The brooding life history strategy may have allowed the persistence of *C. rubrum* in marginal environments and when subjected to heavy fishing pressure, because planula display lower rates of mortality and higher settlement success than related broadcast spawning species. Nevertheless, these populations are highly susceptible to extirpation due to the selective removal of the largest colonies by SCUBA divers, followed by collection of progressively smaller colonies; these smaller colonies produce exponentially fewer larvae per reproductive event than large colonies and they reproduce only a limited number of times before being removed from the population. Furthermore, *C. rubrum* exhibits a single annual discrete reproductive event unlike other corals that are brooders, and local sources of planula are needed to maintain populations due to limited potential for long-distance dispersal. Deep populations may be even more vulnerable to extirpation, since they occur at much lower densities; they may experience allee effect (depensation) if harvest further reduces colony density below levels needed for successful fertilization. An increase in the minimum size of legal harvest (to at least 10 mm diameter and 10 cm height) is needed to rebuild overexploited stocks of *C. rubrum* and provide insurance against catastrophic disturbances. This measure would maximize reproductive output by increasing colony size, allowing colonies to develop third order branching patterns, and increasing the number of times a colony reproduces before removal by collectors. Harvest should be limited in deeper areas (> 50 m) where densities are lower until population dynamics and life history traits from the deep populations are better understood. Other management approaches, such as an increase in the number and size of no-take marine protected areas, are needed to maintain

high reproductive output and compensate for losses due to fishing pressure and other stressors outside of protected areas.

Introduction

Habitat forming corals are modular organisms made up of multiple, identical interconnected units (polyps) that form massive, plating, encrusting, and branching colonies. These corals are permanently attached to the bottom with exception of a short dispersal period during their larval phase. Like unitary animals, corals can be classified as r- or k-selected depending on their life history strategy, although some species exhibit a continuum across these traits. Most k-selected corals form large, long-lived colonies that expend considerable energy in growth and maintenance, and less in reproduction. These include some of the dominant framework corals found on shallow reefs (e.g. *Montastraea annularis*), many of which are hermaphroditic (Szmant 1991). K-selected corals broadcast millions of gametes into the water column during a single discrete event, once per year, which are fertilized externally. These larvae spend an extended period in the water column during their development phase, and have a high potential for long-distance dispersal, but they tend to exhibit very high rates of larval mortality and low settlement success. K-selected corals tend to live for decades to centuries, often sustaining partial mortality that increases over time, but colonies continue to grow indefinitely, and the likelihood of total colony mortality declines with size (and age) (Bak and Engel 1979; Bak and Meesters 1998). These corals must also achieve a certain minimum size before first reproduction, but individual colonies can reproduce indefinitely, as long as they remain above that minimum size.

In contrast, r-selected species are often considered “weedy species” that begin reproducing at a smaller size. These corals invest more energy in reproduction and less in growth, but they tend to have relatively short life spans. They are often the first species to colonize an area after a disturbance because they have naturally high production rates and great inter-annual variation in recruitment driven by stochastic environmental factors (Musik 1999). R-selected species include most brooders; these species have separate male and female colonies, where fertilization is internal, and females release well-developed planula. They produce fewer gametes per reproductive event as compared to broadcast spawners, but larvae have higher rates of survival and colonies often reproduce monthly on a lunar cycle to overcome shortfalls in larval release. Larvae are competent shortly after release and settle within close proximity to the parent, which may also enhance their success by colonizing habitats where their parents were most successful.

