The role of trophic interactions between fishes, sea urchins and algae in the northwest Mediterranean rocky infralittoral

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Chapter 1- General introduction.

The discipline of ecology is habitually divided up into a whole range of different specialities, and this thesis forms part of what is commonly known as “community ecology” (Diamond and Case 1986). To be more precise, my work has centred on the degree to which the trophic relationships that exist between the organisms constituting a food web govern the structure and dynamics of the communities they form. I approached the subject from an experimental point of view and all the work was carried out in the field by means of what are referred to as “natural experiments”, with all the advantages and disadvantages that this supposes. The chosen ecosystem was the coastal marine benthos or, to be more specific, rocky infralittoral communities, a propitious place in which to work since this setting has seen the production of some highly important contributions to community ecology, above all in the development of experimental techniques (review by Castilla 2000).

Owing to the existence of previous investigations, my work, strictly speaking, does not break any new ground, since the subject matter has already been well studied in other oceans (see Castilla 2000 for a revision). Paradoxically, the Mediterranean, the cradle of the natural sciences (Aristotle, 350 BC) and home to the invention of scuba diving by Gagnan and Cousteau in 1944, has generally not been witness to any of the most important advances in experimental benthic science. Whilst not wanting to question the universality of discoveries regarding benthic communities made in other waters, it can surely not be an excessive precaution to attempt to understand the way regional peculiarities - the Mediterranean is a very singular sea in many ways (Margalef 1985) – affect general principals.

One highly significant way in which benthic experiments in the Mediterranean are playing a part in current debate is the role that marine reserves or protected marine areas (PMAs) can be expected to play as management tools in ecosystems adversely affected by human action. In this sense, my work shares a characteristic with many others: the use of marine reserves as experimental sites that can be compared with nearby unprotected zones in order to try and judge their worth.

As a final reflection on the main object of study in my thesis it is worth remarking that the system under study relates on a trophic level macroscopic algae – the main primary producers in the phyto-benthos – to their herbivores, which in the coastal Mediterranean benthos are essentially a sea urchin (*Paracentrotus lividus*), a fish, the salema (*Sarpa salpa*), and a guild of omnivorous fish that include optional grazers of algae and predators on sea urchins. My study investigated the interactions taking place between all the actors in this complex community and not just the interactions occurring between a certain group of species, although inevitably, given its central position, the sea urchin *Paracentrotus lividus* has been the focal point of our efforts. As a means of simplifying, throughout this paper I often refer to the “triangle” ‘algae-sea urchins-fish’, which is described in more detail in Annex 1.

I feel that my work has two main applications. Aside from any knowledge gained from the experimental study of the interactions within a complex community under natural conditions, our results have, firstly, a clear role to play in the management of coastal areas and biological conservation in general. It is known that high densities of sea urchins can cause a regression and a loss of diversity in algal communities (that can be compared to the effects of desertification on the biodiversity of forest ecosystems). Studying experimentally the mechanisms that regulate these interactions is a way of searching for valid management criteria. Secondly, we looked at the relevance of the role played by changes of anthropic origin such as eutrophication or overfishing in the proliferation of sea urchins and the regression of algal communities.

The theoretical framework: trophic models

The causes (or the factors) that govern ecosystem structure and dynamics have been much studied in community ecology. Whenever this subject has been studied from the point of view of energy flows and trophic interactions, two lines of thought have historically come into conflict (albeit only superficially): to summarise, some authors believe that the control of the structure and dynamics of a community is determined from the top of the trophic chain (top-down) by predators, whilst others claim that the whole system is controlled from the bottom (bottom-up) by inputs of energy.

TOP-DOWN control models

The seminal work within this line of thought that defends the idea that communities are regulated by predators is possibly that by Hairston et al. (1960). This model states that the Earth is green, that is to say, that vegetation dominates (in terms of total biomass) the majority of ecosystems because carnivores limit the abundance of herbivores. This control reduces grazing pressure and permits plant communities to flourish. This view postulates that it is the interaction between different trophic levels that determines the composition and abundance of plant communities: carnivores are regulated by competition, while herbivores and plants by predation.

BOTTOM-UP models

A controversy arose immediately between the defenders of this top-down model and those who advocated a completely opposite model. Many authors (i.e. White 1978, Hairston and Price 1992) maintain that it is the variations in the energy input into the system originating from primary producers and the subsequent thermodynamic limitations involved in transferring energy throughout the food web that regulates the quantity of biomass a trophic level can sustain. Thus, these variations control the structure and dynamics of the ecosystem and control – limited by productivity - moves upwards from the bottom.

Mixed models

The positioning of these two models as two mutually exclusive alternatives gave way to more flexible points of view. The basic model proposed by Hairston and collaborators was modified by Fretwell (1977) and then formulated mathematically by Oksanen *et al*. (1980) in order to include limitations imposed from below. This mixed model (Exploitation Ecosystem Hypothesis) recognises that the availability of resources may determine the number of trophic levels. However, faithful to the “top-down” hypothesis (control by predators), it still predicts alternating dominance by vegetation or herbivores according to the number of trophic levels: community structure will be determined by the productivity of the system.

Other authors, in recognition of the fact that both processes work simultaneously, have developed the “bottom-up – top-down” hypothesis (McQueen *et al*. 1986 1989, De Melo *et al*. 1992), in which they suggest that the bottom-up processes (competition) are stronger and dominate the lower levels of the food web, whereas the top-down processes dominate at higher levels. On the basis of their experimental work Menge and Sutherland (1976, 1987) and Menge and Olson (1990) put this model into practice in the sphere of benthic ecology, introducing physical disturbances into the calculations and describing how the relative importance of the different processes that regulate communities along environmental gradients vary.

Trophic cascades: evidence of “top-down” control

A logical consequence of the hypothesis proposed by Hairston *et al*. (1960), in which they state that communities are controlled by predation, is the transmission of a shock wave of effects from top to bottom throughout any network with three or more trophic levels. This wave will become apparent in the positive correlation between the biomasses of two non-contiguous trophic levels separated by a third trophic level, with which the correlation will be negative. To put it more simply, there will be a positive correlation between levels occupying even and odd positions on the trophic scale. This is what is known as the trophic cascade, which, in a very intuitive fashion, corresponds to the old saying, “my enemy’s enemy is my friend”. In a more formal fashion, the trophic cascade is defined as the propagation of indirect mutual relationships between non-neighbouring trophic levels in a food web (Schoenner 1993, Menge 1995).

The existence of trophic cascades would constitute the most observable evidence for the top-down control of communities. Thus, ecologists have always searched ecosystems for experimental evidence that demonstrates the existence of cascades, although this type of research has yet to provide a clear consensus on the question. The first evidence came from the work of Paine (1966, 1974) in intertidal benthic systems. In limnetic systems experiments that involved removing fish from the ‘fish-zooplankton-phytoplankton’ chain provided a good deal of evidence for the existence of trophic cascades in lakes (Carpenter *et al*. 1985, 1987, Leibold *et al*. 1997, Power *et al*. 1985, 1987, Brett and Goldmann 1997), rivers (Power 1990, 1992, Rosemond et al. 1993) and temporary pools (Cochran-Stafira and von Ende 1998, Hulbert and Mulla 1981).

Subsequently the effects of cascades have been described from terrestrial systems with chains such as ‘birds-insects-plants’ (Atlegrim 1989, Marquis and Whelan 1994), ‘spiders-insects-plants’ (Schmith *et al* 1997, 2000, Carter and Rypstra 1995), ‘lizards-insects-plants’ (Chase 1998), ‘wolves-ants-firs’ (McLaren and Peterson 1994) or ‘nematode parasites-ants-bushes’ (Strong *et al*. 1996).

Despite all this evidence, trophic cascades have never been shown to be a universal phenomenon. Some authors sustains that they occur in certain, very productive systems characterized by low specific richness, very lineal trophic connectors and poor spatial heterogeneity (Strong 1992, Polis and Strong 1996, Persson 1999), whereas others have suggested certain mechanisms such as the role of omnivores that may compensate for or even eliminate cascades (Dihel 1993, Agrawal 2003).

Trophic cascades in marine systems

Trophic relationships between corals or benthic algae, sea urchins (the main herbivores) and sea urchin predators – that is, the 'algae-sea urchin-fish' system that is the main objective of this study – have provided some of the best evidence for the existence of trophic cascades in marine systems. As we will show in this paper, the underlying cause for the existence of this chain is the special role played by sea urchins, which are both potent herbivores capable of completely modifying algal communities and are also controlled by predators.

The study of these relationships is one of the classical lines of study in marine ecology (reviews: Lawrence 1975, Lawrence and Sammarco 1975, Schiel and Foster 1986, Sala *et al*. 1998, Pinnegar *et al*. 2000). The question began to be debated during the 1970s within the framework of the temperate seas surrounding the USA, where proliferations of sea urchins had denuded large extensions of macroalgal meadows and transformed them into communities dominated by incrusting calcareous algae (Lawrence 1975, Bernstein *et al*. 1981). This change of the community meant a great loss in structure and diversity because kelp beds and their associated flora and fauna all disappeared.

The disappearance of predators (sea otters) was identified as the cause of the proliferation of the sea urchins: since the otters controlled the sea urchins, excessive otter-hunting led to a sharp increase in sea urchin populations and thus also increased grazing pressure on algal communities. Work done in other temperate waters has shown that these mechanisms work in more or less the same way elsewhere, with a variety of other sea urchin predators including otters (Estes and Palmisano 1974, Estes at al. 1978, Estes at al. 1998, Breen *et al*. 1982, Duggins 1988), fish (Sala 1996, 1998, Tegner and Dayton 2000, Shears and Babcock 2002, 2003) and lobsters (Mann and Breen 1972, Mann 1977). In tropical seas, similar mechanisms are at work with fish as predators, sea urchins and, as primary producers, hermatypical corals (McClanahan and Mutiga 1989).

Quantitative models and the role of humans

The predictions of the “top-down” trophic models and, in particular, the effects of trophic cascades, take on a greater importance in light of the role of man as the top predator in all littoral ecosystems (Vitousek *et al* 1996, Jackson and Sala 2001, Jackson *et al*. 2001). In order to predict the effects of anthropic activity and to establish management criteria for coastal sites, deterministic models have been developed based on the “top-down” control hypothesis and the logic of the predator-prey model as proposed by Lotka and Volterra (Margalef 1974). These models (McClanahan 1992, McClanahan and Sala 1997) predict different terminal states for the structure and dynamics of algal communities according to the human activity, which, via the cascade effect, controls the abundance of the predators acting upon herbivore species. At the two extremes of this process two opposite states are portrayed: 1) systems with no overfishing and abundant predators which control sea urchins that have well-developed algal communities and 2) overfished systems with high sea urchin densities and overgrazed algal communities dominated by incrusting calcareous algae and other ephemeral species.

Aside from describing these two terminal states, these models also predict the conditions needed for one state to transform into another: increased fishing reduce predators abundance and provokes a subsequent increase in herbivores leading to a degradation in algal communities; the reverse process consists of the creation of protected areas that enable predator populations to recover; as a result sea urchins are controlled and well-developed algal communities replace once overgrazed areas.

Box 1: The 'algae-sea urchin-fish' triangle in the Mediterranean

In the rocky infralittoral communities at depths between 5 and 10 m in the northwest Mediterranean Basin (and, in particular, in Catalonia), the three trophic levels we studied (primary producers, herbivores and low-order carnivores) play home to around a hundred species of macroalgae (see Appendix 1) and two species of sea urchin (*Paracentrotus lividus* and *Arbacia lixula*) and one of fish, the salema (*Sarpa salpa),* as the main macro-herbivores: furthermore, there are over 40 other species of omnivorous fish, and of particular importance are the members of the Labridae family including, above all, the Mediterranean rainbow wrasse (*Coris julis*) (see Appendix 2). What follows is a brief description of the most singular characteristics of these communities and what we know of their interactivity, as well as a selection of the most representative works that may help provide the reader who is not familiar with Mediterranean benthic systems with guidance. It is divided into four sections: macroalgae, herbivores, omnivorous fish guilds and their interactivity.

Macroalgae

The infralittoral algal communities in the northwest Mediterranean Basin are species rich, reaching densities of over 200 species per 1,000 cm^2 (Ballesteros 1992). In the infralittoral zone there are up to 11 well-differentiated algal communities distributed from depths of 0.5 m to 30 m (Ballesteros 1992). The extreme miniaturisation of Mediterranean algal communities (Coppejans 1980, Boudouresque *et al*. 1980, Ballesteros 1992) means that the minimum necessary size of sampling areas in which all the representatives of the community appear is very small, around 140 to 400 cm^2 (Coppejans 1977, Verlaque 1987a, Ballesteros 1992, Sant 2003).

Productivity in Mediterranean algal communities is very variable and, as a guide, we can quote values of between 0.3 and 0.7 gC/m^2 per day for communities at depths of 20 to 50 m (Drew 1968), 1 to 3 gC/m^2 per day for photophilous communities (Johnston 1969 Ballesteros 1992) or even much higher values up to 10 gC/m^2 per day in midlittoral communities of *Cystoseira* and *Rissoella* (Johnston 1969 Boudouresque 1969, Bellan-Santini 1968, Ballesteros 1992).

Algal communities in the Mediterranean are distributed in very marked zonal patterns defined by abiotic factors such as the quantity of light, hydrodynamism and the availability of nutrients, all of which are determined by depth (e.g. Ros *et al*. 1984, Ballesteros 1992, Ballesteros and Zabala 1993, Garrabou *et al*. 1998) and limit algal growth (Ballesteros 1989, 1992). These limiting factors, along with the type of substrata, have made it possible to classify algae into different ecological groups (Feldmann 1937, Boudouresque 1984, Verlaque 1987a). This zonation is a reflection on the different structures and compositions of algal communities; dynamics vary from community to community, with those at greater depth characterised by more structural components, greater seasonality and generally slower dynamics (Zabala and Ballesteros 1989, Garrabou 1997). Moreover, owing to the significant inherent seasonality in the marine benthos, productivity peaks in spring and drops to a low in winter, each low/high point being followed, respectively, by maximum and minimum biomass levels (e.g. Feldmann 1937, Boudouresque 1971b-c, Ballesteros 1989b, 1992, Ballesteros and Zabala 1993, Rodríguez-Prieto 1992, Sant 2003). Ballesteros (1991) produced a model of community structure and dynamics that reveals a seasonal oscillation delimited by two productivity phases. Thus, there is a production phase in spring leading to a developed community with maximum biomass levels in the summer. At the end of summer growth stops and a diversification phase begins that involves a loss of biomass but an increase in species richness leading to more diversified communities during winter. Depending on composition and biomass, each community is organised within a space delimited by the axes of production/diversification and biomass/heterogeneity.

The communities we studied have been described by Gili and Ros (1982), Sala (1996) and Sala and Boudouresque (1997), and correspond to transitions between the communities *Padino-Cladostephetum hirsutae* J. Feldmann 1937 and *Rhodymenio-Codietum vermilarae* Ballesteros 1989a (Sala and Boudouresque 1997; see Box 2 for more details). This community may harbour over 200 species, has a minimum biomass of 546 g dry wight/m^2 and a maximum of 765 g dry weight/m^2 at the end of summer (without taking into account incrusting species), and has average productivity of around 150 gC/m^2 per year (Ballesteros 1992).

Over the last few years there has been a notable penetration of allochthonous species into this community, some of which are invasive (Verlaque 1994, Boudouresque and Verlaque 2002) and have modified completely the structure and dynamics of the infralittoral algal communities (e.g. Lemee *et al*. 1996, Ceccherelli and Cinelli 1998). This is the case of, for example, *Asparagopsis armata*, *Caulerpa taxifolia* and, more recently, *C. racemosa*: the first of these three has acclimatised very well to the Medes Islands and annually at the end of spring covers 100% of the substratum at a depth of between 0 and 10 m (Sala and Ballesteros 1997).

Sea urchins

Paracentrotus lividus is a generally dark-coloured, regular-shaped echinoderm with a diameter of up to 7.5 cm. It is found throughout the whole of the Mediterranean, as well as the northeast Atlantic from Ireland to the coasts of Morocco and the Canary Islands (reviewed by Boudouresque and Verlaque 2001). This large range reveals its great physiological diversity (e.g. Tortonese 1965, Mortensen 1943, Allain 1975). It can be found at depths of between 0 and 30 m, and occasionally it will survive at even greater depths (Gamble 1965, Tortonese 1965, Allain 1975, Régis 1978, Harmelin *et al*. 1980). Its chosen habitat are coastal reefs dominated by photophilous algae and *Posidonia oceanica* meadows (Caillaud 1856, Mortensen 1927, Kempf 1962, Neill and Larkum 1965). Young sea urchins take refuge under boulders and plant cover or within *Posidonia* meadows to escape predation (Kempf 1962, Gamble 1965, 1966, Verlaque 1984, 1987a, Azzolina 1988, San Martin 1995). Adults are often found in more exposed sites since they are protected from their many predators by their size (Sala 1996, Palacín *et al*. 1997).

This is a very abundant species with densities that can vary from just a few scattered individuals to dozens of individuals per square meter (Boudouresque *et al*. 1992, Kempf 1962, Harmelin *et al*. 1980, Palacín *et al.* 1997, Sala *et al.* 1998, Kitching and Ebling 1961), although occasionally densities become even higher, especially in shallow water (Benedetti-Cecchi and Cinelli 1995, Fenaux *et al.* 1987, Turon *et al.* 1995).

Growth rates are variable in this species and depend on temperature, food quality and gonadal development (Fernandez 1996). Furthermore, the type of habitat may also modify food availability and thus affect somatic and gonadal development (Turon *et al.* 1995, Guetaff *et al.* 2000). However, this species generally grows about one centimetre a year, although during the first years of its life growth is more rapid, whereas during its last years it is slower (Fenaux *et al.* 1987, Azzolina 1988, Turon *et al.* 1995, Fernandez 1996). Individuals may live for over 10 years (Turon *et al.* 1995, Fernandez 1996) and reach sexual maturity at five months *in vitro* (Azzolina 1987, Cellario and Fenaux 1990), although it is possible that *in situ* this stage is reached later. It is a dioecious species with a larval phase; its pluteus larvae live as plankton for periods of between 20 days and a month (Pedrotti 1993, Fenaux *et al.* 1985). Reproduction occurs via a synchronised release of gametes into the sea that gives rise to external fertilisation occurring usually in spring (Allain 1975, Byrne 1990, Lozano *et al.* 1995) or in the autumn and spring if there are two release phases (Fenaux 1968, Régis 1979, Crapp and Willis 1975, Semroud and Kada 1995).

It is thought to be a herbivorous species (Mortensen 1943, Kitchling and Evling 1961, Kempf 1962, Ebling *et al.* 1966, Neill and Larkum 1966, Neill and Pastor 1973, Verlaque and Nédelec 1983, Verlaque 1987a,b), although it does have certain preferences (see revision by Boudouresque and Verlaque 2001), and in high-density situations it can totally destroy algal cover and create barren patches with feeding rates of between 25 and 161 mg dry weight per individual per day (Verlaque 1984, 1987a). Bare patches are then taken over by incrusting calcareous algae, forming a low biomass of soft, erect algae, these formations have been described from throughout the distribution of *Paracentrotus lividus* (Kempf 1962, Neill and Larkum 1966, Gamble 1966, 1967, Lewis 1976, Verlaque 1987a).

P. lividus avoids predators by being most active at night (Dance 1987, Ebling *et al. 1*966, Kichling 1987 but see Crook *et al.* 2000, Barnes and Crook 2001). In general it is very adaptable and possesses high reproductive potential and a great ability to colonise and establish itself permanently. As Boudouresque and Verlaque (2001) comment, "... *P. lividus* is an incredibly opportunistic generalist, with a very wide range of adaptive responses to environmental conditions. It can do everything and anything".

Another sea urchin species present in these communities is *Arbacia lixula*. It is very similar to *P. lividus*, although it tends to occupy more sciaphile habitats in warmer areas (Francour 1994). In our study area it is present only in low densities (Sala *et al.* 1998), although it can be very abundant – more so even than *P. lividus* - in other areas of the Mediterranean (Bulleri *et al.* 1999).

Fish

Mediterranean fish communities are very diverse and their trophic relationships with whole system are very variable; likewise, the trophic connections between the elements of fish communities are highly complex (revised by Stergiou and Karpouzi 2002). The species that are most relevant in these systems are described below.

The salema (*Sarpa salpa*) is distributed from the Black Sea through the whole of the Mediterranean and west to the coasts of Africa and Europe (Tortonese 1975). Typically, it is a gregarious coastal species that swims in hundred-strong shoals. It is especially abundant in *Posidonia* meadows where average densities reach up to 100 individuals per 250 m^2 (Tomàs 2004) and is rarely found below depths of 20 m (Corbera *et al*. 1996). It is essentially herbivorous (Verlaque 1990, Sala 1996) and feeds basically only on algae and phanerograms, although it may ingest small associated invertebrates and epiphytes. It spawns twice a year, in spring and summer, and recruits appear between May and June and October and November on sheltered, heterogeneous reefs. Immediately, the fry, which are omnivorous, group together and move away from the coastline (Corbera *et al*. 1996).

The white seabream (*Diplodus sargus*) is distributed throughout the Mediterranean as far as the eastern coasts of Africa (Tortonese 1975); the subspecies *D. s. sargus* is endemic to the Mediterranean. Like most other Sparidae, this is a coastal species living near the surface and rarely found below a depth of 50 m (Corbera et al. 1996). It is much sought after by fishermen, and in protected areas it can reach densities of up to 50 individuals per 250 m^2 (Garcia-Rubies 1996). It is omnivorous (Rossechi 1985, Coetzee 1986, Manna and Buxton 1992, Sala 1996, Sala and Ballesteros 1997) and is considered to be the most significant predator of sea urchins (Sala 1996, Sala 1997). At high density, populations of this species can exert a certain control over sea urchin populations (Sala *et al*. 1998). It spawns between March and June, and recruitment occurs in mid-May on sheltered, heterogeneous reefs in shallow seas (Corbera et al. 1996, Vigliola *et al*. 1998, Macpherson 1998, Planes *et al*. 1999).

The common two-banded seabream (*Diplodus vulgaris*) has a wide geographical range, occupying the whole Mediterranean Basin as well as Atlantic coasts from the Basque country to as far south as Angola (Tortonese 1975, De la Paz 1975). It is a coastal species inhabiting reefs at depths of between five and 30 metres, although it may occasionally reach depths of 70 m (Corbera et al. 1996). It is abundant with densities that can reach 35 individuals per 250m^2 (Garcia-Rubies 1999) and swims in large shoals, often mixed with white seabreams (*D. sargus*). It is omnivorous and has a similar diet to *D. sargus*, although owing to their preferences for different depths, these two species do compete (Sala 1996, Sala and Ballesteros 1997). Both these species of seabream have been described as significant predators of *P. lividus* (Sala 1997, Dance 1987). *D. vulgaris* spawns twice a year, at the beginning and end of autumn, and recruitment occurs in two phases at the beginning and end of winter on heterogeneous reefs or *Posidonia oceanica* meadows at greater depths than *D. sargus* (Corbera et al. 1996, Vigliola *et al*. 1998, Macpherson 1998, Planes *et al*. 1999).

The sharpsnout seabream (*Diplodus puntazzo*) is found throughout the Mediterranean as well as in the tropical Atlantic and other western Atlantic coasts (Bauchot and Pras 1980). It is generally a solitary species, strictly coastal, and inhabits reefs and sometimes sandy bottoms, as well as *Posidonia* meadows to a depth of up to 50 m (Bauchot and Pras 1980). It is less common than its congeners, reaching densities of up to 4.5 individuals per 250 m^2, and is the most herbivorous *Diplodus* species. It will also eat not inconsiderable quantities of invertebrates and is the only species of the group that eats sponges and Anthozoa (Sala 1996, Sala and Ballesteros 1997). It breeds at the end of summer and recruitment occurs in mid-October on shallow, sheltered reefs (Corbera et al. 1996, Vigliola *et al.* 1998, Macpherson 1998, Planes *et al.* 1999).

The Mediterranean rainbow wrasse (*Coris julis*) is one of the most abundant fish along rocky coastlines in the northwest Mediterranean; it is also present along Atlantic coasts from the Canary Islands to as far north as Norway (Bauchot and Pras 1984). It is a typically benthic species, very active, with a broad bathymetric range, being found at depths of 0 to 50 m and even below 100 m (Corbera et al. 1996). It has a complex social structure in which a secondary male defends a territory whose size is dependent on population density (Lejeune 1985). This species, as in the case of the ornate wrasse (*Thalassoma pavo*), is carnivorous and feeds principally on small invertebrates such as molluscs, echinoderms and crustaceans (Bell and Harmelin-Vivien 1983, Khoury 1987, Pinnegar and Polunin 2000). It is thought to be one of the main predators of juvenile sea urchins (Sala 1996, Sala 1997). Breeding takes place at the beginning of summer and recruits appear at the end of summer. Although it has no real commercial interest, this species is often caught by rod and line. Protection measures seem to be effective as fish have been seen to be larger on average in no-fishing areas (Garcia-Rubies 1996).

Symphodus ocellatus and the five-spotted wrasse (*Symphodus roissali*) are two small, highly abundant Labridae that inhabit infralittoral reefs, although, unlike *C. julis* and *T. pavo*, these species are omnivorous and have a greater tendency to graze (Bell and Harmelin-Vivien 1983, Pinnegar and Polunin 2000).

The brown wrasse (*Labrus merula*) is a large Labridae with an essentially Mediterranean distribution, although it can also be found in nearby sectors of the Atlantic. It is strictly coastal and inhabits reefs dominated by photophilous algae or *Posidonia* meadows. It is strictly carnivorous and feeds on crustaceans, molluscs, Polychaeta and echinoderms (Bell and Harmelin-Vivien 1983). It is sensitive to underwater fishing and thus is more abundant and on average larger in protected areas.

Trophic cascades in the Mediterranean and the role of marine reserves

Many studies in the Mediterranean rocky littoral have demonstrated that large piscivorous and invertebrate-feeding fish are more abundant within MPAs compared to sites outside (e.g. Bell 1983, Francour 1994, Harmelin et al. 1995) *Diplodus* species have been shown to be major predators of adult sea urchins (particularly *Paracentrotus lividus*), whilst the wrasse *Coris julis* has been suggested to be a major predator on juvenile sea urchins (Sala 1997b). Although sea urchins are not the main prey of sparid fishes (Sala and Ballesteros 1997), Sala and Zabala (1996) found that within the Medes Island Marine Reserve, fish (mainly *D. sargus*, *D. vulgaris* and *C. julis*) accounted for 100% of all urchin predation. Furthermore, at adjacent non-protected sites with a low density of predatory fish, *P. lividus* populations were shown to be 3-4 times higher than at sites in the Medes Reserve (Sala and Zabala 1996).

When at high densities, sea urchins have been shown to remove large erect algae and induce the formation of coralline barrens (Verlaque 1987). Transition from coralline barrens back to erect algal assemblages is possible when sea urchins are eliminated or their populations are strongly reduced as has been shown by both experimental and natural removal (e.g. Kempf 1962, Nédélec 1982). However, the situation becomes greatly complicated by the grazing activity of fishes, mostly *Sarpa salpa* but also *Diplodus* species (Sala and Ballesteros 1997, Sala and Boudouresque 1997). Sala and Boudouresque (1997) showed that where cages excluded fish (and sea urchins), populations of fleshy erect macroalgae developed and dominance by the unpalatable red alga *Asparagopsis armata* was greatly reduced. This coincided with the observation of a seasonal proliferation of *Asparagopsis* and dominance by fine turfs or calcareous algal species in MPAs where grazing fish were more abundant. Sala (1997a) found that within fish exclusion cages, most epifaunal groups (e.g. amphipods, gastropods, decapods and ophiuroids) also became more abundant although few differences were detected between MPA and unprotected areas. Sala (1997a) attributed to a combination of reduced predation but also the dynamics of the fleshy erect algae which provide a structural habitat and food for many of the invertebrates considered.

An energy-based simulation of the Mediterranean rocky sublittoral system helped to predict how depletion especially of invertebrate-consuming fish such as *Diplodus spp* might result in dominance by sea-urchins, which would dramatically reduce algae, epifauna and gross and net primary production (McClanahan and Sala 1997). The indication is that once a high population of sea-urchins has developed, recovery of those fish that eat algae and epifauna might be slowed down or even made impossible because their food resources drop below the minimum threshold necessary for in situ population development (McClanahan and Sala 1997). Therefore, Mediterranean rocky-sublittoral assemblages have been considered to exist in one of two states: (1) an overgrazed community with high abundance of sea urchins and low algal biomass, and (2) a ‘complex’ community with an abundance of fish and dominance by fleshy algae (McClanahan and Sala 1997). Sala et al. (1998a) critically reviewed the literature concerning the effects of fishing on sea-urchin populations and the recent expansion of coralline barrens and concluded that other processes including pollution, diseases, large-scale oceanographic events and availability of refuges from predation, are also likely to be important. This has been somewhat borne out by the findings of Sala et al. (1998b) who suggested that sea urchin populations in the Medes Islands exhibit striking short-term fluctuations in abundance in both protected and unprotected sites, such that other factors including recruitment variability may outweigh the effects of fish predation.

Medes Islands marine Reserve

Infralittoral seaweeds in spring

Halopteris scoparia, Cystoseira sp., Taonia atomaria, Sphaerococcus coronopifolius

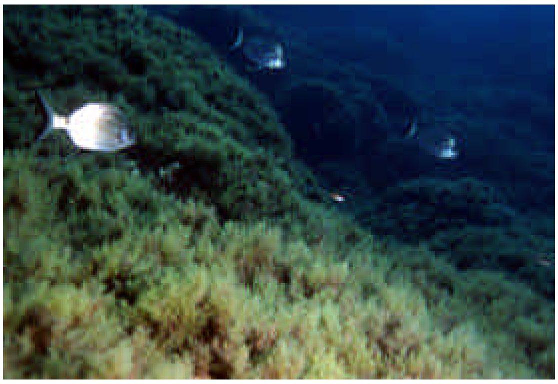
Corallina elongata, Dictyota dichotoma, Padina pavonica, Codium vermilara, Asparagopsis armata

Sarpa salpa eating on transplanted algae

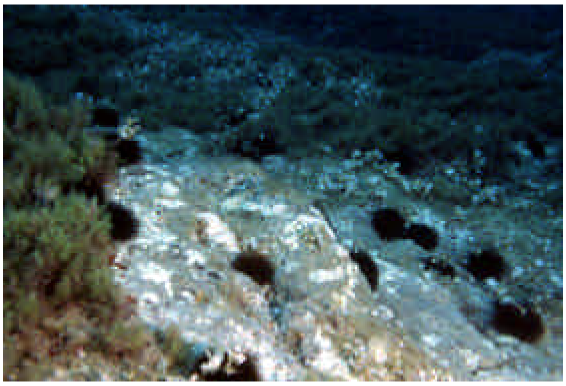
Diplodus sargus

Coris julis male (center) and femeale

Tagged sea urchin Paracentrotus lividus



Cystoseiretum forest in Scandola Marine Reserve



Transition between Cystoseiretum forest and overgrazed community by Paracentrotus lividus in Scandola Marine Reserve

Fish enclosure in Portitxol cave, Medes Islands Marine Reserve enclosure

Artificial sea urchins collector inside a fish

An overview of the challenges ahead

Despite the many investigations carried out into these Mediterranean systems, we still lack enough information to develop a complete vision of the workings of these communities. This thesis therefore concentrates on the areas that, in my opinion, have yet to be fully studied.

1) Nonfulfillment of predictions made by trophic models for the Mediterranean

In many parts of the Mediterranean during the 1960s and 1970s there was a considerable increase in sea urchin populations, which proceeded to decimate algal communities dominated mainly by species belonging to the genus *Cystoseira* (Giaccone 1971, Katzmann 1974, Gros 1978, Augier and Boudouresque 1967, 1970a,b, 1976a,b, Mastaller 1974, Zabodnik 1977, Torunsky 1979, Verlaque and Nédelec 1983). As we have seen in the preceding section (Annex 1), the trophic models that describe the dynamics of algal communities (McClanahan and Sala 1997) predicted this occurrence and attribute it to the drastic reduction in fish stocks caused by overfishing, which in turn leads to a proliferation of sea urchins. These very same models also predict that a recovery in predator populations will reverse this process. That is to say, in areas such as marine reserves in which fish communities are well developed, sea urchins will be controlled by predator fish and coralline barrens will once again be covered by well-developed algal communities.

However, there is a growing body of evidence that suggests that these predictions are not fulfilled. For example, sizeable barren areas appear in some marine reserves with high fish densities, and examples can be found along all the protected coastlines in the Mediterranean. We can fins examples in the oldest protected areas such as the Port-Cros National Park (France), the Banyuls-Cerbère reserve (France), some areas of the Illes Medes Marine Reserve (Spain) or the Scandola Natural Reserve (Corsica, France) (see chapter 8), but also in the more recently created reserves as Ustica Marine Reserve (Sicily, Italy), the Cabrera National Park (Balearic Islands, Spain), the Cabo de Palos-Islas Hormigas marine Reserve (Murcia, Spain) and the Bouches de Bonifacio International Marine Park (Corsica-Sardinia; France-Italy). Furthermore, well developed algal communities in overfished areas are also frequent.

Thus, the predictions made by these models do not exactly match the realities of the northwest Mediterranean and we must accept that other factors, as yet not taken into account by the models, exist and will also be decisive role if we attempt to understand the composition and dynamics of these algal communities (Sala et al. 1998). One of the most important objectives of my thesis was, therefore, to explore these alternative factors.

2*) The methodological limitations of previous experimental work*

Although most of the trophic interactions examined in this thesis have already been investigated experimentally in Mediterranean ecosystems, the simple nature of these experiments and their short time scales raises the suspicion that some of the results obtained could vary if temporal and spatial scales were lengthened. Some of the problems with experiments carried out thus far are as follows:

Excessively small cages and enclosures used in the manipulation of predator and prey densities could alter experimental conditions: two of the most frequent examples are the refuge effect for invertebrates and the accumulation of sediments (discussed in Kennely 1991).

Previous experimental designs did not take into account the relative effects of fish and sea urchins; this interaction implies, albeit indirectly, the use of large-scale enclosures as needed to control fish and urchins densities.

The response of algae to grazing in simplified species-species interactions or in functional groups (erect-turf-barren patches) has been studied; rarely, however, have whole algal communities been investigated. This is due to the great phytobenthic diversity present in the Mediterranean, which means that at present the monitoring of algae at community level is a problem that has not yet well resolved (but see Sala and Boudouresque 1997). Nevertheless, we should not ignore competition between algae, which may lead to situations that are very different from those resulting from the simple effects of grazing by herbivores. This becomes more obvious whenever herbivores are selective. By altering the competitive relationships existing between different species of algae, herbivores may facilitate (as shown by Sala and Boudouresque 1997) or inhibit certain species of algae at community level, an effect that would be impossible to demonstrate in simple experiments limited to the outcome of grazing in pairs of species.

Seasonality alters the composition and dynamics of communities and also affects relationships between algae species: thus, this factor cannot be satisfactorily separated from the effects produced by herbivores. The interaction between grazing and seasonality may mask or enhance the effects of herbivores.

The duration of previous experiments was too short to be able to incorporate seasonal oscillations or long-term tendencies to change.

The starting point of this work was the PhD thesis written by Enric Sala, set also around the Medes Islands and in the same environment (infralittoral communities at depths of 5 to 10 m) (Sala 1996). His work was a fundamental contribution to the understanding of these ecosystems, and raised new questions that must now be investigated experimentally or further studied by means of new experiments at different scales.

In my work I have tried to use experiments on spatial scales ranging from 10 to 100 m^2 and with a temporal scale of three years as a way of revealing the factors that may be responsible for the nonfulfillment of existing trophic models. I installed large enclosures in the Medes Islands Marine Reserve in order to control fish and sea urchin densities. Furthermore, I monitored natural algal communities on a pluri-specific basis in situ for three complete productive cycles in order to incorporate the effects of seasonality, and to be able to observe synergistic effects that small-scale studies may not reveal. Above all, I aimed to determine experimentally the effects that sea urchins and fish have separately and jointly on algal communities. Finally, I also put special emphasis on mechanisms such as settlement, predation and migration that control the dynamics of sea urchin populations, as well as on the processes that regulate juvenile populations.

Objectives and the structure of the thesis

The interactions between the organisms situated on two different trophic levels of a community can be looked at from various overlapping perspectives, despite the fact that in itself the community is a whole that cannot be separated into unrelated parts. The study of a community must be undertaken with various different objectives in mind, although, inevitable, results have to be presented sequentially.

My work is structured bottom upwards, following the order of the organisms that constitute the food web. So, the structure and cycle of algal production and its interaction with herbivores will be the first area dealt with. Subsequently, we will tackle the population dynamics of sea urchins, the main grazers in the system. As a means of studying the factors that control this latter dynamic, we will study sea urchin mortality induced by carnivorous fish, as well as the capacity of man to reverse relationships between herbivores and algae by promoting the recovery of fish populations or by directly eradicating sea urchins.

1-"Top-down" or "bottom-up" control in algal communities in the Mediterranean infralittoral, or the role of seasonality in the effects of herbivores on algal communities

Mediterranean algal communities have traditionally been studied from two different perspectives that up to now have always been seen as independent. On the one hand, many specialists in the field of the ecology of Mediterranean algae (see Ballesteros 1991, 1992, Sant 2003 and references therein) have studied the structure and dynamics of algal communities in terms of the physiological limitations imposed by the environment, thereby implicitly assuming that control in the community comes from below. On the other hand, deterministic trophic models (such as that of McClanahan and Sala 1997) depict the control of algal communities as being the result of biotic predatory relationships existing at higher trophic levels – in other words, control coming from above.

However, this separation is over simplistic (due to the limited capacity of the experiments employed) and highlight the need to study the structure and dynamics of algal communities by taking into account both of these perspectives, as in the precedent set by Verlaque (1987a). In fact, the most probable outcome is that both types of controls operate simultaneously and are anything but independent of each other and there will surely be some kind of interaction that ensures that each process acts on the others. For example, the combined effects of climate (variable throughout the year), the different strategies employed by algae (perennial, seasonal or opportunistic), the different types of herbivores and the omnivorous nature of fish guilds will provide answers that would possibly not be revealed by experiments in which each of these factors was analysed independently.

In order to respond to these questions, we set up an experiment that would allow us to:

1 - integrate and discriminate between the effects of sea urchins and herbivore fish.

2 - integrate and discriminate the effects of the omnivorous fish guild as herbivores and as sea urchin predators.

3 – parcel off and analyse representative portions of the algal communities and avoid “wall effects” by increasing the size of enclosures.

4 - separate the effects of herbivores from those of intrinsic seasonal variation in algal communities by increasing the length of the experiment (pluri-annual).

The second chapter of the thesis presents the results of the experiment designed to evaluate simultaneously the effects of grazing (“top-down”) and the effects of climate (“bottom-up”) on the dynamics and structure of algal communities. This experiment was complex and for almost two and a half years - the time period needed to separate three consecutive phases of productivity (a period long enough to ensure the incorporation of seasonality into the effects of herbivores) - we closed off with vertical nets three small coves on the Medes Islands so that fish could not enter. Inside and outside these enclosures we manipulated sea urchin densities and carried out monthly controls of algal communities in situ of the 40 or so species that can be monitored visually. Due to the effort that this work implied and the multiplicity of factors studied, the results of this experiment form the central part of the thesis.

Given the obligation to not alter conditions within the enclosures during the three experimental seasons, the study of the algae had to be carried out by means of visual examinations and so we were unable to calculate productivity or the loss of biomass caused by herbivores. In order to obtain quantitative results regarding the evolution of the biomass and estimates of grazing rates, I took advantage of the experimental installations to carry out a complementary investigation based on artificial surfaces on which measurable quantities of certain algae could be transplanted and manipulated. This experiment, aimed at quantifying the separate and combined effects of sea urchins and of herbivorous and omnivorous fish, was limited by methodological constraints to just a few species, and is discussed in chapter 3.

2 – The processes that regulate populations of the main herbivore, the sea urchin Paracentrotus lividus

Given that *Paracentrotus lividus* are considered the most important benthic herbivore along infralittoral Mediterranean reefs, an understanding of the dynamics of their populations is fundamental if we are to appreciate the dynamics of the system as a whole. Sea urchin populations, as in the majority of species, are regulated by processes of recruitment, mortality and migration. Despite the fact that the general patterns of these processes have already been much studied, there are some factors whose roles we still do not fully understand (for example, space and refuges) and others have not yet been fully integrated into models: these factors might be the cause of some of the mismatches observed between models and reality. We have placed especial emphasis on the processes that occur during the first phases of the benthic life of sea urchins (whilst their diameter without spines measures less than 2 cm), since this is the least-studied aspect of the ecology of these animals and a phase that we suspect might play a crucial role in the regulation of its populations.

Thus, our experiments were aimed at reaching a better understanding of settlement processes (chapter 4), the mortality caused by predation during the post-settlement phase (chapter 5) and migrations and behaviour associated with movements (chapter 6). Lastly, and as a complement to previous experiments, we have analysed in the evolution of the size of two sea urchin populations (chapter 7) over a long period of time (12 years).

2.1 – Variability in settlement

In chapter 4 we describe the temporal and spatial patterns of *Paracentrotus lividus* settlement in both a marine reserve and an unprotected area. During their life cycle, sea urchins have a planktonic phase of long-range dispersal that enables the species to colonise areas far from their breeding zones. During this planktonic phase, larvae are subject to a series of factors (food availability, mortality, passive dispersal by currents and eddies, and so forth) that cause potentially very uneven entry into the benthos. As a result, settlement may actually destabilise sea urchin populations since variations in the size of settlements may lead to changes in the dynamics of adult populations. On the one hand, the arrival of only a few larvae may limit the renovation of adult populations (Underwood and Fairweather 1989), while important episodes of settlements may increase adult densities and result in episodes of overgrazing (Watanabe and Harrold 1991). On the other hand, very heterogeneous settlement patterns can lead similarly heterogeneous spatial distribution of adults in a particular area.

By means of artificial collectors that permitted the intensity of settlement to be calculated, we monitored settlement in three points in Medes Islands Marine Reserve for three years in order to calculate levels of interannual variability in settlement. Two other experiments also allowed us to determine the spatial variability in settlement patterns on horizontal and bathymetric axes.

2.2 – The role of predation and refuges

In chapter 5 we study the control that predation by fish on the youngest, post-settlement sea urchins may exert on overall sea urchin populations. Predation has been described as the most important control factor at work in sea urchin populations (Sala and Zabala 1996). Owing to the large variation in settlement patterns, only control by predators can check powerful recruitment pulses. The main predators of *Paracentrotus lividus* are fish and, more specifically, Sparidae species such as the white seabream (*Diplodus sargus*), which prey on larvae over 1 cm, and small Labridae such as the Mediterranean rainbow wrasse (*Coris julis*), that preys on juveniles (Sala 1997). Nevertheless, the availability of refuges is also of crucial interest, and can interact with both the size of the sea urchins and of the fish that prey upon them.

If we take into account the fact that the greatest mortality of sea urchins takes place during the post-settlement phase (which probably as a population bottle-neck), then the demographic impact of this mortality – insignificant in terms of biomass - may well be quantitatively much more important than predation on adult sea urchins.

In order to understand what controls the dynamics of sea urchin populations it is essential to discover which species of fish prey on sea urchins during the post-settlement phase and their relative importance. Likewise, we must also investigate the importance of size on the relationship between sea urchins and fish and how this factor may be affected by the availability of refuges (i.e. the structural complexity of the substrate). These concepts are obviously vital for any potential strategic environmental planning, above all if we consider that the impact of different types of fishing will affect each fish species differently.

The most realistic estimations of the impact of predation on sea urchin populations are based on tethering experiments carried out under over-simplified conditions that may exaggerate the importance of predation. Factors such as spatial heterogeneity or the availability of refuges may reduce the mortality rates obtained by these experiments. The consideration of refuges is complicated by the fact that their actual role may depend on the size of both the sea urchins and their predators. We suspect that these secondary effects modifying only “indirectly” mortality rates may explain the discrepancies observed between the predictions taken from models and our findings in the field. This would explain, for example, the high density of sea urchins in the Medes Islands, an area with fish in abundance, as well as the heterogeneous sea urchin densities in areas that are exposed homogeneously to high (protected areas) or low fish densities (unprotected coasts).

Chapter 5 describes various experiments that include refuges and sea urchin size. The effect of refuges has been studied in four distinc natural substrates with increasing structural complexity. On the basis of experiments with sea urchins of different sizes, with shell diameters ranging from 2 to 10 mm, we have discovered which species of fish prey on what size sea urchins. As well, we have carried out experimental studies on the relative importance of predation inside and outside the Medes islands reserve in order to determine the effects of fishing and the existence of protected areas on predation rates.

2.3- Behaviour and the scale of sea urchin movements

In chapter 6 we aim to establish the behavioural patterns of *Paracentrotus lividus* in terms of its home range, seasonal movements and migratory movements.

Despite being all but sessile and with limited mobility, sea urchin movements - whether as a response to a lack of resources or to other factors we do not yet understand (Palacin et al. 1997, Barnes and Crook 2001) - may profoundly alter population structures. According to the scale and direction, their movements could contribute to regularising (density-dependent movements aimed at redistributing resources) or destabilising (migratory waves) densities and, in passing, prevent or cause the appearance of coralline barrens.

On the other hand, on a smaller scale, movement to escape from predators may affect grazing pressure on algal communities. It has been observed that sea urchins avoid predators by hiding in crevices or under boulders and adults, thereby reducing their home range and the grazed area (Sala 1996, Sala and Zabala 1996). Interest amongst ecologists in these trait-mediated indirect interactions (Abrahms et al. 1996) has increased over the last few years in the light of discoveries of facilitation in terrestrial (e.g. Schmitz et al. 1997), limnetic (e.g. Turner et al. 2000) and intertidal (e.g. Trussell et al. 2003) systems, whereby the presence of predators causes a reduction in grazing activity that may be just as important for primary producers as the direct effects of predation on herbivores (reviewed by Werner and Peacor 2003).