Modular Organisms

In addition to selected advantages associated with the different modes of reproduction, there are numerous advantages to a modular life history, such as the ability to survive with partial mortality. However, these organisms require very specific conditions for successful settlement (e.g hard substrate, low rates of sedimentation and algal biomass, and a narrow temperature range); once they settle and begin growing, they are generally unable to relocate if the conditions become unfavorable. They do exhibit the potential to adapt to their environment through various mechanisms such as modifications in growth form. For instance, some species of corals that contain zooxanthellae (symbiotic algae) form hemispherical colonies in shallow water, becoming more plate-like in deeper environments to maximize their surface area for optimal light capture. Branching corals may form short, thickened, robust branches in shallow areas with high wave exposure and longer, slender branches in calm protected environments. Branching species also often dominate large areas and individual colonies attain large dimensions (Gilmore and Hall 1976). Large sizes increases resistance to all but the most devastating physical disturbances and implies greater longevity, while small size implies either a cessation in growth, slow growth, or high colony mortality (Szmant 1986).

Modular organisms also exhibit highly complex growth patterns that can mask the age–size relationships that are characteristic of unitary organisms such as fishes (Hughes and Jackson 1980; Hughes 1984, 1990; Hughes and Tanner 2000). For instance, predation, disease, and other chronic disturbances that cause partial mortality can result in colonies of an identical age with dramatically different sizes or branching patterns. The combination of such variability in partial mortality and annual variation in recruitment makes it unlikely that a coral population ever achieves a stable age distribution, unless they are driven to an altered population structure dominated by small individuals that never reach their full potential for growth such as that observed in certain shallow *C. rubrum* populations (e.g. Calafuria, Italy; Santangelo et al. 2004). Because they are permanently attached to the substrate, they are also more susceptible to total colony mortality associated with human activities, such as collection, than motile fisheries species.

Reproduction and Recruitment

While short-term population dynamics of large, massive, or fast-growing branching species is influenced mostly by rates of recruitment, their ability to colonize new areas or areas that were catastrophically disturbed, and their ability to persist depends on the degree of success of reproduction (Szmant 1986). Reproductive strategies vary across genera and families of corals, with some species reproducing sexually through brooding and others via broadcast spawning, and some also capable of asexual propagation through fragmentation, polyp bailout, and other mechanisms. A coral's reproductive strategy is not necessarily correlated with polyp size or morphology, but reproductive differences may imply important differences in evolutionary selective pressures (Szmant 1986).

The family Coralliidae is one example of gonochoric corals that have a well defined seasonal pattern of sexual reproduction, which occurs only once per year (Santangelo et al. 2003; Torrents et al. 2005; Tsounis 2005; Tsounis et al. 2006b). Within the family, most species are thought to be broadcast spawners, while *C. rubrum* is the only representative known to be a brooder (Grigg 1993). This unique trait has major implications for the survival of *C. rubrum* when exposed to catastrophic acute disturbances (e.g. unusual temperature anomalies) and pressure associated with harvesting. First, the planula released by *C. rubrum* have a much shorter pelagic stage, which allows them to bypass high rates of mortality associated with planktonic development. They also exhibit higher recruitment rates, at least in shallow water, because they tend to settle in locations where their parents were successful. Nevertheless, there are also several factors that limit reproductive output in *C. rubrum*. Most corals that brood larvae are smaller than broadcast spawners; they reproduce on a lunar cycle, with many reproductive cycles per year, to compensate for the lower larval production per gametogenic cycle as compared to broadcast spawners that release millions of gametes (von Moorsel 1983; Szmant 1986; Richmond and Hunter 1990). *C. rubrum* only reproduces once per year, which results in much lower annual levels of larval production. Populations of brooders also tend to have shorter dispersal phases, which results in a high degree of genetic separation on a short spatial scale, and the maintenance and survival of these populations requires local sources of healthy reproductive populations to replace colonies that die or are collected.