Surprisingly, given their importance, the movements of *Paracentrotus lividus* have been thus far little studied (Palacín et al. 1997, Shepherd and Boudouresque 1979, revised by Boudouresque and Verlaque 2001), and neither its mobility nor its behavioural response to predators have ever been taken into account (in models) as factors affecting the dynamics of algal communities. In this thesis, sea urchin movements is a key factor since, depending on their scale, it may bring into perspective results obtained from other experiments. That is to say, until we establish precisely the patterns of mobility occurring in this species of sea urchin, we will not be able to fully understand the real importance of either settlement or predation in the regulation of sea urchin populations.

In chapter 6 we describe a series of experiments that were designed to palliate this lack of knowledge. By marking individuals, we were able to locate sea urchins spatially and thus determine their patterns of movement. An experiment at a circadian scale, which embraced periods of rest (by day) and activity (by night), allowed us to establish sea urchins' home ranges. We carried out the experiment inside and outside the marine reserve in order to demonstrate that the presence of predators provokes a trait-mediated effect on the home range of these herbivores. At the same time, a parallel experiment enabled us to study the migratory capacity of these sea urchins in the mid-term (months).

2.4 - Actual population evolution: settlement vs. predation

The experiments described in the proceeding chapters produced very conclusive results. On the one hand, they confirmed that sea urchin movements are of very little importance, a fact that simplifies greatly the understanding and modelling of sea urchin dynamics. On the other hand, our results showed that both variability in settlement patterns and the impact of predation by fish on settled young sea urchins are powerful factors that are potentially capable of, respectively, destabilising and controlling the dynamics of sea urchin populations.

Nevertheless, our experiments were unable to resolve the dilemma of who (or what) controls the demographic dynamics of sea urchin populations. The reason for this is clear: if settlement and predation produce antagonistic effects, then one of these two factors must prevail over the other. However, given that our experiments treated these two processes separately, we were unable to diagnose exactly the resulting balance of effect between the two. To have manipulated simultaneously both the amount of settlement and predation in a controlled experiment would have been extremely difficult. Moreover, such short-term experiments often tend to mask effects that occur at greater spatial and temporal scales. It thus seems clear that only a long-term analysis of patterns and fluctuations in natural populations subject simultaneously to all the factors under study will allow us to determine the true importance of each of the processes we have discussed in relation to the dynamics of sea urchin populations.

In chapter 7 we analyse the results of a long-term study (12 years) of the density and size structure distribution of sea urchins inside and outside the Medes Islands. Our aim was to test whether deterministic models are accurate when they predict the control of sea urchins by predators, or whether destabilising factors connected with settlement or refuges were more decisive factors, as our results seemed to suggest. This study was part of a monitoring programme of the natural heritage of this reserve and was designed to discover variations in the abundance and structure of sea urchin populations. Given that it was carried out inside and outside the reserves, we were able to analyse the effects of predation and fishing. Likewise, the fact that it was carried out in habitats with highly contrasting degrees of roughness meant that we could also analyse the role of refuges. Finally, as a long-term programme studying a great variety of different-sized settlements, we were able to analyse simultaneously the effects of variation in settlements.

3 –The application ofthe results in management programmes

Finally, in chapter 8 we discuss the applicability of trophic models in the strategic management of a protected coastal area.

Our chosen location was the Scandola Marine Reserve in Corsica, where extensive coralline barrens are visible on reefs otherwise dominated by mature forests of the perennial alga *Cystoseira balearica*. These coralline barrens (with high densities of sea urchins) are well-defined and there are clear boundaries with neighbouring well-developed forests (almost sea urchin-free): this phenomenon in a marine reserve abounding with fish struck us as being an excellent place to evaluate experimentally the predictions made by trophic models concerning a possible reversion of barren patches to well-constituted meadows. Thus, in this chapter we present the results of an experimental eradication of sea urchins, designed to test whether a sudden drop in the population of adult sea urchins might forcibly stimulate the return of *C. balearica* meadows. The results of this experiment are potentially important for the management of protected areas as the eradication of sea urchins may turn out to be a useful tool in combating the spread of barren patches. The three years of the experiment also allowed us to investigate the mechanisms that enable barren patches to persist.

4. Putting the pieces together: a new conceptual framework and proposals for future research

This thesis ends with a section that is too long to be considered as just another chapter. Unlike the previous chapters, this part of the thesis does not deal with any specific research area; rather, it consists of a general discussion of the results presented in previous chapters, here analysed conjointly in an attempt to situate them within a single coherent global framework.

This lateral view of our results is highly appropriate given the formal rigidity of scientific literature (to which the previous chapters of this thesis conform) that prevents us from extracting cross-references from subjects that, despite having been compartmentalised by experimental impositions, are in fact closely interconnected. In my opinion, the main interest in my work and its most original results lie in these cross-references. Thus, I have allowed myself the liberty of presenting the discussion in a speculative fashion that differs from the rigorous experimental work included in previous chapters. A research paper of this nature must not only test and describe its initial hypothesis, but must also identify the weaknesses of that hypothesis: it must likewise generate new hypotheses that will form the basis of any future research. My hypothesis aims to explain the scenarios we found in the different localities of the northwest Mediterranean we studied, and I have added the idea of a historical or successional axis (in which anthropic action plays a highly important role) to the two main axes – conditions of productivity (“bottom-up”) and predator pressure (“top-down”) - that have been the subject of discussion throughout this thesis.

The speculative nature of my ideas can be justified by the lack of any palaeoecological data or historical ecological sources from the Mediterranean that might lend support to connections between the supposed general regression of algae dominated by species belonging to the genus *Cystoseira*, the advance in sea urchin populations and human activity. The discussion ends with a list of subjects to be tackled in the future that I believe must be investigated forthwith.

Box 2: The study area

Aside from the experiments in chapter 8, which were undertaken in the Scandola natural reserve in Corsica, all of the fieldwork included in this thesis was carried out in the Medes Islands Protected Area and nearby coastline. The Scandola reserve (Fig. 1) is located on the westernmost point of the island of Corsica (42°14'-42°25'N, 8°37'-9°00'E). Fishing has been banned since 1975 and fish communities, although not as dense as in the Medes Islands, are well developed here (Francour 1994). The substrate of this coastline consists of steeply shelving volcanic (basalt) rocks and granites, generally quite smooth that are dissected by many crevices. The photophilous species in this reserve are dominated by various species of algae belonging to the genus *Cystoseira*, which succeed one another along the depth gradient (Sant 2003). The infralittoral zone where experiments were carried out, located at a depth of 5 to 10 m, is dominated by well-developed *Cystoseira* meadows alternating with barren patches provoked by dense populations of *Paracentrotus lividus*.

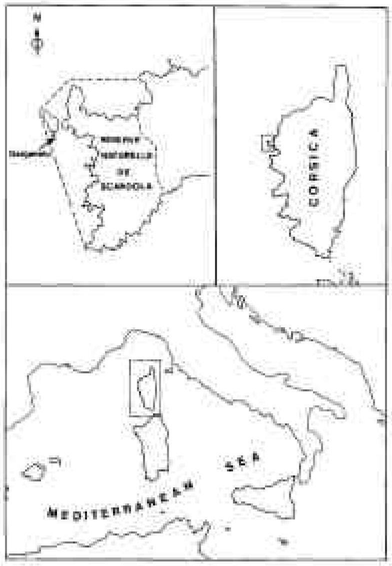


Figure 1. Location of the Scandola marine reserve: the arrow marks the site of the experiments.

The Medes Islands are situated approximately 1 km east of L’Estartit (40º 02, 55’’ N, 3º 13’ 30’’ E, Catalonia, NW Mediterranean). This small archipelago (with a total emerged area of 21.9 ha) consists of a series of islets that correspond to a continuation of the Montgrí massif into the sea. La Meda Gran (18.71 ha) and La Meda Xica (2.59 ha) are the two main islets, while the rest (Carall Bernat, Tascons Grossos, Tascons Petits, El Medallot and Les Ferranelles) occupy only 0.62 ha in total.

The main climatic and hydrographic characteristics are summarised in works by Pascual and Flos (1984), Pascual *et al.* (1995) and Garrabou (1997). The average annual rainfall is around 600 mm (average for the period between 1996 and 1995). There is no clear seasonal pattern to rainfall, although autumn tends to be the rainiest season with maximum figures usually recorded in October (average monthly rainfall 103.8 mm).

Gales are infrequent and only those associated with northerly or easterly winds are severe. Waves are not generally very high, although they do have much greater effects on the distribution of biological communities than tides, which are relatively insignificant (10 to 20 cm maximum tidal range). The prime causal factor in hydrodynamism is wave direction. In a bathymetric gradient, hydrodynamism decreases exponentially with depth. Calculated in terms of erosion units of balls of calcium sulphate (Ballesteros and Zabala, unpublished data, in Garrabou 1997), the maximum measured hydrodynamism at a depth of 2 m is 350 mg of calcium sulphate per hour, while at a depth of 30 m it is 110 mg of calcium sulphate per hour. Average monthly values for hydrodynamism show a seasonal pattern clearly correlated with the greater frequency of storms during winter and autumn, with maximum values during these seasons that are between 50 and 100% higher than figures recorded for spring and summer.

The average annual temperature of the sea is 16.5º C (average between 1966 and 1995), with maximums in summer (August) reaching an average of 24º C and, in winter (February), minimums of 12º C. The annual thermal oscillation is 12º C. Between April and June a thermocline develops at a depth of around 20 m that has a thermal difference of 7-8º C. This thermocline is present throughout the summer and tends to sink to depths of up to 50 m. At the end of the summer, the cooling atmosphere encourages a greater vertical mix of temperatures and by the end of November, the whole column of water is once more fully mixed.

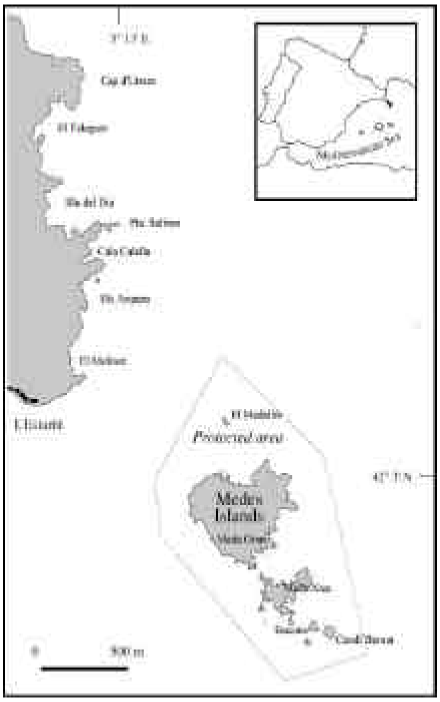


Figure 2 – Location of the Medes Islands and the coastline of the Montgrí massif. The arrows indicate the coves where the enclosures were installed.

Average salinity varies between 37.5 and 38%, although the water mass around the Montgrí massif and, above all, the Medes islands is heavily influenced by outflow from the mouth of the river Ter (situated a few miles southwest of the islands). In epochs of heavy rain, the salinity can drop to 33-34% and exceptionally to 22%.

Concentrations of dissolved organic nutrients (nitrates, nitrides and phosphates) vary with the seasons much more than they do with depth (and, above all, in the range of depths used in our study): levels increase between autumn and the beginning of spring and then start to drop once spring begins until the end of summer, at which point the minimum and undetectable values are reached. Maximum values are similar to those described for other Mediterranean coastal waters (Margalef 1974, Ballesteros 1992, Garrabou 1997), although always near the top of the range.

The average concentration of nitrates is 0.92 mols/l, but varies greatly between 9 mols/l and undetectable levels. The average concentration of nitrides is 0.31µmols/l and values range from 0.84µmols/l to undetectable levels. The average concentration of phosphates is 0.13 µmols/l and values range from a maximum of 0.30 µmols/l to undetectable levels.

The average coefficient of light extinction at depth is 0.12 m^{-1}, which corresponds to an annual average visibility for a Secchi disc of 14.1 m.

Experimental conditions

Fishing has been prohibited around the Medes Islands since 1983: the size of the protected area was extended in 1991 (Law 19/1990 Generalitat de Catalunya). As a result, fish populations have recovered and today recorded densities and sizes are some of the highest in the whole of the Mediterranean (Garcia-Rubies and Zabala 1990, García-Rubies 1996). Notwithstanding, fish populations along the neighbouring, unprotected coastline are much smaller and exhibit symptoms of overfishing (Garcia-Rubies 1996). The contrast between bottom-dwelling fish biomass in areas inside and outside the protected area – areas that are otherwise very similar – provides excellent experimental conditions for testing the effects of fish on infralittoral communities.

Amongst the different benthic communities that merge into each other along the bathymetric gradient of the Medes Islands (see Annex 1; Fig. 3), our study focussed on the infralittoral community on exposed rocks situated at depths between 5 and 10 m (see following paragraph). Within the Medes reserve we chose three coves with narrow entrances that could be closed off with vertical nets; they also had to be large enough to harbour a good representation of the communities under study and well-protected from gales. We chose the coves of Portitxol, Sant Istiu and Cova de la Reina (Fig. 2) given that they faced in approximately the same direction (SE-S), were of similar depths (between 5 and 7 m) and had reefs consisting of large blocks covered in similar photophilous algal communities. In these three coves we carried out the majority of our experiments involving herbivore exclusion and transplants, as well as the temporal monitoring of settlement and predation. The remaining experiments were carried out on substrates with similar characteristics.

Figure 3 – Schematic view of the vertical zonation of the Catalan coast. Taken from Ballesteros and Zabala 1993.

The infralittoral rocky bottom communities

The main characteristics of the phytocoenosis of photophilous algae communities situated at a depth of 5 – 10 m and occupied by large bouldres are described in Ballesteros *et al.* 1984, Sala 1996 and Sala and Boudouresque 1997.

The dominant algal community at depths between 5 and 10 m in the Medes Islands and the neighbouring coastlines of the Montgrí massif are made up of photophilous and hemiskiaphyte algae and have been described as a transition between *Padino-Cladostephetum hirsutae* J. Feldmann 1937 and *Rhodimenio-Codietum-vermilarae* Ballesteros 1992. Overall, this communities harbours over 100 species of algae (Ballesteros 1992) that are organised spatially in different strata: an erect stratum dominated by perennial and annual species, an arborescent stratum, a stratum of epiphyte and turf-forming algae and a final stratum of incrusting species, some of which are incrusted with carbonates (Table 1).

Table 1 – The main species of algae in photophilous and hemisciaphilic communities in the Medes Islands.

Stratum	**Strategy**	**Principal species**
Erect	Perennial	*Halopteris scoparia*, *Halopteris filicina*, *Codium vermilara*, *Codium bursa*, *Codium effusum*, *Cystoseira compressa*, *Cystoseira sp*
	Annual	*Dictyota dichotoma*, *Dictyota fasciola*, *Taonia atomaria*, *Padina pavonica*, *Asparagopsis armata*
Turf	Perennial	*Corallina elongata*, *Peyssonnelia borneti*
	Annual	*Rhodymenia ardissonei*, *Cryptonemia lomation*, *Falkenbergia rufolanosa* stadium, *Plocamium cartilagineum*
Epyphitic	Annual	*Sphacellaria* spp. *Ceramium* spp; *Herposiphonia secunda*
Encrusting	Perennial	*Lithophyllum incrustans*, *Mesophyllum alternans*, *Hildenbrandia canariensis*, *Zanardinia prototypus*
	Annual	*Aglaozonia parvula* stadium, *Aglaozonia melanoidea* stadium

The faunal fraction of this community represents just a small part of the total biomass despite exhibiting a high level of biodiversity. In response to the complex spatial structure generated by algal communities, invertebrates adopt different colonisation strategies (Ballesteros *et al*. 1984). Thus, invertebrates can be grouped into different strategic groups according to size, the habitat they occupy, food, adaptation to seasonality and mobility (Table 2).

The fish fauna of the infralittoral communities around the Medes Islands has been studied by García-Rubies (1996). This author, following the criteria established by Harmelin (1987), grouped fish species into six groups according to their position on the substrate and their use of space (Fig. 4). The most abundant species in the communities we studied were those of groups 3 and 5, amongst which the following species stand out due to the density of their populations, their biomass or role as predators: the Sparidae *Diplodus sargus*, *D. vulgaris* and *D. puntazzo*. As abundant and important are the herbivore *Sarpa salpa* and the small Labridae *Coris julis, Symphodus tinca* and *Serranus cabrilla* (Table 3).

In the same locality the microhabitats chosen for settlement by the larvae of the most important species and the survival and dispersal of juveniles belonging to the genus *Diplodus* (Garcia-Rubies and Macpherson 1995) have also been studied. The food of the most abundant species was studied by Sala (1996) and a certain degree of niche separation in the way the space was exploited by the principal species of the genus *Diplodus* was observed (Sala and Ballesteros 1997). The list of fish species detected during this study are shown in annexes 1 and 2 to chapter 1.

Table 2 – The main species of invertebrates present on reefs dominated by photophilous and hemisciaphilic communities in the Medes Islands.

Functional group				**Species**
Habitat	**Feeding**	**Seanoallity**	**Mobility**	
Encrusting	Suspension feeders	Perennial	Sessile	Sponges (*Crambe crambe*), Tunicata and Bryozoa
Cryptophile	Variable	Perennial	Low Mobility	Polychaeta (*Nereis zonata*, *Ceratonereis costae*, *Lepidonotus clava* i *Spirobranchus polytrema),* Mollusca (*Jujubinus gravinae* i *Muricopsis cristatus*, *Haliotis tuberculata*, *Dendrodoris limbata*, *Conus ventricosus),* Echinodermata (O*phiotrix fragilis*, *Amphipholis squamata, Asterina gibbosa*, *Coccinasteria tenuispina)*
Movile fauna within algal turfs and animals	Variable	Annual	Low Mobility	Hydrozoa, Sponges, Crustacea (*Dexamine spiniventris*, *Hyale* sp., *Maera inaequipes*, *Lilljeborgia brevirostris*, *Caprella* spp., *Ammothella longipes*, *Cymodoce truncata* i *Dynamene bidentata*), Mollusca (*Flavellina affinis*, *Herbsia costai*, *Coryphella pedata)*, Polychaeta (*Lysidice ninetta*, *Platynereis dumerili*)
Sessile erect macrofauna with vertical or laminar growth	Suspension feeders	Perennial	Sessile	Sponges (*Ircinia fasciculata*, *Hamigera hamigera*, *Anchinoe ficticius*), Cnidaria (Hydrozoa, *Aiptasia diaphana*, *Anemonia sulcata*, *Balanophilia regia*, *Maasella edwarsi*), Bryozoa (*Crisi occidentalis*, *Pentapora ottomulleriana*, *Schizobranchiella sanguinea*, *Turbicellepora magnicostata*), Mollusca (*Ostrea edulis*, *Spondylus gaedeoropus*, *Mytillus galloprovincialis*, *Arca noae*), Tunicata (*Micrcosmus sabatieri*, *Polycarpa pomaria*, *Pyura dura*, *P. microcosmus*, etc.) and sedentary Polychaeta (Serpulidae, Sabellidae)
Mobile macrofauna	Predators	Perennial and annual	High mobility	Crustàcis Decapoda (*Pilumnus hirtellus*, *Alpheus dentipes*, *Calcinus oratus*, *Thoralus cranchii*, etc.), Mollusca (*Aplysis punctata*, *Octopus vulgaris*), Echinodermata (*Arbacia lixula*, *Paracentrotus lividus*, *Genocidaris maculata*, *Echinaster sepositus)*
Epibiont	Suspension feeders	Annual	Sessile	Sponges, Hydrozoa (*Eudendrium capillare*, *Campanularia hemisphaerica*, *Halecium beani*, *Aglaophenia pluma),* Mollusca, Bryozoa *(Scrupocellaria reptans*, *Crisia occidentalis, Amathia lendigera), Tunicats (Botryllus spp.)*

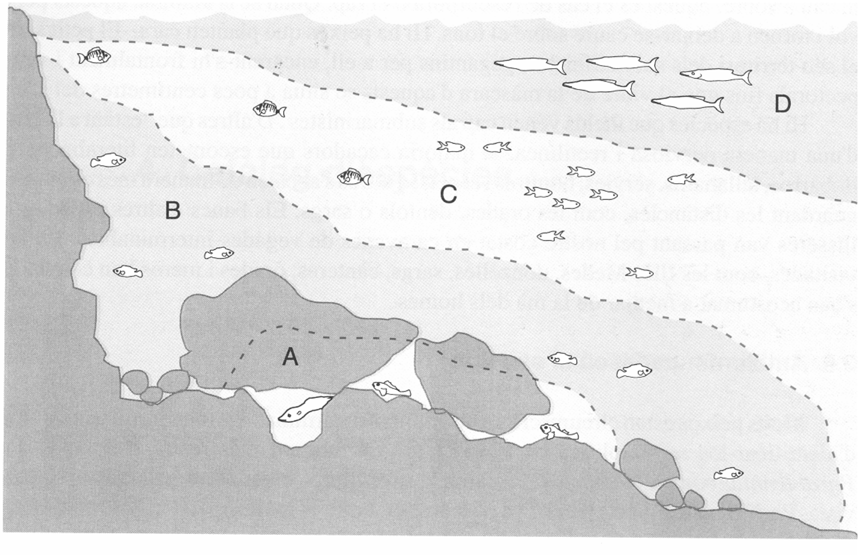


Figure 4 – The six spatial categories within the community of onshore fish species on reefs in the western Mediterranean (according to Harmelin 1987; redrawn by Jordi Corbera in Corbera et al. 1992).

Table 3 – The six spatial categories within the community of onshore fish species on reefs in the Mediterranean, and the commonest species around the Medes Islands and on the Montgrí coastline.

Category	**Group**	**Principal species**
D	Nectonic	Centracanthidae: *Spicara ssp.;* Sparidae: *Boops boops, Oblada melanura;* Mugilidae: *Mugil sp.;* Carangidae: *seriola dumerili;* Serranidae: *Dicentrarchus labrax*
C	Nectonic sedentary	Pomacentridae: *Chromis chromis;* Serranidae: *Anthias anthias*
B	Nectobenthic with moderate vertical movements	Sparidae: *Diplodus annulars, Diplodus cervinus, Diplodus puntazzo, Diplodus sargus, Diplodus vulgaris, Dentex dentex*
	Nectobenthic with low vertical movements	Mullidae: *Mullus surmuletus*
	Nectobenthic species with low desplacemnent	Serranidae: *Serranus cabrilla, Serranus scriba, Epinephelus marginatus;* Sciaenidae: *Sciaena umbra*
A	Sedentary	Labridae,*Coris julis, Ctenolabrus rupestris, Labrus bimaculatus, Labrus merula, Labrus viridis, Symphodus cinereus, Symphodus doderleini, Symphodus mediterraneus, Symphodus melanocercus, Symphodus ocellatus, Symphodus roissali, Symphodus rostratus, Symphodus tinca, Thalasoma pavo;* Scorpaenidae: *Scorpaena porcus, Scorpaena scrofa, Scorpaena notata;* Gobiidae: *Gobius bucchichi;* Blenniidae: *Parablennius gattourgine, Parablennius incognitus, Parablennius pilicornis, Parablennius rouxi;* Tripterygiidae: *Tripterygion spp.* Congridae: *Conger conger;* Muraenidae: *Muraena helena;* Gadidae: *Phycis phycis*

Chapter 2- Multiple controls of community structure in a sublittoral marine environment

Abstract

The structure and dynamics of ecological communities can be determined by both top-down (e.g., predation) and bottom-up (e.g., nutrient inputs) processes, which can act sinergistically and across spatial and temporal scales. Here we aimed at understanding the roles of bottom-up vs. top-down control in a sublittoral marine community with a marked seasonality in energy inputs, which harbors a diverse algal community, and strong herbivores. We hypothesized that in this seasonal environment top-down control regulates total biomass and community structure (relative abundance of species). To test these hypotheses we conducted an experiment in a Mediterranean sublittoral rocky community by orthogonally manipulating densities of the major consumers of benthic algae (fishes and sea urchins) in 100 m^2 enclosures in a marine reserve, and monitored algal communities at the lowest taxonomic level possible over two and a half years. Most algae showed a marked annual cycle with a biomass peak in Spring and biomass low in Winter, following seasonal nutrient pulses. Previous studies showed that fluctuations in algal biomass are immediately followed by similar fluctuations in epifaunal invertebrates. These results indicate the existence of bottom-up processes. Sea urchins clearly reduced the abundance of most algae and total algal biomass, although the abundance of some opportunistic species and encrusting corallines increased by a facilitation process. This indicates the existence of top-down processes. The effect of fish grazing on algal abundances was significantly weaker. Sea urchin grazing was inhibited when predatory fish were present. Multivariate analysis showed that the interaction between seasonal nutrient inputs and herbivory induced the formation of four algal communities dominated by non-random groups of species. In a multivariate space, algal communities grazed by sea urchins and algal communities where urchins were absent moved in opposite directions. However, all communities showed seasonal oscillations (cycles) nested within their general (successional) trajectories. In summary, in this Mediterranean rocky sublittoral community, community organization was determined by the synergistic interaction between top-down and bottom-up processes: top-down control regulated total algal biomass and determined the general trajectory of ecological succession of algal communities, while bottom-up control produced fluctuations of community trajectory nested within the main successional trajectory.

Introduction

One of the key issues in ecology is the role of resource (bottom-up; Fretwell 1977) vs. predator (top-down; Hairston et al. 1960) control in the structure and dynamics of populations and communities (Matson and Hunter 1992). Bottom-up and top-down forces do not act in isolation, and they vary within and among systems (e.g. Power 1992, Menge 1992, 2002). The important issue is thus to determine under which conditions predators or resources will dominate community regulation (Hunter and Price 1992, Power 1992). The conditions that cause variation in the relative strength of predator and resource control include variation in energy inputs into the system, the life history of species, and food web structure (Power 1992, Polis 1999). For instance, the effects of energy input fluctuations (e.g., nutrients) on primary producers will depend on their life history (e.g., ephemeral vs. perennial plants) and on nutrient dynamics (Polis 1999). In addition, our understanding of the relative roles of bottom-up and top-down processes depends on the temporal scale. Predation impacts on community structure that become evident only after years or decades may be masked (and thus go undetected) by seasonal fluctuations (presumably attributable to bottom-up control) occurring at shorter time scales, as has been shown in terrestrial communities (e.g. McNaughton 1985, 1998, Terborgh et al. 2001). Understanding multiple controls of community structure across temporal scales is hence essential for understanding and predicting ecological succession and the evolution of natural communities.

While in terrestrial and in freshwater systems the importance of bottom-up processes in determining the community structure and their interaction with top-down processes has been largely demonstrated (e.g. Stiling and Rossi 1997, Moon and Stiling 2002, Gratton i Deno 2003, Rosemond et al. 2001, Flecker et al. 2002), in marine benthic systems there are only a few evidences at the smallest spatial scales (Benedetti-Checci 2000, Menge et al. 1997a, Nielsen 2001, 2003, Nielsen and Navarrete 2004) and specially in subtidal commnities (McGlathery 1995, McCook 1996, Lotze and Sommer 2001, Seitz and Lipcius 2001). Although there is a number of studies where nutrient availability and predator abundance have been manipulated at small spatial and temporal scales (small-cage experiments; e.g. McClanahan et al. 2003, Nielsen 2001, McGlathery 1995), it is difficult to manipulate bottom-up factors at larger scales. The comparison of sites located far apart and exposed to different environmental conditions can provide some clues about the role of bottom-up processes (Menge and Olson 1990, Dayton et al. 1999, Menge et al.

1999, Menge 2000), although geographic distance can introduce uncontrolled factors that may confound the experimental results.

In temperate seas, however, it is possible to test the role of bottom-up factors taking advantage of natural conditions, since the factors driving primary benthic productivity (e.g., irradiance, temperature, nutrient availability, and water motion) fluctuate seasonally. Therefore it is possible to carry out experiments manipulating top-down factors (e.g., predator abundance) and monitoring seasonal factors in a single locality, thus avoiding uncontrolled factors associated with spatial heterogeneity. In this study we aimed at understanding the roles of bottom-up vs. top-down control in a sublittoral marine community with a marked seasonality in energy inputs, which harbors a diverse algal community with perennial and ephemeral species, and strong herbivores and predators.

The Western Mediterranean sublittoral is dominated by complex benthic communities composed of many hundreds of species of algae and invertebrates (Ros et al. 1985, Ballesteros 1992). The sea urchin *Paracentrotus lividus* is the most important grazer in this system, and at high densities it can turn complex algal assemblages into coralline barrens by grazing (Verlaque 1987). Overfishing of sea urchin predators can result in increases of sea urchin abundance and subsequently in the formation of coralline barrens, indicating the existence of top-down control (Sala et al. 1998). On the other hand, the Western Mediterranean is subjected to seasonal fluctuations of temperature and nutrients, which result in an annual benthic succession consisting of marked cycles of algal biomass (Zabala and Ballesteros 1989, Ballesteros 1989, 1992). These seasonal changes in algal biomass are followed by similar changes in the biomass of small epifauna (Sala 1997). This indicates the existence of important bottom-up processes.

Changes in community structure in the Mediterranean sublittoral have been described separately at different time scales as the alternation between the two endpoints of a successional continuum, from the most simplified to the most complex structure. At a time scale of years, community structure alternates between coralline barrens and complex algal communities (Sala et al. 1998). At a time scale of months, benthic communities alternate between the annual minimum algal biomass and the annual biomass peak (Ballesteros 1991). However, there have been no attempts to integrate the effects of both seasonal nutrient fluctuations and predation to understand what controls community structure across temporal scales.

The objective of this study is to determine the role of top-down and bottom-up processes in the regulation of the structure of a community subjected to seasonal energy inputs, and to predict changes in community structure over time. In addition, we aimed at describing successional trajectories in community structure as a result of the continuous interaction between both control mechanisms over time. We hypothesize that in this seasonal environment top-down control regulates total biomass and community structure, but it does not cancel seasonal biomass fluctuations induced by bottom-up processes. In addition, we hypothesize that bottom-up effects are nested in the general trajectory of ecological succession which is mainly determined by top-down control. To test these hypotheses we conducted an experiment in a Mediterranean sublittoral rocky community manipulating densities of the major consumers of benthic algae (fishes and sea urchins) over two and a half years.

Material and methods

Study sites and assemblages

The study was carried out in Medes Islands Marine Reserve (42º 16’ N, 03º 13’ E), Catalonia, NW Mediterranean Sea (Fig. 1), where fishing is prohibited since 1983.

. Our study sites were small coves with large boulders and S-SW orientation. Infralittoral algal assemblages in the rocky bottoms of the reserve are described in Ballesteros et al. (1984) and Sala and Boudouresque (1997). The study was carried out on algal assemblages at 5-8 m depth. These assemblages are composed of distinct strata: an erect stratum with several species of algae both annual (*Dictyota dichotoma*, *Dictyota fasciola*, *Taonia atomaria*, *Padina pavonica*, *Asparagopsis armata*) and perennial (*Halopteris scoparia*, *Halopteris filicina*, *Codium vermilara*, *Codium bursa*, *Codium effusum*, *Cystoseira compressa*, *Cystoseira* sp.), a stratum of understory algae (*Rhodymenia ardissonei*, *Corallina elongata*, *Cryptonemia lomation*, *Falkenbergia rufolanosa* stadium, *Plocamium cartilagineum*, *Peyssonnelia bornetii*), and an encrusting stratum (*Zanardinia prototypus*, *Aglaozonia parvula* stadium, *Aglaozonia melanoidea* stadium, and crustose corallines). This algal assemblage is composed of up to a hundred species (Ballesteros 1992).

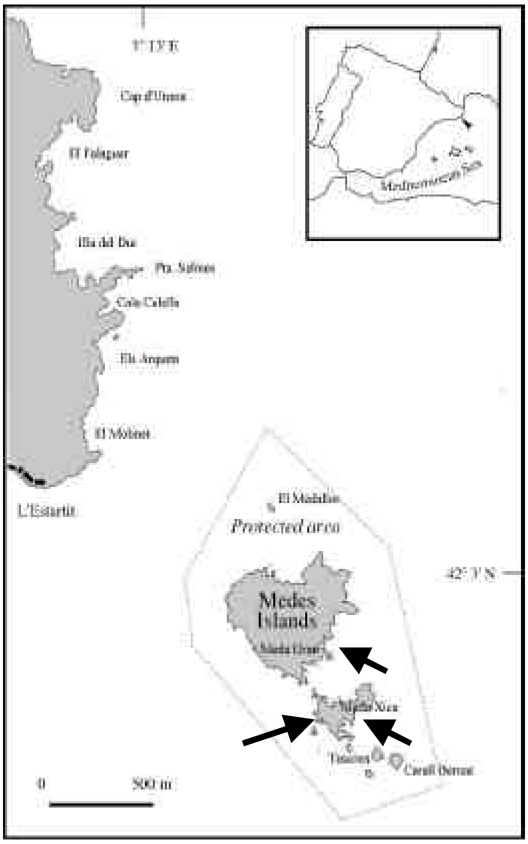


Figure 1- Location of study sites in the Medes Island Marine Reserve, Catalonia, NW Mediterranean Sea. Dotted lines show the limits of the reserve, where all fishing is prohibited.

Fish assemblages at the study site are described in Garcia-Rubies and Zabala (1989), Garcia-Rubies (1996), and Garcia-Rubies (1999); diet and grazing impacts in Sala (1996), Sala and Ballesteros (1997), Sala and Boudouresque (1997). The major benthic-feeding fishes are sparids, mainly *Diplodus* spp.; *Sarpa salpa*, the major strictly herbivorous fish, is also present although in lower abundance (Apendix 1).

Experimental design

To determine the relative impacts of fish and sea urchin grazing on algal assemblages we conducted a grazer exclusion experiment from June 1998 to September 2000. We manipulated the density of herbivorous/omnivorous fishes (Table 1 and figure 2) and the sea urchin *Paracentrotus lividus*, the most abundant sea urchin in the region (Sala et al. 1998).

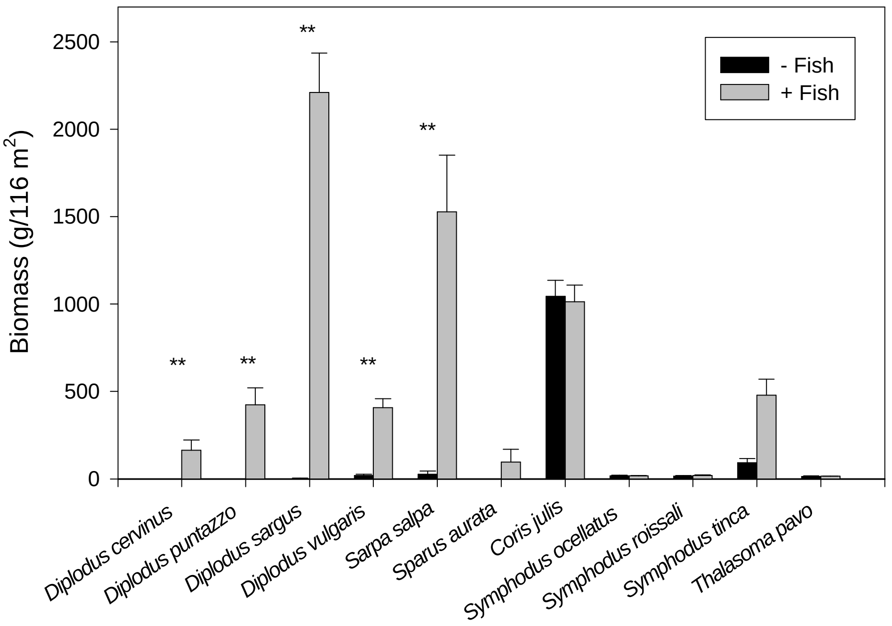


*Figure 2- Biomass of the major benthic feeding fishes inside and outside experimental enclosures in Medes Islands Marine Reserve. ** Asterisks indicates statistical significance in an ANOVA analysis (** p<0.01).*

*Table 1- Biomass (mean ± SE) of the most abundant benthic-feeding fishes inside and outside the experimental enclosures. Results of two-way ANOVA testing the net exclusion effect and time on the biomass of the most abundant species (Site = 2 d.f., Treatment = 1 d.f., n=72). Significance: *p<0,05, **p<0,01,ns = not significant.*

	Biomass (g/116m^2)		Treatment	Year	Treatment x Year
	Inside	Outside	F	F	F
Diplodus cervinus	0 (0)	164.22 (58.04)	**8.14****	2.10 ns	2.10 ns
Diplodus puntazzo	0 (0)	423.19 (97.30)	**21.31****	**3.57***	**3.571***
Diplodus sargus	2.19 (1.43)	2211.43 (224.56)	**3732.55****	0.41ns	0.41ns
Diplodus vulgaris	19.67 (6.61)	406.28 (53.12)	**492.43****	0.17 ns	0.17 ns
Sarpa salpa	25.52 (18.94)	1527.67 (324.41)	**118.92****	2.27 ns	2.27 ns
Sparus aurata	0 (0)	96.17 (73.52)	3.82ns	0.39ns	0.39ns
Coris julis	1043.68 (91.98)	1013.13 (94.94)	0.098ns	**4.95***	0.15ns
Symphodus ocellatus	18.23 (3.15)	17.07 (2.67)	0.14ns	0.53ns	0.11ns
Symphodus roissali	15.38 (3.15)	19.43 (3.30)	0.37ns	0.62ns	0.12ns
Symphodus tinca	92.77 (22.93)	479.34 (90.55)	0.100ns	0.42ns	0.11ns
Thalasoma pavo	12.76 (4.10)	14.33 (0.3.62)	0.912ns	0.25ns	0.29ns

Grazer exclusions were replicated in the three experimental coves (Estiu, Reina and Portitxol, Fig. 1). The experiment consisted of four orthogonal combinations of fishes and sea urchins: no grazers (-Fish-Urchins, -F-U), only sea urchins present (-F+U), only fish present (+F-U), both sea urchins and fish present (+F+U) (Fig. 3).

Fish exclusions were made by closing half of small coves (cove size = 140-220 m^2) with polystyrene trawler nets 2.5 cm mesh size, 6-8 m in depth and 11-16 m in length. Nets were attached using steel cable to autoexpansive nails anchored into the substratum. The upper part of the net was continuously kept on the surface by plastic buoys. The experiment thus tested the effects of medium-large (up to 45 cm total length) herbivorous and omnivorous fishes only. Exclusion nets were cleaned and checked daily, and replaced every other month to prevent significant fouling. Enclosures were checked daily for large fishes, which were removed when occasionally migrated into the exclusion area. Nets were broken by strong storms in three occasions, but they were replaced within three days. Moreover, storms occurred only in winter and fall, when fish activity was lower (Garcia-Rubies 1996). Roofless herbivore exclusion nets have negligible light-shading effects (Lewis 1986). Increased densities of micrograzers represent a potentially confounding factor in the interpretation of experimental manipulations involving caging treatments (Dayton and Oliver 1980, Brawley and Adey 1981), but the size of our exclosures diminishes the likelihood of such artifacts usually associated with previously used small cages. The mesh size of the nets allowed free passage to juvenile sparids and several small labrids that are carnivores (Sala 1996). The abundant *Coris julis* and other wrasses, predators of gastropods, small crustaceans and echinoderms (Sala 1996), moved freely trough exclusion areas and were commonly observed feeding within the exclusions. Treatments including fishes were located immediately adjacent to the fish exclusions.

To create the treatments including sea urchins we built 16 m^2 enclosures using 10 cm-tall plastic fences 2 cm mesh size, supported by steel rods anchored into the substratum. We added sea urchins in each enclosure to recreate average densities of 12 individuals/m^2. To create the treatments without sea urchins we removed all sea urchins on several large boulders and built partial fences to account for any potential caging artifact. Because we sampled algal assemblages far from the edges of the enclosures, and these fences do not interfere with light and water movement (Sala and Boudouresque 1997), we assumed that caging artifacts were negligible. Sea urchin exclusion areas were checked weekly and all new urchins removed. The four experimental treatments were then located as follows: -F-U and -F+U in closed cove, and +F-U and +F+U in open cove (Fig. 3).

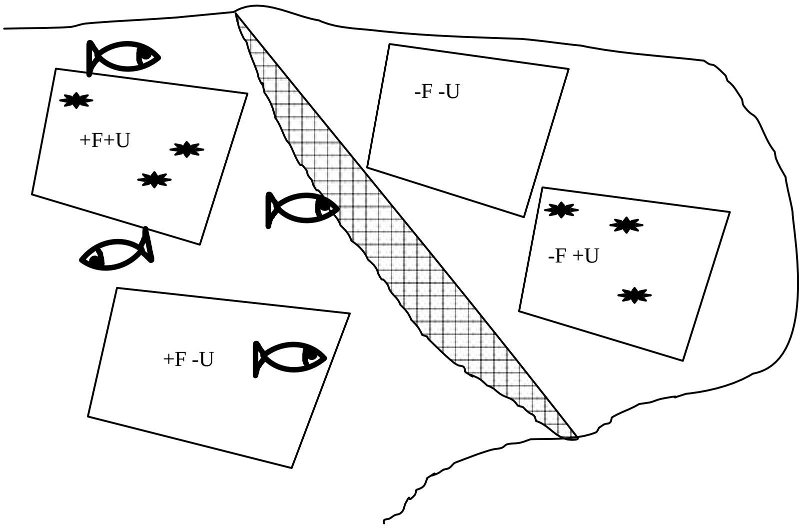


Figure 3-. Schematic design of the experimental treatments on each cove. -F-U = fishes and urchins absent, -F+U = only urchins present, +F-U = only fishes present, +F+U = both fishes and urchins present.

Quantification of community structure

To determine the effects of the experimental treatments on the algal assemblages we monitored algal composition and abundance monthly (weather permitting) from May 1998 to September 2000. The monthly sampling interval was intended to incorporate the seasonality of algal dynamics in the region (Ballesteros 1992, Sala and Boudouresque 1997). Algal cover was quantified using 25 ? 25 cm quadrats divided in 25 5 ? 5 cm subquadrats (Sala and Ballesteros 1997). Four replicate quadrats were randomly placed at each treatment and site, and the percentage of cover of each taxa estimated as the percentage of the number of subquadrats where a taxa was present relative to the total number of subquadrats sampled. Due to the extreme diversity of Mediterranean algal communities at small spatial scales (Boudouresque and Fresi 1976, Coppejans 1977, Verlaque 1987, Ballesteros 1992), the sampling area of 2500 cm^2 fulfills the requirements of minimum area for quantification of community structure (Ballesteros 1992). Algal species were also pooled in two groups on the basis of their seasonality (see Results and Appendix 2).

Sea urchin density and size distribution was quantified monthly using randomly placed 1m^2 quadrats (n = 4 per site and treatment). Abundance and size of herbivorous and omnivorous fish were determined by visual censuses using the fixed point method (Harmelin-Vivien et al. 1985). A diver stopped at a point chosen haphazardly and identified, counted and estimated the size of all fishes within a radius of 6 m. Fish biomass was estimated using length-mass equations (Sala unpubl. data, Garcia-Rubies 1996, Bayle 2001). Density of most benthic-feeding fishes in the Medes Islands do not show significant variability trough the year (Garcia-Rubies 1996), hence we conducted censuses once a year from 1998 to 2000.

To ensure that all sites had algal communities with similar starting composition and structure, we quantified algal abundance in all sites and tested for differences between sites prior to building the experimental treatments. To test for differences in the structure of algal communities we used a non-parametric one-way Analysis of Similarity (ANOSIM) (Clarke 1993) including all major algal species (Table 2). We did not find significant differences in algal abundance and community structure between sites (Global R=0,14; p=0,21). There were no significant differences in sea urchin density between sites prior to manipulation (mean density = 10.41 ind/m^2; ANOVA $F_{5,54}$=0.62, p=0.68).

Data analysis

To test for differences in sea urchin and fish abundance between treatments we used two-way ANOVA with time and treatment (fixed factors) as independent variables. To test for the effects of grazing on the algal community we used a 3-way ANOVA with urchins, fishes and time as fixed factors. The assumption of homogeneity of variances was checked using Cochran’s C-test and data transformations were performed when necessary. For the species showing strong seasonality, only samples conducted during the growth period were used in the analysis.

To determine the relative importance of bottom-up (seasonality) versus top-down (grazing) factors, relationships among algal species and environmental variables were analysed by Redundancy Analysis (RDA) (ter Braak 1994) using the ordination program CANOCO for windows version 4.0 (ter Braak and Smilauer 1994). RDA assumes a linear model for the relationship between the response of each taxa and the ordination axes, and is used if the gradient lenght in the data is short (<3 SD units) (ter Braak and Prentice 1988). The results of the RDA are presented as correlation biplots of species, sites, and environmental variables (Verdonschot and Ter Braak 1994). The eigenvalue of an ordination axis in RDA is the proportion of the total variance explained by that axis and indicates its relative importance. An unrestricted permutation test was used to test the validity of the total ordination. This technique is fully explained by Ter Braak (1990) and Verdonschot and Ter Braak (1994). Fish and sea urchin presence (as a qualitative variable), nitrate, nitrite and phosphate concentration, irradiance and surface water temperature were included as environmental variables. Physico-chemical data for the Medes Islands Marine Reserve were obtained from Garrabou (1997) and Pasqual (1998-2000 unpubl. data). Furthermore, time was included at two different scales: 1) seasons (spring, summer, fall and winter), coded as dummy variables (0 or 1); and 2) time elapsed since the beginning of the experiment in years. Forward selection of environmental variables was used to ascertain the minimum set of variables that better explain the species data. The statistical significance of the environmental variables to be used in the final analysis was determined using a Monte Carlo permutation test.

To analyse pluriannual changes in the algal community in the experimental treatments, RDA analysis was not appropriate because the weight of the treatments and the environmental variables on the analysis aggregated excessively the samples and masked time tendencies. Thus, we used a Principal Component Analysis (PCA) to assess longer term effects of grazing and seasonality on the structure of algal communities. All multivariate analysis were performed on non-transformed data. Algal species with relative cover <1% or occurring in only one sample were excluded from the analysis.

Results

Monitoring of the experimental conditions

Sea urchin densities in all experimental treatments did not show significant changes over time (ANOVA, interaction treatmentxtime p=0.99, time p=0.98) (figure 4). A total of 46 fish species were observed at the study sites (Apendix 1). The biomass of the major herbivorous and omnivorous fishes was significantly different after the creation of the fish exclosures, and maintained throughout the experiment (Table 1, Figure 2). Small labrids, which can move through the nets, did not show significant differences between treatments (Table 1; Figure 2).

Effects of experimental factors on algal species abundance

Changes in cover of the most abundant algal species over the 28-month study period are shown in Fig. 5. Time was a highly significant factor in explaining the cover of most species, since most species showed strong seasonal patterns of production and biomass loss. However, articulated calcareous algae (such as *Corallina elongata* and *Jania rubens*) and encrusting corallines (such as *Litophyllum incrustans* and *Mesophyllum alternans*) did not show a predictable seasonal pattern.

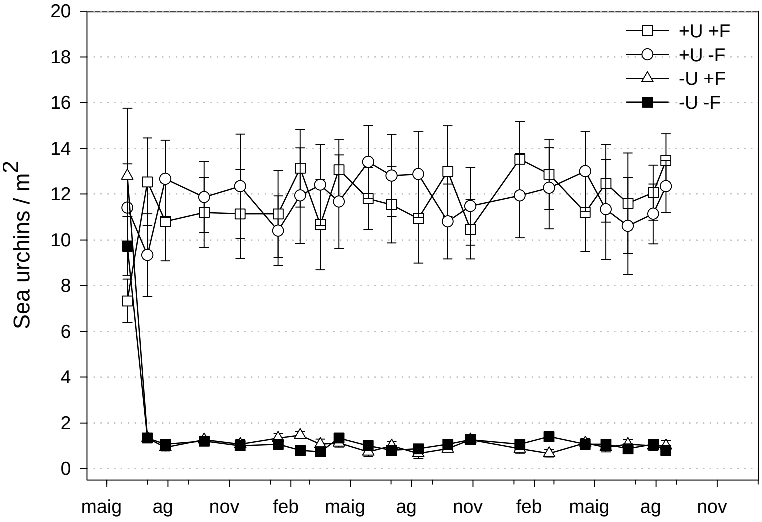


Figure 4- Mean density (±SE) of the sea urchin Paracetrotus lividus in the different experimental treatments over time (n=4).

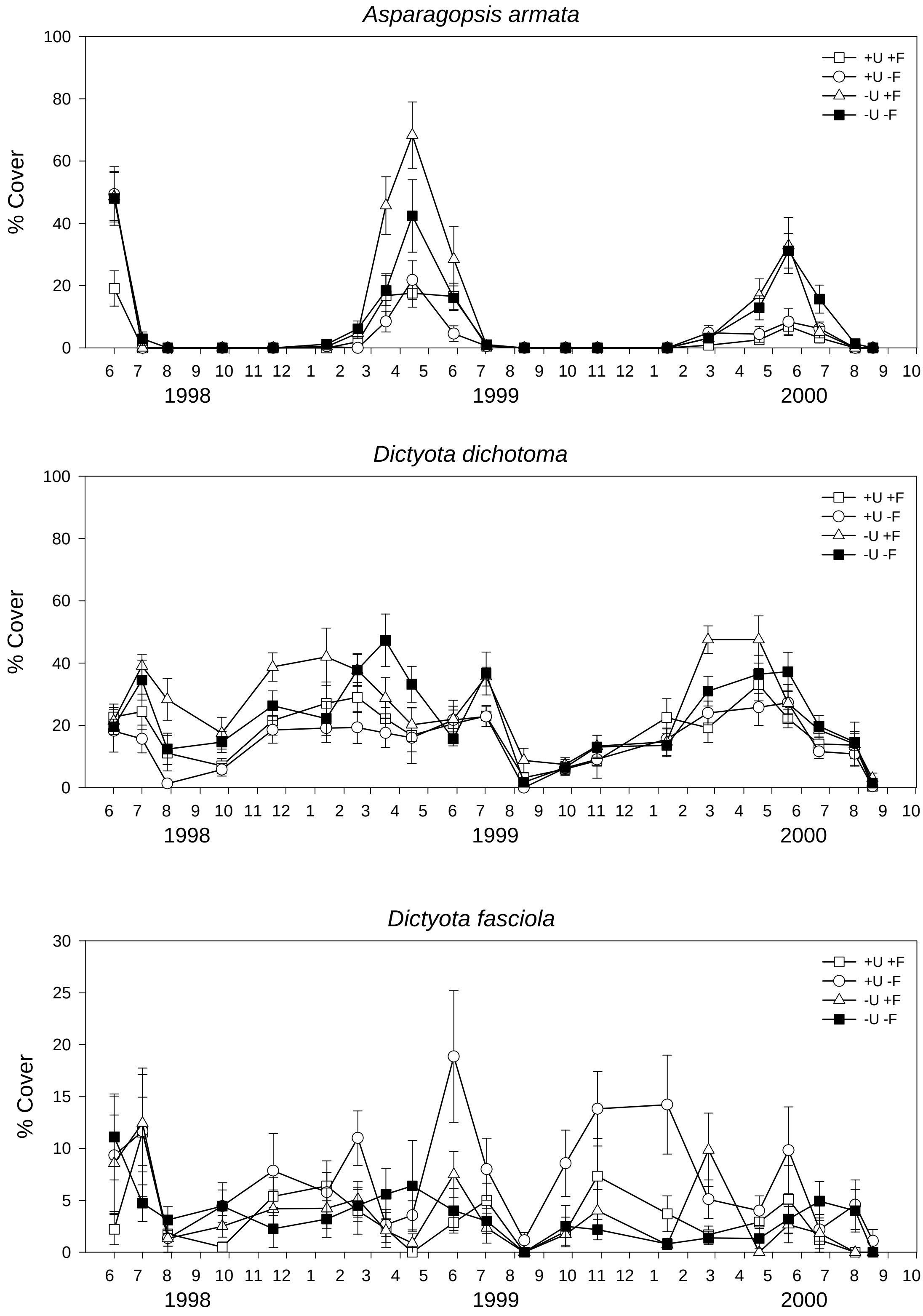


Figure 5- Temporal variation in cover (mean ± SE) of the major algal species in the experimental treatments. -F-U = fishes and urchins absent, -F+U = only urchins present, +F-U = only fishes present, +F+U = both fishes and urchins present. Months: 1=Jan trough 12=Dec

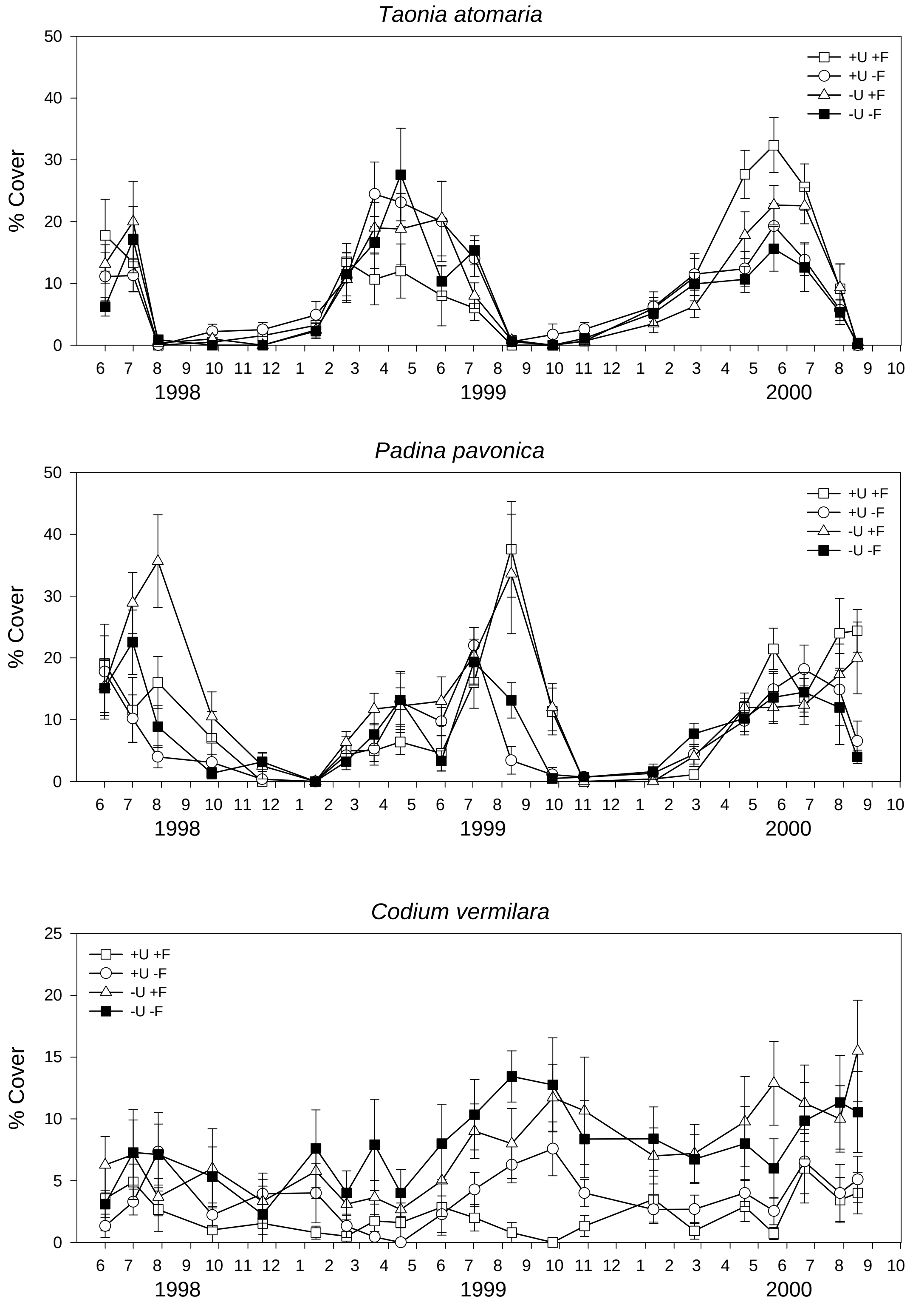


Figure 5 (cont.)- Temporal variation in cover (mean ± SE) of the major algal species in the experimental treatments. -F-U = fishes and urchins absent, -F+U = only urchins present, +F-U = only fishes present, +F+U = both fishes and urchins present. Months: 1=Jan trough 12=Dec

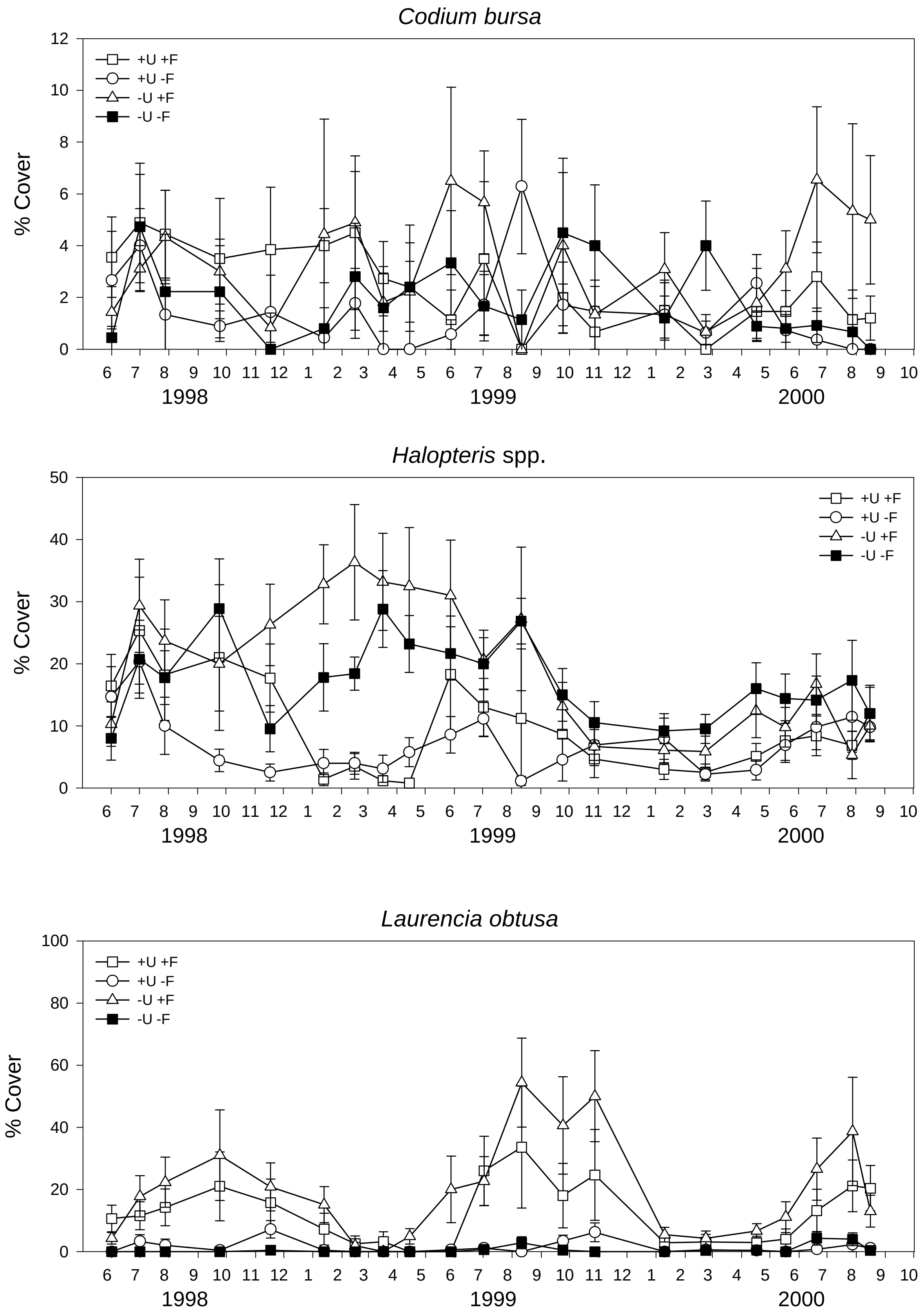


Figure 5 (cont.)- Temporal variation in cover (mean ± SE) of the major algal species in the experimental treatments. -F-U = fishes and urchins absent, -F+U = only urchins present, +F-U = only fishes present, +F+U = both fishes and urchins present. Months: 1=Jan trough 12=Dec

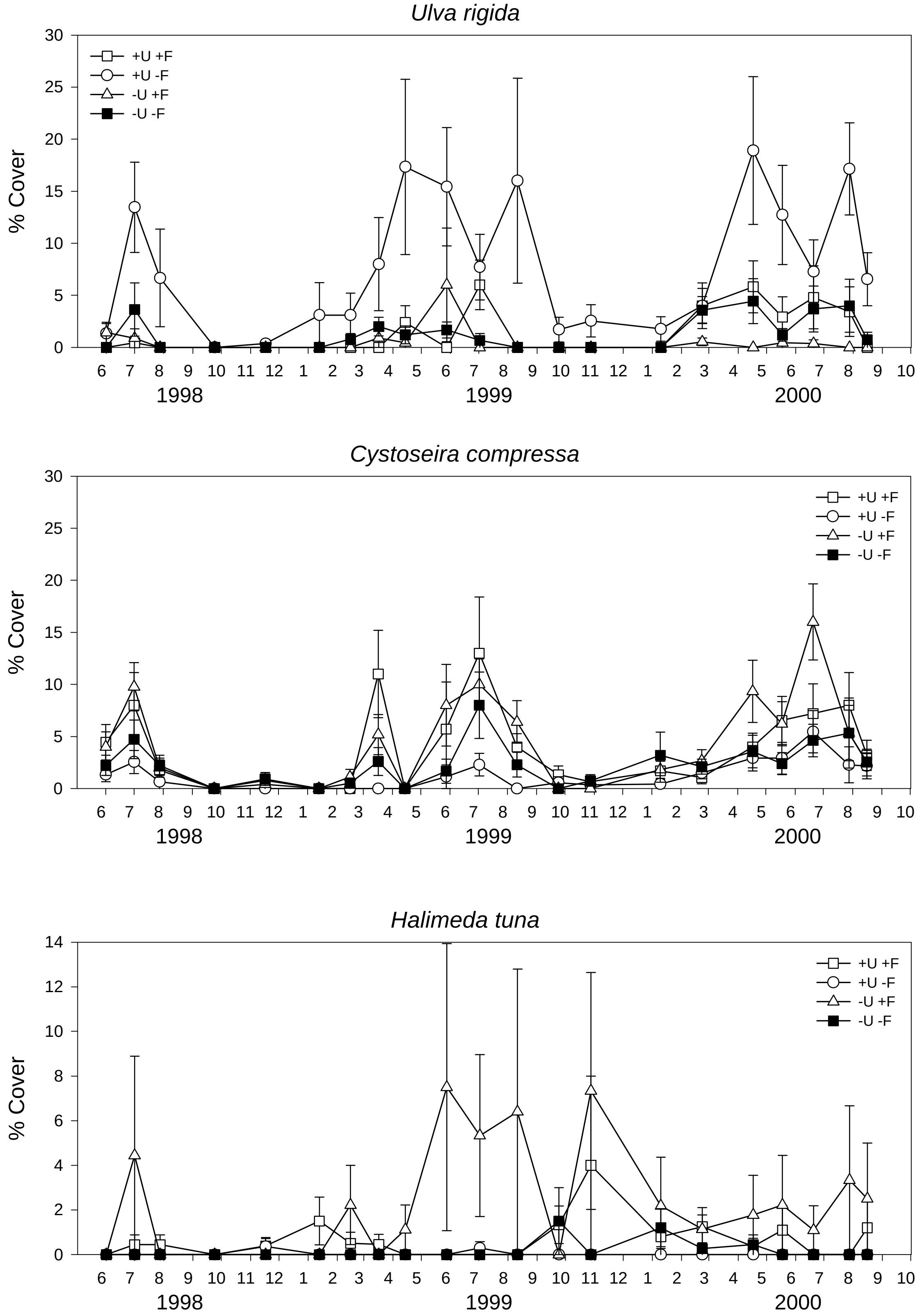
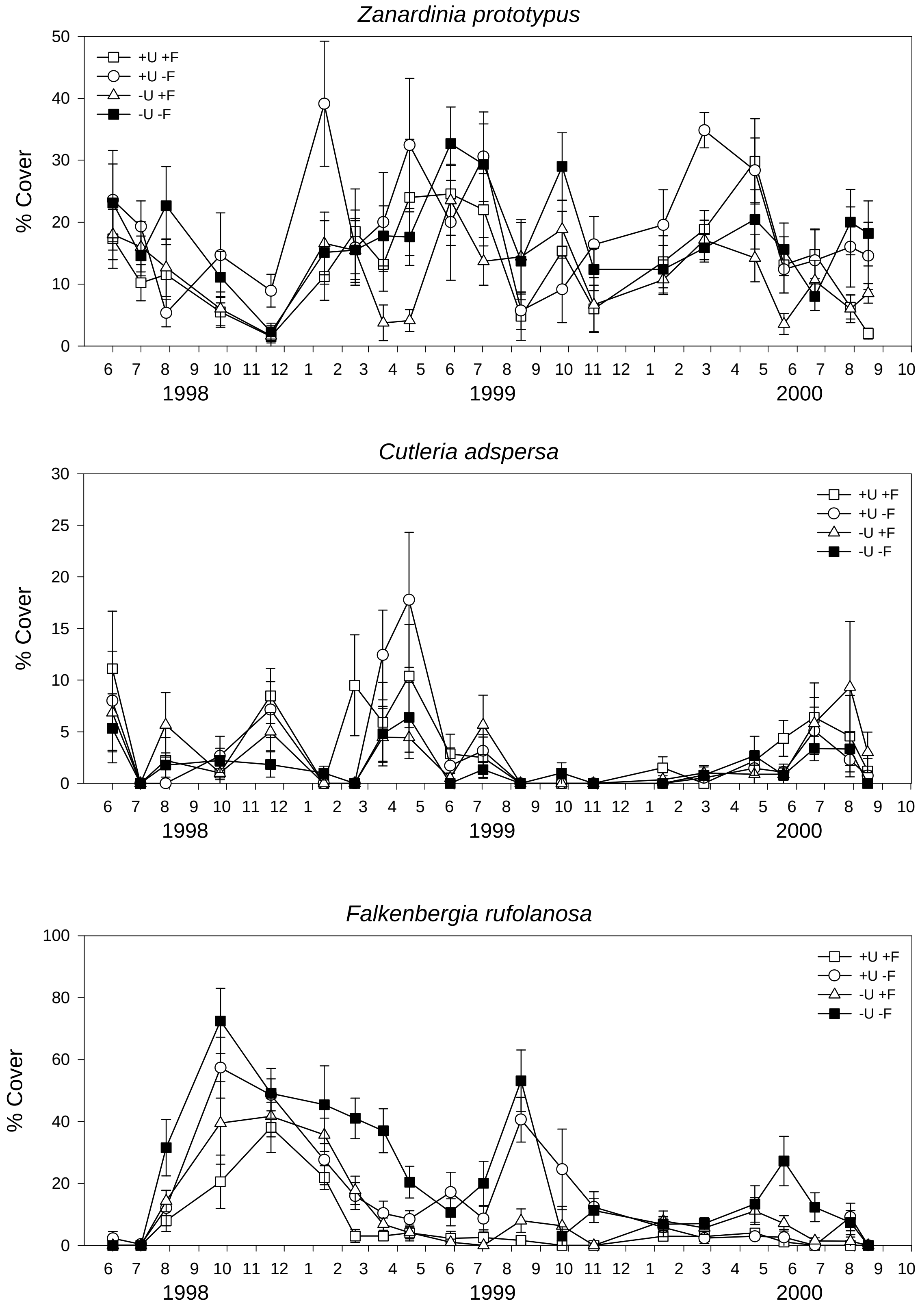


Figure 5 (cont.)- Temporal variation in cover (mean ± SE) of the major algal species in the experimental treatments. -F-U = fishes and urchins absent, -F+U = only urchins present, +F-U = only fishes present, +F+U = both fishes and urchins present. Months: 1=Jan trough 12=Dec



Zanardinia prototypus

Cutleria adspersa

Falkenbergia rufolanosa

Figure 5 (cont.)- Temporal variation in cover (mean ± SE) of the major algal species in the experimental treatments. -F-U = fishes and urchins absent, -F+U = only urchins present, +F-U = only fishes present, +F+U = both fishes and urchins present. Months: 1=Jan trough 12=Dec

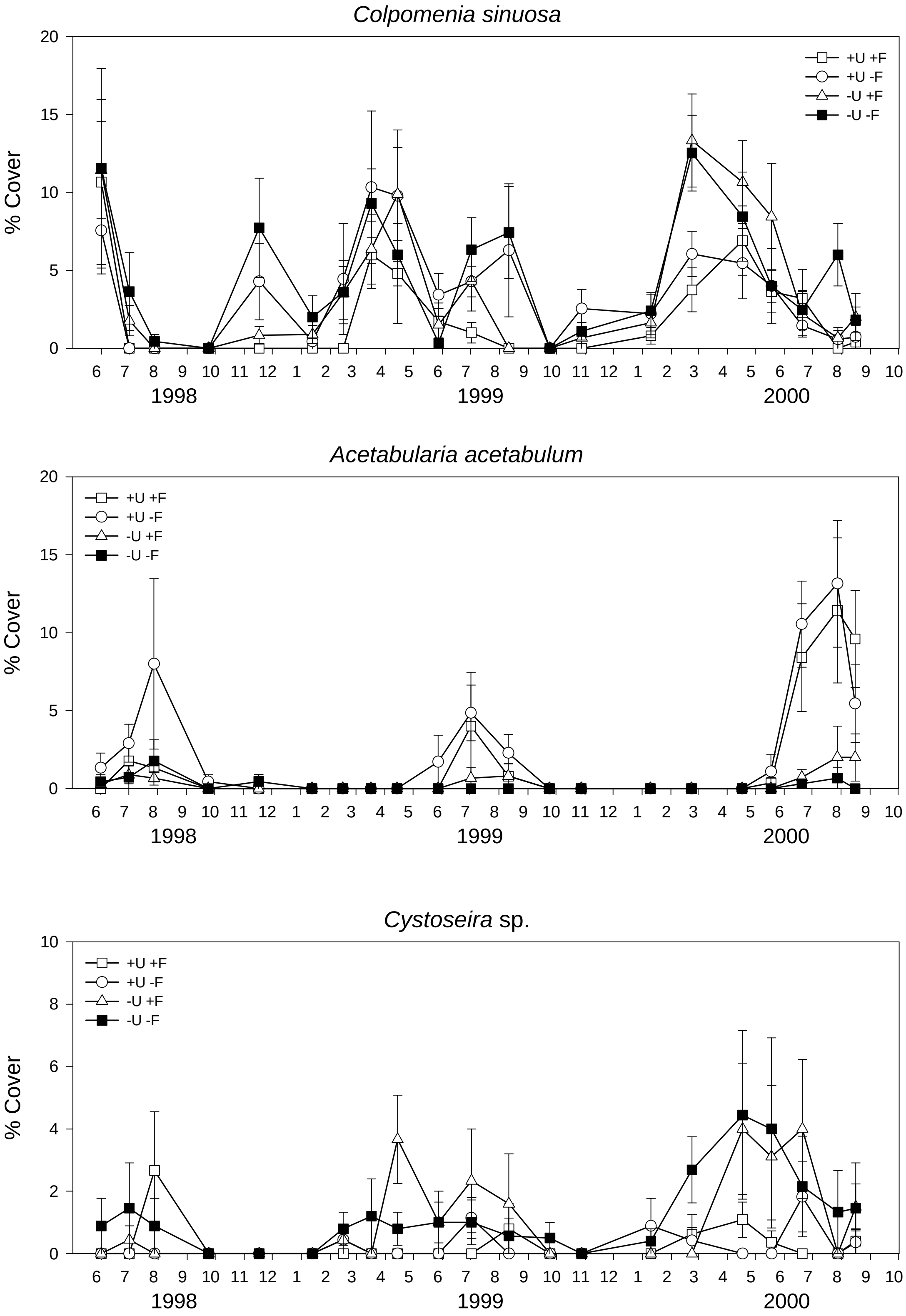
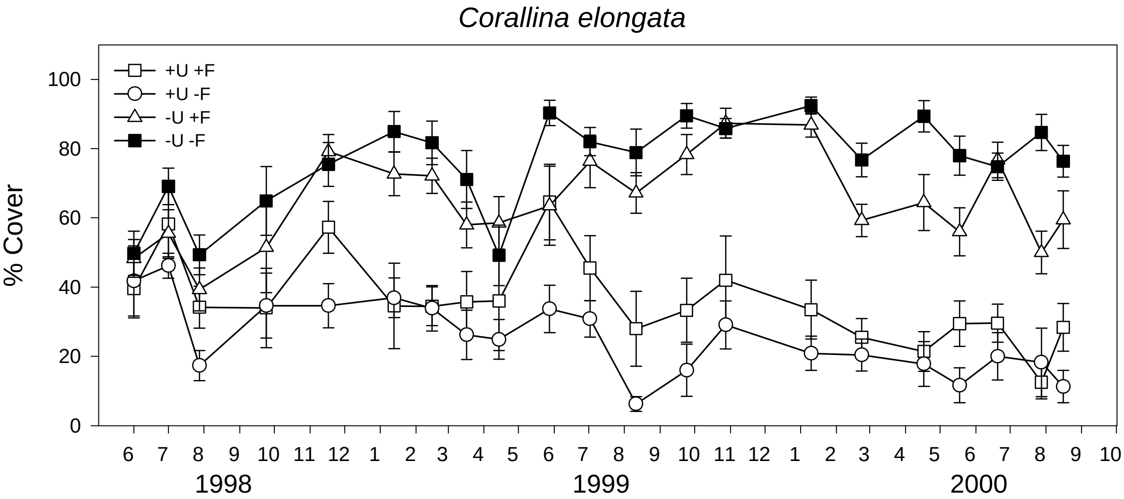
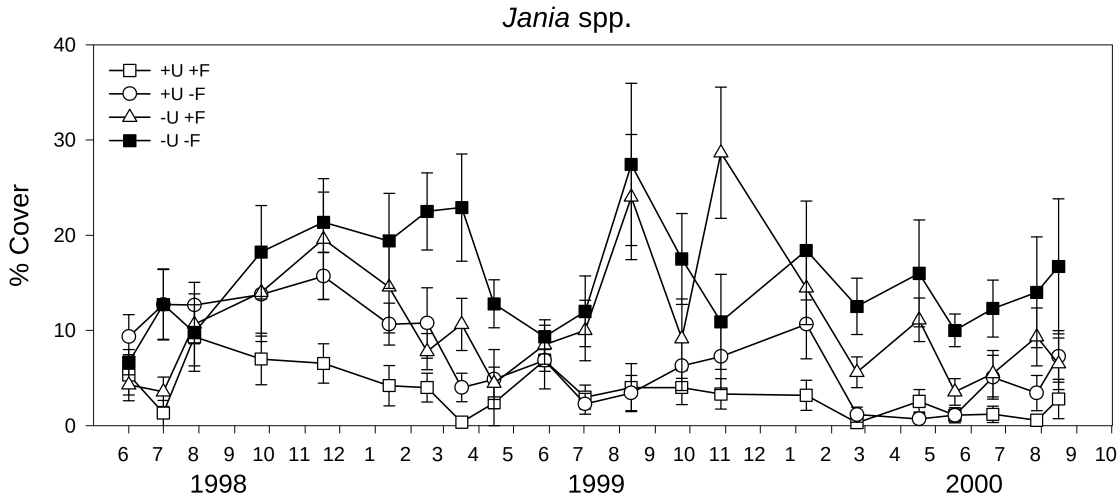


Figure 5 (cont.)- Temporal variation in cover (mean ± SE) of the major algal species in the experimental treatments. -F-U = fishes and urchins absent, -F+U = only urchins present, +F-U = only fishes present, +F+U = both fishes and urchins present. Months: 1=Jan trough 12=Dec


Corallina elongata


Jania spp.

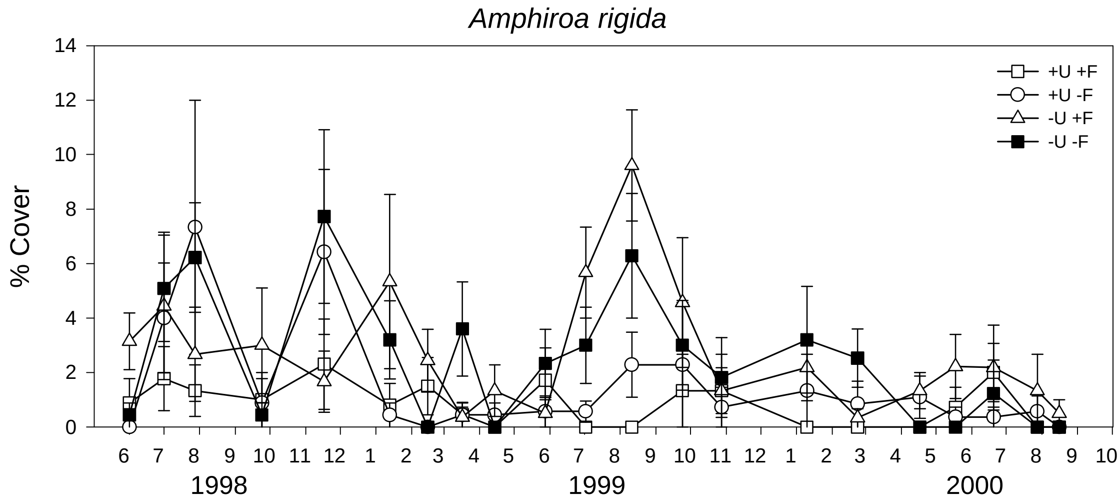

Amphiroa rigida

Figure 5 (cont.)- Temporal variation in cover (mean ± SE) of the major algal species in the experimental treatments. -F-U = fishes and urchins absent, -F+U = only urchins present, +F-U = only fishes present, +F+U = both fishes and urchins present. Months: 1=Jan trough 12=Dec

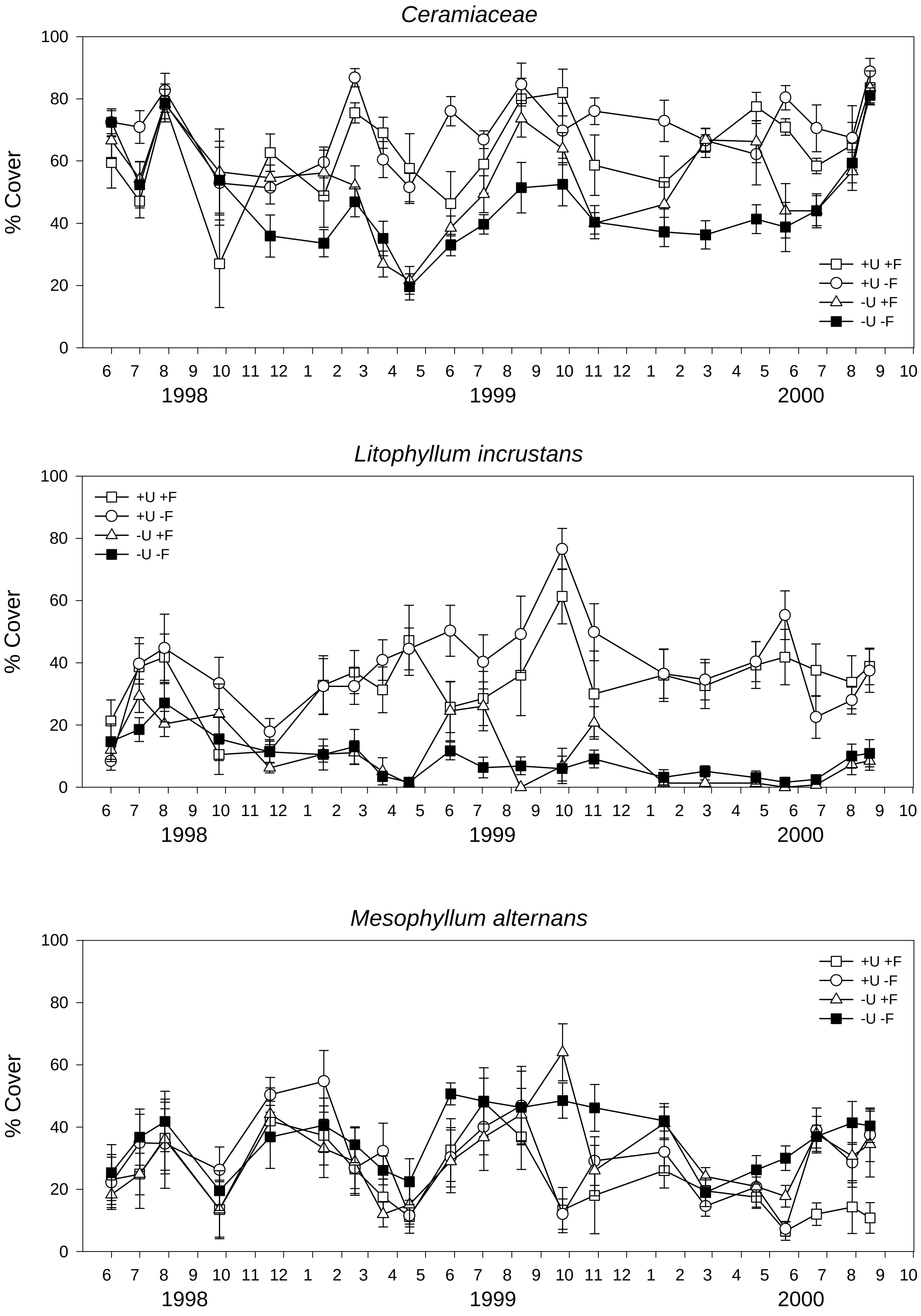


Figure 5 (cont.)- Temporal variation in cover (mean ± SE) of the major algal species in the experimental treatments. -F-U = fishes and urchins absent, -F+U = only urchins present, +F-U = only fishes present, +F+U = both fishes and urchins present. Months: 1=Jan trough 12=Dec

There were three main temporal patterns of algal growth: annual, perennial and perennial with seasonal canopy. Annual species had a strong production period, tipically during spring (e.g., *Asparagopsis armata, Dictyota dichotoma, Taonia atomaria, Colpomenia sinuosa*), although a few species had biomass peaks during late summer (*Padina pavonica, Acetabularia acetabulum, Ulva rigida*) and winter (*Laurencia obtusa,* Ceramiaceae). Cover decreased significantly or completely after the production period. In a pluriannual scale, seasonal species seemed not to be affected by grazers, since there was no significant interaction between time and grazing treatments (Table 2). Thus, their growth potential may be maintained over the years even if herbivores can reduce the magnitude of their biomass peak. Perennial species (such as *Codium vermilara, Codium bursa, Halopteris scoparia, Halopteris filicina, Corallina elongata, Jania rubens, Zanardinia prototypus, Lithophyllum incrustans* and *Mesophyllum alternans*) maintained its cover throughout the year. Because of their low growth rates (Ballesteros 1992) and longer time of exposure to grazers, these species are more susceptible to herbivory. Moreover, the effects of grazers on the cover of perennial species may be accumulative in a pluriannual scale. Perennial species with seasonal canopy included C*ystoseira* sp. and *Cystoseira compressa*. These species develop seasonal canopies but also have perennial thalli which persist during winter.

The response of algal species to grazers was highly variable. Sea urchins clearly reduced the cover of most species, although the cover of some opportunistic species increased in a facilitation process (Fig. 5, Table 2).

By grazing most of the erect and turf algae, sea urchins may have eliminated the dominant competitors and allowed filamentous algae such as Ceramiaceae, *Acetabularia acetabulum* and *Ulva rigida* to increase. The encrusting coralline *Lithophyllum incrustans*, which dominates sea urchin barrens, also increased its cover throughout the experiment. This crustose alga can resist the bulldozing effect of sea urchins that eliminates its competitor *Mesophyllum alternans*.

The effect of fish grazing on algal cover was less important, although annual species such as *Colpomenia sinuosa, Taonia atomaria, Padina pavonica, Ulva rigida, Dilophus fasciola* and *Zanardinia prototypus* were significantly depleted in the +F-U treatment (Fig. 5, Table 2). The significant interaction between fishes and time indicates that major biomass losses occurred during the Spring algal growth period. The cover of some species such as *Padina pavonica*, *Cystoseira compressa* and *Laurencia obtusa* was larger in the fish treatments, suggesting a facilitation process similar to that induced by sea urchin grazing.

The interactions between fishes and sea urchins produced complex responses. For some species, such as the articulated coralline *Corallina elongata*, sea urchin grazing caused larger reduction of the cover in the absence of fishes (Fig. 5, Table 2). This interaction may have a high significance in determining the structure of the algal communities, since *C. elongata* is a dominant species in the community. As described above, the reduction of erect algae by sea urchins may benefit filamentous and opportunistic algae such as *Ulva rigida*, which had greater growth in the sea urchin-only treatments (Fig. 5, Table 2). However, fishes efficiently reduced the cover of these algae, thus the facilitation effect of sea urchins is higher in the absence of fishes. Total algal cover shows a significant response to time and sea urchin grazing, but no significant interaction between any of the factors (urchins, time, fishes).

Table 2- Results of ANOVA on the effects of sea urchins, fishes and time on the percent cover of most abundant algae. Species marked with [1] *were tested only during the seasonal growth period (except L. obtusa which was tested during summer, fall and winter). *p<0,05, **p<0,01, ***p<0,001,* ^{ns} *not significant.*

	Time	Urchins	Fish	Time x Urchins	Time x Fish	Urchins x Fish	T x U x F
	F	F	F	F	F	F	F
A. armata[1]	**33.2****	**19.9****	0.3^{ns}	1.2^{ns}	1.1^{ns}	0.0^{ns}	0.6^{ns}
D. dichotoma[1]	**11.0****	**21.3****	0.8^{ns}	1.0^{ns}	1.0^{ns}	0.9^{ns}	0.5^{ns}
C. sinuosa[1]	**5.6****	**4.3***	**4.3***	0.4^{ns}	0.9^{ns}	0.0^{ns}	0.4^{ns}
T. atomaria [1]	**28.3****	0.2^{ns}	0.1^{ns}	0.4^{ns}	**2.0***	2.1^{ns}	0.7^{ns}
D. fasciola	**5.2****	0.6^{ns}	**9.6****	0.9^{ns}	0.5^{ns}	2.5^{ns}	0.7^{ns}
P. pavonica[1]	**2.5****	1.3^{ns}	**15.9****	1.3^{ns}	**2.9****	0.5^{ns}	0.5^{ns}
A. acetabulum [1]	**0.0****	**0.0****	0.3^{ns}	**0.0***	1.0^{ns}	0.0^{ns}	1.0^{ns}
U. rigida[1]	1.2^{ns}	**17.9****	**22.3****	0.6^{ns}	0.4^{ns}	**6.7***	0.6^{ns}
L. obtusa [1]	1.2^{ns}	0.6^{ns}	**50.7****	0.2^{ns}	0.5^{ns}	**4.6****	0.3^{ns}
C. vermilara	**3.4****	**82.9****	3.8^{ns}	1.4^{ns}	1.0^{ns}	0.6^{ns}	0.5^{ns}
H. scoparia	**1.7***	**45.8****	1.1^{ns}	0.9^{ns}	0.5^{ns}	2.9^{ns}	0.4^{ns}
***Cystoseira* sp.**[1]	1.1^{ns}	**11.9****	0.0^{ns}	0.9^{ns}	0.3^{ns}	0.1^{ns}	0.5^{ns}
C. compressa[1]	**3.6****	**4.9***	**12.3****	0.3^{ns}	0.8^{ns}	1.1^{ns}	0.4^{ns}
Z. prototypus	**2.0****	1.0^{ns}	**9.1****	0.6^{ns}	0.2^{ns}	0.0^{ns}	0.4^{ns}
C. elongata	**2.3****	**311.4****	0.9^{ns}	**2.6****	0.6^{ns}	**22.8****	0.4^{ns}
***Jania* spp.**	**2.8****	**72.6****	**18.0****	**1.7***	1.1^{ns}	0.9^{ns}	0.6^{ns}
Turf algae	**5.7****	**57.4****	0.0^{ns}	**1.8****	1.1^{ns}	**12.6****	0.6^{ns}
L. incrustans	1.3^{ns}	**100.5****	0.7^{ns}	**2.6****	0.3^{ns}	0.5^{ns}	0.7^{ns}
All species	**5.47****	**165.2****	0.14^{ns}	1.05^{ns}	1.14^{ns}	2.61^{ns}	0.76^{ns}
Seasonal	**11.68****	**12.40****	24.71^{ns}	0.84^{ns}	1.14^{ns}	**12.99****	0.55^{ns}
Perennial	**2.70****	**136.5****	**10.56****	1.46^{ns}	0.76^{ns}	0.25^{ns}	0.78^{ns}
***Cystoseira* spp.**	**7.634****	**14.4****	**6.36***	0.56^{ns}	0.98^{ns}	**4.54***	0.50^{ns}

Effects of experimental factors on algal community structure

A significant proportion (41.5%) of the variance in the data is explained by the two first axes of the RDA, the first axis alone explaining 29.8% (Table 3, Fig. 6).

All environmental variables were shown to be statistically significant by a Monte Carlo permutation test of the residuals ($p<0.01$). Presence of sea urchins was the most important variable, as it accounted for the 27 % of the variance. Temperature and irradiance were also important as they explained 8% of the variance respectively. Nutrient concentrations, year and fishes had no significant correlation with any of the first two axes. Fish presence explained only the 8.11 % of the variance. Sea urchins were strongly and negatively correlated with axis 1 ($r = - 0.83$, Table 3), suggesting that this axis represents the top-down (urchin herbivory) control of algal communities. Major variables related to productivity (irradiance, temperature and phosphate) are correlated with axis 2, which appears to represent the bottom-up (seasonality) control of algal communities (Table 3).

Table 3- Results of redundancy analysis (RDA) on algal cover and environmental and experimental variable.

		Axis		Total variance
	1	2	3	
Eigenvalues	0.298	0.117	0.067	
Species-environment correlations	0.875	0.874	0.794	
Cumulative percentage variance of species data	29.83	41.5	48.2	
of species-environment relation	55.0	76.6	88.9	
Sum of all unconstrained eigenvalues				1
Sum of all canonical eigenvalues				0.542
Interset correlation of environmental axis with species axis				
Urchins	-0.830	0.037	-0.153	
Fish	-0.027	0.085	0.559	
Irradiance	-0.168	0.426	0.364	
Temperature	-0.165	-0.552	0.353	
PO4	0.025	-0.358	0.155	
NO2	0.213	-0.025	-0.429	
NO3	0.171	0.101	-0.422	
Year	-0.127	0.201	0.337	

The ordination of the physico-chemical variables in the RDA diagram shows an annual pattern, in which seasons succeed each other in a counter-clockwise pattern (Fig.6). Spring was significantly correlated with irradiance, Summer with temperature, and Fall and Winter with nutrient concentration and temperature. These results reflect the peaks of the environmental variables: irradiance peaks in late spring, temperature in late summer, and nutrient concentration in late fall and winter (Ballesteros 1992, Garrabou 1997).

The RDA shows a gradient in algal community structure in relation to the two main factors. Sea urchin grazing benefited grazing-resistant species such as encrusting corallines (e.g., *Litophyllum incrustans*) and opportunistic turf species such as *Acetabularia acetabulum* and *Ulva rigida*. In contrast, perennial species such as *Corallina elongata*, *Halopteris scoparia*, *Codium vermilara* and *Jania rubens* were more abundant in the absence of sea urchins. Seasonal erect algae such as *Taonia atomaria, Asparagopsis armata*, *Colpomenia sinuosa* and *Dictyota dicothoma* are significantly and positively related to seasonal energy inputs. These species are weakly correlated with sea urchin presence, indicating that sea urchin grazing has stronger effects on perennial than on seasonal species.

Effects of experimental factors on pluri-annual patterns of community structure

The first principal component (PC1) discriminated for sea urchin grazing (Fig. 7).