Brooders are also more sensitive to changes in density, because the chance for successful fertilization is much lower. Colonies that are broadcast spawners synchronously release a large a pool of gametes that have a high likelihood of direct contact and fertilization and an obligatory development period before they become competent to settle (Willis 1990). *C. rubrum* is more similar to a pine tree that releases pollen. The pollen is ready immediately and becomes less viable with time. It requires a chance encounter with a female colony for successful fertilization, which will occur only if colonies are located within close proximity or water currents are suitable to transport sperm to female colonies. The magnitude of the dispersal for a brooder like *C. rubrum*, in terms of number of larvae dispersing and distance travelled, is much less than larvae of broadcast spawning corals (Willis 1990)

Size-dependent Reproduction

One of the most critical biological aspects for a sessile (attached) organisms that form complex, branching colonies and have long life-spans is colony size, as 1) reproductive output continues to increase with size and age; 2) growth to a larger size conveys a greater resistance to disturbance; and 3) it implies longevity. This is partially due to the modular nature of *C. rubrum*, where each polyp is interconnected with other polyps by a series of canals that are responsible for the translocation of water and nutrients, allowing all polyps to function together as a single, larger unit. These colonies must reach a certain size before they become sexually mature, but once that size is achieved they can reproduce indefinitely. In branching gorgonians, reproductive output increases exponentially with size and the largest colonies in the population are thought to produce 90% or more of the offspring (Babcock 1991; Coma and Gili 1995; Beiring and Lasker 2000; Santangelo et al. 2003; Torrents et al. 2005; Bruckner 2009).

Although *C. rubrum* is a brooder, it exhibits many traits in deep water that are similar to other gorgonians that are broadcast spawners (including other species of *Corallium*), presumably because fishing pressure and large scale environmental disturbances are less common which allows these corals to achieve much larger sizes. Most species in the family Coralliidae are in the low-productivity range as colonies are relatively slow-growing and long-lived, with population turnover estimated to occur once every 15-25 years (Grigg 1976) or longer, based on more recent estimates of age (Marschal et al. 2004). Brooding and early reproduction may be an adaptation that allows the coral to occupy marginal habitats in shallow water, because the colonies can never achieve a large size before dying (Santangelo 2003), which results in a much more rapid population turnover. These populations usually display high rates of recruitment (0-32 recruits/m^2 per yr from 1995 to 1999 in Spain (Linares et al. 2000), and 0-12.5 recruits/m^2 per yr from 1979 to 2000 in France (Garrabou et al. 2001)), although recruitment occurs in pulses with no successful settlement in some years, up to 95% of the larvae die before settling (Tsounis 2005), and 66-70% of the new recruits die over the first four years of life (Bramanti et al. 2005). Small colonies that dominate shallow areas of the Mediterranean today are also more vulnerable to total colony mortality, and their contribution to future generations is much less than larger colonies because they contain substantially fewer reproductive modules (polyps).

Significant differences in the size of *Corallium rubrum* colonies have been reported between locations and depths, and most areas affected by coral fishing and recreational diving have shown a general trend of declining size structure over the last four decades. For instance, colonies collected in the 1950s and 1960s were frequently up to 50 cm height and 2 cm diameter. A 1962 collection off Costa Brava, Spain consisted of colonies with basal diameter of 10-45 mm (mean = 16 mm) and height of 10-50 cm (mean = 11.5 cm) with the largest corals estimated at 50-80 years in age (Garrabou and Harmelin 2002). Colonies sampled off Costa Brava were still substantially larger in 1986 than that observed today with 85% of the colonies having a basal diameter > 5 mm (García-Rodríguez and Massò 1986). Shallow populations from Costa Brava (10-25 m depth) are now skewed towards small corals (mean height = 3.1 cm, max = 20 cm; mean diameter = 4-5 mm), most of which are young (< 8 years old) and only 35% have basal diameters > 5 mm. Colony height increases with depth to 4 cm height at 25-50 m and 6 cm at 50-90 m; the largest colonies (13-16 cm height) are found in non-harvested areas below 50 m depth (Rossi et al. 2008). Colonies in an adjacent protected area (Medas Island, Spain) closed to fishing for 15 years were 20-50% larger (mean = 4 cm height, max = 20 cm) than colonies at similar depths in fished areas off Costa Brava. Populations examined in 1998 in fished areas off France (Riou archipelago) were larger (mean height = 6 cm; range = 4-13 cm) than that reported for Spain (although small colonies were not examined in this study), but these colonies were still only about half the size of a similar habitat in France protected from fishing since 1983 (mean = 11.8 cm, range = 8-17 cm).