The samples in the presence of sea urchins are mostly on the left of the plot, whereas the samples without sea urchins are on the right side. The second principal component (PC2) discriminated samples on a temporal basis. Samples from Spring are on top of the plot and samples from Fall at the bottom. We drew a line for each treatment, from each sampling time to the next. The result shows that algal communities in all treatments exhibited an annual cycle, in turn shifting towards one side of the ordination space among years (Fig. 8).

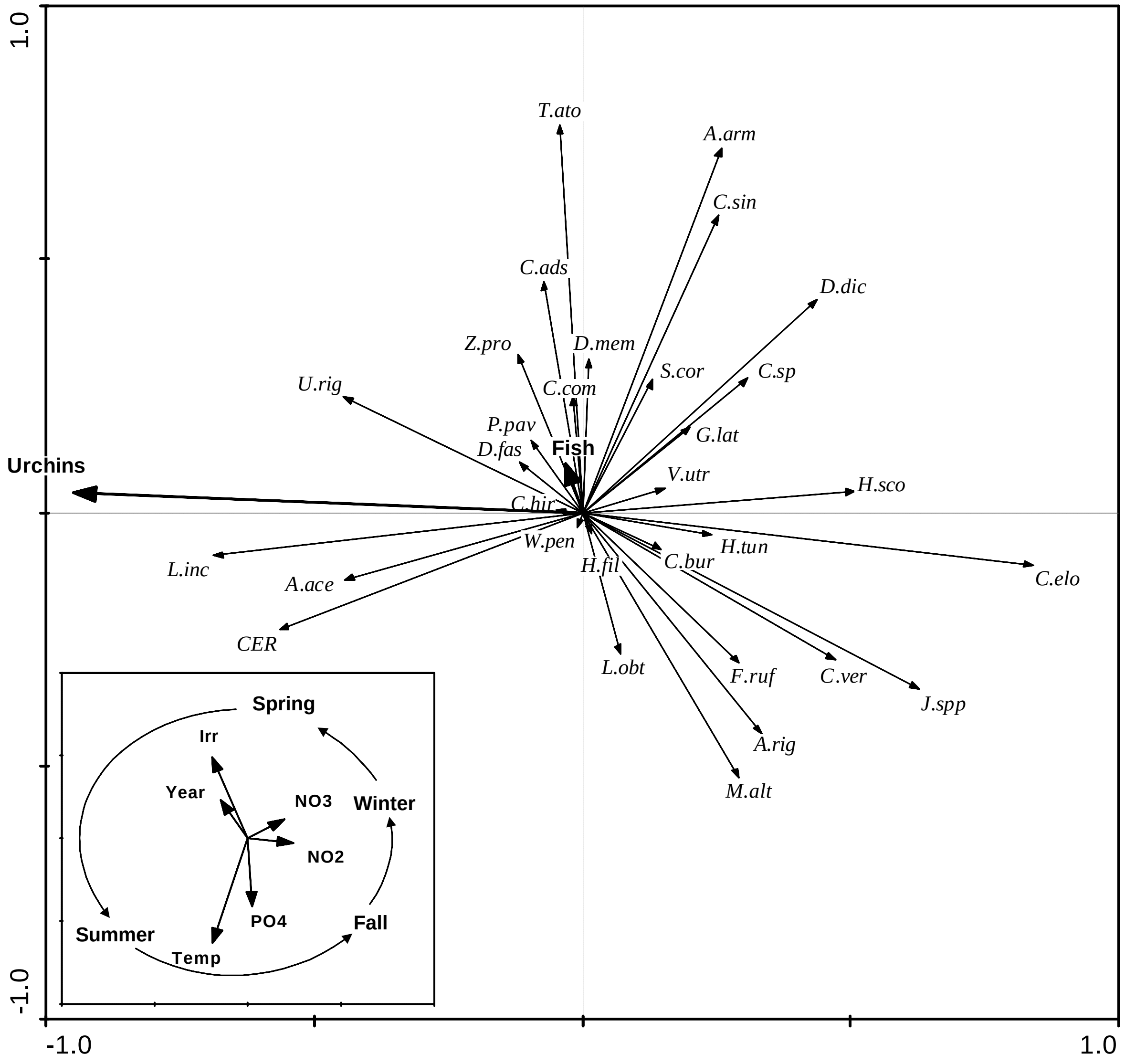


Figure 6- Redundance analysis biplot showing the ordination of algal species and the role of sea urchins and fishes. The inset shows the distribution of environmental variables, and the ecological succession throughout an annual cycle. Species codes: *A.ace*=Acetabularia acetabulum, *A.rig*=Amphiroa rigida, *A.arm*=Asparagopsis armata, *Cer*=Ceramiaceae, *C.hir*=Cladostephus hirsutus, *C.bur*=Codium bursa, *C.eff*=Codium effusum, *C.sin*=Colpomenia sinuosa, *C.ver*=Codium vermilara,*C.elo*=Corallina elongata,*C.ads*=Cutleria adspersa, *C.com*=Cystoseira compressa, *C.sp*=Cystoseira sp., *D.dic*=Dictyota dichotoma, *D.fas*=Dictyota fasciola, *D.mem*=Dictyopteris membranacea, *F.ruf*=Falkenbergia rufolanosa, *G.lat*=Gelidium latifolium, *H.fil*=Halopteris filicina, *H.sco*=Halopteris scoparia, *H.tun*=Halimeda tuna, *J.spp*=Jania spp., *L.obt*=Laurencia obtusa, *L.inc*=Litophillum incrustans, *M.alt*=Mesophillum alternans, *P.pav*=Padina pavonica, *S.cor*=Sphaerococcus coronopifolius, *T.ato*=Taonia atomaria, *U.rig*=Ulva rigida, *V.utr*=Valonia utricularis, *W.pen*=Wrangelia penicillata, *Z.pro*=Zanardinia prototypus.

Environmental variables: Temp=temperature, Irr=irradiance, NO3=nitrate, NO2=nitrite, PO4=phosphate.

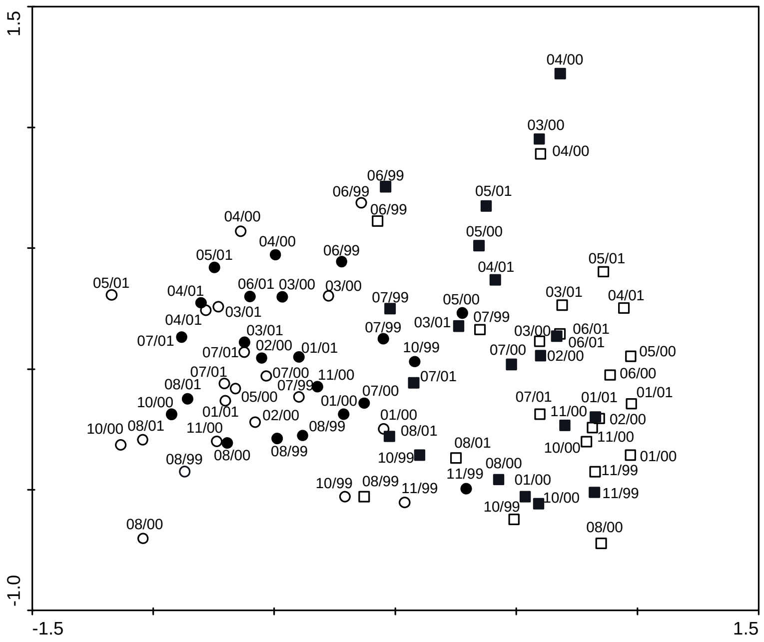


Figure 7- Ordination (PCA) biplot of sampling sites trough time. Codes for species are the same as in fig. 5. Codes for sites: square=-Fish –Urchins, solid square= +Fish-Urchins, circle=-Fish +Urchins, solid circle=+Fish +Urchins. Number correspond to the month and year of sampling (mm/yy).

The treatments with sea urchins moved the communities to the right of the origin point, whereas the treatments without sea urchins caused a leftward movement. These results suggest that the pluriannual movement represents the main succession of the community, within which the annual succession is nested. The departure from the origin points of the samples at the beginning of the experiment were caused by the addition or removal of herbivores, mainly sea urchins. Because sea urchin grazing drives the community to lower successional stages (e.g., Verlaque 1987), we assume that a rightward movement in the PCA plot means an advance towards more advanced successional stages. The removal of sea urchins caused a sudden departure of the community towards more advanced successional stages, and after that the annual cycles showed narrow displacements along PC1, regardless of fish abundance. Sea urchin grazing, in contrast, showed wider annual cycles, probably because of the short time blooms of seasonal algae.

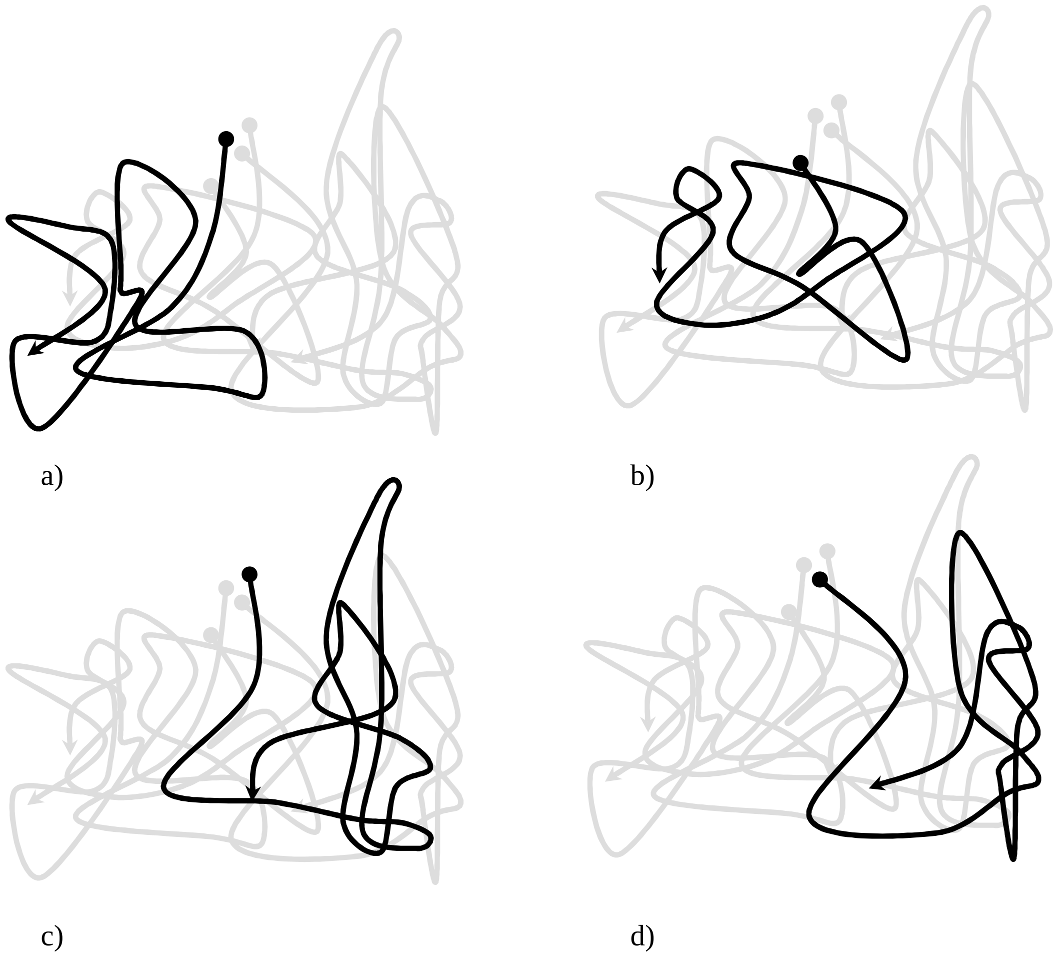


Figure 8- Ordination (PCA) diagram of the axes 1 and 2 showing the succession pattern in each treatment. The bold line indicates the succession pattern in sites over the months for a) +Fish +Urchin, b) –Fish +Urchins, c) –Fish –Urchins and d) +Fish –Urchins treatments.

Discussion

There has been much debate over the role of “top-down” (predator control) vs. “bottom-up” (resource control) processes in determining the structure of ecological communities (Power 1992, Hunter and Price 1992). Several models have been proposed to explain how communities are regulated. The first conceptual model was that of Hairston et al (1960), which focused on trophic interactions based on predation regulation through trophic cascades (i.e. top predators ultimately regulate primary production). In intertidal marine communities, these models were implemented introducing the effects of environmental stress, which can modify the strength of biological processes (i.e. competition and predation) from high to low importance in an increasingly disturbed environment (Connell 1975, Menge and Sutherland 1976, 1987, Lubchenco 1986, Witman and Grange 1988). Other community regulation models were based on different environmental gradients of nutrients and productivity effects (Fretwell 1977, 1987, Oksanen et al. 1981). These models predict an increasing number of trophic levels in an increasing gradient of productivity, with an alternate control of competition and predation. In marine environments, recent empirical work shows that bottom-up processes can be important in determining community structure, increasing productivity and biomass of primary producers and herbivores, even in a smallest scales (Menge et al. 1997 a,b 2002, Nielsen 2003).

It is evident that 'bottom-up' and 'top-down' processes act simultaneously, but their relative roles vary among and within biological systems (Hunter and Price 1992, Persson et al. 1996) and may be context-specific (Menge 1992, Menge et al. 1997, Leonard et al. 1998, Nielsen 2001). Furthermore, recent models have involved the effects of omnivory (Menge et al. 1996, Polis and Strong 1996), food supply (Bustamente et al. 1995, Polis and Strong 1996), and the influence of positive interactions (Bertness and Callaway 1994).

Our results show that, in a Mediterranean rocky sublittoral community, both top-down and bottom-up processes are apparent and affect community structure synergistically. Herbivory regulated total algal biomass and community structure, but it did not cancel seasonal fluctuations induced by resource fluctuations. In addition, seasonal cycles of algal biomass evolved following a main successional trajectory determined by herbivore abundance.

Top-down processes: fishes vs. sea urchin grazing

Sea urchins are the major benthic herbivores of Mediterranean rocky sublittoral communities (Verlaque 1987, Benedetti-Cecchi and Cinelli 1995). At large densities, *P. lividus* can remove all erect algae and induce the formation of a coralline barren (Verlaque 1987). In the western Mediterranean, the sparid fish *Sarpa salpa* is the only strict, important herbivore, although species of the genus *Diplodus* also consume a significant algal biomass (Verlaque 1987, Sala and Ballesteros 1997). Although it has long been assumed that herbivorous fishes have negligible roles in the organization of benthic communities in temperate seas, recent studies have indicated the opposite (e.g., Sala 1996, Sala and Boudouresque 1997, Ruitton et al. 2001). In the Medes Islands

Marine Reserve, small scale experiments showed that fish grazing determines the structure of algal communities by reducing the abundance of abundant species of seasonal fleshy algae and facilitating the seasonal dominance of an introduced chemically-defended alga, *Asparagopsis armata* (Sala and Boudouresque 1997). While fish grazing produces changes in the structure of the algal community, it does not necessarily modify total algal biomass. *P. lividus* grazing, in contrast, universally reduces algal biomass.

Our experiments support the role of *Paracentrotus lividus* as a major factor in determining algal community structure, by reducing biomass of most species and favoring the dominance of grazing-resistance species and opportunistic turf algae. But our results disagree with some previous results concerning fish grazing. Fish grazing alone did not produce significant changes in total algal biomass, thus supporting Sala and Boudouresque's (1997) findings. However, fish grazing alone did not cause significant changes in the biomass of seasonal algae. In contrast, our fish exclosures produced dominance of *Asparagopsis armata* only in 1999. These differences might be caused by the scale of the experiments. Sala and Boudouresque (1997) herbivore exclusion cages were 1,000 cm^2, whereas our fish teatments were about 100 m^2 and the sea urchin treatments within were 16 m^2. Furthermore, Sala and Boudouresque's (1997) exclosures were maintained only during the algal production period. The shorter term, smaller caging experiments in this seasonal environment may have enhanced the effect of fishes (Kennelly 1991). However, Sala and Boudouresque (1997) showed that the effects of fish grazing were greater with increasing fish abundance. There is indeed strong spatial heterogeneity in fish abundance in the Medes Islands Marine Reserve (García-Rubies 1996). The greatest effect of fish grazing found previously, the dominance of *A. armata*, occurred in Tascons, the site with the largest fish abundance in the reserve and one of the largest in the Mediterranean (Sala and Boudouresque 1997, García-Rubies 1996). The coves were we carried out the experiments in this study had significantly lower fish densities than Tascons, thus we would expect weaker effects of fish grazing. A combination of the above factors may explain why the effects of fish grazing in our experiments were weaker than previously reported. In any case, our results confirm that sea urchins are stronger herbivores than fishes in this Mediterranean sublittoral community, and that herbivory clearly influences algal community structure.

Top-down processes: trophic cascades

Predation can regulate the abundance of major herbivores of the dominant primary producers through trophic cascades (Estes et al. 1998, McClanahan and Shaphir 1990, Steneck 1998, Pace et al. 1999). In the Mediterranean, large densities of predatory fishes have the potential to control sea urchin populations and reduce sea urchin grazing, which in turn produces an increase in algal biomass (Sala and Zabala 1996, Sala et al. 1998). Because the density of sea urchins in our +U treatments was maintained artificially, we could not test whether predation by fishes controls sea urchin abundance and consequently the structure of algal communities. In addition, even fish enclosure had not effect on the sea urchins predator *Coris julis* densities, it did not modified our results because they predate only on small juvenile urchins and small invertebrates (Sala 1997). However, our results indirectly support the existence of trophic cascades. On one hand, we showed that the absence of urchins induces the formation of a benthic community totally different from a sea urchin-grazed community. This indicates that when predatory fishes reduce sea urchin abundance to very low levels, trophic cascades will occur. On the other hand, the cover of perennial algae, such as *Corallina elongata*, was significantly larger in the +F+U than in the –F+U treatment.

The presence of predatory fishes in the +F+U treatment appears to have inhibited sea urchin grazing. Because sea urchin density was maintained artificially, these effects were not caused by predation, but probably by a trait mediated indirect interaction (Abrams et al. 1996). The simple presence of a predator can produce a sheltering response and lowered activity in a prey (e.g. Schmitz et al. 1997, Raimondi et al. 2000, Trussell et al. 2003). In the Mediterranean, it has been shown that *Paracentotus lividus* individuals graze on open surfaces during the day in the absence of predators, whereas most individuals are sheltered in the presence of abundant predators (Sala and Zabala 1996). When predators are abundant, *P. lividus* moves to exposed surfaces only at night, which reduces the spatial extent of grazing to about one meter around the shelters (Sala 1996). We observed the same type of behaviour in our +F+U treatment. Even when sea urchins could not shelter, their activity and movements were reduced.

Bottom-up processes: seasonal resource cycles

Our results confirm that Mediterranean algal communities show seasonal cycles of biomass every year, regardless of herbivore abundance (Ballesteros 1991). The algal communities in every treatment oscillated between two annual extremes: a peak of algal biomass in Spring and a minimum of algal biomass in Winter. However, as we will discuss below, the magnitude of the biomass difference between the two annual extremes and of the oscillation in community structure was determined by herbivory.

While studying bottom-up processes, we did not investigated the effects of resource fluctuations beyond algal growth. However, Sala (1997) showed that, in the study region, seasonal increases in algal biomass (Sala and Boudouresque 1997) were followed by rapid increases in the biomass of small epifauna, regardless of fish density. Because of the duration of the study we could not address longer term effects of the increase of algal biomass (in treatments with low herbivory) on higher trophic levels such as fishes. Nevertheless, the effects of the seasonal fluctuations in environmental resources on the community were evident.

Top-down vs. bottom-up: composition of algal communities

The interaction between resource availability and herbivore abundance induced the formation of algal communities dominated by non-random groups of species. The PCA ordinated algae in four main groups with particular characteristics as a response to the interaction between herbivory and productivity, similar to the functional groups proposed by Grime (1977) for terrestrial ecosystems.

1- Stress-tolerant conservatives: perennial species that dominate under conditions of permanent disturbance, such as sea urchin grazing (e.g., the encrusting coralline *Lithophyllum incrustans*).

2- Competitive conservatives: perennial species that dominate competitively in the absence of stress and disturbance. These are strictly perennial (e.g., *Halopteris scoparia*, *Mesophyllum alternans*, *Corallina elongata*, *Jania rubens*) or species with perennial thalli and seasonal canopy (*Cystoseira* spp.).

3- Resource opportunists: seasonal species that take advantage of seasonal peaks of resources (e.g., *Dictyota dichotoma*, *Taonia atomaria*, *Asparagopsis armata*). Their short life cycle allows them to escape herbivory.

4- Herbivory opportunists: seasonal species that do not proliferate necessarily during the Spring bloom but grow rapidly after the elimination of other species by grazing (e.g., *Acetabularia acetabulum*, *Padina pavonica*, *Ulva rigida*, *Ceramiaceae* turfs). Although these species are facilitated by sea urchin grazing, they may be vulnerable to fish grazing.

Sustained grazing by sea urchins will eventually promote stress-tolerant conservatives while competitive conservatives will be progressively excluded; herbivory opportunists can take advantage of sea urchin presence if grazing is not too intensive; and resource opportunists succeed to escape relatively strong grazing by intense productivity during seasonal resource peaks. Similar trends would be predicted in the presence of both sea urchins and fishes. In contrast, sustained grazing by fishes in the absence of sea urchins will enhance competitive conservative species, while stress-tolerant conservatives will become less important. The success of resource opportunists is irrespective of the nature of grazers.

Previous classifications of algae in functional groups (Littler and Littler 1980, 1984, Steneck and Watling 1982, Steneck and Dethier 1994) were not suitable to our species. We did not identify microscopic algae and there are no large leathery algae in the study region, thus all species belong to similar size groups. Hence we could not apply the morphologic criteria proposed by Steneck and Dethier (1994). The histological types described by Steneck and Dethier (1994) could be found in species of very different size and life span, and species belonging to the same histological type were found throughout the ordination plane in our multivariate analysis. The applicability of functional groups was hindered in other studies because groups were more useful where species were pooled in functional rather than morphological groups (Phillips et al. 1997, Padilla and Allen 2000, Airoldi 2001).

Finally, algae not only respond to herbivory but also to competition. The morphological features that are advantageous against herbivory are probably different from those which give competitive advantage. Often, herbivory facilitates the increase in biomass of some species by eliminating the dominant competitor (e.g., the substitution of *Mesophyllum alternans* by *Lithophyllum incrustans*). However, there are species groups (e.g. incrustant and turfs) that coexist without apparent competition (Airoldi 2000).

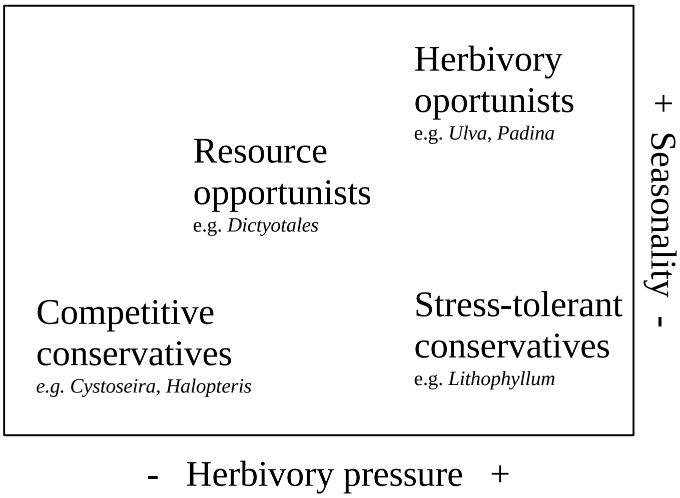
Top-down vs. bottom-up: a synthetic model

In the NW Mediterranean, algal biomass and community structure markedly fluctuates seasonally (Feldmann 1937, Zabala and Ballesteros 1989, Ballesteros 1991, 1992, Garrabou 1997). Ballesteros (1991) proposed a conceptual model where algal community structure oscillates between two extremes. During the season where environmental resources such as irradiance, water temperature and nutrients are optimal (generally Spring), algal biomass peaks and diversity (H') is at its minimum because of the dominance of a few seasonal species. In contrast, during Winter algal biomass is at its minimum but diversity is highest because there is no clear dominance in biomass by any species. Ballesteros' (1991) model adequately explains the general annual dynamics of algal communities even without considering top-down processes.

More recently, McClanahan and Sala (1997) developed an energy-based model that ignored seasonal biomass fluctuations, exclusively based on top-down control. The model proposed the existence of two successional extremes: 1) a coralline barren with small fish biomass, large sea urchin biomass, and low benthic biomass, and 2) a complex community with large fish biomass, low sea urchin biomass, and large benthic biomass. The shift between these two states would be driven by top-down trophic interactions (where the top predators are fishes) induced by fishing type and intensity (Sala et al. 1998). The main driving factor is the density of predatory fishes. When fish abundance is large, predation on sea urchins induce the maintenance of complex algal communities; when fish abundance is low, sea urchin populations may increase and turn complex algal communities into coralline barrens. This model ignores variation in primary productivity and bottom-up factors, and explains general dynamics at larger scales.

Our results allow us to propose a synthetic model that incorporates both top-down and bottom-up factors and provide more predictive power across scales. Ballesteros (1991) assumed that under constant environmental conditions, each algal community and its annual biomass cycle is a stable point (*sensu lato*), but also suggested that disturbances such as herbivory can produce shifts between stable points. Our results suggest the existence of a continuum of successional stages, rather than multiple stable points. When herbivory is reduced (like in our –U treatments), communities will exhibit successional trajectories starting from different points of origin, but eventually converging in a "stable domain" similar to the complex community described by

McClanahan and Sala (1997). When herbivory is maintained at high levels (like in our +U treatment), communities will move towards a coralline barren. Although the duration of our experiments did not allow sea urchins to create a barren, we observed that communities were significantly grazed and moving towards the elimination of erect algae. When herbivore abundance is maintained above an overgrazing threshold, communities will eventually oscillate annually around the same successional stage. The two extremes in the successional continuum are hence the coralline barren (a true stable point) and the complex community (a stable neighborhood).



In summary, top-down processes determine successional stage and trajectory at pluriannual scales, and bottom-up processes produce seasonal fluctuations in community structure at monthly scales within the main successional trajectory. The amplitude of the annual cycles and the transition from one successional stage to another is a function of disturbance. Although abiotic factors have been shown to induce changes in the structure of benthic communities, in this study the relative abundance of fishes and sea urchins was the major factor. Because maintaining the experimental conditions was extremely time-consuming we could not replicate the experiments in other Mediterranean localities. We believe, however, that the conceptual model proposed here is applicable to other Mediterranean sites, and that the effects of herbivory will decrease along a gradient in algal productivity.

Appendix

Labridae	*Coris julis*
	Ctenolabrus rupestris
	Labrus bimaculatus
	Labrus merula
	Labrus viridis
	Symphodus cinereus
	Symphodus doderleini
	Symphodus mediterraneus
	Symphodus melanocercus
	Symphodus ocellatus
	Symphodus roissali
	Symphodus rostratus
	Symphodus tinca
	Thalasoma pavo
Sparidae	*Boops boops*
	Dentex dentex
	Diplodus annularis
	Diplodus cervinus
	Diplodus puntazzo
	Diplodus sargus
	Diplodus vulgaris
	Oblada melanura
	Sarpa salpa
	Sparus aurata
	Spondyliosoma cantharus
Atherinidae	*Atherina boyeri*
Scorpaenidae	*Scorpaena porcus*
	Scorpaena scrofa
	Scorpaena notata
Serranidae	*Epinephelus marginatus*
	Serranus cabrilla
	Serranus scriba
Moronidae	*Dicentrarchus labrax*
Apogonidae	*Apogon imbervis*
Sciaenidae	*Sciaena umbra*
Mullidae	*Mullus surmuletus*
Centracanthidae	*Spicara maena*
Pomacentridae	*Chromis chromis*
Gobiidae	*Gobius bucchichi*
Bleniidae	*Parablenius gattourgine*
	Parablenius incognitus
	Parablenius pilicornis
	Parablenius rouxi
Tripterygiidae	*Tripterigion spp.*
Mugilidae	*Chelon labrosus*
Muraenidae	*Muraena helena*

Appendix 1- Fish species censed in the experimental areas.

Chlorophyta

Acetabularia acetabulum (Linnaeus) Silva [a]
Bryopsis sp. [b]
Codium bursa (Linnaeus) Kützing [b]
Codium effusum (Rafinesque) Delle Chiaje [b]
Codium vermilara (Olivi) Delle Chiaje [b]
Dasycladus vermicularis (Scopoli) Krasser [a]
Flabellia petiolata (Turra) Nizamuddin [b]
Halimeda tuna (Ellis et Solander) Lamoroux [b]
Ulva rigida C.Agardh [a]
Valonia utricularis (Roth) C.Agardh [a]

Phaeophyta

Asperococcus turneri (Smith) Hooker [a]
Cladostephus hirsutus (Linnaeus) Prudhonne van Reine [b]
Colpomenia sinuosa (Mertens ex Roth) Derbis et Solier in Castagne [a]
Cutleria adspersa (Mertens ex Roth) De Notaris [a]
Cystoseira compressa (Esper) Gerloff et Nizamuddin [b]
Cystoseira sp. [b]
Dictyopteris membranacea (Stackhouse) Batters [a]
Dictyota dichotoma (Hudson) Lamouroux [a]
Dictyota fasciola (Roth) [a]
Halopteris filicina (Grateloup) Kützing [b]
Halopteris scoparia (Linnaeus) Sauvageau [b]
Padina pavonica (Linnaeus) Thivy [a]
Sphacelaria cirrosa (Roth) C. Agardh [b]
Taonia atomaria (Woodward) J.Agardh [a]
Zanardinia prototypus (Nardo) Nardo [b]

Rhodophyta

Asparagopsis armata (Harvey) Schmitz a
Bonnemaisonia asparagoides (Woodward) C.Agardh [a]
Sphaerococcus coronopifolius Stackhouse [b]
Plocamium cartilagineum (Linnaeus) P.Dixon [b]
Laurencia obtusa (Hudson) Lamouroux [a]
Liagora viscida (Forskål) C.Agardh [a]
Amphiroa rigida Lamouroux [b]
Ceramiaceae [a]
Corallina elongata Ellis et Solander [b]
Falkenbergia rufolanosa (Harvey) F.Schimitz-stadium [a]
Gelidium latifolium (Greville) Bornet et Thuret [a]
Jania spp. [b]
Lithophyllum incrustans Philippi [b]
Mesophyllum alternans (Foslie) Cabioch & Mendoza [b]
Peyssonnelia sp.[b]
Polysiphonia sp. [a]
Wrangelia penicillata C.Agardh [a]

Appendix 2- Major benthic algae species in the study community monitored during experiment. Seasonal strategies related algal species were pooled into two groups for data analysis: [a] *seasonal,* [b] *perennial*

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Chapter 3- The effects of sea urchins and fish in depleting palatable algae on a Mediterranean subtidal community

Abstract

Here I studied the relative and combined effects of sea urchins and fish on algal biomass in the Medes Island Marine Reserve. For this purpose I used tethering experiments with palatable algae in large enclosures that contained an orthogonal combination of sea urchins and fish.

Sea urchins contributed more to the decline of algae while the effects of fish were more moderate but nevertheless non-negligible, as a decrease in algal biomass was observed in the fish treatments at all sites. Surprisingly, the effects of fish and sea urchins on algal biomass reduction were not additive. The presence of fish inhibited the impact of sea urchins while losses in algal biomass were minor in the combined treatments.

These results confirm the drastic depletion of palatable algae caused by sea urchins and highlight the contribution of herbivorous and omnivorous fish to this process. Furthermore, since sea urchin densities remained constant during the experiment, our results support the notion of facilitation in subtidal communities -an effect caused by the escape response of sea urchins in the presence of fish.

Introduction

Herbivores contribute greatly to the structuring of vegetal communities in a wide range of habitats (e.g. McNaughton & Georgiadis 1986). In subtidal marine systems, fish and sea urchins are the main herbivores and they influence the abundance and composition of algal assemblages (e.g. Lubchenco & Gaines 1981, Choat 1982, Verlaque 1987, Andrew & Jones, 1990, Ruitton et al. 2000).

Sea urchin effects on seaweeds is a well documented phenomenon in a wide variety of habitats (Lawrence 1975, Schiel & Foster 1986, Andrew 1993). At high densities, they are capable to deplete all erect algae forming barren areas dominated by calcareous encrusting algae (Lawrence 1975, Verlaque 1987, Tegner et al. 1995). Contrarily, the role of fishes in structuring algal communities is still a debated question (Jones and Andrew 1990, Sala 1996, Sala & Boudouresque 1997, Ruitton et al. 2000).

As herbivorous, fish can reduce algal biomass (reviewed by Horn 1989, Hay 1991). As predators, fish can control sea urchin populations by predation, thus reducing herbivore pressure through trophic cascades (e.g. McClanahan & Sala 1997, Sala et al. 1998).

Most ecosystem functional models are based on top-down structuring forces, and predict an alternating-control trophic levels (i.e. consumers on one trophic level regulate the abundance of prey on the trophic level immediately below and cause an alternating sequence of predator control and release from predation down trough to the basal trophic level of primary producers) (Hairston et al. 1960, Oksanen et al. 1981, Carpenter et al. 1985, Power 1992, Menge 1995, McClanahan & Sala 1997).

Nevertheless, fish occupies more than one trophic level (i.e. herbivorous, omnivorous and carnivorous) and consequently the interactions caused by fishes are not simply linear. The heterogeneity within and between the trophic levels together with other factors, such as size-structure heterogeneity or the behaviour-mediated interactions, can all lead to departures from the alternating-control trophic levels expectation (e.g. Strong 1992, Osenberg & Mittelbach 1996, Persson 1999, Menge 2000, Trussell et al. 2003). Thus, as predicted by theoretical and empirical evidence, omnivory may dampen trophic cascades because it may treat and damage simultaneously the shared resource by different ways (Diehl 1992, Stein et al. 1995, Polis & Strong 1996, Holt & Polis 1997).

Major body of experimental evidences of the effects of omnivores in trophic webs has been reported in freshwater systems (e.g. Diehl 1992, 1995, Lodge et al. 1994, Hill & Lodge 1995); however, examples of terrestrial and marine systems are still scarce (Jennings et al. 1997, Pinnegar & Polunin 2000).

In temperate subtidal communities, several studies have addressed the role of fish in structuring temperate algal communities (Jones & Andrew, 1990, Sala, 1996, Sala & Boudouresque, 1997, Ruitton et al. 2000). However, few test the combined effects of herbivorous fish and sea urchins (but see Ruitton et al. 2000), and no one experimental.

In the Mediterranean Sea, sparid fish are the main predators on adult sea urchins and are simultaneously herbivores (Sala & Zabala 1996), thus increasing trophic connections in the food web. To quantify the relative contribution of herbivorous and omnivorous fish and sea urchins on the depletion of algal biomass, and their combined effects, we performed tethering experiments using large enclosures (>15m^2) with an orthogonal combination of fish (herbivorous and omnivorous) and sea urchins (herbivorous).

Material and methods

The study was carried out in Medes Islands Marine Reserve (42º 16’ N, 03º 13’ E), NW Mediterranean Sea (Fig. 1), where fishing is prohibited since 1983. We selected three sites (Racó del Portitxol, Cova de la Reina and Sant Estiu) which had large rocky boulders, with similar orientation (S to SW) and depth (5-8 m).

Fish assemblages at the study site are described in chapter 1 and in Garcia-Rubies and Zabala (1989), Garcia-Rubies (1996); diet and grazing impacts in Sala (1996), Sala and Ballesteros (1997) and Sala and Boudouresque (1997). The major benthic feeding fishes are sparids, mainly *Diplodus* spp.; *Sarpa salpa*, the only true herbivorous fish, is also present at high abundances (Fig.2).

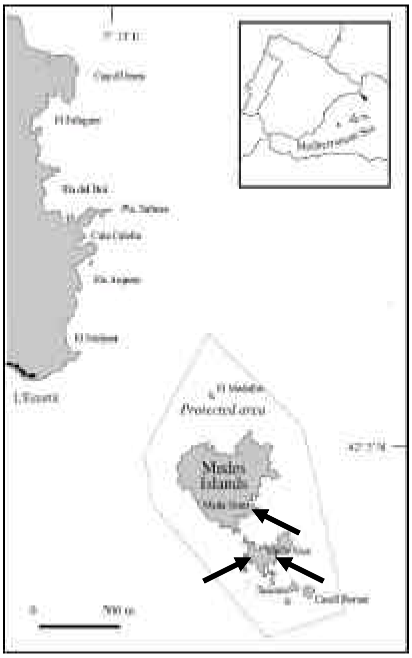


Figure 1- Location of study sites, inside Medes Island protected area, NE Spain, NW Mediterranean Sea. Doted lines represents the limits of the Medes Islans Protected Area, where all fishing is prohibited. Arrows mark experimental sites where experiments were replicated.

Experimental design

To determine the relative impacts of fish and sea urchin grazing on algal assemblages, grazer exclusion experiments were performed over four weeks in July 1999.

We manipulated herbivorous and omnivorous fish and the sea urchin *Paracentrotus lividus* (de Lamarck 1816), the most abundant sea urchin in the region (Sala et al. 1998). Grazing exclusion was replicated at the three experimental sites (Estiu, Reina and Portitxol, Fig. 1). The experiment consisted of orthogonal combinations of the presence/absence of each group. Four groups were established: no grazers (-Fish-Urchins, -F-U), sea urchins only (-F+U), fish only (+F-U), sea urchins and fish (+F+U) (Fig. 2).

Fish exclusion treatments were made by closing small coves (70-110 m^2) with nets. Polystyrene trawler nets of 2.5 cm mesh size, 6-8 m depth and 11-16 m length were attached to autoexpansive nails anchored into the substratum using steel cable. The upper part of the net was continuously kept on the surface using plastic buoys. The experiment thus tested the effects of large herbivorous and omnivorous fishes only. Exclusion nets were cleaned and checked daily, and replaced every other week to prevent significant fouling. Roofless herbivore exclusion nets have negligible light-shading effects (Lewis 1986). Although increased densities of micrograzers are a potential confounding factor in the interpretation of experimental manipulations involving caging treatments (Dayton & Oliver 1980, Brawley & Adey 1981), the size of our enclosures diminished the likelihood of artifacts usually associated with previously-used small cages. The net mesh size used in this study allowed free passage to juvenile sparids and several labrids that are carnivores (Sala 1996). The abundant *Coris julis* and other wrasses, predators of gastropods, small crustaceans and echinoderms (Sala 1996), moved freely trough exclusion areas and were commonly observed feeding within exclusions.

To create the treatments including sea urchins, 16 m^2 enclosures were built using 10 cm-tall plastic fences 2 cm mesh size supported by steel rods anchored into the substratum. Because algae assemblages were not sampled near the edges of the enclosures and these fences did not interfere with light and water movement (Sala & Boudouresque 1997), we assumed that caging artifacts were negligible. Sea urchin enclosures were built in and outside exclusion coves. To create the treatments without sea urchins we removed all sea urchins on several large boulders.

Sea urchin densities similar to those found before the experiment (9-14 urchins m^{-2}) and with similar size distributions were maintained in the sea urchin enclosure throughout the study. These enclosures were checked daily and new sea urchins were added when predation by fish was detected.

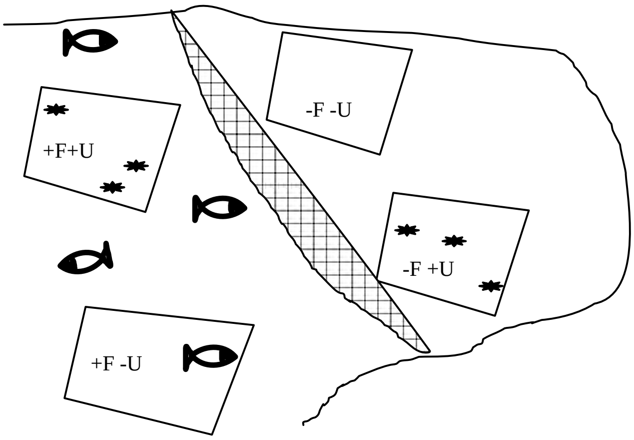


Fig 2- Schematic design of one set of experimental enclosures in which the presence of fish and sea urchins are orthogonally controlled, allowing combinations of sea urchins and fish presence for treatments: -F-U = no herbivores presence, -F+U = only sea urchins present, +F-U = only fish present, +F +U = both sea urchins and fish present.

The abundance and size of herbivorous and omnivorous fish were determined by a 4 replicated census per site and treatment (inside and outside enclosure). Each census was performed by standing at a fixed point and counting all fish in an area of 50 m^2. A total of 46 species were observed at the stations. Fish biomass was estimated using length-mass equations (Garcia-Rubies 1996, Bayle et al. 2001). For simplicity, here we present only the results of the main herbivorous fish *Salpa sarpa* and the omnivorous *Diplodus sargus* (Linnaeus 1758). These fish did not show differences in abundance between sites, but significant differences between enclosed and non-enclosed sites were observed (Table 1, Figure 3).

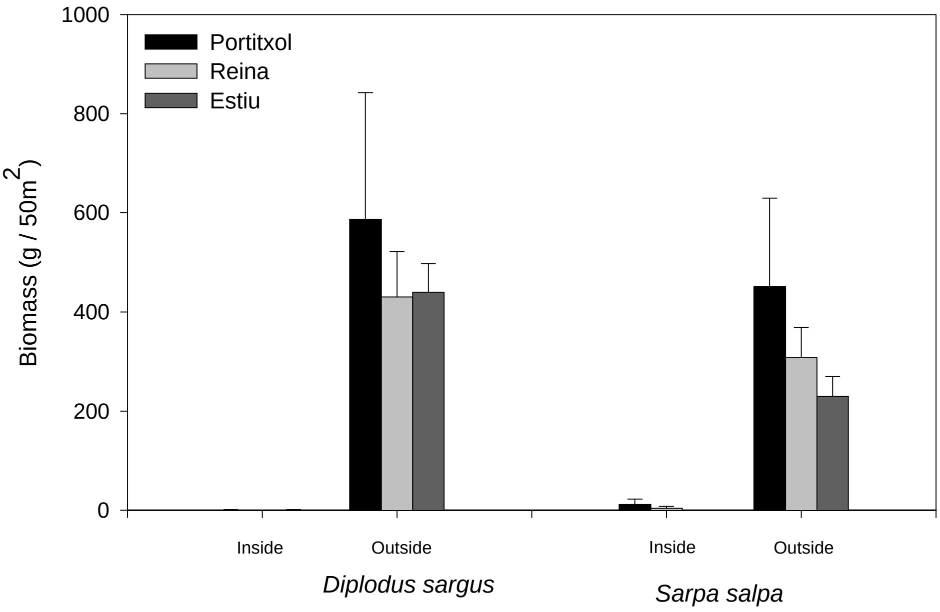


Figure 3- Mean biomass (g / 50m^2 ± SE) of Diplodus sargus *and* Sarpa salpa *inside and outside the fish exclusion treatments on each experimental site.*

Table 1- Results of 2-way ANOVA testing differences of D. sargus *and* S.salpa *biomass between enclosed and control treatments (fixed factor) and between sites (random factor). Data were log transformed to support heteroscedasticity.*

Diplodus sargus	Df	MS	df err	MS err	F	p
Site	2	0,123	18	0,378	0,327	0,7255
Treatment	1	33,381	2	0,226	147,653	0,0067
Site x Treatment	2	0,226	18	0,378	0,599	0,5601

Salpa sarpa	df	MS	df err	MS err	F	
Site	2	0,377	18	0,258	1,460	0,2584
Treatment	1	26,471	2	0,020	1305,499	0,0008
Site x Treatment	2	0,020	18	0,258	0,079	0,9247

Experiments were performed with *Cystoseira* sp. and *Padina pavonica* (Linnaeus) Thivy because these are the most abundant palatable algae during summer (Sala and Boudouresque 1997) and they occur in the vicinity of grazing trials at all the study sites. It was assumed that the rates of algal consumption measured were not confounded by differences among habitats in background availability of these plant species. *Cystoseira* sp. has not been clearly determined. Sala and Boudouresque (1997) determined it as *Cystoseira spinosa* Savaugeau, but recent studies identified it as *Cystoseira squarrosa* De Notaris (Hereu unpl. data).

Consumption rates of both algae were measured with a standardized assay for herbivorous fish grazing modified from Hay (1981) and Lewis (1986). Algae were collected entire by the means of a hammer and chisel. Fleshy algae were spun dry for 1 minute and weighed to the nearest 0.1 g. Nine randomly disposed thalli were attached by a nylon line in plastic mesh holders attached to a ceramic 40 cm x 20 cm plate. During the experiment, algae height was measured weekly using a ruler. At the end of the experiment, the plants were removed, and reweigh, and the differences between initial and final weights were compared.

20 thalli from each species per treatment per site were installed (n=480). In order not to confound the effects of grazing with accidental losses, disappeared thalli were not counted in the analysis.

Data analysis

To determine the effect of algae height trough each experiment we conducted a separate three way Repeated Measures Analisis of Variance (RMANOVA, von Ende 1993) for each specie. A prior test for heteroscedasticity was performed using Levene's test, and no transformation data was necessary.