Differences in total reproductive output are directly related to colony size structure and the degree of branching. *Corallium rubrum* are gonochoric brooders that were reported to first produce gonads at 2-10 years age (minimum 2-3 cm height, 1.8-3.6 mm diameter), with colonies achieving 100% fertility at 4-6 cm height. The total number of polyps increased exponentially with colony size from about 25-90 polyps in a small (2-3 cm height) single branched colony to over 4000 in a 12 cm tall colony with over 35 branches, and 15,000 for colonies 30 cm in height. Even in the Ligurian Sea, where colonies never exceed 10 cm in height and most had few branches, the number of planula increased 7 fold from the smallest reproductively mature colonies (1.4-2.3 mm diameter, 24 planula) to the largest (> 4.6 mm diameter, 158 planula) (Santangelo et al. 1993). While small colonies may be the most important component in terms of reproductive contribution in some shallow populations today (Santangelo et al. 2007), this is only because the small colonies are numerically dominant, versus very few larger colonies. Nevertheless, when compared to their potential to achieve larger sizes the contribution of these small colonies to future generations would be much less if a population exhibits a more normal size frequency that is not skewed towards juvenile colonies. They are also less likely to sustain the synergistic impacts of fishing, natural stressors and climate change, and degraded areas have a delayed potential for recovery due to limited potential for long distance dispersal.

Relationships between Size and Density

Abundance and biomass are usually important factors in assessing population status and trends of fishery species. However, for sessile colonial species, size and relationships with density are more important measures, as size is a major determinant of first reproduction, reproductive output, and colony survival, and density is related to the likelihood of fertilization. In the case of *C. rubrum*, smaller colonies tend to occur in large aggregates because they settle relatively close to their parent; these smaller-sized colonies lack a branching morphology and exhibit higher rates of natural mortality. As they increase in size, they require more space, but survival also increases with size. If they are able to reach a large size, populations will ultimately become less dense, with a lower overall abundance throughout a bed, but populations will potentially have a higher number of polyps overall. For instance, a single large colony 300-500 mm in height can contain more polyps (up to 10,000 or more) than 100 or more small colonies that are 30-50 mm height (approx. 100 polyps), like those found today in the Mediterranean. The increase in polyps is partially related to size (larger colonies have more polyps overall), but large colonies lack polyps at the basal portions and polyps may be more dense but smaller at the branch tips. Most importantly, polyp number also increases in proportion to the degree of branching, which is much more extensive in large colonies. For these reasons, size/age structures give a better indication of population decline, as the fishery is size-selective (largest colonies are removed first) and a decline in the number of large colonies may result in an increase in small colonies as more space becomes available to support settlement of larvae.

Data on the population structure are also more useful in identifying a changing proportion of mature/immature colonies, which is more functional as a basis for management decisions that need to ensure minimum recruitment, especially for sessile animals that require a certain density to ensure fertilization success (Bruckner 2009; Tsounis et al. in press). Abundance data cannot be directly compared among populations or within individual beds over time, due to their patchy occurrence within these beds, differences in the available habitat within an area occupied by this coral, and highly variable features such as crevices and outcrops that are not uniformly distributed throughout the habitat. Also, numbers of colonies per unit area are unlikely to provide an indication of the population status or trends due to their life history traits, which include: 1) a sessile (attached) existence; 2) density-dependent recruitment within localized areas that result in dense populations of small, unbranched colonies; 3) the ability to form of large, highly branched, three-dimensional colonies that are long-lived and will reproduce annually for the duration of their lifespan, in the absence of physical disturbance (collection).