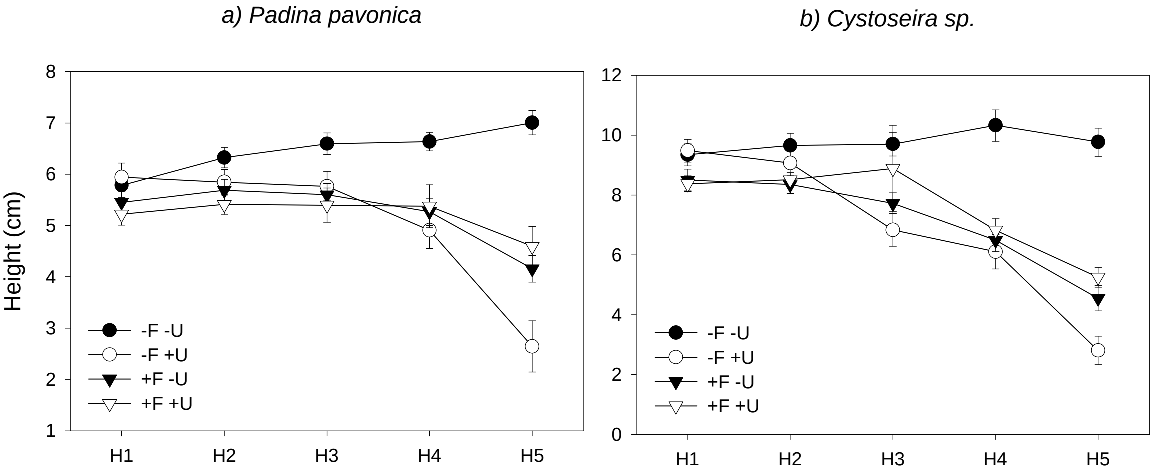
Treatments (sea urchins and fish presence) were the between-subject factor, and time (i.e. sampling events) the repeated-measures (within-subject) factor. To test if data matrix met circularity, we used Mauchly's test of sphericity. When sphericity was violated, we made a Huynh-Feldt adjustment by multiplying the numerator and denominator degrees of freedom by epsilon (e) (von Ende 1993), then F values and probabilities were calculated.

The weight increase during experiments (final - initial wet weight) was used to test the biomass increment (increase by growth – decrease by herbivory) for each specie. Treatment effects were tested using three-way ANOVA of sea urchins and fish (presence vs absence) as fixed factors. Site, as random factor, was nested to urchins and fish.

Results

In all the experiments, treatments had a clear influence on algae height and weight (Figs. 4 and 5). The effects of fish and sea urchins were highly significant (Tables 2 and 3, between-subject effects), furthermore there was a significant interaction, indicating that the simultaneous presence of both fish and sea urchins modified their effects (Tables 2 and 3, within treatment effects: time x sea urchins x fish).

Both sea urchins and fish reduced algal height that decrease during experiment, while in herbivore exclusion treatments algae height increased. Furthermore, while sea urchins reduced algal height in the fish removals, the pattern was more moderate when fish and urchins occurred together (Fig. 4).


a) Padina pavonica

b) Cystoseira sp.

Figure 4- Height increment (mean ± SE) of transplanted algae on each treatment during the four weeks study period on a) Padina pavonica *(n=207) and b)* Cystoseira sp. *(n= 176) (-F-U = no herbivores presence, -F+U = only sea urchins present, +F-U = only fish present, +F +U = both sea urchins and fish present).*

Table 2- Repeated measures ANOVA of the impact of fish and sea urchins on Padina pavonica *height in Medes Island Marine Reserve. Bold values indicate significant differences. Data do no show homogeneity of treatment variances (Sphericity test, p= 0.00; df=9). Huynh-Feldt corrected probabilities (P H-F) are given for both the univariate within subject analysis (H-F epsilon = 0.71).*

Between-subjects Source	*df*	MS	*F*	*P*
Fish	1	72,81	6,81	**0,010**
Urchins	1	139,23	13,01	**0,000**
Fish x Urchins	1	126,78	11,85	**0,001**
Error	202	10,70		
Within-sujects Source	*df*	MS	*F* H-F	*P* H-F
Time	4	52,19	21,271	**0.000**
Time x Fish	4	0,46	0,19	0,946
Time x Urchins	4	27,34	11,14	**0,000**
Time x Fish x Urchins	4	53,69	21,88	**0,000**
Error	808	2,45		

Table 3- Repeated measures ANOVA of the impact of fish and sea urchins on Cystoseira sp. *height in Medes Island Marine Reserve. Bold values indicate significant differences. Data do no show homogeneity of treatment variances (Sphericity test, p= 0.00; df=9). Huynh-Feldt corrected probabilities (P H-F) are given for both the univariate within subject analysis (H-F epsilon = 0.58).*

Between-subjects Source	*df*	MS	*F*	*P*
Fish	1	222,45	7,98	**0,005**
Urchins	1	364,32	13,07	**0,000**
Fish x Urchins	1	686,30	24,62	**0,000**
Error	196	27,87		
Within-sujects Source	*df*	MS	*F* H-F	*P* H-F
Time	4	384,75	42,76	**0,000**
Time x Fish	4	19,22	2,14	0,075
Time x Urchins	4	84,15	9,35	**0,000**
Time x Fish x Urchins	4	124,60	13,85	**0,000**
Error	784	9,00		

Weight increment of both *Padina pavonica* and *Cystoseira* sp. showed the same pattern as height control. Herbivores treatments showed a net decrease in weight, while herbivore exclusion treatments increased (Fig. 5, Table 4). Furthermore, in this analysis was also evident the interaction between sea urchins and fish, since in the presence of fish the effect of sea urchins is lower that when occurs alone (Table 4).

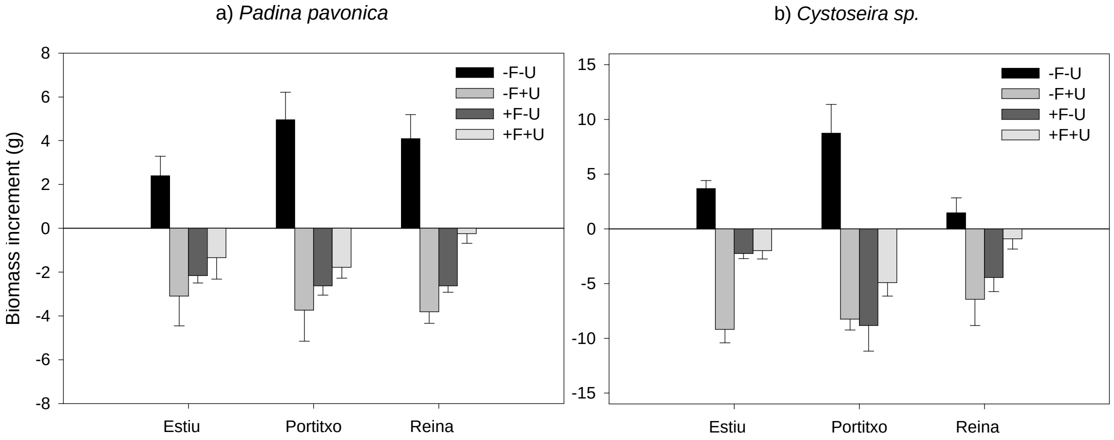


Figure 5-. Biomass increment (mean ± SE) of transplanted algae a) Padina pavonica (n=207) and b) Cystoseira sp. (n= 176) on each treatment and each site. (-F-U = no herbivores presence, -F+U = only sea urchins present, +F-U = only fish present, +F +U = both sea urchins and fish present).

Table 4- Results of nested ANOVA comparing weight increment between Fish and Urchins treatment and Site of a) Padina pavonica *and b)* Cystoseira sp.. *Bold values indicate significant differences.*

Factor	df	MS	df err	MS err	F	p-level
a) *Padina pavonica*						
Site	8	0,21	195	0,19	1,09	0,3690
Fish	1	4,50	8	0,21	21,2	**0,0017**
Urchins	1	6,56	8	0,21	30,9	**0,0005**
Fish x Urchins	1	22,96	8	0,21	108	**0,0000**
b) *Cystoseira sp*						
Site	8	1,17	188	0,25	4,75	**0,0000**
Fish	1	5,15	8	1,17	4,39	0,0694
Urchins	1	14,70	8	1,17	12,54	**0,0076**
Fish x Urchins	1	31,49	8	1,17	26,87	**0,0008**

Discussion

The effect of herbivorous fish in temperate seas, and particularly in the Mediterranean, is a debated issue (e.g. Sala & Boudouresque 1997, Sala et al 1998, Ruitton et al. 2000). While sea urchins are considerate the major grazers in infralittoral temperate communities, herbivorous fish were considerate browsers of minor importance (e.g. Choat 1982, Gaines & Lubchenco 1982, Horn 1989, but see Jones & Andrew 1990). However, recent studies in the Mediterranean show the great contribution of herbivorous fish in structuring infralittoral algal communities (Verlaque 1990, Ruitton et al. 2000, Sala & Boudouresque 1997).

In addition, most studies on herbivory have addressed fish and sea urchins separately. Given that fish and sea urchins share habitats their interaction could lead to responses that are not detected by isolated experiments. This experimental design allowed the study of the contribution of sea urchins and fish separately and their combined effects under natural conditions on two palatable algae species. Although species-species relationships do not reflect the whole community pattern, the tethering experiments allowed us a finest control than coverture in quantifying biomass increment (Hereu 2004).

Large enclosures with roofless nets closing caves allowed us to perform the algal transplants in optimal conditions. At all sites, all algal thalli in herbivore exclusion treatments showed a significant increase in height and weight. On the basis of this observation we can conclude that there were no artifacts caused by manipulation while transplanting algae. Taking account of the short live cycle of these seasonal growing algae, four weeks was time enough to test the effects of herbivory.

The greatest effect on algae decline was detected in sea urchin treatments since all algal thalli showed a significant decrease. The grazing of *Paracentrotus lividus* is characterized by the removal of whole plants, including their bases, a process described as “bulldozing” (Verlaque 1984). Thus, thalli grazed by sea urchins were almost entirely depleted and only a small base attached by the nylon line remained in the holders.

The effects of fish were more moderate, even more important than expected while showed net differences in all sites. In contrast to sea urchins, fish did not deplete whole thallus, but reduced only the apical part of the alga. These differences could be explained by the feeding behavior of fish: they bite but do not graze, therefore, algal growth can continue. Although the effects of fish on algal assemblages were not as great as those caused by sea urchins, our results indicate that herbivorous fish can contribute to determining the biomass of palatable algae.

Although results are consistent with the effects of herbivorous fish on seaweed reported elsewhere (Sala & Boudouresque 1997, Ruitton et al. 2000, Verlaque 1990), they should be interpreted with care since we tested the herbivory effects on only two palatable species. Like most trophic cascades experiments, species-species level shows strong interactions, but at whole community levels the effects of herbivory may provoke different overcomes (Kennelly 1991, Polis & Strong 1996, but see Anderson 1999). Furthermore, this experiment was performed during the summer, when most algal growth is limited (Ballesteros 1991). Similar experiments during spring showed a less clear effect of herbivores, probably because the high algal growth compensates the loss caused by herbivory (unpubl. data).

Sala & Boudouresque (1997) and Sala & Ballesteros (1997) suggested that herbivorous fish are selective and prefer a range of palatable species, which includes *Padina pavonica* and *Cystoseira* spp. Thus, this study of tethering of palatable species had a clear result in which there is a clear reduction of algae biomass. In a previous study, herbivorous fish had no clear effect at whole community level since partial analysis of single species showed variable responses, and total algal cover did not differ in the presence or absence of fish (Hereu 2004), probably because of the compensatory growth of other less palatable species (Sala & Boudouresque 1997).

Surprisingly, the effects of fish and sea urchins on algal biomass reduction were not additive. This observation may be explained by the effect of omnivorous fish such as *Diplodus vulgaris*. This species is not only abundant at the study sites, it also depletes palatable algae and is the main sea urchin predator (Sala & Zabala 1996, Sala 1997).

Because of their direct, lethal effects on sea urchins, as described by current trophic models (e.g. Sala & Zabala 1996, Maclanahan & Sala 1998), the highly abundant omnivorous sparidae could benefit plants indirectly. This mechanism is included in conventional theory on trophic density-dependent interactions models (i.e. Hairston et al. 1960, Oksanen et al. 1981). Nevertheless, since sea urchin densities were maintained artificially during the experiments, these results cannot be explained by the direct and lethal effects of fish.

Carnivores can also favor algal assemblages indirectly through the behavioral responses of herbivores to avoid predation. The escape response of sea urchins in the presence of predators (e.g. Hagen & Mann 1994, Sala 1996, Barnes & Crook 2001) may explain these unexpected results. Many authors describe nocturnal activity of *Paracentrotus lividus* to avoid diurnal predators (e.g. Dance 1987, Sala 1996, but see Crook et al. 2000). Furthermore, in zones of high fish density, *P.lividus* reduces its foraging range (Sala 1996, Hereu 2004).

Because the results were not as we expected, we did not analyze the behavior or foraging range of sea urchins, nor did we address fish-urchin attacks. Nevertheless, patchy distribution and foraging behavior were observed in combined treatments.

The mechanism by which sea urchins detect predators is not still clear, but their responses are probably mediated by a combination of conditioning and sensitivity to biochemical cues (Kats and Dill 1998). For example, Hagen et al. (2002) described the defensive behavioral responses of sea urchins by chemical detection of active predators (wolfish and crab). Chemical information is released during predatory attacks from conspecifics, or emitted by active predators, which have been chemical labeled by their recent diet.

The contribution of omnivory to structuring food webs has been discussed in a theoretical framework (e.g. Strong 1992, Diehl 1993, Persson et al. 1996, Polis & Strong 1996, Persson 1999, Polis 1999), and increasing evidence indicates that it may be a powerful force in freshwater systems, (e.g. Vadas 1990, Diehl 1992, 1995, Lodge et al. 1994, Hill & Lodge 1995). However, there is still little experimental evidence to support this notion, particularly in benthic marine assemblages (reviewed by Menge 2000).

As predators, omnivorous fish may cause a change in the behavior of individual herbivorous species and consequently a reduction in their grazing range, which, consequently, affects the whole food web. Trophic cascades are affected by flexible behavior in one or several levels in both aquatic and terrestrial systems (Carpenter et al. 1987, Turner and Mittelbach 1990, Moran et al. 1996, Beckerman et al. 1997, Schmitz et al. 1997), indicating that trait-mediated indirect interactions (TMIIs, Abrahms et al. 1996) may give rise to strong trophic cascades (reviewed by Werner & Peacor 2003).

Facilitation processes structure communities (e.g. Bruno et al. 2003). Recent experimental evidence in freshwater (e.g. Turner & Mittelbach 1990, McIntosh &

Townsend 1996, Peacor & Werner 1997, 2000, 2001, Peckarsky et al. 2002, Turner et al. 2000) and terrestrial systems (Beckerman et al. 1997, Schmitz et al. 1997, Schmitz & Suttle 2001) highlight the importance of these mechanisms. Nevertheless, in marine systems there is scarce information and this is mainly in intertidal communities (Raimondi et al. 2000, Dill et al. 2003, Trussell et al. 2003). For example, Trussel et al. (2003) described facilitation in the crab-snail-barnacle and algae food web, in which predator cues reduce the foraging behavior of snails; a response that indirectly benefits barnacles and algae.

In summary, our results support the notion of facilitation in subtidal communities. This facilitation is caused by the escape response of sea urchins when predators are detected. Omnivorous fish may cause distinct direct or indirect effects on the alternate food levels. On the one hand, they reduce sea urchins populations, but also reduce its homing range by behavioral effects

Chapter 4- Temporal and spatial variability in settlement of the sea urchin *Paracentrotus lividus* in the NW Mediterranean

Abstract

Settlement into the benthic habitat may be an important process in regulating sea urchin abundance, which potentially modifies the structure of benthic communities. Strong settlement events may increase sea urchin abundance beyond a certain threshold, leading to the formation of coralline barrens (overgrazed communities with a dominance of encrusting coralline algae). To understand the role of settlement in regulating sea urchin populations we first need to determine settlement variability. Temporal variation in settlement of the sea urchin *Paracentrotus lividus* was monitored at three sites in the Medes Islands, NW Mediterranean, during three settlement seasons (March 1998 through October 2000). Spatial variation in settlement was studied in 1999 at 50 sites along a gradient of exposures to waves and currents, inside and outside the archipelago, and separated by distances from tens to thousands of meters. Bathymetric distribution of settlement was also studied in 2000 at six sites at 5, 10, 15 and 20 m depths. Settlement of *P. lividus* occurred in a single annual peak within 3 weeks in May–June. Differences in settlement between years were more than two orders of magnitude. Spatial variability was found at all scales investigated, showing strong patchiness at the smallest spatial scales (tens of meters). Sea urchins settled preferentially at depths between 5 and 10 m. Substratum type, level of protection, and adult population densities were not significant in determining settlement. However, settlement was found to be related to the degree of exposure to waves and currents, indicating that physical processes are very important at the spatial scales investigated. This greatly variable settlement is a necessary, although not sufficient, condition to create gradients of adult *P. lividus* abundance. Further studies should be designed to investigate the interaction between settlement strength and post-settlement mortality

Introduction

Sea urchins have a key role in structuring infralittoral benthic communities. At high densities they can turn complex algal communities into coralline barrens with low complexity and diversity (Lawrence 1975; Harrold and Pearse 1987; VanBlaricom and Estes 1988). It has been suggested that abundant predators can regulate sea urchin abundance and inhibit the creation of coralline barrens (Duggins 1980; Tegner and Dayton 1981; Tegner and Levin 1983; Estes et al. 1998; Sala et al. 1998). However, mosaics of complex algal communities and coralline barrens have been observed at some sites where predator abundance is high (Foster 1990; Sala et al. 1998). This can occur if the effects of sea urchin settlement patterns overcome in the short term the longer term controlling effects of post-settlement mortality (e.g. Menge 2000). A necessary, although not sufficient, condition for these coralline barrens to develop is, hence, that the strong settlement episodes take place, and that sea urchin settlement exhibits great variability in time and space. This paper is part of a larger study designed to investigate the interaction between predatory fishes, sea urchins and algae in the Mediterranean sublittoral. It has been shown that the abundance of a sea urchin (*Paracentrotus lividus*) and the processes controlling it, such as settlement and predation, play key roles in determining the structure of the whole community structure in this system (Sala et al. 1998). Here, we present the results of a study aimed at describing the spatio-temporal variability of sea urchin settlement.

Settlement is an important process in determining adult population structure and dynamics (Underwood and Denley 1984; Connell 1985; Gaines and Roughgarden 1985; Roughgarden et al. 1985), and it can be extremely important in situations with high larval supply and low post-settlement mortality (Paine and Vadas 1969; Talbot et al. 1978; Vance 1979; Verlaque 1984; Andrew 1993), but it can also be important in shaping communities when supply is limited (e.g. Roughgarden et al. 1985). Sea urchin settlement can be highly variable at both temporal and spatial scales (Ebert 1983; Keesing et al. 1993; Balch and Scheibling 2000; Lamare and Barker 2001).

In the Mediterranean infralittoral, the most important grazer is the sea urchin *P. lividus* (Lamarck) (Verlaque 1987). Episodes of strong *P. lividus* proliferation leading to severe regression of algal assemblages have been reported repeatedly (Kempf 1962; Nédelec 1982; Vukovic 1982; Verlaque 1984, 1987). Spatial and temporal variability in settlement of *P. lividus* might be a key factor in the fate of infralittoral Mediterranean communities, which has not yet been adequately quantified. Both the unpredictability of the number of settlement events (one or two peaks a year) and the duration of the larval stage of *P. lividus* (20–40 days; Fenaux et al. 1985; Pedrotti 1993) suggest the potential for highly variable settlement episodes (Lozano et al. 1995; Sala and Zabala 1996; Lopez et al. 1998). The objectives of the present study were to quantify the variability of *P. lividus* settlement at different spatial scales (along the depth gradient and from tens to thousands of meters in a geographical sense) and at different temporal scales (intra- and inter-annual).

Materials and methods

Study site

The study was carried out in the Medes Islands Marine Reserve and on the nearby coast (NW Mediterranean Sea) (Ros et al. 1984). The reserve, where fishing has been prohibited (93.2 ha) since 1983, is located 1 km offshore from the town of l Estartit (42°16 N; 03°13 E) and encompasses a group of small calcareous islands (total surface <20 ha). The unprotected nearby coast is also calcareous and harbors the same types of habitats. The study was carried out on rocky bottoms between 5 and 20 m in depth, which were colonized by a rich algal assemblage dominated by erect algae, articulated calcareous algae and small filamentous algae (Sala and Boudouresque 1997).

Settlement collectors

Settlement of *Paracentrotus lividus* was determined using artificial collectors. Artificial collectors are a non-destructive method, easily installed and replaced, and the samples are easily and quickly analyzed. Artificial collectors, by providing both standardized surface and rugosity, reduce factors affecting settlement and appear to be sufficient for obtaining a reliable relative index of settlement (Harrold et al. 1991). Nevertheless, the possibility that other processes affect settlement in collectors (e.g. predation on settlers, natural mortality) cannot be excluded. Other studies of settlement of echinoderms have used different collectors: oyster shells (Loosanoff 1964), rigid plastic (Tegner 1989), plastic light diffusers (Bak 1985), plastic matrix and articulated coralline algae in a PVC pipe (Harrold et al. 1991), artificial grass (Ebert et al. 1991) and scrub brushes with nylon bristles (Ebert et al. 1994). After an initial experiment with oyster shells, plastic matrix, artificial grass and different types of scrub brushes in 1997 (Table 1), scrub brushes with vegetal bristles were selected as the most effective and easily treatable collectors for *P. lividus* (ANOVA, $F_{4,15}=10.84$, $P<0.01$). Brushes had an 18×6 cm wooden base with 2.5-cm-long vegetal bristles. The advantage of this type of collector is that no special manufacture is required, it is cheap, and easily available for extensive replication (Ebert et al. 1994). Each collector was composed of groups of four brushes attached to nylon lines. The lines were anchored at the bottom and suspended in the water column with a small subsurface float. On each line, the first pair of brushes was 30 cm above the bottom and the second pair 10 cm above the lower pair.

Table 1- Paracentrotus lividus. *Mean and standard deviation of sea urchin settlers in different types of collectors (n=4), installed during a period of 2 weeks at the Medes Islands Marine Reserve during spring 1997.*

Collector type	Mean	SD
Wood	14.00	3.56
Wood and plastic bristles	10.25	1.26
Plastic	4.00	2.94
Artificial grass	2.50	1.73
Oysters	6.25	3.86

Brushes were collected in situ, placed in individual plastic bags in an ice chest, and transported to the laboratory for sorting. To remove recruits from the collectors individual brushes were cleaned in a high-pressure freshwater shower, rubbing bristles by hand. A prior experiment comparing this method with that of Ebert et al. (1994) using a sonic cleaner showed no significant differences in sea urchin recovery rate between treatments (t-test, t=1.32, P=0.21). Following cleaning, the water was filtered through a 250 µm sieve, and sea urchins and other organisms were collected and preserved in 70% ethanol. Identification and measurement procedures of settled sea urchins and other echinoderm species were carried out under the microscope.

Temporal variability of settlement

Three sites with similar topography (boulders >10 m3), orientation (approximately S), wave exposure, depth (5–10 m) and algal assemblages [a transition between Padino–Cladostephetum hirsutae Feldmann (1938) and Rhodimenio–Codietum vermilarae Ballesteros (1989)] were randomly chosen for the study of temporal variability among all possible sites sharing these habitat characteristics (Fig. 1). Water temperature was recorded weekly with a CTD from a hydrographic station located ~2 miles offshore and north of the Medes Islands (J. Pascual, unpublished data).

Patterns of settlement were monitored from March 1998 through October 2000. At each site, collectors were sampled and new collectors were installed weekly during the highest settlement period (spring–late summer) and every other week during the rest of the year. Some gaps occurred in the temporal series as a result of losses caused by storms that prevented retrieval of collectors. Gaps occurred mostly during winter, but never during the potential period of peak settlement (Fig. 2).

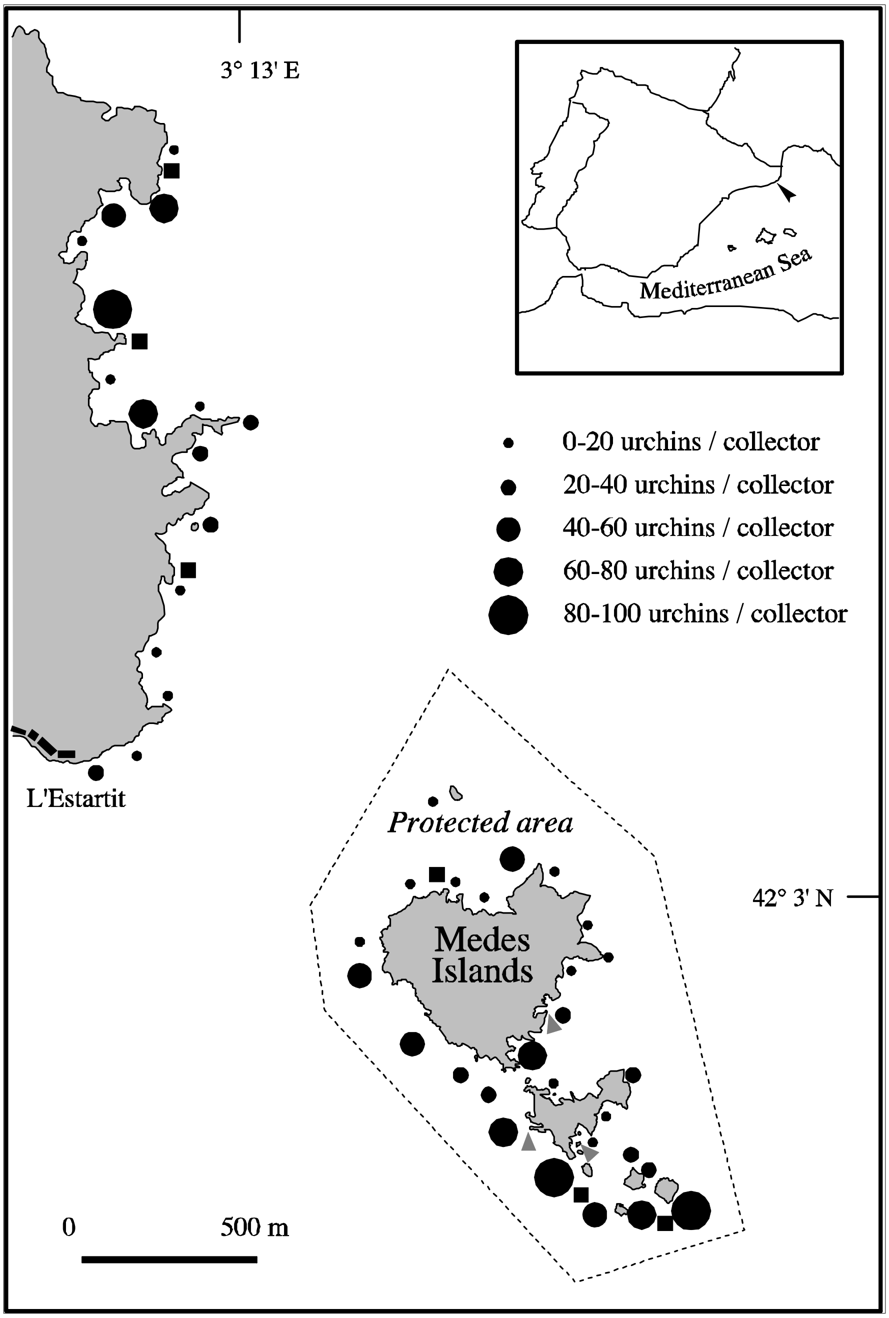


Fig. 1- Paracentrotus lividus. *Location of sampling sites for the study of temporal variability (gray triangles), spatial variability (circles) and bathymetric variability (squares) in settlement. The diameter of circles reflects the number of sea urchins settled per collector.*

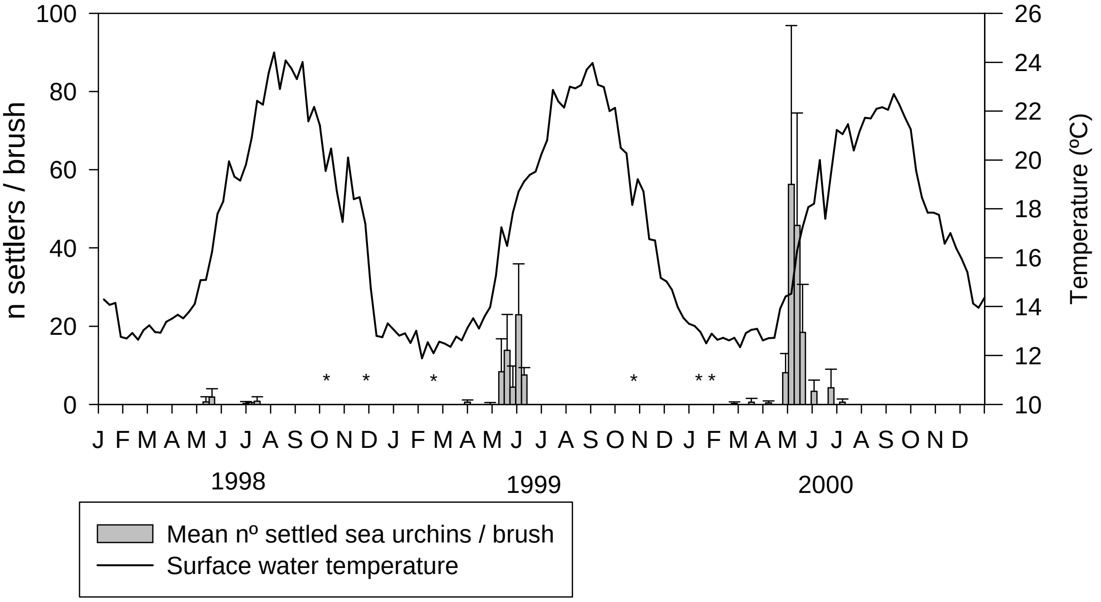


Fig. 2- Paracentrotus lividus. *Abundance (weekly mean±SE) of sea urchins settled on collectors in the Medes Islands Marine Reserve, and water temperature during the study period. Asterisk indicates periods without data.*

Spatial variability of settlement

To monitor spatial variability in *P. lividus* settlement an experiment was carried out during the 1999 settlement peak. Fifty collectors (200 brushes in total) were distributed at 50 randomly selected sites at least tens of meters from the nearest collector (Fig. 1). We placed 32 collectors in the marine reserve and 18 in the adjacent unprotected area, randomly distributed in different orientations and at different wave exposures, from depths of 6 to 9 m. All collectors were deployed on 17 May and collected on 27 May 1999. To determine the variability in settlement with depth, collectors were deployed at four depths (5, 10, 15 and 20 m) at three sites in the Medes Islands and three sites along the nearby coast (Fig. 1) on 11 May and collected on 21 May 2000. Five sites in the spatial-variability study and one site in the depth-gradient study were not used in the analysis because of the loss of collectors due to rough seas.

Variability of settlement among benthic substrata

We carried out an experiment to determine the variability of settlement on different substrata. The experiment was carried out in spring because this is the period of largest abundance of *P. lividus* larvae in plankton samples (Lopez et al. 1998). Three different substrata, simulating a gradient of habitat complexity corresponding to erect algal assemblages, coralline barrens, and a habitat with no structural complexity (no algae), were placed on ceramic 30×30 cm plates. A total of 9 thalli per plate of the brown alga Halopteris scoparia were used to simulate an erect algal assemblage, and 12 empty oyster shells (covered with encrusting corallines) per plate were used to simulate a coralline barren. Brown algae are known to be poorer inducers of sea urchin metamorphosis than articulated calcareous algae (Harrold et al. 1991), which were also abundant in the algal assemblage. Our choice was justified because Corallina elongata thalli were easily lost and also because the brown alga H. scoparia was the dominant architectural builder in the assemblage. Thalli of H. scoparia were tied at the base using monofilament and then attached to a plastic grid placed on the plate. Oyster shells (individual valves) were tied and fixed to the plastic grid with their external side, covered with encrusting coralline algae, exposed to the open water. Settlement plates were placed on the bottom, and, prior to collection, the underside was cleaned to eliminate settlers sheltered therein. Five collectors per treatment were placed at each sampling site (Cova de la Reina, Sant Estiu and Racó del Portitxol) for a period of 10 days (15–25 May 1998), and then collected.

The settlement–abundance relationship of adult sea urchins

To determine whether the variability in sea urchin settlement was associated with the variability in adult sea urchin abundance, we conducted visual censuses of adults. Numbers and sizes of adult *P. lividus* were quantified by SCUBA diving along randomly located 50×1 m transects at 11 sites inside and outside the marine reserve, where settlement collectors had been placed. Sampling (three transects per site and date) was carried out in the settlement season. We hypothesized that settlement is decoupled from the local abundance of reproductive adults (>3 cm in diameter, Lopez et al. 1998).

Data analysis

To test for differences in sea urchin settlement between site (random factor) and years (fixed factor), two-way ANOVAs were performed. Due to strong seasonality, only samples conducted during the settlement period were used in the analysis. To test for differences between sampling sites in the experiment of spatial distribution, one-way ANOVA was performed.

To understand the heterogeneity of settlement, we determined the spatial autocorrelation structure for *P. lividus* settlers using the Spatial Autocorrelation Analysis Package (SAAP version 4.3 by D. Watemberg). Moran s I autocorrelation coefficient was calculated for 19 distance classes. Moran s I ranges from –1 to 1, 0 indicating no correlation, negative values indicating negative autocorrelations, and positive values indicating positive autocorrelation. A positive autocorrelation indicates that settlement at each sampling site has greater similarity to that in other sites than could be expected by chance (Legendre and Legendre 1998). To test for differences in sea urchin settlement between sites (random factor) and depth (fixed factor), a two-way ANOVA was performed.

To test for differences in settlement between substrata, a two-way ANOVA was performed, with site (random factor) and substratum type (fixed factor) as independent variables. To test for differences in the number of settled *P. lividus* between level of protection (reserve vs. unprotected area), orientation (N, E, S, W) and exposure, an ANOVA was performed. We determined orientations between 315°N and 45°N, between 45°E and 135°E, between 135°S and 225°S and between 225°W and 315°W.

For all analyses, Cochran s tests were conducted prior to ANOVA to test the assumption of homogeneity of variance. When necessary, data were log-transformed to satisfy this assumption. When differences were significant, post hoc comparisons were made using the Student–Newman–Keuls (SNK) test.

Results

Temporal variability in settlement

Settlement of *Paracentrotus lividus* exhibited a clear seasonal pattern, with a consistent single settlement peak from May to early July (Fig. 2), when surface water temperature starts to increase (settlement peak occurred between 14°C and 18°C).

The number of settled sea urchins showed significant differences through time ($F_{2,4}$=22.31, P<0.01) and between sites ($F_{2,79}$=4.22, P<0.05), but the interaction was not significant ($F_{2,79}$=0.673, P=0.637). Settlement of *P. lividus* in the Medes Islands showed strong interannual variation, settlers being scarce in 1998 (mean±SD: 3.00±2.76 collector^{-1}) and 12 and 47 times more abundant in 1999 (38.30±26.72) and 2000 (141.37±77.07), respectively (Fig. 2). Sea urchin larvae collected with artificial collectors in all experiments ranged between 230 and 583 µm (mean±SD: 374±48). We could not determine the existence of distinct pulses of larval arrival, because samples were collected weekly and it was impossible to know the size of the urchins immediately after settlement.

Spatial variability in settlement

P. lividus settlement varied significantly from site to site, the number of settled urchins ranging from (mean±SD) 6.3±3.8 to 109.0±12.1 urchins collector–1 (ANOVA, $F_{44,128}$=9.11, P<0.01) (Fig. 1). These results reinforce those above on a different scale, since sites were separated by distances from tens to thousands of meters (Fig. 1). There was no autocorrelation in the shortest distances (Fig. 3); thus, we can assume a highly heterogeneous distribution of settlement, even at a scale of tens of meters.

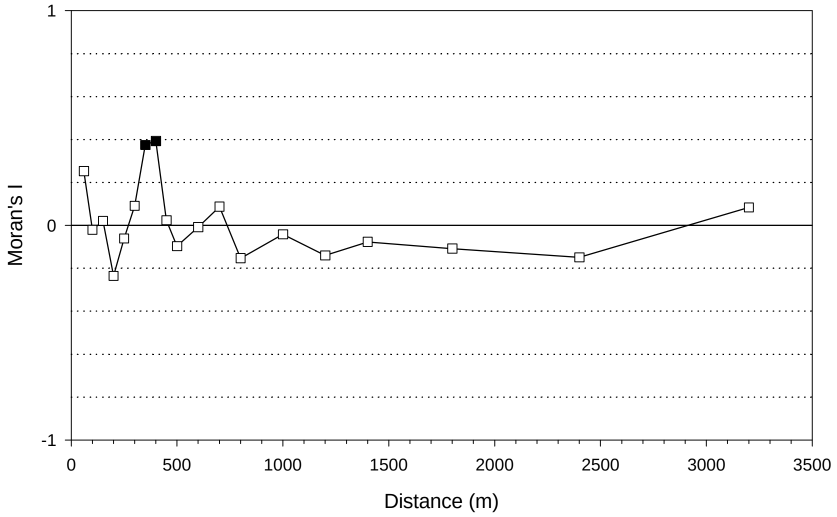


Fig. 3- Paracentrotus lividus. *Correlogram showing the spatial correlation of sea urchin settlers at the different sampling sites. Moran's autocorrelation coefficient I is shown in relation to 19 distance classes (class with variable). Moran's I coefficient is based on a minimum of ten centroid pairs. Filled squares represent significant autocorrelation coefficients at the P=0.05 level, after applying the Bonferroni correction to test for the overall significance of the correlogram.*

P. lividus settled at greater abundance at 5 and 10 m than at deeper habitats at all sites (Fig. 4) (ANOVA, $F_{3,12}$=70.23, P<0.001). The analysis also showed significant differences between sites ($F_{4,56}$=13.28, P<0.001), although there was no interaction between depth and site ($F_{12,56}$=1.05, P=0.414).

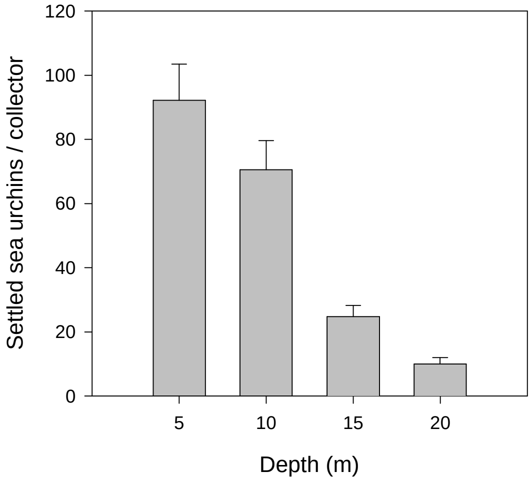


Fig. 4- Paracentrotus lividus. *Number of sea urchins settled (mean±SE per collector; n=19 per treatment) along a depth gradient at the Medes Island and nearby unprotected sites.*

Settlement showed no significant differences between the Medes Islands and the nearby coast (ANOVA, $F_{1,171}$=3.33, P=0.07). However, settlement was significantly different between orientations of sampling sites (ANOVA, $F_{3,169}$=6.77, P<0.01). Settlement in sites oriented N was significantly lower in comparison to those oriented S, E and W, the latter showing the strongest settlement (SNK test, P<0.01) (Fig. 5). Settlement at exposed sites (mean±SD: 43.57±32.08 settlers collector–1) was significantly higher than in bays and at protected sites (31.00±28.08 settlers collector–1) (ANOVA, $F_{1,171}$=11.46, P<0.01).

Substratum selection

Settlement of *P. lividus* did not show significant differences between experimental substrata ($F_{2,4}$=0.16, P=0.86), nor interaction between substrata and site ($F_{4,36}$=1.32, P=0.28), although there were significant differences among sites ($F_{2,36}$=13.33, P<0.001) (Fig. 6). These results suggest that *P. lividus* larvae do not have substrate preferences for settlement. Thus, spatial variability in settlement must be due to factors other than larval substratum selection behavior.

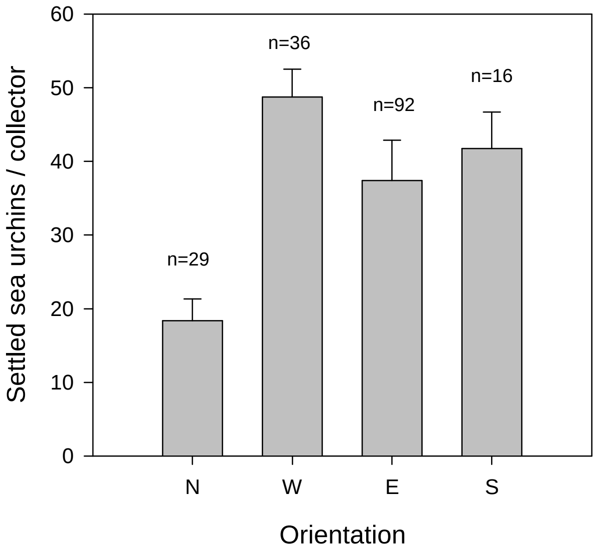


Fig. 5- Paracentrotus lividus. *Number of sea urchins settled (mean±SE per collector) within sample sites, but with different orientations.*

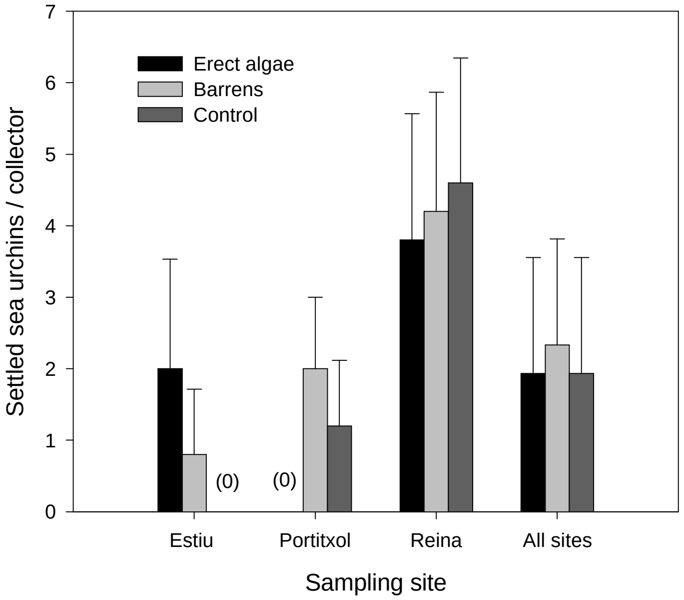


Fig. 6- Paracentrotus lividus. *Number of sea urchins settled (mean±SE per collector; n=5 per treatment) on different substrates at three sites in Medes Islands.*

The settlement–adult population size relationship

The number of settled *P. lividus* showed no significant correlation with local abundance of adult sea urchins (Pearson s $F=_{4.53}$; df=1,9; P=0.062), although the probability was very close to the 5% significance level (Fig. 7). The percentage of variance explained by the model was very low (r^2=0.33), thus suggesting that adult densities and settlement are decoupled at the spatial scales investigated in this study.

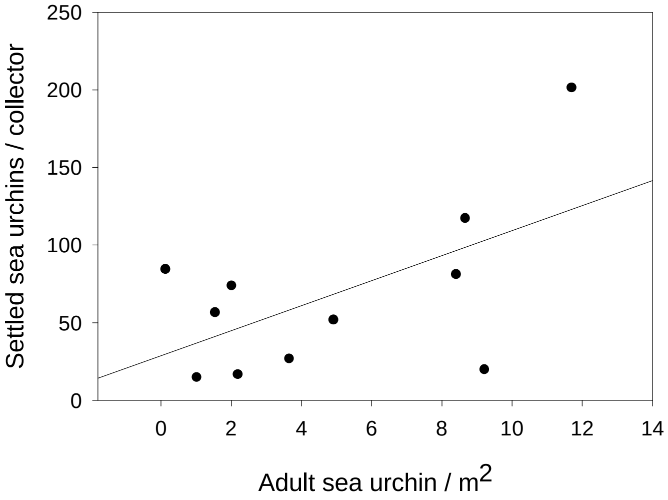


Fig. 7- Paracentrotus lividus. *Relation between number of settlers collected during the settlement season in 1999 and adult sea urchin densities.*

Discussion

The intensity of *Paracentrotus lividus* settlement in the Medes Islands Marine Reserve and nearby unprotected area was highly variable in time (more than two orders of magnitude in number of settlers per collector), within and between years. However, >90% of the yearly settlement occurred in a single peak within 3 weeks in May–June. These results confirm recent reports of a single settlement peak during early summer (Lozano et al. 1995; Sala and Zabala 1996; Lopez et al. 1998), in contrast to previous studies conducted in other Mediterranean regions suggesting a longer settlement period or two distinct peaks in spring and fall (Fenaux 1968; Crapp and Willis 1975; Verlaque 1984; Guetaff et al. 2000). Discrepancies among studies could be explained by the variability in the time and intensity of smaller secondary settlement episodes (Lopez et al. 1998), which were not detected in the present study. However, they may also be an artifact of data collection methods, since studies reporting two settlement peaks did not monitor settlement, but the gonadic cycle of reproductive adults. Seasonality of sea urchins settlement has also been shown for other species for which temporal settlement patterns are predictable at sites located hundreds of kilometers away (Ebert et al. 1994). Settlement in the study region shows a clear synchronicity with planktonic echinoid larval peaks during spring (Lopez et al. 1998), although we did not find the second settlement phase to correspond to the second peak of planktonic larval abundance described by Pedrotti (1993).

Spatial variability in settlement of *P. lividus* was striking at all scales investigated, from tens to thousands of meters. The lack of significant autocorrelations between sampling sites located tens of meters apart indicates settlement heterogeneity of a very small patch size (tens of meters). Our results contrast with those of Keesing et al. (1993), who found that echinoid settlement showed spatial variability at a scale of thousands of meters, but not at smaller scales. Spatial autocorrelations are notoriously affected by singularities in the data (i.e. a very localized clump of individuals) and where they happen to occur. Thus, we do not give the 300–400 m correlation any special significance. The most significant result of this analysis is the absence of correlation at even the smallest spatial scales.

The striking spatial heterogeneity of *P. lividus* settlement is probably a result of the heterogeneity in the distribution of sea urchin larvae in the water column, which could be explained by several influences such as the aggregative feeding behavior of larvae (Metaxas and Young 1998; Starr et al. 1990), heterogeneous mortality in plankton by predation (Tegner and Dayton 1981), food limitation (Ebert 1983; Olson and Olson 1989; Lopez et al. 1998) and purely physical factors such as circulation (Pedrotti and Fenaux 1992; Balch et al. 1999). Our results also suggest that coastal topography, in particular orientation and exposure to waves, may be important in determining settlement, since the ranking of abundance of settlers among the three permanent sites was maintained throughout the study period.