In Spain, depth was found to be only weakly correlated to population abundance while there was a stronger correlation with size, with larger colonies found in deeper water where fishing pressure was lower (Tsounis et al. 2006b). The weak relationship between density and depth may be due to small scale variation in environmental and habitat attributes. In very shallow areas (18-25 m) colonies occur in dense aggregations in cracks and crevices, under overhangs and on the walls and ceiling of small caves, where they form very small patches. In contrast at depths below 35 m, colonies occur in the open at lower densities but they cover a larger area and are larger in size. This trend was apparent several decades ago, where densities in Palma de Mallorca were reported at 55 colonies per square meter at 40 m depth and 20 colonies/m^2 at 60 m depth along the Costa Brava, while 90-100 colonies/m^2 were observed in Corsica (FAO 1984). These abundances are much lower than reported in the Ligurian Sea (Santangelo et al. 1993), but those populations may consist of 2/3 or more juvenile colonies. One of the limitations of these data is related to differences in sampling regimes; the scraping technique detects all corals, small and large, while other methods under count recruits. Furthermore, recruitment in the densest populations (Ligurian Sea) appears to be an order of magnitude higher than other areas and juvenile mortality is lower (Bramanti et al. 2006), but some of these dense shallow populations are much more susceptible to mass mortality events and partial mortality from sponges and other factors (Garrabou et al. 2001) and population turnover is very rapid, with few colonies ever achieving a minimum diameter of 7 mm.

Recommendations for Improved Management

- Increase minimum size of harvest to 10 mm basal diameter and 10 cm height: With exception of new measures adopted in Sardinia, most other locations in the Mediterranean that use size limits in their national coral management plans establish a minimum size of harvest for *C. rubrum* at 7 mm basal diameter. In one of the earliest demographic study of *C. rubrum*, García-Rodríguez and Massò (1986) documented the harvest of colonies that were 5-14 years in age which they concluded were well below maximum sustainable yield (MSY). Based on recent age studies that indicate *Corallium* colonies are 2-4 times older and growth rates are 2.6-4.5 times lower than previously thought (Marschal et al. 2004; Roark et al. 2006). Tsounis et al. (2007) estimated MSY of 98 years, whereas the current practice of harvesting colonies once they achieve a 7 mm basal diameter (11 year old colonies) results in only 6% of the potential yield. This increase in size would allow colonies time to develop branches, reach 100% sexual maturity, and reproduce multiple times before collected.

- Reduce collection at depths above 50 m depth: These populations are reported to be overexploited throughout the Mediterranean. Collection needs to be limited until colonies reestablish a larger size structure. Once these areas recover, collection should be limited to small portions of the total habitat and large-size colonies only (e.g. above 10 cm height).

- Create networks of protected areas (MPAs): MPAs should encompass all depths/habitats occupied by *Corallium* and portions of each bank where *Corallium* is collected. Existing no take areas (protected areas) for *C. rubrum* are relatively small and it is unclear whether they are sited such that they would replenish fished areas, given the high degree of genetic structure and evidence that populations are self seeding (Costantini et al. 2007).

- Rotational harvest: It is unclear how effective this measure would be unless rotational periods exceed 30-40 years to allow full recovery of populations as colonies in areas protected from fishing for 15-30 years are still less than half the reported historic size (Caddy 1993; Francour et al. 2001; Tsounis et al. 2006a).

- Limit harvesting in deep water: Proposals to limit collection to 80-130 m (mixed gas diving) appear to be short sighted at this time because we know too little about these populations. This move to deeper water may be a reflection of the depleted nature of the resource – all acceptable (large) colonies have been removed from shallow water and collectors are now targeting areas that have not been fished for 20 years or more (e.g. since elimination of the dredge). Harvest in these areas should be restricted until population structure is quantified and more data as both growth rates and recruitment may be much different in deep water due to environmental variations.

- Establish monitoring plans: Baseline studies on population dynamics must be completed before a new area is open to fishing. Conservative estimates of landings from these areas should be adopted based on the size of the bank that contains *Corallium*, its abundance and size structure. Collection areas should then be monitored on an annual basis to determine collection impacts and to modify measures as needed to prevent a shift in size structure as that observed in shallow water.