According to these results, it is not surprising that there was no significant correlation between settlement and local abundance of reproductive *P. lividus* at the spatial scales considered (tens to thousands of meters). The planktonic life span of *P. lividus* larvae (20–40 days, Fenaux et al. 1985; Pedrotti 1993) can allow significant dispersal distances. Although *P. lividus* larvae could be retained locally but settle heterogeneously because of local processes, the available evidence suggests that reproduction and settlement of *P. lividus* are decoupled at spatial scales smaller than thousands of meters.

P. lividus settlement had a clear peak between 5 and 10 m, which indicates that *P. lividus* larval behavior may exert some control on settlement, although our results also suggest that substrate is not a determinant cue for *P. lividus* settlement.

Differences in numbers of settlers between natural substrata and brushes may be due to the different textures and the locations with regard to the bottom. While brushes were suspended in the water column, plates were disposed on the bottom and were thus accessible to possible micropredators and sedimentation. Nevertheless, these two methods were designed to test different hypotheses, and not to obtain absolute settlement densities.

What are the implications of this heterogeneity in settlement for the distribution and abundance of *P. lividus* populations? The depth-related settlement pattern is similar to patterns of adult *P. lividus* abundance, with the highest counts in shallow habitats and decreasing abundance below 10 m (Kempf 1962; Gamble 1965; Harmelin et al. 1980; Chelazzi et al. 1997). Since the mobility of *P. lividus* is low (on the scale of a few meters; Dance 1987; Sala 1996), settlement appears to be a major factor in determining the distribution and relative abundance of *P. lividus*. However, our results do not allow us to define the role of settlement in determining absolute abundance of *P. lividus*. Although both strong and variable settlement may be necessary conditions for the sudden outbursts of *P. lividus*, they are not necessarily sufficient stimulants, because the transition from a large abundance of *P. lividus* recruits to adult numbers will also be affected by processes not considered in this study, such as post-settlement predation. Prior studies have pointed out the important role of post-settlement events (mostly mortality) in shaping adult sea urchin populations (Cameron and Schroeter 1980; Rowley 1989). Mortality of post-settled sea urchins can be very high (Rowley 1990). In the Mediterranean, mortality of recruits has been estimated to be at least 75% over the first 6 months (Sala and Zabala 1996) and >99% over the first year after settlement (Lopez et al. 1998). Further demographic and experimental studies are needed to determine whether the patchy, strong settlement episodes reported here have long-term demographic and community-wide consequences.

Chapter 5- The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins

Abstract

We studied the effect of abundance of predatory fishes and structural complexity of algal assemblages on the survival of juveniles of the sea urchin *Paracentrotus lividus* on Mediterranean infralittoral rocky bottoms. Post-settled juveniles (2-10 mm) were placed on four distinct natural substrates with increasing structural complexity (coralline barren, algal turf, erect fleshy algal assemblages and small crevices) inside and outside the Medes Islands Marine Reserve. Predation on these sea urchins increased at greater abundance of predatory fishes, and decreased with greater structural complexity. The refuge provided by structural complexity, however, decreased with increasing size of sea urchin recruits. Predation on the smallest post-settlers was carried out almost exclusively by small fishes (< 20 cm), mainly the labrid *Coris julis,* while the dominant predator of larger juveniles was the sparid *Diplodus sargus.* Our results demonstrate the cascading effects caused by prohibition of fishing in marine reserves, and highlight the potential role of small predatory fishes in the control of sea urchin populations.

Introduction

Sea urchin abundance is highly variable in time and space (Pearse and Hines 987; Turon et al. 1995; Sala et al. 1998a). Small variation in sea urchin abundance can have considerable effects on benthic communities, because beyond a density threshold sea urchin grazing can transform complex communities, dramatically decreasing biodiversity in many systems such as algal communities (e.g.Lawrence 1975; Andrew and Choat 1982; Himmelman et al. 1983), seagrass beds (e.g. Camp et al. 1973; Macia and Lirman 1999; Alcoverro and Mariani 2002), and coral reefs (e.g. Hughes et al 1987; Carpenter 1990; McClanahan and Shafir 1990). In spite of its ecological importance, the relative contributions of the processes that regulate sea urchin abundance, such as predation and recruitment, are yet unclear.

Predation is a key process in determining sea urchin population structure and dynamics (e.g., Tegner and Dayton 1981; McClanahan and Shafir 1990; Shears and Babcock 2002). It has been suggested that predation on juveniles is the major bottleneck in sea urchin populations (Tegner and Dayton 1981; McClanahan and Muthiga 1989; Sala 1997, Lopez et al. 1998), and that it might dampen large fluctuations in density which result from variability in recruitment (Sala and Zabala 1996; Lopez et al. 1998). Therefore, sea urchin populations should be smaller in the presence of abundant predators (McClanahan and Sala 1997). In marine reserves, where predatory fishes are more abundant and larger than in unprotected areas (e.g., Halpern and Warner 2002), sea urchin densities are generally lower than in the latter (McClanahan and Muthiga 1989; Sala and Zabala 1996; Shears and Babcock 2002; 2003). However, predation is not the sole factor regulating sea urchin densities. Diseases (e.g. Lessios 1988) or recruitment variability (e.g. Turon et al. 1995) can also modify sea urchins populations. There is evidence of large spatial and temporal fluctuations of local sea urchin densities in marine reserves (e.g., Sala et al. 1998a) because of factors such as refuges from predation, which may reduce predation rates (Sala et al. 1998b).

The availability of shelter is a key factor in determining predation rates (Roberts and Ormond 1987; Hixon and Beets 1993; Beck 1995) and hence the distribution and abundance of sea urchins (Tegner and Dayton 1981; Carpenter 1984; McClanahan and Kurtis 1991; Andrew 1993). When shelter is available, sea urchins hide and graze around it, thus contributing to the formation of local barrens (Andrew 1993; Sala 1996). The proportion of sheltered sea urchins is greater with decreasing size because small sea urchins are more susceptible to predation by fishes than large adults (Sala and Zabala 1996; Shears and Babcock 2002). Furthermore, the availability of shelters may be limitant for adult sea urchins

The sea urchin *Paracentrotus lividus* (Lamarck) is the most common grazer in the Mediterranean infralittoral (e.g. Kempf 1962; Verlaque 1987). At high densities, this species overgrazes complex algal assemblages composed of several hundred species, and turns them into barrens dominated by a few species of encrusting algae (Kempf 1962; Neill and Larkum 1965; Verlaque 1987; Sala 1996). Barren grounds, together with large sea urchin populations, occur mainly in areas with few urchin predators (reviewed by Sala et al. 1998b; Pinnegar et al. 2000). However, there is also evidence of barrens in marine reserves with large fish densities (Sala et al. 1998a). The objective of this study was to determine the effects of predator abundance and structural complexity of the habitat (algal assemblages) on the survival of juvenile *P. lividus*. We hypothesize that survival of juveniles is lower with increasing predator abundance, and that increasing structural complexity (availability of shelter) decreases predation rate.

To test this hypothesis, we carried out experiments in the NW Mediterranean, in a marine reserve and in an unprotected area with significant differences in the abundance of predatory fishes.

Material and methods

Study site

The study was carried out in the Medes Islands Marine Reserve and the nearby Montgrí unprotected area (NW Mediterranean Sea). The reserve (created in 1983), where fishing is prohibited, is located 1 km offshore from the town of L'Estartit (42º 16' N, 03º 13' E) and encompasses a group of small islands. The study was conducted on rocky bottoms 5 to 10 meters in depth, harboring a mosaic of patches (10^3 – 10^5 cm^2) dominated by distinct types of algal assemblages, including 1) coralline barrens dominated by encrusting corallines (*Lithophyllum incrustans*, *Mesophyllum alternans*, *Spongites notarisii*), 2) turf algal assemblages dominated by small filamentous algae (e.g., Rhodomelaceae, Ceramiaceae, Ulvaceae), and 3) erect algal assemblages dominated by a canopy of perennial (e.g., *Cystoseira compressa*, *Codium vermilara*) and seasonal (e.g., *Dictyota dichotoma*, *D. fasciola*, *Asparagopsis armata*) macroalgae and understory species (e.g., *Corallina elongata*, *Rhodymenia ardissonei*, *Halopteris filicina*) (Sala and Boudouresque 1997).

Predatory fish abundance

To quantify the abundance of urchin-feeding fishes in the reserve and the unprotected area, we counted and estimated the size of all fishes along randomly located 50 ? 5 m transects using SCUBA diving (Harmelin-Vivien et al. 1985). We conducted 5 transects in each of two randomly selected sites at both the reserve and the unprotected area (n=10 transects per level of protection). The different substrate types form small patches (< 10m2) and fishes move between patches, hence we assumed that there are no differences in fish density between substratum types within sampling sites. Fish biomass was calculated using length-biomass relationships from E. Sala (unpubl. data) and Bayle et al. (2001).

Predation experiments

Juvenile *Paracentrotus lividus* 2 to 10 mm in diameter (test without spines) were collected using SCUBA diving from crevices and beneath boulders in the study areas.

All experiments were conducted in summer because fish activity (Garcia-Rubies 1996) and *Paracentrotus lividus* recruitment (Lopez et al. 1998) are strongest. Nocturnally active urchin-feeding fishes are uncommon (Savy 1987, Sala 1997); therefore experiments and field observations were conducted during daylight.

Juvenile *Paracentrotus lividus* were placed on the bottom using tweezers and covered with 40 x 40 x 30 cm plastic cages 1cm mesh size. After 5 minutes a diver located 10 m away lifted the cage using a string, thus exposing the urchins to predators. We believe we avoided artefacts caused by attraction of fish to divers, and obtained independent estimates of predation. Fish did not appear to be attracted to the cage, and therefore we believe that predation was not biased by the experimental procedure. A digital video camera (Sony VCR 900) in an underwater housing (Gates Diego Housing) was placed close to the cage, and experiments were filmed by remote control for 20 minutes (divers left the site after pulling the cage and exposing urchins to predators). In the laboratory, we watched the videotape and noted the time at which each sea urchin was consumed by fish, identified predator species, and estimated their size using a plastic ruler placed at the study site. Preliminary trials showed that in most treatments sea urchin survival showed asymptotes before 20 minutes after the beginning of the experiments, suggesting that the experiments were run long enough to allow us to detect differences between treatments.

To test how predation may be modified by the structural complexity of the habitat, four types of substrate (see above for details) were selected on each area, by increasing degree of protection from predation: 1) coralline barrens without shelter (no crevices), 2) algal turfs, 3) erect macroalgal assemblages, and 4) crevices. In the treatment with crevices, sea urchins were placed inside the crevices; in all other treatments sea urchins were placed on the substrate. In both areas (inside and outside the marine reserve), we conducted five experiments in each habitat type. In each experimental replicate, 10 juvenile sea urchins (2-4 mm diameter) were placed in each treatment (habitat type). To test for differences in survival of juvenile *Paracentrotus lividus* between treatments and degree of predator abundance, 2-way ANOVAs were performed, with predator abundance (reserve/large, unprotected area/low) and habitat type as independent variables, and survival at the end of the experiment as the dependent variable.

To test the relationship between sea urchin size and survival in the different habitat types, we conducted experiments as described above, using two size classes (2-6 and 6-

10 mm), in the marine reserve (n=3 replicates per size class and habitat type). To test for differences in sea urchin survival among sizes and substrata, 2-way ANOVAs were performed. Cochran's test was conducted prior to ANOVA to test the assumption of homogeneity of variance. When necessary, data were log-transformed to satisfy this assumption.

To determine the relationship between predatory fish size and sea urchin size, we conducted a non linear regression between fish length and sea urchin diameter, using data from experiments where sea urchin size was measured and estimation of fish size was possible. We also conducted additional experiments using sea urchins from 10 to 13 mm in diameter.

Results

Abundance of predatory fish

The major *P. lividus* predator, *Diplodus sargus*, showed similar densities in the reserve and the unprotected area (ANOVA, $F_{1,18}$=1.36 p=0.26). However, mean size was significantly larger in the reserve, and hence biomass was higher in the reserve ($F_{1,18}$=13.02 p=0.002; Fig. 1). The biomass of *Coris julis* ($F_{1,18}$=10.8, p=0.005), *Labrus merula* ($F_{1,18}$=7.57, p=0.013) and *Thalassoma pavo* ($F_{1,18}$=7.56, p=0.013), the other main *P. lividus* predators (Sala 1997), was also significantly higher in the marine reserve than in the nearby unprotected area (Fig. 1). The biomass of other known predators was similar among reserve and unprotected area. Nevertheless, the total biomass of predatory fish was higher in the reserve, mainly due to the contribution of *D. sargus* (Fig. 1).

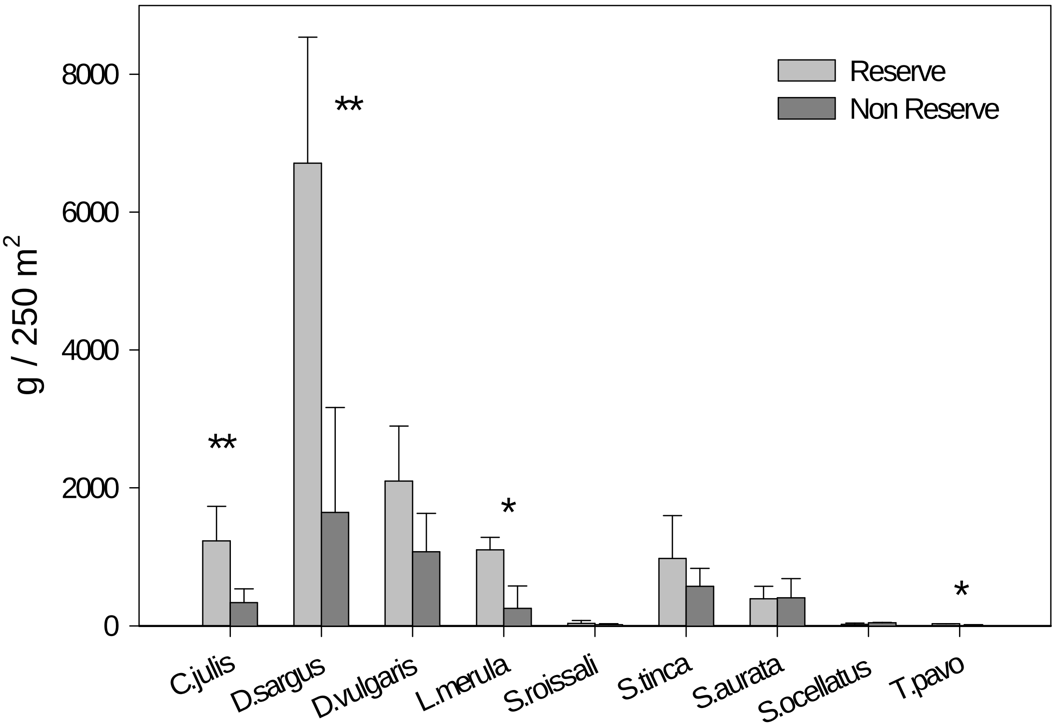


Figure 1- Biomass of predatory fishes (mean ± SD) inside and outside the Medes Islands Marine Reserve. Asteriscs indicates statistical significance in an ANOVA analysis (p<0.05; ** p<0.01).*

Effects of predation and habitat structural complexity on sea urchin survival

The predatory fish observed during the experiments were the labrids *Coris julis, Labrus merula, Symphodus roissali* and *Thalassoma pavo,* and the sparids *Diplodus sargus* and *D. vulgaris.* Predation rates on juvenile *Paracentrotus lividus* were greater in the marine reserve than in the unprotected area for all substrate types except crevices (Fig. 2¸ Table 1).

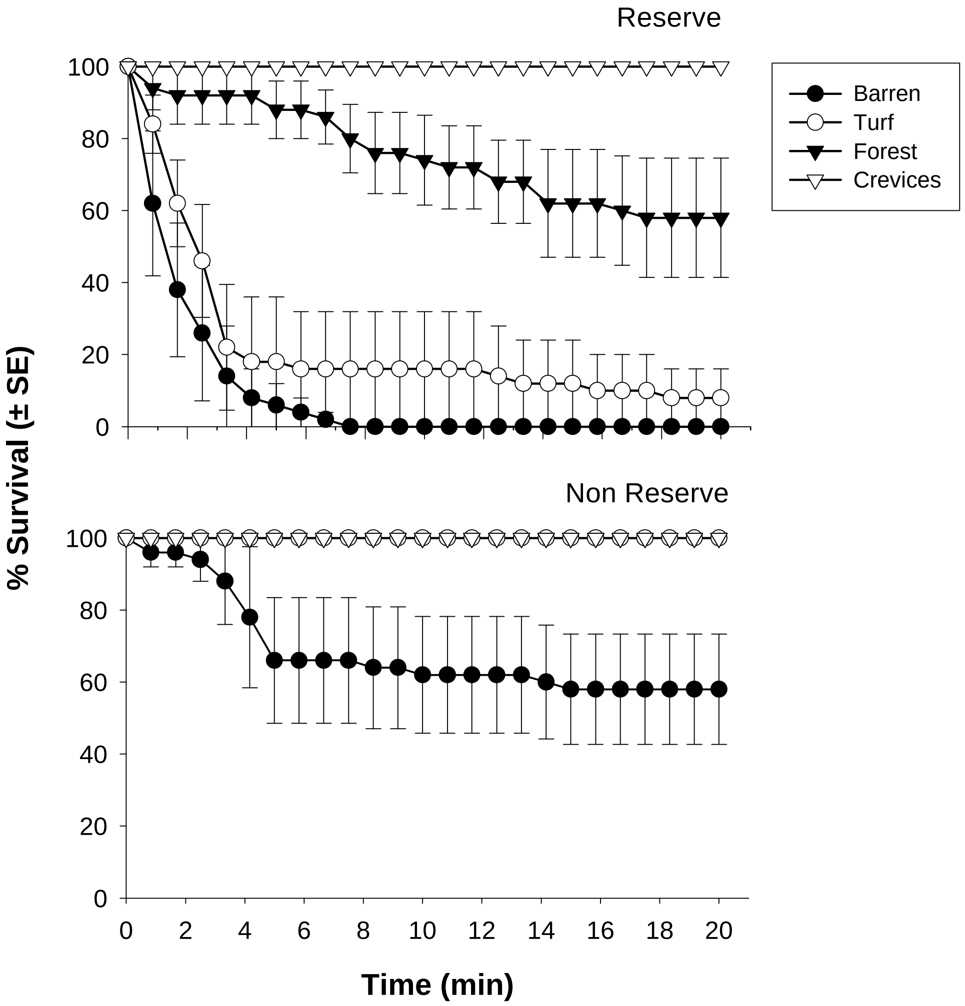


Figure 2- Mean survival (± SE, n = 5) of juvenile (2-4 mm) Paracentrotus lividus *in distinct habitat types the Medes Islands Marine Reserve and the unprotected area nearby.*

Table 1- Results of ANOVA comparing the effect of substrate type in protected and unprotected areas on the survival of juvenile Paracentrotus lividus.

Factor	df	MS	F	p-level
Protection (P)	1	40.83	45.10	<0.01
Substrate (S)	3	18.27	20.19	<0.01
P x S	3	644.40	10.16	<0.01
Error	32	0.905		

Table 2- Survival of juvenile Paracentrotus lividus *in each substrate type and size class inside (MR) and outside (NR) the Medes Islands Marine Reserve. Barren: coralline barren; Turf: algal turf; Erect: erect palatable algae.*

		2-6 mm		*6-10 mm*	
		% Mean	Std. Dev.	% Mean	Std. Dev.
MR	Barren	0.00	0.00	0.00	0.00
	Turf	6.66	16.32	0.00	0.00
	Erect	58.00	33.11	11.66	16.02
	Crevices	100	00.0	100	0.00
NR	Barren	56.66	30.76		
	Turf	100	0.00		
	Erect	100	0.00		
	Crevices	100	0.00		

The survival of sea urchins was higher with increasing structural complexity of the algal assemblage, being minimum on coralline barrens where shelter absent, and maximum inside crevices which provide the highest degree of physical protection. In the unprotected area where predatory fish were less abundant, all juvenile *P. lividus* in vegetated substrates survived the experiment, whereas in the reserve they experienced predation in all vegetated treatments (Fig. 2, Table 2). In the reserve, percentage survival was not significantly different for turf assemblages and barrens ($F_{1,8}$=1.00; p=0.34) (Table 2).

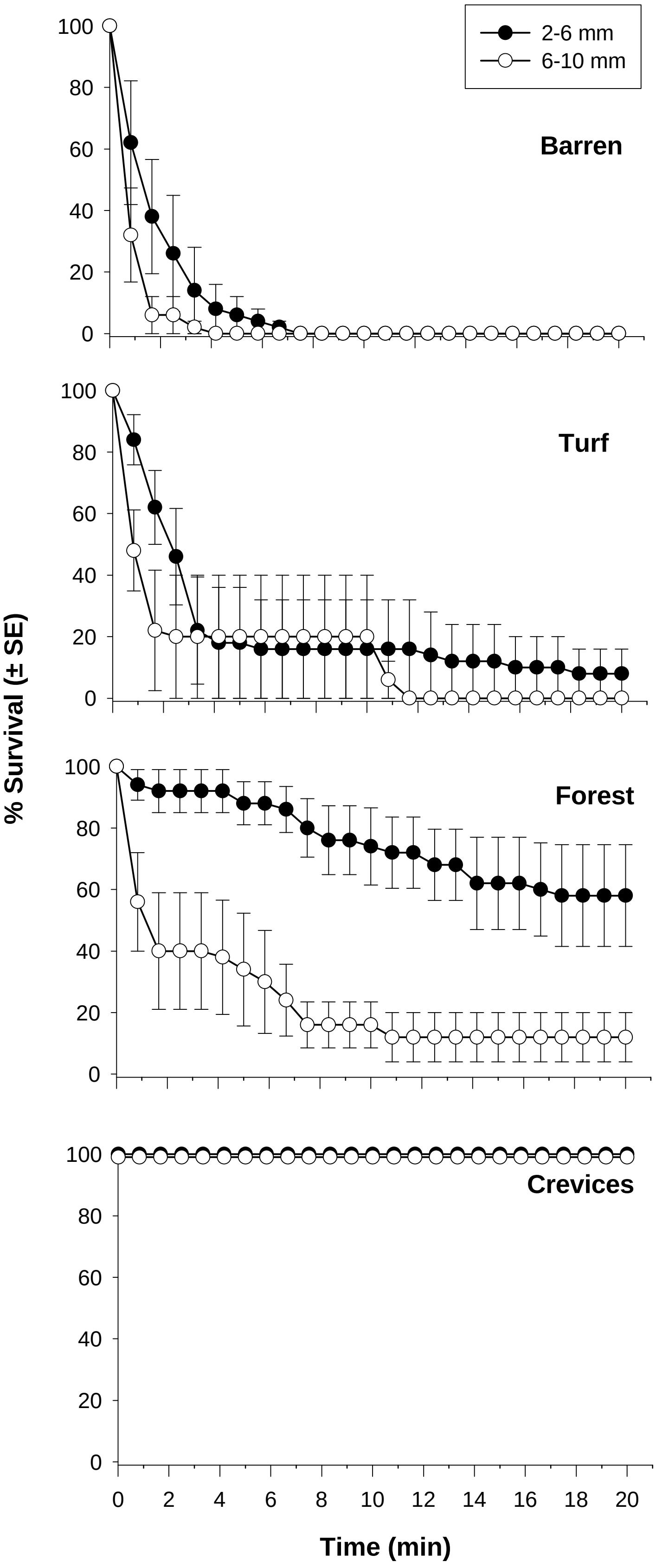


Figure 3- Mean survival (± SE, n = 5) of juvenile Paracentrotus lividus *belonging to two size classes (2-6 mm and 6-10 mm) in distinct habitat types in the Medes Islands Marine Reserve.*

Table 3- Results of ANOVA comparing the effect of substrate type on the survival of small (2-6 mm) and larger (6-10 mm) juvenile Paracentrotus lividus.

Factor	df	MS	F	p-level
Substrate	3	25328,44	125,13	<0.01
Size	1	2091,80	10,33	<0.01
Substrate x Size	3	1484,06	7,33	<0.01
Error	40	1484.06		

Predation was highest during the first 5 minutes of the experiments (Figs. 2-3). In the reserve, predation on sea urchins 6-10 mm in diameter was greater than on smaller ones (2-6 mm) (Fig. 3, Table 3), indicating that predation is driven by visual cues. Sea urchin survival was similar in barrens and algal turfs regardless of size, whereas survival of smaller sea urchins was greater in erect algal assemblages. Crevices provided effective refuge for both size classes.

Predator-prey size relationship

The identity of the major predators changes with increasing sea urchin size (Fig. 4). Although *Diplodus sargus* is the most important predator of adult *Paracentrotus lividus* (Sala and Zabala 1996, Sala 1997), *D. sargus* does not feed effectively on small juveniles (< 4 mm). The labrid *Coris julis* is the most effective predator of small juvenile *P. lividus*. The importance of *C. julis* as a predator decreases while that of *D. sargus* increases with increasing sea urchin size. As reported previously by Sala (1997), *P. lividus* > 10 mm are consumed mostly by *D. sargus.* Other fish species have a low contribution to total predation (0-20 %) (Fig. 4). Although *L. merula* was not observed eating sea urchins > 12 mm in this study, they are known to prey on larger sea urchins (Sala 1997).

The relationship between predatory fish size (all species) and sea urchin size was statistically significant although the variance explained by the model was low (r^2=0.31, p<0.001; Fig. 5). There was a significant correlation between predator and sea urchin size within taxa (r^2=0.32, p<0.001 for *C. julis* and *T. pavo*; and r^2=0.06, p = 0.003 for *D. sargus*). In *C. julis*, females predominantly ate the smallest sea urchins, while larger males monopolised predation of urchins of 9-10 mm in size.

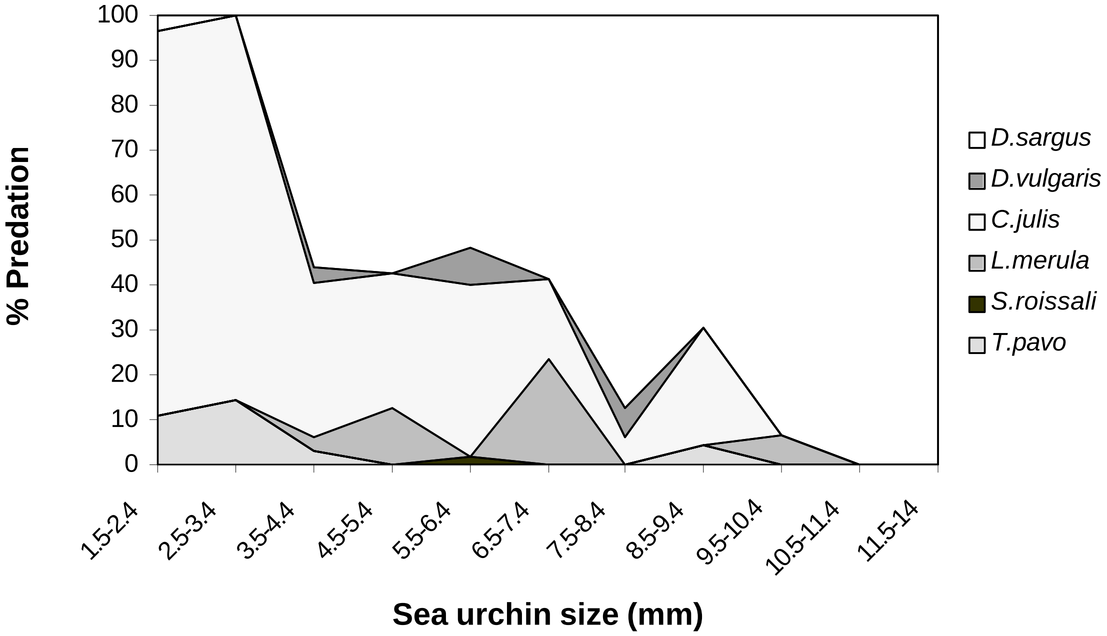


Figure 4- Proportion of mortality caused by major predatory fish species on juvenile Paracentrotus lividus *of different sizes.*

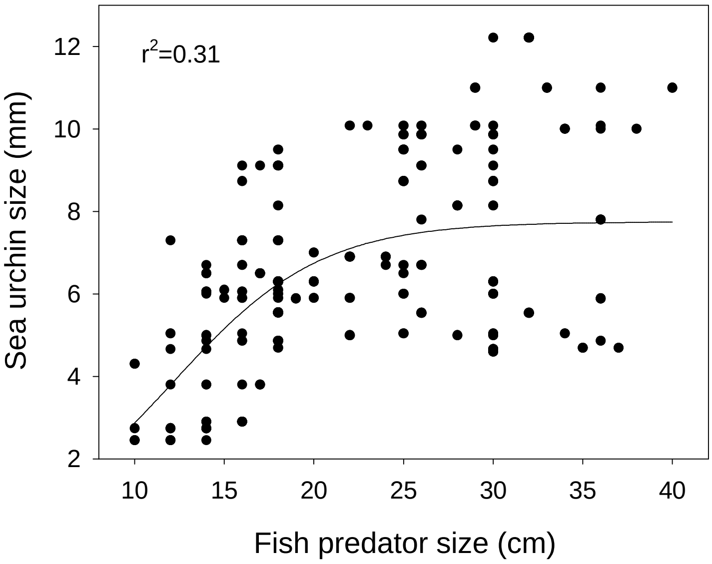


Figure 5- Size relationship between Paracentrotus lividus and predatory fishes during predation experiments in the Medes Islands Marine Reserve.

Discussion

The abundance of predatory fishes and the structure of algal assemblages influenced survival of juvenile *Paracentrotus lividus*. Survival was higher with increasing habitat complexity and at lower fish biomass. Adult *P. lividus* also had greater mortality rates in the presence of abundant predatory fishes (Sala and Zabala 1996). Our results support the hypothesis that, although medium to large fishes are the most effective predators of adult sea urchins, smaller fishes such as wrasses can play a major role in the regulation of recruitment by eating the smaller size classes (Sala 1997).

As demonstrated for other species and systems, the presence of shelter can reduce predation mortality (McClanahan and Shafir 1990; Hixon and Beets 1993; Andrew 1993; Beck 1995). In the present study increasing structural complexity of the habitat also increased survival of juvenile sea urchins, at least in the short term. Because *Paracentrotus lividus* larvae do not appear to exhibit habitat preferences for settlement (Hereu et al. 2003), we would expect the density of sea urchin recruits to be larger on sites with shelter. However, the substantial mortalities of *P. lividus* settlers during the first weeks after settlement in erect algal assemblages (Sala and Zabala 1996, Hereu et al. 2003) may be due to other factors such as predation by micropredators, such as polychaetes and crustaceans, which inhabit erect algal assemblages.

Our results involve only the first 20 minutes after the beginning of experiments. The fact that predation by fishes virtually ended after less than 20 minutes suggests that sea urchins secured shelter and were no longer detected by fishes. However, the presence of micropredators probably causes additional mortality over time. Absolute predation rates were not obtained from our experiments because algal assemblages are not the only shelter available to juvenile sea urchins; crevices and spaces beneath small boulders also provide abundant shelter. In fact, predation in marine reserves with a high abundance of predatory fishes may not reduce absolute sea urchin densities, because most are sheltered in crevices and beneath boulders (Sala and Zabala 1996, Sala et al. 1998a). However, simple predation experiments, like those carried out here, can provide a standardised protocol to assess the strength of predation in coastal ecosystems.

The partitioning of predation on *Paracentrotus lividus* by fish species and sizes can have implications for the regulation of sea urchin populations as a function of fishing pressure. Small fishes eat small juveniles, and there is an escape size beyond which small fishes cannot effectively kill sea urchins (Sala 1997, this study). Therefore, in fished areas sea urchins will reach a refuge from predation at smaller sizes because predators in unprotected areas are smaller (García-Rubies 1996, Sala 1997). Our results also support the idea that the commonly neglected effects of line fishing, which targets mainly small fishes such as *C. julis* (Harmelin et al. 1995, Harmelin 1999), could influence *P. lividus* population abundance (Sala 1997) and subsequently the structure of the benthic community (Sala et al. 1998b).

Our results support the potential role of marine reserves in the regulation of sea urchin populations and hence in preventing the development of sea urchin barrens, as predicted by models (McClanahan and Sala 1997; Sala et al. 1998b). In Mediterranean marine reserves, predatory fishes are more abundant and greater in size than in unprotected areas (e.g., Garcia-Rubies and Zabala 1990; Francour 1991; Harmelin et al. 1995), therefore predation rates on sea urchins are greater in these reserves (Sala and Zabala 1996, this study). The significantly lower survival observed in the Medes Islands Marine Reserve relative to that in unprotected sites is a clear example of the predation effects that follow effective protection of coastal habitats (Pinnegar et al. 2000). We believe that the strength of predation on juvenile sea urchins by fishes is a good estimator of fish build-up and trophic changes in marine reserves.

Chapter 6- Movements patterns of the sea urchin *Paracentrotus lividus* in the NW Mediterranean

Abstract

Sea urchins can alter the composition and dynamics of algal communities by grazing. Changes in their displacement capability can influence their grazing and thus their effect on algal communities. The daily and monthly movement of *Paracentrotus lividus* inside and outside a marine reserve in the NW Mediterranean Sea was studied in order to determine the role of predation in sea urchin movements and its potential grazing impacts.

During the three-month study, the total distance travelled by sea urchins ranged from 71.8 to 673.6 cm (mean = 379.2 cm, SD = 221.3). Home ranges (distances from the initial position) were between 50 and 302 cm (mean = 150.7 cm, SD = 99.4). Movements were not directional but random, with a mean of 150 cm around the initial position.

The activity of *Paracentrotus lividus* was significantly higher at night than during daylight. Total displacement at the end of the experiment was significantly higher in the unprotected area than in the reserve, as was the home range. The linear distance travelled in a 24-h period ranged between 6 and 220 cm with a mean home range of 51 cm. These results agree with those of other authors, and allow us to rule out major migratory processes of sea urchin populations in this area. Nevertheless, these results underline the role of predatory fishes in reducing herbivory pressure by trophic cascades, reinforcing the evidence that sea urchin escape behaviour may be an important factor in structuring algal communities.

Introduction

Sea urchins in temperate seas are capable of transforming erect algal communities into barren grounds (*e.g.* Lawrence, 1975; Andrew & Choat, 1982; Verlaque, 1987). Since the transition from erect algal communities to barrens is a function of sea urchin density, the dynamics of sea urchin populations may determine the structure of benthic communities.

Some models of organization of benthic communities suggest top-down control, where predators can control sea urchin populations and, by cascading effects, prevent the formation of overgrazed areas (*e.g.* Estes & Palmisano, 1974; Duggins, 1980; McClanahan & Sala, 1997). However, strong settlement events can increase sea urchin densities regardless of predators, especially when predation is attenuated by high availability of refuges (Sala *et al.*, 1998a). The existence of sea urchin barrens in marine reserves where predatory fishes are abundant (Sala *et al.*, 1998b) suggests that other processes such as migrations or escape behaviour may be crucial in determining sea urchin densities and consequently the composition and structure of benthic communities.

There is evidence for the formation of dense feeding aggregations that move as fronts, consuming all erect macrophytes in their path. Off the Atlantic coast of Nova Scotia, destructive grazing by feeding aggregation fronts of *Strongylocentrotus droebachiensis* is a recurrent phenomenon (Mann, 1977; Bernstein *et al.*, 1983; Vadas *et al.*, 1986; Scheibling *et al.*, 1999). Other migration fronts are described in seagrass communities (Alcoverro & Mariani, 2002; Peterson *et al.*, 2002). Because sea urchins can persist in barrens and prevent algae recolonization, destructive grazing can cause large-scale shifts in community status (Mann, 1977).

Moreover, sea urchin movements on a lower scale can also be a determinant factor in structuring algal communities because their grazing capability is a function of the surface ranged. Even in marine reserves, where predatory fish densities are high, if the half-distance between refuges is smaller than the home range of sea urchins, the formation of sea urchin barrens is enhanced (Andrew, 1993). Thus, factors that modify sea urchin movements and reduce their grazing range, such as predation (Nelson & Vance, 1979; Carpenter, 1984, Scheibling & Hamm, 1991), food availability (Mattison *et al.*, 1977; Russo, 1979; Harrold & Reed, 1985; Andrew & Stocker, 1986) or water flow (Kawamata, 1998) may help determine algal communities' structure and dynamics.

In the Mediterranean infralittoral, the sea urchin *Paracentrotus lividus* is the most important benthic herbivore (*e.g.* Kempf, 1962; Verlaque, 1987). Evidence is available on *P. lividus* migrations from recruitment areas to adult habitats (Fernandez *et al.*, 2001). Nevertheless, adult movements appear to be related to movements allowing adjustment of zonation patterns (Chelazzi *et al.*, 1997) or to recovering zones after removals (Palacin *et al.*, 1997), but not to active migratory fronts as described for other species.

At a circadian level, *P. lividus* has nocturnal activity patterns to avoid diurnal predators (Kempf, 1962; Gamble, 1965; Dance, 1987; but see Barnes & Crook, 2001a).

Although there is evidence that the presence of predatory fish can reduce the grazing range of *P. lividus* to about one meter around refuges (Sala, 1996), little experimental evidence of *P. lividus* movement patterns exists. Laboratory studies show that *P. lividus* movement may be important and that it is mediated by light, which can determine both direction and speed of movement (Domenici *et al.*, 2003). Nevertheless, field studies show that *P. lividus* travel short distances around a small area, with relatively random movements (Dance, 1987).

In this study I examined the movement of *P. lividus* on daily and monthly scales by monitoring tagged individuals inside and outside a marine reserve. The aim was to determine the role of predation in sea urchin movements and potential grazing impacts..

Methods

The study was carried out in the Medes Islands Marine Reserve and the nearby unprotected area (NW Mediterranean Sea). The reserve (created in 1983), where fishing is prohibited, is located 1 km offshore from the town of L’Estartit (42º 16’ N, 03º 13’ E) and encompasses a group of small islands (Fig. 1). Fish assemblages at the study site are described in Garcia-Rubies and Zabala (1990), Garcia-Rubies (1999) and in chapters 1 and 5; the major benthic-feeding fishes are sparids, mainly *Diplodus* spp., although other small *P.lividus* predators such as labrid fishes are also present in high abundance (Chapters 2 and 5).

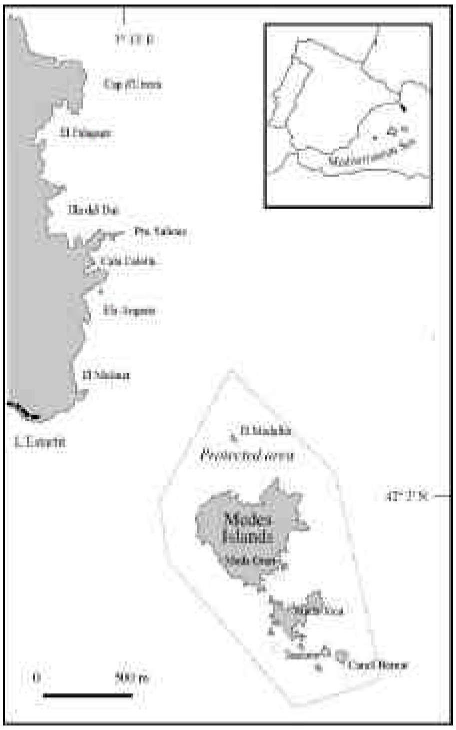


Figure 1- Location of study sites, inside and outside the Medes Island protected area, NE Spain, NW Mediterranean Sea. Dotted lines represent the limits of the Medes Islands Marine Reserve, where all fishing is prohibited.

Monthly activity

Experiments were carried out using adult Paracentrotus lividus sea urchins (50–60 mm diameter) on horizontal rocky bottoms at 4–6 m depth in the unprotected area. The substrate was covered with erect algal communities (a transition between the Padino–Cladostephetum hirsutae J. Feldmann, 1938, and Rhodymenio–Codietum vermilarae Ballesteros, 1989). Movement rates on a monthly scale were determined at two sites in the unprotected area (Falaguer) adjacent to the Medes Islands Marine Reserve (Fig. 1, full squares) from March to June, 2001, by tagging 40 individuals with anchor tags in situ (Olsson & Newton, 1979; James, 2000; Duggan & Miller, 2001). This method consisted of inserting a nylon anchor in a 3 mm diameter hole drilled near the top of the urchin in the interambulacrum with a submersible tagging gun. Although sea urchins suffered a high mortality, this method was selected because it is more perdurable in time than others (Dix, 1970; Cuenca, 1987).

A stainless steel bar was fixed in the study area as a reference to measure polar coordinates (direction [± 5°] and distance measured to the nearest cm) of sea urchin movements. Sea urchin position was recorded every other week during a period of three months. After determining the position of each individual by polar coordinates, the distance travelled from prior movement positions and the distance from the starting position (as a measure of home range) were calculated.

To reduce possible tagging artefacts, only movement data from one week after tagging were used. At the end of the experiment, 24% of the tagged sea urchins had died. Individuals dying from infections due to tagging were observed moving and feeding, and James (2000) demonstrated that this technique had no observable effect on sea urchin behaviour. The greatest sea urchin mortality occurred during the first several days after tagging (35% of total sea urchins tagged), and survivorship after the first week was higher. To avoid any other tagging artefacts, only the data on the seven individuals that survived the 3-month experiment were used. None of the survivors showed necrosis around the anchor hole.

Daily movements

To determine the circadian cycle of P. lividus movements and the home range, tagging studies were conducted in summer 2000 at two sites in the Medes Islands Marine Reserve and at two sites in the nearby unprotected area, in the same type of habitat described above (Fig. 1, full circles).

Tagging for this short-term study followed the method described by Gamble (1965), which consisted of sliding small pieces of plastic sleeve insulation from electric wire over individual spines. This method does not damage sea urchins, but is less perdurable because the tags detach in a few days. They were, however, persistent enough for a 24-hour experiment. All sea urchins were tagged in situ. At each site, 40 individual sea urchins 50–60 mm in diameter were marked and identified. Some tags were lost during the experiments, so only movement data from sea urchins which kept their tags throughout the experiment were used. A stainless steel bar was utilized to locate the position of each individual sea urchin (see monthly activity). Sea urchin position was recorded every four hours during one day (July 15, 2000).

To test for differences in movement between the marine reserve and the nearby unprotected area, a Repeated Measures Analysis of Variance (RMANOVA; von Ende, 1993) was used with movement data for 4-hour periods. Data were log-transformed to satisfy the assumption of heteroscedasticity after conducting Levene's test. Treatment (protection) was the between-subject factor, and time the repeated-measures (within-subject) factor. To test if the data matrix met circularity, Mauchly's test of sphericity was used and a Huynh-Feldt adjustment was made by multiplying the numerator and denominator degrees of freedom by epsilon (von Ende, 1993).

The analysis comparing total displacement and home range between the reserve and unprotected area was performed using one-way ANOVA. To test the assumption of normality and the assumption of homogeneity of variances, Shapiro-Wilk's W-test and Cochran's C-test were performed respectively prior to ANOVA, and in both cases analysis data was log transformed to satisfy this assumption.

Results

Monthly activity

During the three months the total distance travelled by sea urchins ranged between 72 and 674 cm (mean = 379.2, SD = 221.3) (Figs 2 and 3). The linear distances travelled by sea urchins during the every-other-week sampling periods ranged between 0 and 255 cm (mean = 54.2, SD = 52.8 cm). This maximum distance travelled corresponds to a mean daily movement of 18 cm. Home ranges (distances from the initial position) were between 50 and 302 cm (mean = 150.7 cm, SD = 99.4) (Fig. 3). The sea urchins did not show the homing behaviour for individuals living in holes as described by Neill & Larkum (1965). Nevertheless, individuals appeared to stay in a reduced area because the home range was smaller than the linear distance of the area travelled, as shown in a t-test analysis taking into account the total displacement and the home range of the 7 surviving tagged sea urchins at the end of the experiment (t-test: t = 3.83, df = 6, P = 0.008); movements were not directional and were limited to a radius of 1.5 m around the initial position

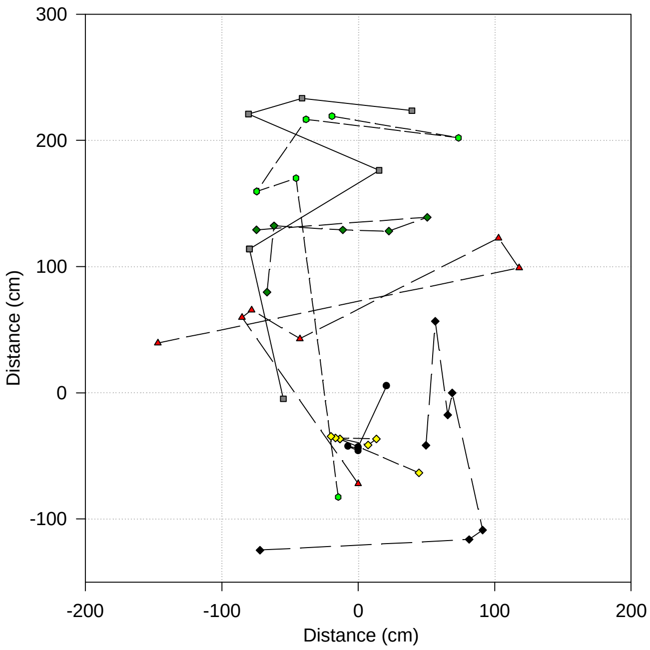


Figure 2- Movement of tagged sea urchins during the 3-month study period. Each symbol corresponds to an individual sea urchin. Position was recorded every other week.

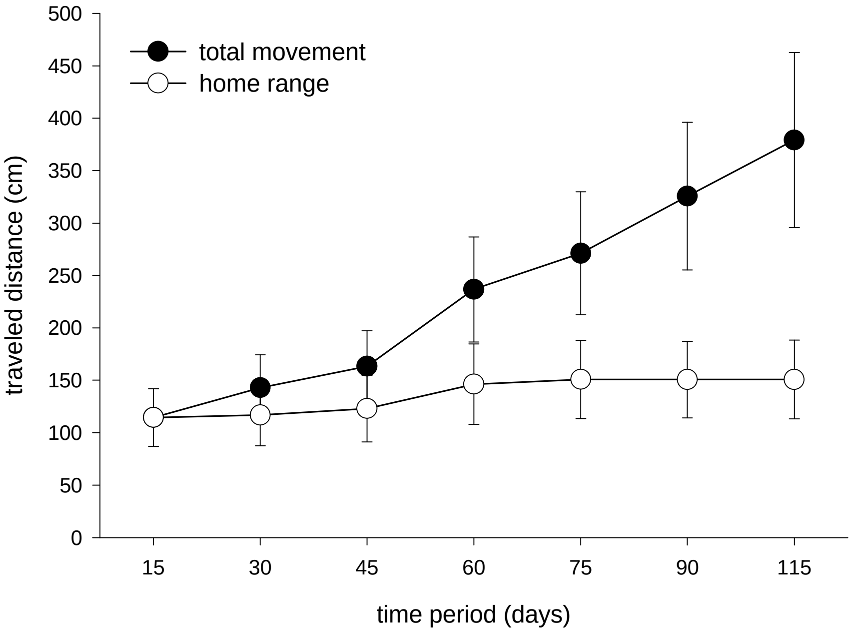


Fig. 3. Mean of total displacement and home range of tagged P. lividus *during the 3-month study experiment in the unprotected area. Bars are standard errors.*

Circadian movements

Although most sea urchins moved, only in a few cases were movements larger than 20 cm (Fig. 4). The RMANOVA test results showed that larger movements were more abundant in the unprotected area site (between subjects). Furthermore, there were significant differences between the different 4-hour periods (within subjects), indicating that movements were higher at night than during daylight (*post-hoc* SNK test). Finally, the non-significant interaction between both factors indicates that this circadian pattern is common to both the marine reserve and the unprotected area (Table 1; Fig. 5).

In the marine reserve, movement during daylight ranged between 0 and 33 cm every four hours (mean = 3.4, SD = 4.7). At night, movement was greater and ranged between 0 and 20 cm every four hours (mean = 4.7, SD = 4.6). In the unprotected area, movements ranged between 0 and 54 cm (mean = 5.0, SD = 8.6) during daylight and between 0 and 205 cm (mean = 12.8, SD = 25.9) at night.

Thus, average speed during daylight hours was 0.02 $cm \cdot min^{-1}$ and 0.05 $cm \cdot min^{-1}$ at night. Nevertheless, movement was greatly variable, and 90% of observed individuals moved less than 20 cm.

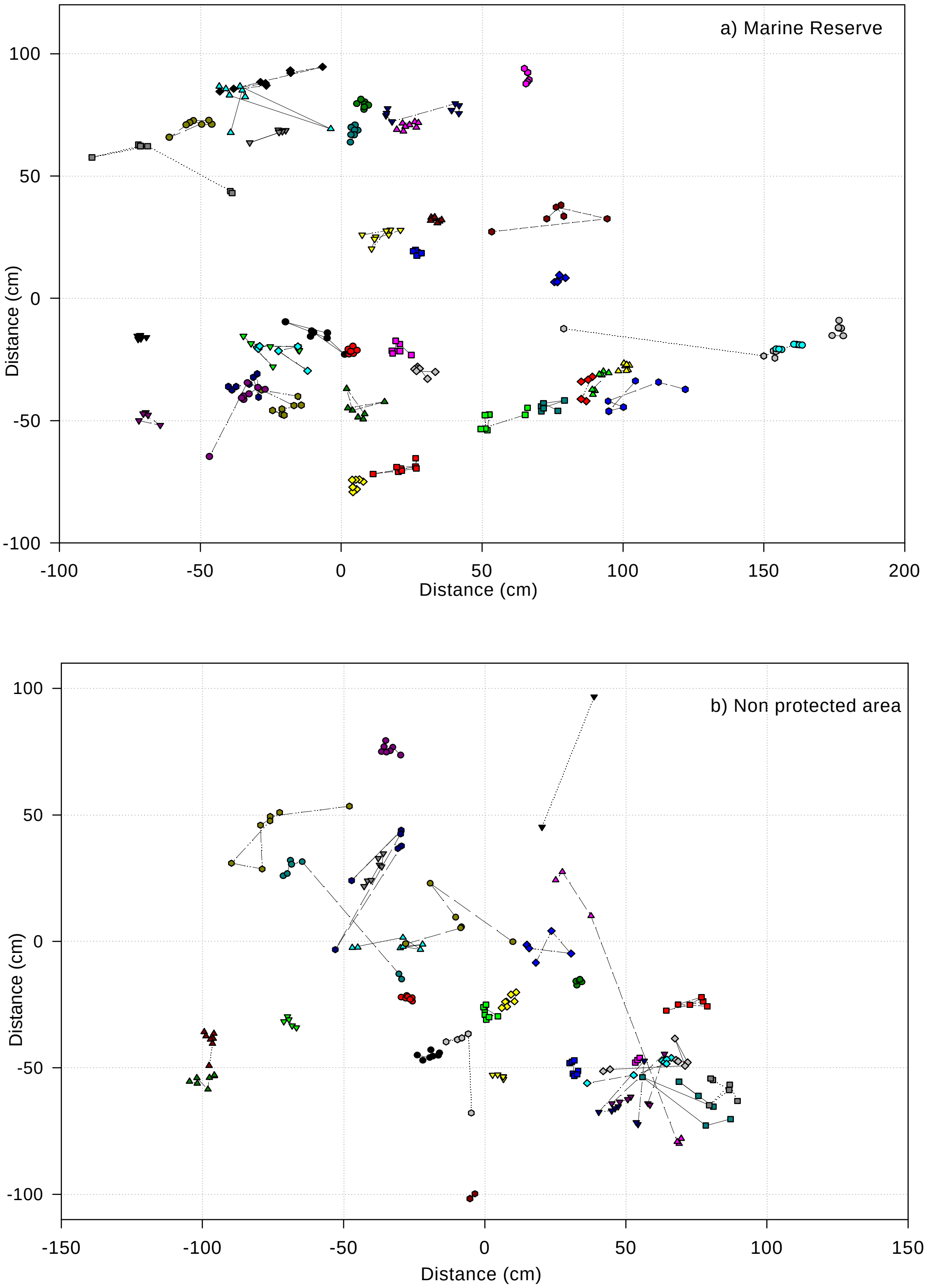


Figure 4- Movement of tagged sea urchins in the 24-hour experiment, represented on x y coordinates in a) Medes island Marine Reserve and b) unprotected area. Each symbol corresponds to an individual sea urchin position each 4 hours period. Distance was measured as cm from spatial reference point.

Table 1. Repeated Measures ANOVA performed to test for differences in travelled distances during the 4-hour periods by tagged sea urchins (time period), between the Medes Islands Marine Reserve and nearby unprotected area (protection level). Huynh-Feldt corrected probabilities (P H-F) are given for both the univariate within-subject analyses (H-F epsilon = 0.95).

between subjects effect	df	MS	F	P
protection level (P)	1	1.835	6.041	0.017
error	54	0.303		
within subjects effect	df	MS	F H-F	P H-F
time period (T)	5	0.784	7.273	<0.0001
P × T	5	0.151	1.405	0.222
error	270	0.107		

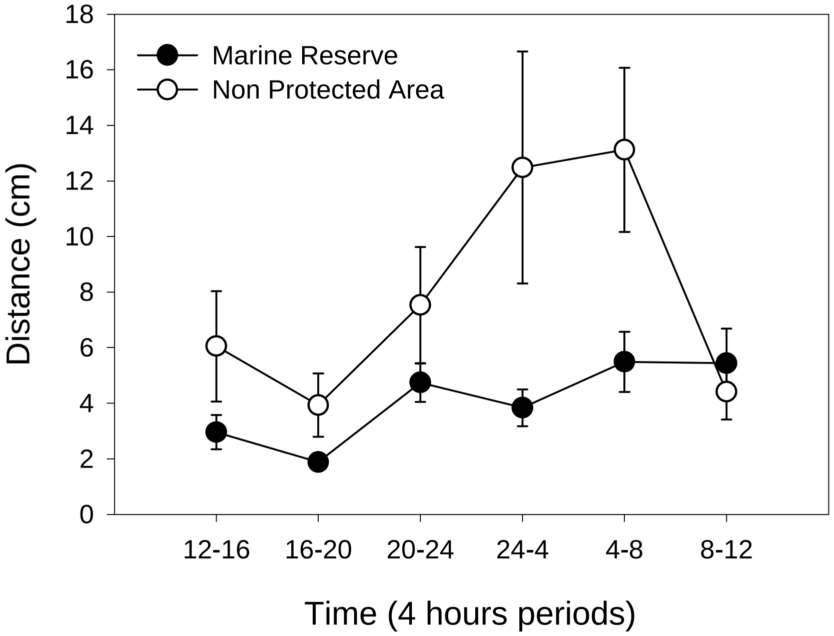


Fig. 5. Mean displacement (± SE) of tagged P. lividus *every four hours inside and outside the Medes Islands Marine Reserve during a 24-h period.*

Total movement at the end of 24 hours was significantly greater in the unprotected area than in the reserve (ANOVA: F= 5.329, P = 0.024, df = 1, 54; SNK post-hoc test), as was the home range (ANOVA: F= 5.419, P = 0.023, df = 1,54; SNK post-hoc test). The linear distance travelled in 24 hours ranged between 5.9 and 220.4 cm (mean = 51.2, SD = 51.1 cm) in the unprotected area and between 7 and 130 cm (mean = 35.9, SD = 29.9 cm) in the marine reserve. However, more than 85% of the individuals travelled less than 100 cm. At the end of the 24 hour period, the home range varied from 0 to 75.9 cm in the reserve (mean = 11.1, SD = 14.0) and from 0 to 196 cm in the unprotected area (mean = 24.9, SD = 42.6), and 80% of the individuals did not exceed 35 cm.

Discussion

On shorter temporal and spatial scales, most sea urchin species show a circadian pattern of activity; more urchins are active during the night as a defence against diurnal predators (Mattison *et al.*, 1977; Nelson & Vance, 1979; Carpenter, 1984). These adaptive shifts in sea urchin behaviour caused by the presence of predators can influence trophic interactions. The presence of predators reduces the sea urchins' diel foraging pattern (Carpenter, 1984; Nelson & Vance, 1979; Sala, 1996; Odgen *et al.*, 1973) and consequently their grazing effect on seaweeds. *Paracentrotus lividus* also had a clear circadian activity pattern, supporting previous evidence that it moves more at night (Kempf, 1962; Gamble, 1965; Dance, 1987; but see Ebling *et al.*, 1966; Kitching, 1987). This nocturnal pattern has been suggested to be escape behaviour from diurnal predators (Dance, 1987). It contrasts with the discovery in Lock Inne (Ireland) of a *P. lividus* population that shows diurnal activity to avoid nocturnal predators (Ebling *et al.*, 1966; Barnes & Crook, 2001a).

The speed values reported here are in the same range as those under natural conditions in Port-Cros, where the speed of *P. lividus* ranged between 0.02 cm·min^{-1} during daytime and 0.13 cm·min^{-1} at night, with peaks of 0.66 cm·min^{-1} (Dance, 1987). This value is lower than that obtained under laboratory conditions (Domenici *et al.*, 2003), where *P. lividus* travelled between 3.7 cm·min^{-1} and 4.6 cm·min^{-1}. Differences in laboratory and field speed experiments can reflect types of substratum and topography but may also be attributable to the difference in the temporal resolution used (Domenici *et al.*, 2003).

In this study the effect of sea urchin size, which is described as a source of variation (Domenici *et al.*, 2003), was not considered, and all experiments were performed with adult sea urchins (50–60 mm diameter). Circadian movements were measured during only one day, and possible variability due to seasonal activity, seawater conditions or other causes of variation were not taken into account.

Furthermore, in the long-term study, given the high level of mortality, tagging clearly caused some stress to individuals. Nevertheless, we accepted these possible effects in seeking a compromise between the tagging effects and the perdurability and veracity in the individuals’ identification. Further research is needed to study the sea urchins' behaviour at an individual level, incorporating more perdurable and trustworthy tagging techniques, without altering the behaviour of tagged individuals.

Paracentrotus lividus has a relatively low mobility on monthly scales. Although total displacement can be important, movement of tagged urchins was confined to a circle of 1.5 m radius or less. These values, however, reflect the minimum distance covered by sea urchins because movements over the 2-week periods were not recorded. These results are similar to those of Dance (1987), who showed that *P. lividus* had a low and random mobility in Port-Cros rocky bottoms. Furthermore, in a similar study, Palacin *et al.* (1997) demonstrated low mobility in the long term; in an eradication experiment, sea urchins recovered to less than 46% original abundance after four and a half years in the most isolated area of the experiment.

This restricted movement capacity supports the hypothesis that coordinated migratory processes are not important in determining *P. lividus* population structure and dynamics in Mediterranean rocky shores.

Nevertheless, there is no consensus about *P. lividus* migratory patterns, especially when considering other systems and geographic areas. Fernandez *et al.* (2001), in a coastal lagoon, described a *P. lividus* migration from a recruitment area, with high sea urchin densities and overgrazed facies, towards growth areas of adult populations with low densities and made up of well-developed seagrass communities.

The behavioural patterns of *P. lividus* populations in the southwest of Ireland do not, however, follow the same pattern. This population shows diurnal activity to avoid nocturnal predators, in contrast to Mediterranean populations (Barnes & Crook, 2001a). Furthermore, a significant diurnal and seasonal pattern was found for its migratory behaviour (Crook *et al.*, 2000; Barnes & Crook, 2001a, 2001 b). These authors described changes in the population structure, population size and population centres of abundance as a consequence of spatial and seasonal variations in migration to the upper surfaces of rocks (Barnes & Crook, 2001). These geographical differences in behavioural patterns highlight the need to understand all variables that may influence individual behaviours and subsequent impact on algal communities.

Random movements during a four-month period show that sea urchin effects are not confined to the small halos formed around them as suggested by some authors (Verlaque, 1984). If we consider the densities in this area (5–14 urchins$\cdot$m^{-2}) (Sala *et al.*, 1998b), and the restricted average foraging range (1.5 m radius), then all bottom surfaces are susceptible to sea urchin grazing. Accordingly, sea urchins could potentially graze all bottom surfaces within a few weeks. This movement should be sufficient to maintain algal communities with an intermediate grazing pressure, not so high as to maintain coralline barrens, but high enough to impede the growth and maintenance of long-lived species such as *Cystoseira* spp.

Sea urchin movements may be an important aspect of the fish-urchins-algae trophic cascades, in addition to other factors such as recruitment and predation (reviewed by Sala *et al.*, 1998a; Pinnegar *et al.*, 2000). Behavioural changes inducing synchronised movements in sea urchin populations are described as a response to predator pressure (Bernstein *et al.*, 1981, 1983; Hagen & Mann, 1994), food availability (Mattison *et al.*, 1977; Harrold & Reed, 1985; Andrew & Stocker, 1986; Vadas *et al.*, 1986) or a combination of both factors (Scheibling & Hamm, 1991). This can provoke outbreaks and form destructive feeding aggregations or fronts (Mann, 1977; Bernstein *et al.*, 1983). Such fronts can be important in determining the composition and dynamics of algal communities. The existence of sea urchin barrens is in itself not necessarily a cause of migration because barrens can be maintained over time by high sea urchin densities (Lang & Mann, 1976; Dayton, 1985; Keats *et al.*, 1990; Leinaas & Christie, 1996). In the study area, no extensive barrens or sea urchin fronts were observed.

The grazing range of *P. lividus* in the marine reserve, where predatory fish abundance is higher (Garcia-Rubies & Zabala, 1990), was smaller than in the adjacent unprotected area. This suggests that the presence of predatory fish mediates sea urchin behaviour by causing urchins to shelter, thus diminishing their grazing impact by an interaction that does not necessarily involve predation (Ebling *et al.*, 1966; Nelson & Vance, 1979; Carpenter, 1984; Sala, 1996). Although we do not know how sea urchins can detect the presence of predators, some authors suggest that chemical cues can provoke escape or aggregative behaviour in other species (Kats & Dill, 1998; Hagen *et al.*, 2002). These behaviourally mediated effects of predators on community dynamics (reviewed by Bruno *et al.*, 2003; Werner & Peacor, 2003) have also been shown in terrestrial (*e.g.* Beckerman *et al.*, 1997; Schmitz *et al.*, 1997) and in freshwater systems (*e.g.* Werner & Anholt, 1996; McIntosh & Townsend, 1996) but are scarce in marine communities (Trussell *et al.*, 2003; Raimondi *et al.*, 2000; Dill *et al.*, 2003).

The present results show that the effects of sea urchins on seaweeds in the presence of predatory fish are lower than in the absence of fish, and reinforce the evidence that sea urchins' escape behaviour may be an important factor in structuring algal communities (Hereu, 2004; Hereu *et al.*, 2004).

The results also increase our understanding of sea urchin dynamics and their interaction with algal communities. They indicate that migration is not an important factor affecting adult *P. lividus* populations. Thus, sea urchin population dynamics are determined mostly by other factors, such as settlement and predation mortality (Sala *et al.*, 1998b). In addition, previous results suggest an interaction between sea urchins and predatory fish, in which fish dampened the grazing pressure of sea urchins by behaviourally mediated processes (Hereu, 2004). This indicates the need to include behavioural effects in current trophic models.

Chapter 7 – Temporal variability in abundance of the sea urchin *Paracentrotus lividus* in the northwestern Mediterranean: comparison between a reserve and an unprotected area

Introduction

The abundance of sea urchins in sublittoral rocky communities is regulated by multiple synergistic factors which affect recruitment rates and mortality. Recruitment (i.e. the addition of new individuals into adult populations) is determined by larval avoidance, substrate selection by settlers and also by post-settler displacements (reviewed by Caley et al. 1996). Mortality may be caused by interspecific competition during the first post-settlement phases (Lopez et al. 1998), by predation (Duggins 1980, Tegner and Dayton 1981, Tegner and Levin 1983, McClanahan and Muthiga 1989, Sala and Zabala 1996) or by other causes such as storms or diseases (Pearse and Hynes 1979, Scheibling and Raimond 1990, Lessios 1988, Boudouresque et al. 1980).

The importance of each of these processes in determining adult sea urchin populations has been studied in many works in addition to the present one (see chapters 4, 5 and 6). Nevertheless, no studies have been carried out to elucidate the relative role of each process in natural populations.

An experimental approach to this type of study is not possible due to obvious logistical restrictions. For example, it is not possible to manipulate planktonic larvae abundance or fish densities in large enough areas. Thus, we tried to investigate the relative role of recruitment and predations in determining the structure and dynamics of sea urchin populations over a pluriannual monitoring of diverse populations under different predation pressures.

Marine Reserves provide an optimal experimental situation to study the role of fish predators in controlling sea urchin populations. Previous studies have suggested that sea urchin densities are lower within marine reserves, where fish densities are higher, than in unprotected areas (Sala et al. 1998b, McClanahan et al. 1999, Shears and Babcock 2002, 2003). Throughout this thesis and in other studies the predation rate on juvenile and adult sea urchins is shown to be higher in Marine Reserves (Chapter 5; Sala. 1997, McClanahan and Muthiga 1989). In this study we also demonstrate the high spatial and temporal variability in sea urchin settlement (Chapter 4). Therefore, to determine the relative role of predation and settlement in establishing sea urchin population structure, we need a pluriannual monitoring of a diverse population under different predation pressure.

Our study analyzed the data of a *Paracentrotus lividus* sea urchin by monitoring the Medes Island Marine Reserve and a nearby unprotected area over a 12-year period. The purpose of this monitoring was to describe the pluriannual variability in sea urchin abundances, and to determine the relative effect of the fish predation and the settlement variability in determining sea urchin population structure and dynamics.

Material and Methods

The study described here was carried out in Medes Islands Marine Reserve and in a nearby unprotected area, NW Mediterranean (Figure 1). In the Marine Reserve fishing has been prohibited since 1983 and fish densities are higher than in unprotected areas (Garcia-Rubies and Zabala 1990; this study). The study was conducted in 2 contrasted habitats: 1) fields of large limestone boulders (Tascons and Freuetó within the reserve, hereafter 'R'; Falaguer and Molinet outside the reserve, hereafter 'NR') and 2) vertical walls (Carall and Vaca, R; Punta Salines and Falaguer, NR).

Boulder habitats were colonized by a rich algal assemblage dominated by erect algae, articulated calcareous algae and small filamentous algae (Sala and Boudouresque 1997, Sala et al. 1998b). This habitat provides a high abundance of refuges (beneath boulders, crevices) where sea urchins can avoid predation. Vertical walls support algal assemblages as well as numerous suspension feeders (Ros et al. 1984). Unlike boulder habitats, vertical walls refuges for sea urchins are highly limited to small crevices and rock concavities.

Abundance and population size-structure of sea urchins were studied in situ by SCUBA diving along random transects (50 x 1 m^2 each) on sea bottoms at depths between 5 and 10 m in each study site. Transects were divided into five 10 m^2 subtransects. Within the first 20 m^2 of each transect, *Paracentrotus lividus* >1cm were counted and their diameter (test without spines) were measured with callipers. In the remaining 30 m^2, *P. lividus* were counted but not measured. Since density was lower, all individuals >1cm were counted and measured within the transects. Diameters were grouped in size classes of 1 cm, and in subtransects of 10 m^2.

In order to reduce the variability of sea urchin densities due to strong recruitment pulses (see Sala et al. 1998b) we performed a size-weight regression to analyse *P.lividus* populations in terms of biomass. We randomly took 100 individuals, including all sizes, and calculated their dry weight by drying them on a stove at 80º C for 24 hours. The resulting dry weights included the weight of the skeletons and the resulting weight function can be expressed as follows: Dry weight = $0.0013D^{2.571}$; r=0,976 n=100, where D is the diameter without spines.

Since only one sample could be taken yearly due to logistical constraints, we decided always to sample during the same season (summer) in part because *P. lividus* shows recruitment peaks at this time (Lozano et al. 1995, Sala and Zabala 1996) and thus we expected visually to find 1-year-old individuals in our transects 1 year after they settled.

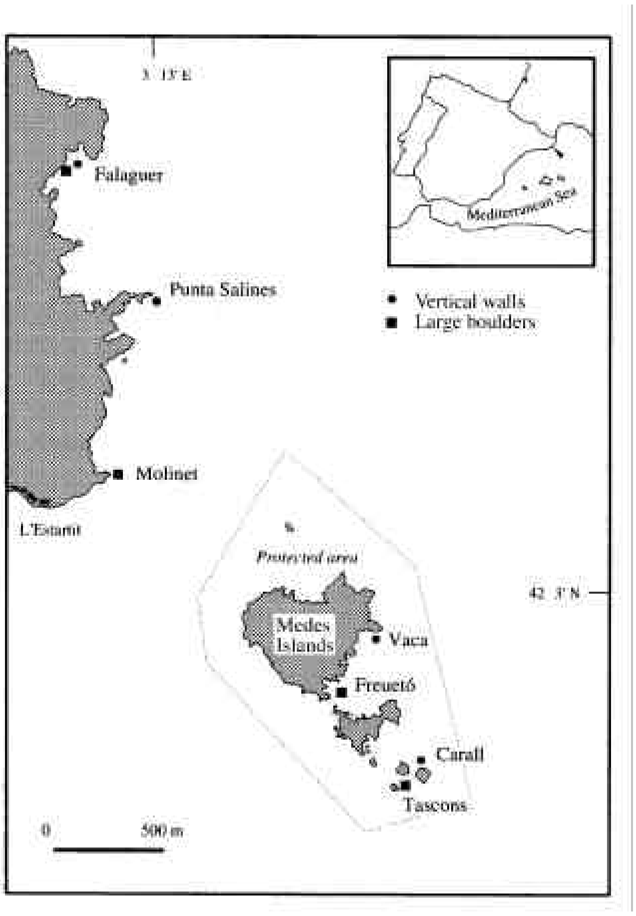


Figure 1- Location of the study sites inside (Tascons, Freuetó, Vaca and Carall) and outside (Falaguer, Molinet and Punta Salines) of the Medes Island Marine Reserve, NW Mediterranean. Dashed lines represent the limits of marine reserve where all fishing is prohibited.

This study forms part of the monitoring program of the Medes Islands Marine reserve.*P. lividus* was monitored from 1991 to 2002 in Tascons (R), Freuetó (R), Carall (R) and Punta Salines (NR) from 1992 to 1997 in Falaguer (NR) and from 1995 to 2002 in Vaca (R) and Molinet (NR).

In 1995 we decided to study the effect of the protected area (i.e. the effects of high density of predatory fish) on sea urchin populations. Thus, we added new sampling sites on the monitoring programme in order to account for spatial heterogeneity within areas. A hierarchical design (at least 2 sites within each of the areas) was needed in order to test properly any differences in density and mean size of *Paracentrotu lividus* between specimens from/in protected and unprotected areas.

In many sites studied, *P. lividus* populations showed a bimodal size class distribution, with two peaks in the smallest and the largest size classes. As is suggested, this bimodal distribution is due to the different dynamics of juveniles, which have a higher predation pressure, and adults which have reached an escape size whereby predation pressure is reduced (Tegner and Dayton 1981, Cole and Keuskamp 1998, Andrew and Choat 1982, Tegner and Levin 1983).

Thus, we can expect that the effect of protection (i.e. the higher abundance of predatory fish) will be different depending on sea urchin size. To investigate this effect, we carried out different analyses by grouping sea urchins into two size classes: from 1 to 3 cm of test diameter, and larger than 3 cm (the escape size sensu Sala 1996).

To test for temporal variability in density, mean size, and biomass within each site, 1-way ANOVAs were performed. To test for differences in density, mean size and biomass between areas (protected versus unprotected), ANOVAs were performed between 1995 and 2002, where data were available for 2 sites inside the reserve and 2 sites outside the reserve. Within this analysis, the site (random factor) was nested within the level of protection (fixed factor; protected or unprotected) in order to account for differences between areas.

The homogeneity of the variance was tested beforehand (Cochran's test) and whenever necessary, data was transformed by the function log (x+1). In the cases where data were not homogeneous after transformation we reduced the level of significance to $p>0.001$. Differences between groups were tested by post-hoc Student-Newman-Keuls (SNK) test.

In order to determine the relationship between adult *P.lidus* densities and predator fish densities we performed a regression between the number of sea urchins >2 cm and *D.sargus* biomass in sites where fish densities data were available (extracted from Garcia-Rubies 1996, Garcia-Rubies et al. 2002 and this study).

In order to estimate the mortality in the smallest size classes (which are more affected by fish predation and have a linear growth), we calculated differences in numbers between the size class of 2-3 cm and the size class of 1-2 cm of the previous years from the same site. We assumed that all individuals of the 1-2 cm size classes will cross to the 2-3 cm size class next year.

To calculate the effect of protection and topography on the mortality rate, we performed an ANOVA with the mean mortality for each site.

We also performed a correlogram with the number of recruits (1-2 cm) and the number of adults in order to determine whether recruitment pulses are transmitted through time to adult populations.

Results

Differences in *Diplodus sargus* densities inside and outside the Marine Reserve are represented with data from Garcia-Rubies and Zabala (1990), Garcia-Rubies (1996) and Garcia-Rubies et al. (2002).

D.sargus densities were calculated by random 50 x 5 m^2 transects inside and outside the reserve. The number of transects performed were 10 in 1990 (Garcia-Rubies 1996), and 8 in protected areas and 12 in unprotected areas in 1999 and 2002 (Garcia-Rubies et al. 2002).

The different locations of sites where censuses were performed in 1990 and in 1999-2002 may explain the biomass differences in protected area. Nevertheless, *D. sargus* biomass is higher in the protected area, and this difference is maintained over time (Figure 2).

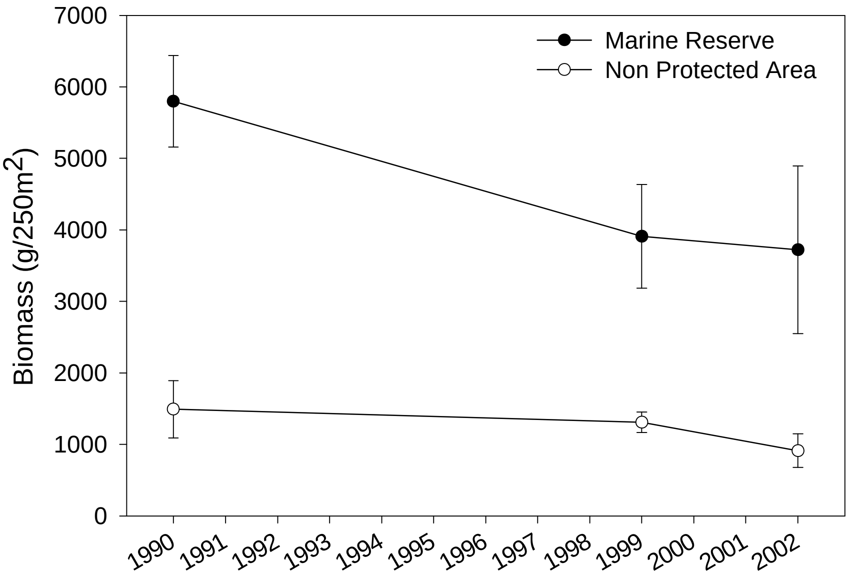


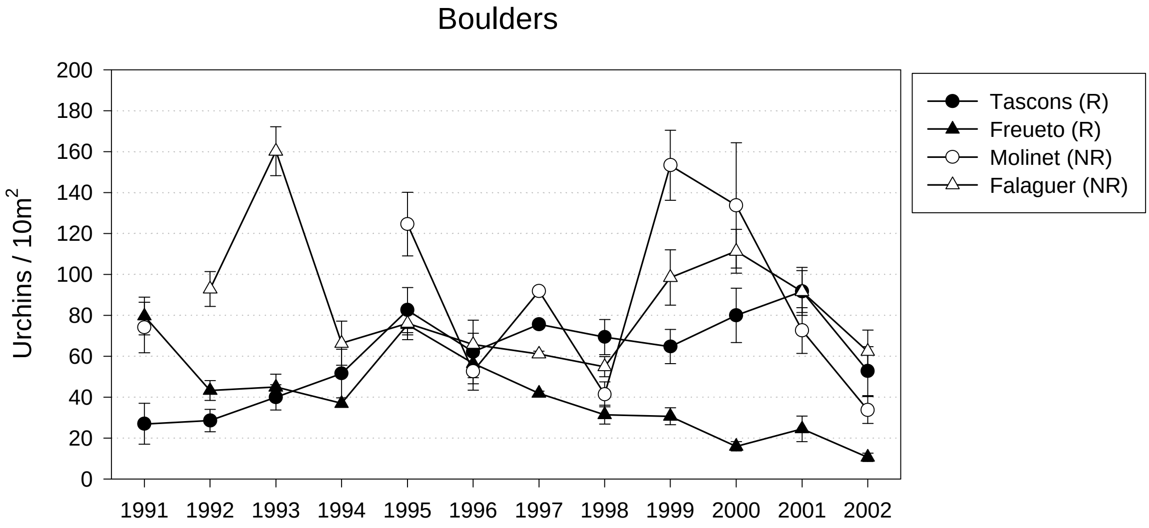
Figure 2- Diplodus sargus *biomass evolution (g/250m^2 ± SE) inside and outside the Marine Reserve over time. Full circles: protected area; empty circles: unprotected area. n=10 in 1990 and n=8 in protected area and n=12 in unprotected area in 1999 and 2002.*

Density

Densities and biomass of *Paracentrotus lividus* for all sampling dates and sites are shown in Fig. 3 and Fig. 4 respectively.

Densities on boulder-covered sea bottoms showed high variability in densities. In Tascons (R) densities steadily increased from 1991 to 1995 and was then maintained to 2002, where a slight decrease was shown ($F_{11,171}$=5.52, p<0.001; SNK test). In Freuetó, (R) density also varied significantly over time dropping by a factor of 2 from 1991 to 1992, then remaining stable until 1994, when it increased by a factor of 2. From 1995, densities showed a constant decrease to 2002, where the minimum values were reached ($F_{11,163}$=17.72, p<0.001). At Falaguer (NR), densities increased in 1993, but later decreased and were constant until 1999, when they increased until 2000, only to decrease again from 2002 ($F_{10,163}$=9.66, p<0.001). In Molinet (NR) densities were highly variable between 1995 and 1998. In 1999 they increased significantly and afterwards showed a regular decrease from 2002, when they dropped to minimum values ($F_{10,163}$=9.66, p<0.001).

On the other hand, in vertical walls, densities remained constant throughout all the years of the study in all sites.



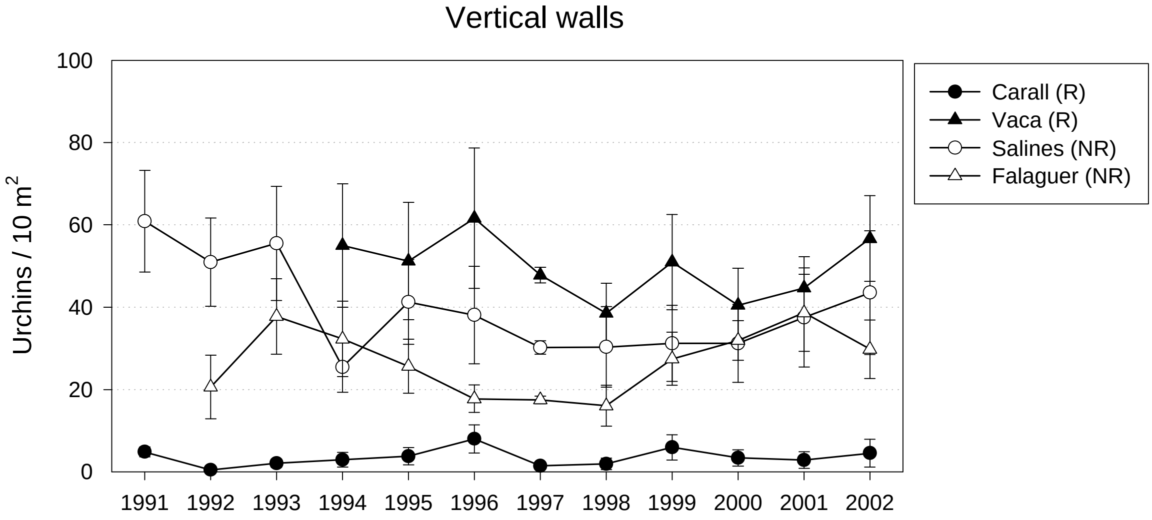


Figure 3- Number of sea urchins (>1 cm diameter) per 10 m2 (mean ± SE) at each site and in the 2 types of habitat (large boulders and vertical walls between 5 and 10 m depth) during the monitoring period (1991 to 2002). Solid symbols represent sites within Medes Islands Marine Reserve (R); open symbols represents sites in the nearby unprotected area (NR).

The higher variance observed in vertical walls relative to big boulders indicates that spatial heterogeneity at 10 m^2 scale is higher on vertical walls, i.e. *P .lividus* are more evenly distributed on big boulders than on vertical walls.

Comparison among areas of *P.lividus* densities on large boulders from 1991 to 2002 showed significant differences among sites within the area (Table 1). Mean density did not differ between the protected and the unprotected area. There was a significant variation in density over time, but temporal trends were not significantly different among areas (Table 1).

Comparison of densities on vertical walls showed differences between sites among areas, but did not show differences in time or in the level of protection (Table 1).

Table 1- Results of nested ANOVA comparing densities of Paracentrotus lividus *between Medes Islands Marine Reserve and the nearby unprotected area and over time (1995 to 2002) on a) large boulders and b) vertical walls.*

a) Boulders	**df**	**MS**	**F**	**p-level**
Year	7	0,763	2,794	**0,0483**
Reserve	1	3,884	2,074	0,2865
Site (Reserve)	2	1,873	39,65	**0,0000**
Reserve x Time	7	0,307	1,124	0,4015
Site (Reserve) x Time	14	0,273	5,782	**0,0000**
Error	442	0,047		

b) Vertical walls	**df**	**MS**	**F**	**p-level**
Year	7	0,082	2,150	0,1055
Reserve	1	1,680	0,191	0,7046
Site (Reserve)	2	8,785	93,45	**0,0000**
Reserve x Time	7	0,058	1,530	0,2358
Site (Reserve) x Time	14	0,038	0,406	0,9731
Error	448	0,094		

Biomass

Biomass showed the same pattern as densities (Figure 4): in large boulders there were significant differences between sites among areas and over time, but there were no differences between the levels of protection (Table 2). On vertical walls there were differences between sites among areas, but not over time or level of protection (Table 2).

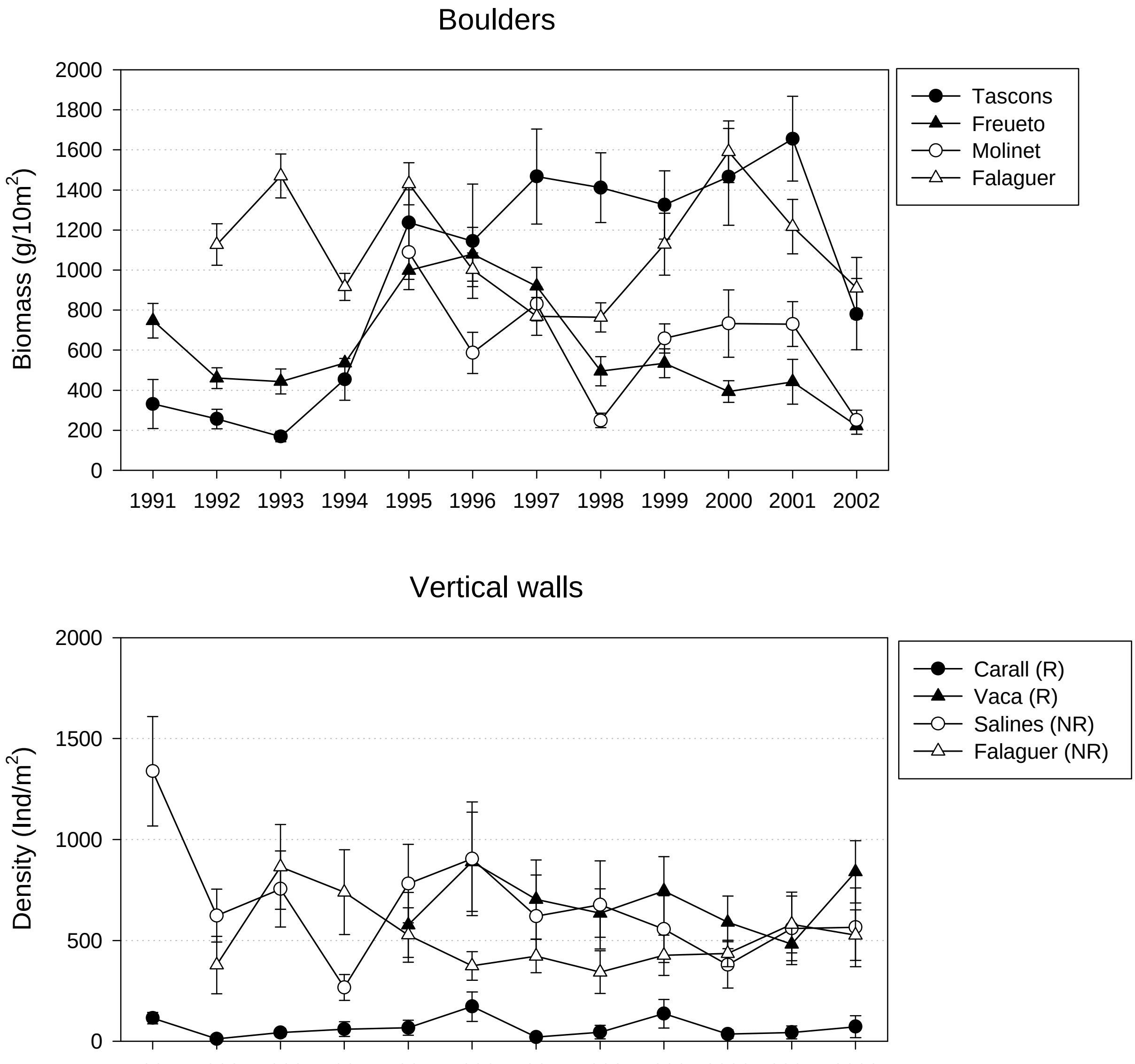


Figure 4- Biomass of sea urchins (>1 cm diameter) per 10 m2 (mean ± SE) at each site and in the 2 types of habitat (large boulders and vertical walls between 5 and 10 m depth) during the monitoring period (1991 to 2002). Solid symbols represent sites within Medes Islands Marine Reserve (R); open symbols represent sites in the nearby unprotected area (NR).

Table 2- Results of nested ANOVA comparing biomass of Paracentrotus lividus *between Medes Islands Marine Reserve and the nearby unprotected area and over time (1995 to 2002) on a) large boulders and b) vertical walls.*

a) Boulders	**df**	**MS**	**F**	**p-level**
Year	7	1,974	2,450	**0,0728**
Reserve	1	0,048	0,010	0,9302
Site (Reserve)	2	4,909	140,051	**0,0000**
Reserve x Time	7	0,394	0,488	0,8277
Site (Reserve) x Time	14	0,806	6,574	**0,0000**
Error	442	0,123		

b) Vertical walls	**df**	**MS**	**F**	**p-level**
Year	7	0,450	0,739	0,6440
Reserve	1	70,08	0,826	0,4593
Site (Reserve)	2	84,80	129,207	**0,0000**
Reserve x Time	7	0,599	0,982	0,4812
Site (Reserve) x Time	14	0,610	0,929	0,5273
Error	448	0,656		

Fish and Urchin relationship

Diplodus sargus biomass showed no significant correlation with adult sea urchins biomass (Pearson r^2=0.36; p=0.12; Fig. 5) or with the whole population biomass including recruits (Pearson r^2=0. 23; p=0.84).

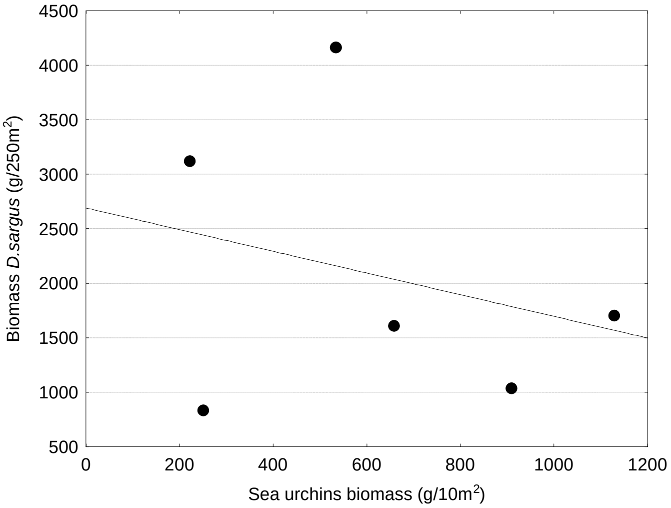


Figure 5- Relationship between adult sea urchins biomass (>2 cm test diameter) and Diplodus sargus *biomass in different transects carried out in Medes Islands Marine Reserve (n= 2) and nearby unprotected area (n= 4).*

Size structure frequency

At Tascons (R), mean size of *Paracentrotus lividus* varied significantly over time ($F_{11,6860}$=45,38; p<0,000). Recruitment episodes occurred in 1992 and 1993 and greatly influenced the size distribution at Tascons (R) (Fig.6). The size frequency distribution graphs illustrate a high frequency of recruits, which provokes a decrease in mean size. After 1994, however, the distribution was bimodal, with a second mode of urchins between 4 and 6 cm in diameter. This second mode of large sea urchins after 1994 was more conspicuous due to a lower recruitment rate during these years.

The analysis of biomass showed a pronounced increment over 1994 ($F_{11,171}$=19.50; p<0.000) probably due to the effect of the/a recruitment peak which occurred in the previous years. These high biomasses are then maintained, probably due to the 1993 cohort, until 2002, when a slight decrease is seen (Fig. 4).

At Freuetó (R) mean size also varied significantly over time ($F_{11,5749}$=27.19; p<0.001). High recruitment rates in 1992 and 1993 produced a size-distribution with a very conspicuous mode of small sea urchins (Fig. 6). However, as recruitment declined after 1993, the size distribution was markedly bimodal, increasing mean size and biomass. After 1997, mean size increased, due probably to the progressive decrease in densities, also provoking a decrease of biomass $F_{11,163}$=11.02; p<0.001) (Fig.4).

The Molinet (NR) population is characterized by high recruitment episodes which provoke a high variability in densities and mean size ($F_{7,7410}$=36.60; p<0.000). Size frequency distribution showed recruitment peaks in 1995, 1999 and 2000 and this changed a bimodal distribution to a unimodal one (Fig. 6). In 2001 and 2002, there were no important recruitment episodes and size frequency distribution became bimodal again. Biomass was also affected by recruitment episodes, increasing when high recruitment peaks occurred ($F_{7,112}$=36.60; p<0.001) (Fig.4).

Falaguer (NR) showed a pulse of recruits in 1992 and 1993 which provoked a decrease in mean size ($F_{10,8407}$=54.07; p<0,000) (Fig.6). After 1993 mean size increase and size frequency distribution became bimodal, with an important peak at 4-6 cm. Biomass evolution was also determined by these recruitment peaks: after 1992 and 1993 they decrease progressively, and after 1998 they increase again ($F_{10,163}$=5.53; p<0.001) (Fig.4).

In vertical walls sea urchin populations were more stable, but also showed some recruitment episodes.

At Carall, *Paracentrotus lividus* size frequency distribution was bimodal, and mean size did not vary significantly from 1995 to 2000 when there was an important recruitment episode that provoked a significant decrease in mean size ($F_{10.509}$=5.13; p<.0000) and changed the size frequency distribution into unimodal. In 2001 and 2002, sea urchin populations showed the same pattern as that prior to 2000 (Fig. 7). There was even a conspicuous recruitment peak, although there were no significant differences in biomass over time ($F_{10,154}$=1,34; p=0.21) (Fig.4), probably due to the low sea urchin density.