- Enforcement: Better monitoring of landings that include data on numbers of colonies, sizes (height and diameter), and numbers of branches, along with total weight, should be undertaken at ports and marinas, instead of voluntary reporting. Divers should be required to submit daily log books, including site locations, and strict penalties should be adopted for offenses. Once a minimum size is established, there should not be a variance allowed (e.g. 20% as included in the Sardinia plan), as this diminishes the value of a minimum size and it is an indication that inadequate numbers of larger colonies exist in an area if collectors are removing smaller corals.

Conclusions

For a modular organism that characteristically forms highly complex, branched colonies, and can reach sizes of 30-50 cm, a mean height of 3-5 cm, as reported from most shallow areas (< 50 m) in the Mediterranean, is equivalent to a loss of 80-90% of the reproductive modules (polyps) of individual colonies, due to the absence of 2nd, 3rd and 4th order branches. These small colonies can become sexually mature at a young age (2-3 cm height), although they don't achieve 100% fertility until about 6 cm height and 10-20 years in age or older. The spawning potential in *C. rubrum* (and other gorgonians) increases exponentially with size, with larger arborescent colonies producing up to 90% of the recruits. Given settlement rates of no more than 5% of the total larval production, and continued removal of colonies by fisheries after they have reproduced no more than one or two times, typical shallow population today may produce 80-90% fewer recruits than in the 1960s, and about half of that produced by populations that have been protected from fishing for 15-20 years and contain colonies twice as large.

Using only colony abundance and density as an indication of population size and viability can be misleading, as dense populations are limited to only *C. rubrum* and these tend to be dominated by small, reproductively immature colonies. For colonial organisms, change in population structure (size frequency distribution) is a more suitable measure of decline than changes in the absolute numbers of colonies. Commercial extraction primarily eliminates the largest corals, followed by smaller colonies over time, but it is the largest, oldest colonies that contribute most to the replenishment of the population. Furthermore, shifts in the size structure of populations due to fishing pressure can be directly compared, while density and abundance cannot. This is because these measures differ depending on how they are assessed (colony density measured over the entire suitable habitat is much less than the density of small patches occupied by the coral within this habitat), and the life stage of the population. In fact, a less-dense population is likely to represent an older, more stable and viable population as open substrates of suitable habitat can support high numbers of recruits, but these exhibit size-related survival that increases as the colonies get larger. Thus, populations with a high abundance and density, such as those seen in Mediterranean shallow water, are an indication of frequent continuing perturbations responsible for rapid turnover of populations and a persistent state of early-stage recovery. This is similar to observations of other corals that brood their larvae; however, most other corals that are brooders are considered early colonizing, "weedy" species, while *C. rubrum* is a long-lived species that may be attempting to adapt to increasing localized (direct human impacts) and global stressors (climate change). These types of populations are much less resilient to other stressors and are more likely to exhibit localized extirpations when compounded by fishing pressure than populations that contain a mix of small (10-50 mm tall), medium (60-140 mm), and large (150-500 mm) colonies, like that formerly observed in the Mediterranean and still present in some deep-water areas that have not been targeted by fisheries for several decades.

Throughout most of the Mediterranean, *C. rubrum* colonies in shallow water now form small, high density aggregations within much larger areas of suitable habitat, while the corals become less dense and larger in size in deeper areas with lower fishing pressure. These dense shallow aggregations are dominated by recruits and small adult colonies, generally no more than 3-5 cm in height with few colonies over 10 cm in height, whereas historically colonies were 20-50 cm in height. Because of the sessile nature of the species, further reductions in density associated with the selective removal of the largest colonies in deeper coral beds may alter reproductive potential due to allele effects. Also, the smaller organisms in shallow water may experience catastrophic mortalities when fishing pressure is compounded by other stressors such as climate change.

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