At Vaca (R) two settlement peaks occurred in 1995 and in 2001 which provoked a decrease in mean size ($F_{7,4872}$=9.21; p<0.001) and an increase of the smallest size classes in the size frequency distribution (Fig. 7). These recruitment peaks do not have any effect on biomass, which showed no differences over time ($F_{8,116}$=1.80; p=0.082) (Fig 4).

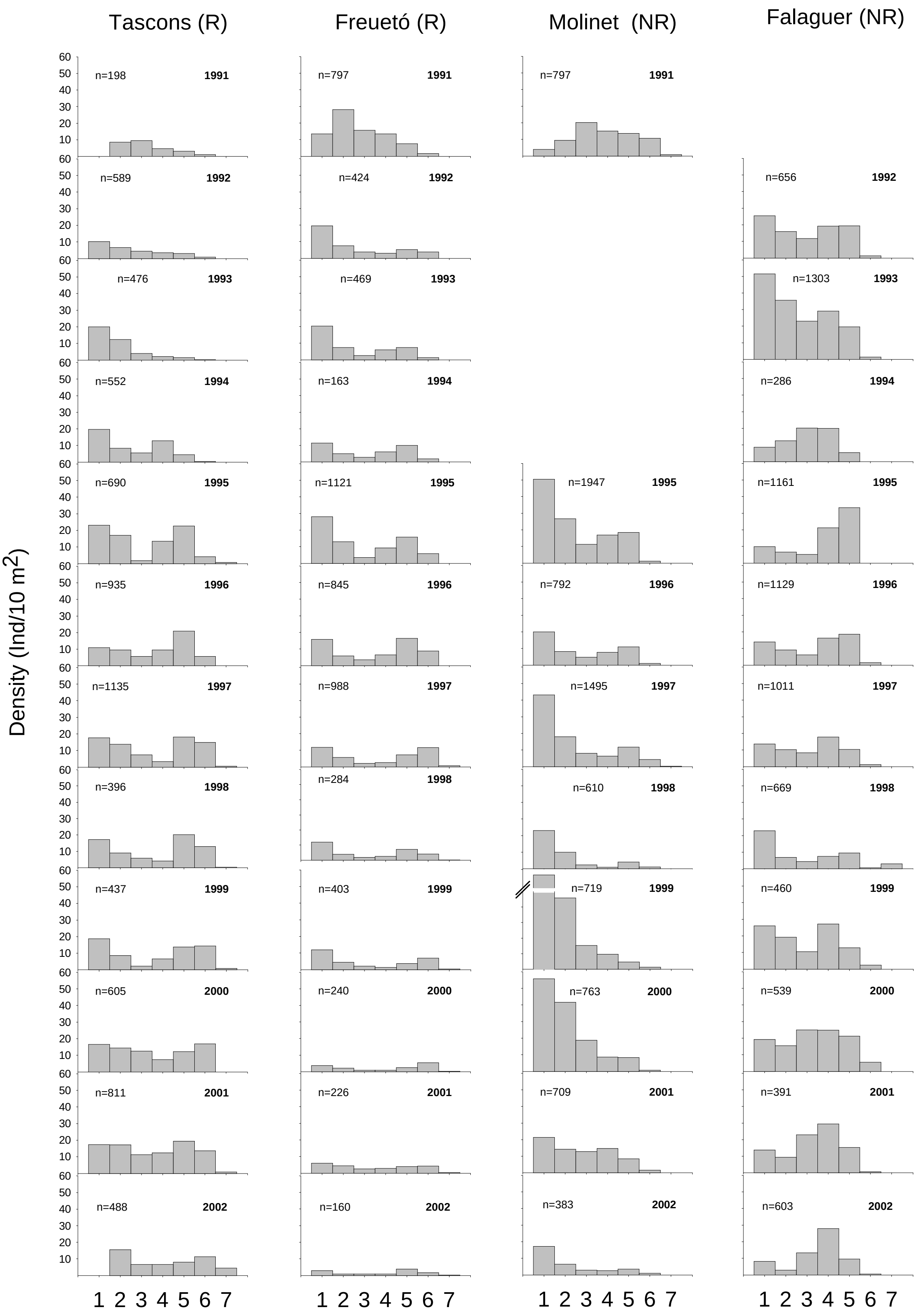


Figure 6- Paracentrotus lividus *(>1cm) density of each test size from 1991 to 2002 on large boulders (between 5 and 10 m depth) within (Tascons and Freuetó) and outside (Molinet and Falaguer) the Medes Islands Marine Reserve. Size classes: 1 = 1-1.9 cm, 2 = 2-2.9 cm, 3 = 3-3.9 cm, 4 = 4-4.9 cm, 5 = 5-5.9 cm, 6 = 6-6.9 cm, 7 = 7-7.9 cm.*

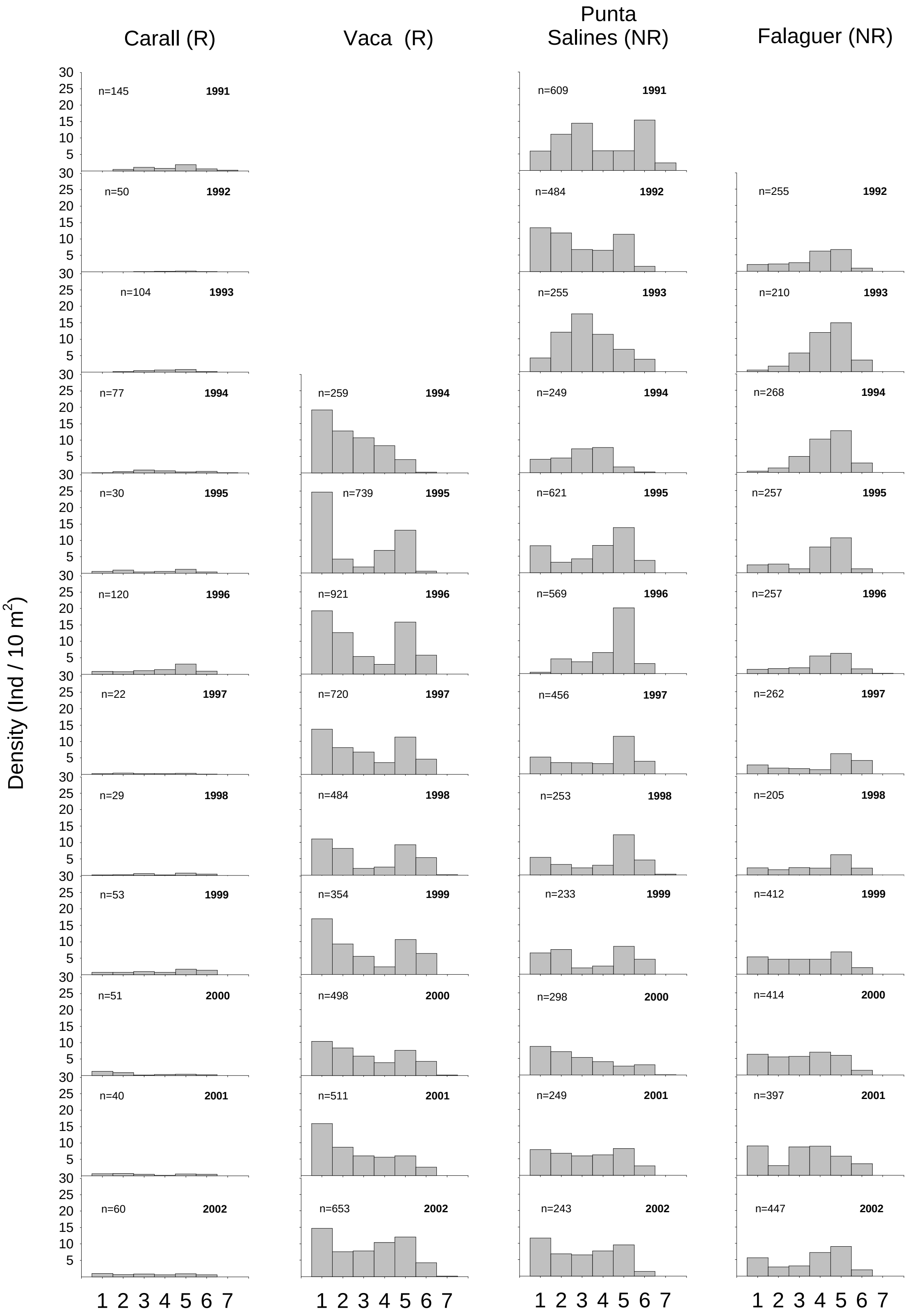


Figure 7- Paracentrotus lividus *(>1cm) density of each test size from 1991 to 2002 on vertical walls (between 5 and 10 m depth) within (Tascons and Freuetó) and outside (Molinet and Falaguer) the Medes Islands Marine Reserve. Size classes: 1 = 1-1.9 cm, 2 = 2-2.9 cm, 3 = 3-3.9 cm, 4 = 4-4.9 cm, 5 = 5-5.9 cm, 6 = 6-6.9 cm, 7 = 7-7.9 cm.*

In Punta Salines (NR) mean sizes also changed due to recruitment peak ($F_{11,4507}$=35,30; p<0,000). In 1991 the size frequency distribution was bimodal, but in 1992 and 1994 there were important recruitment episodes which changed this distribution and decreased mean sizes (Fig 7). After 1995 the size frequency distribution remains bimodal with an important peak in the largest sizes and an increase in mean size. In 2000, there occurred an important recruitment episode that provoked other changes in size frequency distribution and decreases in mean size, that increase putatively in 2001 and 2002. There was no difference in the biomass over time ($F_{11,156}$=1,72; p=0.071) (Fig.4).

At Falaguer the *Paracentrotus lividus* sizes frequency distribution remains stable over time, with an important peak in the largest size classes. In 1999 and in 2000 there occurred two episodes of recruitment which decreased mean sizes ($F_{10,3553}$=24.47; p<0.000) until 2991 and 2002 when the recruits peak decrease, and increase the proportion of largest sizes (Fig.7). There was no difference in biomass over the study period ($F_{10,\ 147}$=1.49; p=0.15) (Fig.4).

Comparison of mean size of *Paracentrotus lividus* on large boulders showed significant differences over time and among sites within areas (Table 2), but also between protected and unprotected areas, where were larger (Table 3). On vertical walls the comparison of *P. lividus mean* sizes showed significant differences over time, and also between protected and unprotected areas, but not between sites within areas (Table 3).

Table 3- Results of nested ANOVA comparing mean size of Paracentrotus lividus *between Medes Islands Marine Reserve and the nearby unprotected area and over time (1995 to 2002) on a) large boulders and b) vertical walls.*

a) Boulders	**Df**	**MS**	**F**	**p-level**
Year	7	0,982	2,335	0,0838
Reserve	1	15,29	0,797	0,4661
Site (Reserve)	2	19,18	520,424	**0,0000**
Reserve x Time	7	1,347	3,204	**0,0303**
Site (Reserve) x Time	14	0,420	11,403	**0,0000**

Error	22754	0,037

b) Vertical walls	**Df**	**MS**	**F**	**p-level**
Year	7	0,802	4,411	**0,0088**
Reserve	1	1,752	2,177	0,2781
Site (Reserve)	2	0,805	22,289	**0,0000**
Reserve x Time	7	0,198	1,086	0,4216
Site (Reserve) x Time	14	0,182	5,037	**0,0000**
Error	10837	0,036		

The effect of protection on juvenile Paracentrotus lividus

The densities of juvenile (<2cm diameter) sea urchins is shown in Figure 8. In general, pattern densities in sites within the reserve are more stable than outside. In Tascons (R), juvenile densities in 1991 is the lowest, but increased after 1992 and remained stable, with some oscillations in 1993-95 and in 2000-2001 ($F_{11,171}$=8.28, p<0.001). In Freuetó (R), juvenile densities in 1991 were maximal, and showed a gradual decrease, except in 1995, since the lowest values occurred in 2002 ($F_{11,163}$=25.76, p<0.001).

However, in Molinet (NR) juvenile densities were more unstable, with marked peaks in 1995, 1997 and 2000-2001 followed by striking decreases ($F_{7,112}$=11.64, p<0.001). Falaguer (NR) also showed important variability, with important peaks in 1993 and in 1999, followed by striking decreases which correspond to low recruitment periods ($F_{10,163}$=27.31, p<0.001).

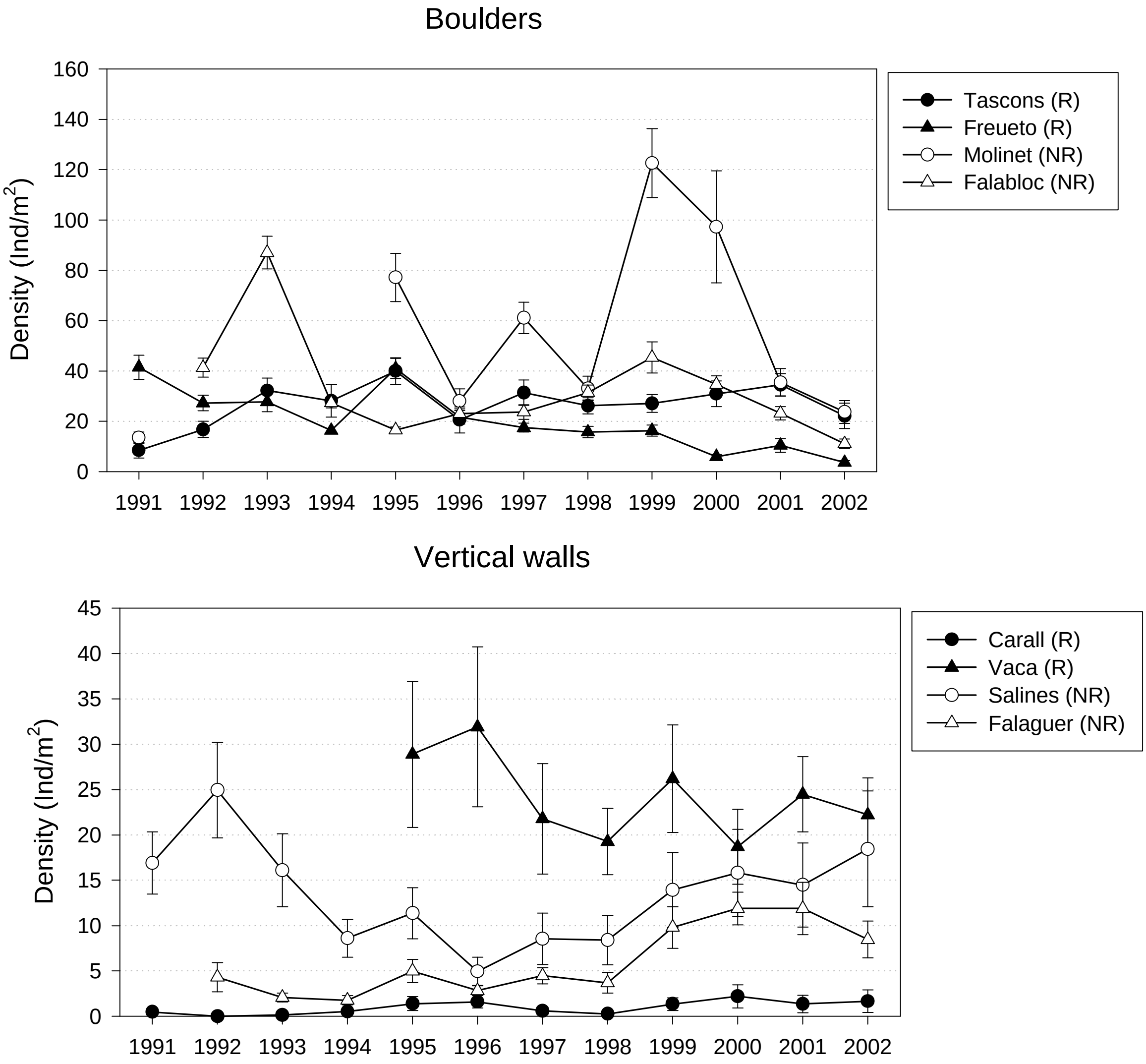


Figure 8- Juvenile (<2 cm test diameter) densities per 10 m2 (mean ± SE) at each site and in the 2 types of habitat (large boulders and vertical walls between 5 and 10 m depth) during the monitoring period (1991 to 2002). Solid symbols represent sites within Medes Islands Marine Reserve (R); open symbols represent sites in the nearby unprotected area (NR).

The effect of protection on recruitment

The effect of protection did not show significant differences on recruitment rates (Figure 4). In large boulders, recruitment showed significant differences between sites within areas, and over time, but did not show differences between the protection levels. In vertical walls the analysis showed a significant interaction between time and the level of protection since in the unprotected area the oscillations were more conspicuous than in the protected area, and showed an increment in the most recent years (Table 4).

Table 4- Results of nested ANOVA comparing juvenile Paracentrotus lividus *(<2 cm diameter) between Medes Islands Marine Reserve and the nearby unprotected area and over time (1995 to 2002) on a) large boulders and b) vertical walls.*

a) Boulders	**Df**	**MS**	**F**	**p-level**
Year	7	1,47	2,55	0,0649
Reserve	1	7,39	2,02	0,2913
Site (Reserve)	2	3,66	55,56	**0,0000**
Reserve x Time	7	0,47	0,82	0,5832
Site (Reserve) x Time	14	0,58	8,74	**0,0000**
Error	442	0,07		

b) Vertical walls	**Df**	**MS**	**F**	**p-level**
Year	7	0,56	3,90	**0,0145**
Reserve	1	0,28	0,01	0,9230
Site (Reserve)	2	23,27	161,76	**0,0000**
Reserve x Time	7	0,54	3,75	**0,0169**
Site (Reserve) x Time	14	0,14	1,00	0,4521
Error	448	0,14		

Relationship between juveniles and adult sea urchins

We did not find any relationship between *Paracentrotus lividus* juvenile (<2 cm diameter) and the adult populations on any site and year except in Vaca (R), where there was a significant correlation in all years. The lag of a clear correlation pattern in the recruits and the density of adult populations over time indicate that the settlement episodes are not transmitted into adult populations.

Table 5- Results of the correlogram between Paracentrotus lividus *juvenile (<2 cm diameter) densities and the adult populations on each site. Correlation indices are calculated for 3 to 4 consecutive years (lags).*

Localitat	**R^2**	**Lags**	**R**	**S.d.**	**t(3)**	**p**
Tascons	0.944	0	1,684	1,520	1,108	0,349
		1	-0,481	1,946	-0,247	0,821
		2	2,303	1,924	1,197	0,317
		3	-0,183	1,874	-0,098	0,928
		4	1,005	1,304	0,771	0,497
Freueto	0.9806	0	1,678	0,514	3,266	0,047
		1	0,786	0,463	1,696	0,188
		2	-1,021	0,656	-1,556	0,218
		3	-0,293	0,426	-0,689	0,540
		4	0,983	0,423	2,325	0,103
Vaca	0.987	0	-0,319	0,080	-3,984	0,058
		1	-0,646	0,096	-6,760	0,021
		2	-0,399	0,091	-4,393	0,048
		3	3,691	0,310	11,894	0,007
Carall	0.876	0	6,565	3,148	2,086	0,128
		1	5,249	4,387	1,197	0,317
		2	-10,049	5,292	-1,899	0,154
		3	14,955	6,599	2,266	0,108
		4	-14,606	6,139	-2,379	0,098
Molinet	0.413	0	-0,057	0,168	-0,337	0,758
		1	0,061	0,161	0,377	0,731
		2	0,142	0,144	0,983	0,398
Falaguer Boulders	0.98	0	-0,874	0,349	-2,508	0,129
		1	1,930	1,597	1,208	0,350
		2	1,425	2,901	0,491	0,672
		3	0,172	1,860	0,093	0,935
		4	0,271	0,366	0,741	0,536
Falaguer Vertical wall	0.7948	0	-0,445	3,126	-0,142	0,900
		1	5,353	5,162	1,037	0,409
		2	2,193	5,347	0,410	0,721
		3	-3,689	7,668	-0,481	0,678
		4	-1,301	7,932	-0,164	0,885
Salines	0.974	0	-1,697	3,738	-0,454	0,681
		1	0,003	1,748	0,002	0,999
		2	1,814	3,860	0,470	0,670
		3	2,760	1,724	1,601	0,208
		4	3,012	2,129	1,415	0,252

Post-settlement mortality

Mortality rates during the first years did not show differences between the *Paracentrotus lividus* populations inside and outside the reserve. On the other hand, mortality showed significant differences between large boulders and vertical walls, where mortality in vertical walls was higher (Table 6).

Mortality rate did not show a significant correlation with the adult *Paracentrotus lividus* biomass in the same year.

Table 6- Results of ANOVA comparing the mean of the Paracentrotus lividus *mortality rate (between size classes 1-2 cm and 2-3 cm) between Medes Islands Marine Reserve and the unprotected area and large boulders and vertical walls.*

	df	**MS**	**F**	**p-level**
Rugosity	1	277765,25	7,29	0,0087
Reserve	1	3749,99	0,10	0,7547
Reserve x Rugosity	1	3612,70	0,09	0,7591
Error	71	38110,12		

Discussion

The existing models of relations between fish, sea-urchins and algae (McClanahan and Shafir 1990, McClanahan and Sala 1997) predict that, via cascade effects, the consequences of fishing or of Marine Protected Area (MPA) protection can be transmitted through lower trophic levels even to algae communities. According to the models, we should expect that in the Medes Islands an MPA where fishing is prohibited and the density of fish is very high will result in a very low density of sea-urchins due to the pressure of fish predation.

This predation effect would also cause the average size of the sea-urchin populations outside the MPA—where the main predator is humankind, in its selection of the largest sizes—to be smaller than inside the MPA—where the predators are fish—because fish predation is focused mainly on the small sizes. But in reality, this does not occur because there are other factors apart from predation that affect the regulation of sea-urchin populations (Sala et al. 1998).

The image, which provides us with the whole time series regarding the role played by protection measures (MPA versus no MPA contrast), is confused, mainly due to the strong variability of the series.

What could explain this variability in the density and structure of sea-urchin population sizes? Ruling out the existence of migratory displacements (the results of Chapter 5 induce us to think that displacements are of little importance), it seems that what bears very great weight in the variability is the variations in recruitment: all of the changes that have been produced in the sea-urchin populations over the course of the years have been produced by high recruitment. To the extent that this series allows affirmation of this observation, it seems that the probability of the occurrence of strong recruit settlement episodes is equal inside and outside of the MPA. Thus, we saw differences in the effect produced: outside the MPA, the alterations caused by the arrival of recruits are strongly marked while, on the other hand, inside the MPA these peaks due to recruitment are more gradual. It would appear that inside the MPA the peak of small sizes that would follow a year of good recruitment is regulated by the pressure of fish predation whereas, thanks to having reached the so-called refuge size (a diameter of 3 cm; Sala and Zabala 1996), predation is much diminished on the size classes that progressively accumulate and contribute to the characteristic bimodal pattern. If this is confirmed, this difference would seem to suggest that while the largest biomass of MPA fishes is unable fully to counteract the destabilizing effects of the massive arrival of larvae, it still produces a certain regulating effect by making the oscillations deriving from this arrival less disruptive.

Topography

The only factor that seems to establish a persistent pattern in the temporal behavior of sea-urchins is topography. The difference between rocky bottoms (high density, small average size) and the vertical walls (lower density, larger average size) did not vary during any year, thus showing great stability.

The absence of refuges in the vertical walls could be the cause of high sea-urchin mortality, above all in the first phases, where we have seen that there is density dependency: the availability of refuges limits the adult populations. On the other hand, in rocky bottoms, where the availability of refuges is very high, mortality in the first phases is density independent, indicating that the abundance of adults is not limited by other factors.

Validity of the Mc Clanahan and Sala model

After ten years of monitoring populations of sea-urchins exposed to what is unquestionably the highest imaginable biomass (measured by density and by size) of fish predators in the Mediterranean (Garcia-Rubies and Zabala 1990), it seems proven beyond doubt that the recovery of the fish populations inside the MPAs is unable to revert to the conditions of high sea-urchin density that led to the situations of overgrazing of algae populations once the latter have become established. As this is a question of one of the predictions of greatest weight in the McClanahan and Sala model (1997) and constitutes a key factor in the hopes placed on the MPAs as tools of littoral management, one negative conclusion of our results could in fact hold great relevance.

While there is a certain lack of connection between the model’s predictions and our results, in terms of the interactions between the pressure due to fishing, fish, and sea-urchins, it is a lack of connection that can be explained if we accept the existence of some key factors in the demographic dynamics of the sea-urchin populations which the model itself does not consider (Sala et al. 1998a).

First, there is the fundamental role played by reruitment. Owing to factors beyond our control, and which will probably not be understood for some time because they depend on the “aleatory” factors of the planktonic phase, recruitment is highly variable both in time and space. The result is that, in any given year and in a concrete place, there may be a massive arrival of recruits that completely changes the population structure of that place. The results of the experiments in Chapter 3 have shown that there is a great variability, both spatially (on scales of dozens of metres) and temporally (from one year to the next), thus ruling out any model that considers the settlement patterns of the populations of the Medes Islands and those of the littoral to be different.

But in addition to the differences in recruitment, we see that the availability of refuges can drastically affect the regulating efficiency of predation (Sala 1996, Sala et al. 1998b). The clearest indirect evidence of what we are saying can be found in the effect of topography on the structure of the populations studied. The only plausible explanation for the differences observed is that in heterogeneous boulders rocky bottom, with high availability of refuges, sea-urchins can take shelter from their predators and sea-urchin mortality due to predation is far lower than in vertical walls devoid of refuges.

If we add these two factors (recruitment + refuges), we see how, in the event of a period of high recruitment in a boulders rocky bottom (an exemplary case would be the Tascons station), the whole high density of large fish in the MPA would be unable to control the demographic explosion of sea-urchin populations that would follow such recruitment.

There is, moreover, an effect of scales which would help to explain the unfulfilled predictions of the Medes Islands MPA model in spite of its possible conceptual correctness. The entire MPA comprises no more than a few hectares within many square kilometres of rocky sea bottom occupied by dense sea-urchin populations. Given the long planktonic life of sea-urchin larvae (Escoubert 1977) and the capacity for passive dispersion made possible by the coastal currents, it becomes inevitable to consider the population of the Medes Islands as a very small part of a metapopulation which maintains a very highly active demographic interchange flow. From this perspective, even if the fish were capable of greatly depressing the reproductive subpopulation of the MPA, they would never come to introduce a regulating effect on recruitment, which would continue to be nourished by external subpopulations that are, obviously, independent of the predation.

Chapter 8- Effects of removing sea urchins (*Paracentrotus lividus*): stability of barren states and *Cystoseira balearica* forest recover in NW Mediterranean

Introduction

In other parts of this thesis we have already seen how the sea urchin *P. lividus* plays a key role in the structure of rocky infralittoral communities. The interaction between sea urchin biomass and algal cover is intense (see chapter on grazing by herbivores) and may lead to a transition between two extreme and characteristic situations: algal ‘forests’ if sea urchins are uncommon, or barrens whenever sea urchin biomass is very high and algal biomass is minimal (see, for example, Verlaque 1987, Sala 1996). This interaction may have enormous repercussions on the conservation of benthic biodiversity, since barren communities are very species-impoverished when compared to well-developed algal forests (Verlaque 1987, Graham 2004). Some authors described a hundred-fold loss at least in plant and animals species (Vukovic 1982, Verlaque 1987; Ballesteros unpublished data). Thus, purely in terms of its overwhelming effects and its spatial magnitude, the destruction wrought on benthic ecosystems by the proliferation of barrens could be compared to the devastating effect of forest fires and desertification on biodiversity in terrestrial Mediterranean ecosystems. Over the last few decades a systematic advance in barren areas has been detected in almost all the seas in the world (Breen et al. 1982, Berstein et al. 1981, Chapman 1981, Ayling 1981, Lawrence 1975, Mann 1977, Paine and Vadas 1969, Watanabe and Harrold 1991, Duggins 1980, Estes et al. 1998) and the Mediterranean is no exception (Gros 1978, Augier and Boudouresque 1967, 1970a,b 1976, Mastaller 1974, Zavodnik 1977, Torunsky 1979, Verlaque 1987). Practically the whole coastline of all the countries on the shores of the Mediterranean Basin have been affected by the appearance of barrens measuring from hundreds of metres to tens of kilometres across (obs. pers.).

Evidence exists that the progressive spread of barrens could have been indirectly favoured by human activity. The eutrophication of coastal waters may lead to greater larval survival rates (Fénaux et al. 1994, Lopez et al. 1998) and to metabolic surpluses, which can then be invested by adults in higher gonadal effort (Semaud and Kada 1987, Meidel and Scheibling 1999, Guetaff et al. 2000, Lozano et al. 1995). One very evident reason is the overfishing of the fish that prey on and thus control sea urchin populations (see chapter 4; Sala and Zabala 1996). Ecological trophic models explain in a generic way the relationship between overfishing and the appearance of barrens as a result of the cascade effect (see introductory chapter). However, here we must take into account a model developed especially for describing the relationship between fishing intensity, fish populations, *P. lividus* populations and the development of algal communities in the Mediterranean (McClanahan and Sala 1997; see the introduction and the many references scattered throughout this paper). This model suggests that marine reserves, which benefit previously overexploited fish populations, may be an efficient management tool in any attempt at halting the spread of barrens in mature algal communities. Nevertheless, barrens do exist in marine reserves.

The appearance of barrens in marine reserves may be caused by a number of factors such as exceptional recruitment pulses (chapter 3; Watanabe and Harrold 1991, Sala et al. 1998b). The availability of crevices favours sea urchin survival, which, once they have reached a certain size (Sala 1996, Sala and Zabala 1997), can move in and out of crevices to graze at will, regardless of the density of predator fish. In these cases the eradication of adult sea urchins could be a useful mechanism for controlling the spread of barrens. The efficiency of any eradication programme can be tested by experimental manipulation such as has been carried out in other areas of the world (Leinass and Christie 1996, Breen and Mann 1976, Duggins 1980, Chapman 1981, Himmelman et al. 1983, Keats et al. 1990).

The specific objectives of this work are as follows:

1- Investigate the existence and extent of barrens in one area of the Medes Islands Marine Reserve.

2- Confirm by means of correlative and experimental evidence (eradications) that the sea urchins that govern the dynamics of these barrens belong to the species *P. lividus*.

3- Estimate the persistence of barrens on a pluri-annual scale and evaluate the continuous or discrete nature of transitions from one state to another. In essence, this task consists of trying to define the level of sea urchin biomass that corresponds to the threshold between the two states.

4- Test on a pluri-annual scale the effects of eradication experiments on algal cover.

Material and methods

The success of our experiment depended on three factors conditions (see below) and so it was only feasible to conduct our research in marine spaces that fulfilled these conditions.

1- Firstly, the definition of the term “barren” is difficult if the algal cover is not permanent and has a marked seasonal component (see chapter on grazing), as often occurs in the Mediterranean. In these situations, the size of the barren patch can only be measured easily during phases of algal proliferation. To get around this problem, we chose to work with communities dominated by perennial algae or by algae that retain their biomass throughout a significant part of their annual cycle. In the Mediterranean, communities dominated by species belonging to the genus *Cystoseira* offer the best conditions for a study of this nature.

2- Secondly, the ability of algae to recolonise barrens is determined by their dispersal capacities and the availability of propagules. Although there is a notable lack of information on these questions, there are indications that the dispersal capacities of the most persistent species of algae (such as the *Cystoseira* species mentioned above) are limited to between 10^1 and 10^2 m. This means that if for historical reasons (for example, centuries of overfishing) barrens have developed far away from the nearest source of “progenitors”, recolonisation will not occur spontaneously even if all the other conditions needed for a reversal of the trend towards increased barrenness are fulfilled.

3- We must also guarantee that overfishing has ceased and that fish populations have really recovered. This is not the case in all Mediterranean marine reserves (Garcia-Charton 1999), be it because they have only been created recently, or because a lack of effective vigilance means that they are, in practice, only ‘paper reserves’ (Bohnsack 1993).

As a result of these three factors we were happy to accept the offer to work in Scandola, a marine reserve (western Corsica) that fulfilled all the criteria we needed.

1- The Scandola marine reserve is located on the western-most point of the island of Corsica (western Mediterranean) between the localities of Calvi and Porto (Fig. 1). Created in 1975, the reserve covers over 1.000 ha, of which 72 ha are classified as an integral reserve (Francour et al. 2001). Within the integral reserve, no plant or animal species may be removed, nor is any commercial activity permitted; anchoring is strictly limited and only scientific diving, bathing and recreational sailing are allowed. Thanks to the efforts of the wardens, fish populations have recovered well and they are now significantly greater in terms of species richness, density, sizes and total biomass than other populations along unprotected stretches of the coastline (Francour 1994).

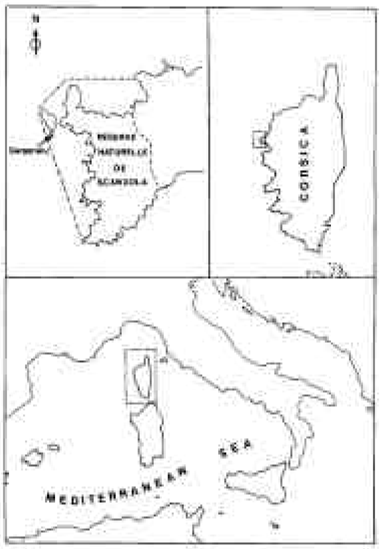


Figure 1- Location of the study site. Extensive censuses were carried out throughout the whole reserve, and the eradication experiments were located at S of Garganellu Island (marked with an arrow). Dashed line represents the limits of the integral Marine Reserve, where all fishing is prohibited.

2- The coast in Scandola is steep and rocky and so in many places the coastal shelf drops over 50 m in depth before coming into contact with bottom sediments. Throughout almost the whole length of this gradient (between 0 and 45 m) the magnificent transparency of the waters enables an unfolding of a succession of benthic communities dominated by extraordinary extensions of perennial algal species belonging to the genus *Cystoseira* (Ballesteros et al. 1998, Sant 2003). Between a depth of 3 and 10 m - the chosen depth range of populations of the sea urchin *P. lividus* - the community *Cystoseiretum balearicae* (Verlaque 1987), first described from and studied in Scandola, appears. This community is dominated by the perennial alga *Cystoseira balearica*, whose sizeable arborescent structure provides shelter for a great diversity of other organisms (Coppejans and Boudouresque 1974, Verlaque 1987).

3- The barrens observed within *C. balearicae* forests have been described as belonging to the community *Neogoniolitho-Pseudolithodermetum adriaticae* (Verlaque 1987). Its most characteristic quality is the absence of fleshy algae owing to the large numbers of sea urchins (and the limpet *Patella aspera*) present, which have been substituted, for example, by encrusting and filamentous algae that are resistant to grazing. The specific richness of this algal community is much lower than in the *C. balearicae* community. The transition between one community and the other is very sudden, occurring in a space of just a few centimetres (Verlaque 1987).

The existence, extension and size of the barrens

In order to evaluate the extension and distribution of barrens in Scandola in 1999 an extensive series of censuses was carried out throughout the whole reserve. A total of 33 points on a map were selected at random at a depth of 6 m; at each point a measuring tape was used to delimit a 50 x 1 m transect. Along each transect the extent to which the measuring tape coincided with forests or barrens was measured; other calculations made were that of the total cover of *Cystoseira balearica* and the density and size of sea urchins, this latter calculation being made by throwing down at random along the whole transect 20 50 x 50 cm^2 measuring squares.

Eradication experiments

The experiment was carried out between 1999 and 2003 on the basis of annual 20-day visits in the month of September (see Ballesteros et al. 2002 for a complete description of the missions). After intensive inspection, two rocky needles situated at the extreme south of the channel between the islet of Gargalu and Cap de Scandola were chosen as the site for the eradication experiment (Fig. 1). The bases of the needles were at a depth of 24 m, while the tips touched the surface of the sea (needle 1) or reached to about 1 m under the surface (needle 2). Needle 1 had high sea urchin densities as well as extensive barrens. Needle 2, on the other hand, situated less than 100m away, boasted algal forests without any signs of barrens. These rocky needles were chosen for the eradication experiment because they were almost totally surrounded by a sandy bottom that was sufficiently large to minimise the effects of sea urchin immigration from neighbouring areas. On each needle four rectangular plots covering 50 m^2 were marked, the plots on needle 1 being located in a barren patch and those on needle 2 in an algal meadow. All plots were located at a depth of between 4 and 10 m and their four vertices were delimited by polyvinyl pegs stuck to the rock by a two-component putty. During the visits, a rope strung between the pegs was used to view the plots. After carrying out the initial control in September 2000 according to the procedures explained below of algal cover and the density and structure of sea urchin sizes, all the sea urchins on the two needles were sacrificed (single eradication: SE) by perforating them with a knife.

The control experiments were carried out on the south face of the islet of Garganellu, situated just under 200 m from needle 1 (Fig. 1). Aside from being the nearest surface to the two needles, the south face of this islet was chosen because of its similar structure: it exhibits the same rock type, similar roughness and the same range of depths, inclinations and orientation as the two needles where the eradication was carried out.

In order to have data with which to compare the effectiveness of the single eradication, two types of control experiments were conceived: controls without eradication (CWE) and repeatedly eradicated controls (REC). The first aimed to give an idea of the evolution that local sea urchin populations would have experienced if they had not been eradicated, while the second was conceived to establish the maximum recovery potential of the algal communities if the sea urchins were removed every year.

Between a depth of 0 and 15 m at the extreme south of the islet of Garganellu the coastal shelf consists of a gentle gradient of quite smooth basaltic rock whose uniformity makes it difficult to imagine that the differences in environmental parameters existing there might affect the abundances of sea urchins and algae. Nevertheless, in 1999 this rock face was covered by a complex mosaic of forests and barrens, adjoining but separated by strongly contrasting boundaries. The size of the blotches ranged from 100 to 2,500 m^2. A total of 24 plots of around 50 m^2 were located at random on the rock face, eight of which were located in forests, eight in barrens and a further eight in transition zones (that we named ‘mixed’ zones). All plots were situated at depths of between 4 and 15 m, with the maximum distance between each being no more than 350 m. The vertices of the plots were delimited by polyvinyl pegs stuck to the rock by a two-component putty. During the visits, a rope strung between the pegs was used to view the plots in order to avoid errors of location during manipulation. After carrying out the initial control in September 2000 according to the procedures explained below of algal cover and the density and structure of sea urchin sizes, the sea urchins in half of the plots (four in forests, four in barrens and four ‘mixed’ plots) chosen at random were eradicated. Since then every year (2000-2003) the sea urchins in these plots have been eradicated again after measuring the algal cover and the density and structure of sea urchin sizes. The other half of the plots were not manipulated on any occasion and are controls without eradication (CWE).

Controls on community structure

Three variables were used to evaluate the evolution of communities: algal cover, the density of populations of the sea urchin *P. lividus* and the size of sea urchin skeletons without spines. Each year, before the eradications were carried out, we measured the algal cover and sea urchin density and size in 50 x 50 cm^2 quadrants placed at random on the rock surfaces. In each of the 32 plots measured (eight in SE, 12 in REC and 12 in CWE), 25 quadrants were analysed, totalling 6.25 m^2.

The algal cover of *C. balearica* was estimated visually in terms of a percentage. A sliding calliper was used to measure the size of all the sea urchins (shell diameter without spines) present in the quadrant (diameter classes of 1 cm; precision ± 0.5 cm). All the large sea urchins were lifted up to see if there were smaller urchins underneath. Given the difficulties involved in counting sea urchins when they are hidden in crevices, sea urchins under 1 cm in diameter were not taken into account in the analysis.

In order to calculate the biomass of sea urchin populations, we calculated the relationship between size and dry weight. At random we sampled 100 sea urchins – including some of all sizes – and calculated their dry weight by drying them on a stove at 80º C for 24 hours. The resulting dry weights included the weight of the skeletons and the resulting weight function can be expressed as follows: Dry weight = $0.0013D^{2.571}$; r=0,976 n=100, where D is the diameter without spines.

Statistical analyses

In order to determine the evolution over a long period of time of the control plots (CWE) in the three different communities, we employed a two-factor ANOVA: zone (random) and year, with the average values for cover and biomass being used as variables. The homogeneity of the variance was tested beforehand (Cochran’s test) and whenever necessary, data was transformed by the function log (x+1).

In order to determine the relationship between algal cover and sea urchin density and biomass, we used a Piecewise linear regression test between the cover of *Cystoseira balearica* and sea urchin density and biomass using the data from the initial controls from all the plots, as well as from the annual controls of the control plots (without eradication).

In order to search for significant differences between the size structure in the sea urchin populations, we employed the Kolmogorov-Smirnov test and used the software package Statistica©.

Results

Existence, extension and sizes of barrens

In total, 25 out of the 33 transects studied in the Scandola marine reserve showed barrens. Together, these patches represented almost 24.7% of the length of the transect area. The structure of the size of the barrens is summarised in Figure 2. Forests were generally larger than the barrens; the majority of barrens were small and could be situated on a scale of 10^1 m.

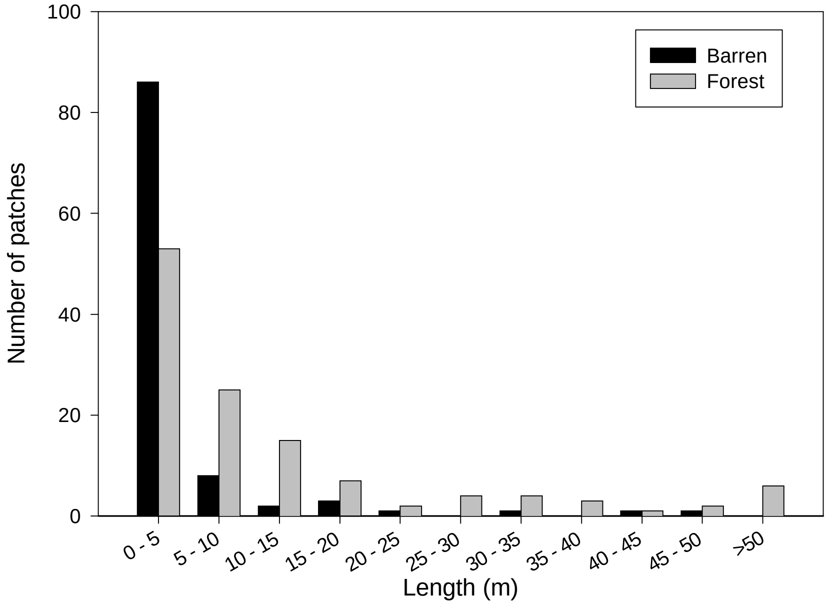


Figure 2- Number and length of patches of C.balearica *forests and barrens at 6 m depth in Scandola Marine Reserve.*

Relationship sea urchins-algal cover

The structure of the communities studied shows very contrasting differences that give credit to the description of “barrens” and “forests” as separate, discrete units. There is a clear correlation between the cover of *C. balearica* and sea urchin density and biomass that explains 74.58% and 87.18% (n=80) respectively of the variance: there is thus a clear causal relationship between the cover of *C. balearica* and the density and biomass of sea urchins (Figure 3).

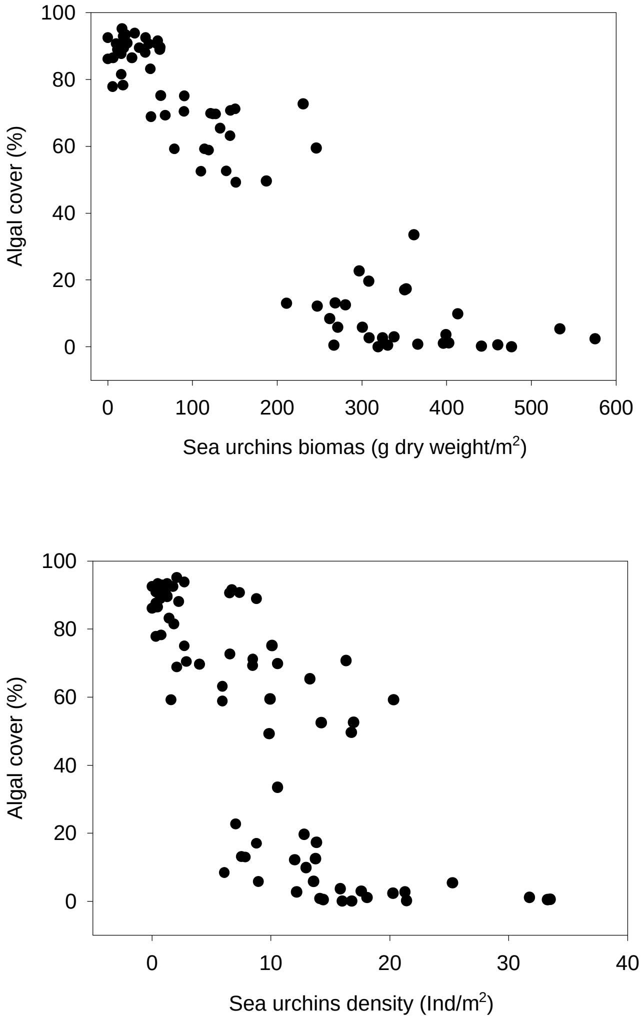


Figure 3- Relationship between Cystoseira balearica *and sea urchins a) density and b) biomass.*

A threshold of sea urchin density of 9.1 sea urchin/m^2 and 174 g dry weight/m^2 exists, beyond which changes in the meadow and barren communities begin to occur.

The striking discontinuity between the two types of communities (in both cover and biomass) shows that there is a clear distinction, consisting of very obvious boundaries, between these two communities. This boundary is more evident when we analyse the biomass of sea urchin populations. On the other hand, the density of sea urchin populations is not quite such a clear descriptor of this threshold, since small sea urchins (1- 2 cm) are very abundant, but affect algal cover much less than adult sea urchins.

Temporal evolution of the communities

The cover of *C. balearica* in the plots that were left as controls (no eradication) remained essentially stable during the four years of the study, although in some cases – above all in the barren communities – some changes were noted in algal cover and in sea urchin density. However, at no time did the percentage cover of barrens rise to more than 20%, while the cover of forests never dropped below 80%. Likewise, sea urchin biomass in barrens never dropped below 250 g dry weight/m^2 and meadow biomass never reached 50 g dry weight/m^2 (Figure 4, Table 1).

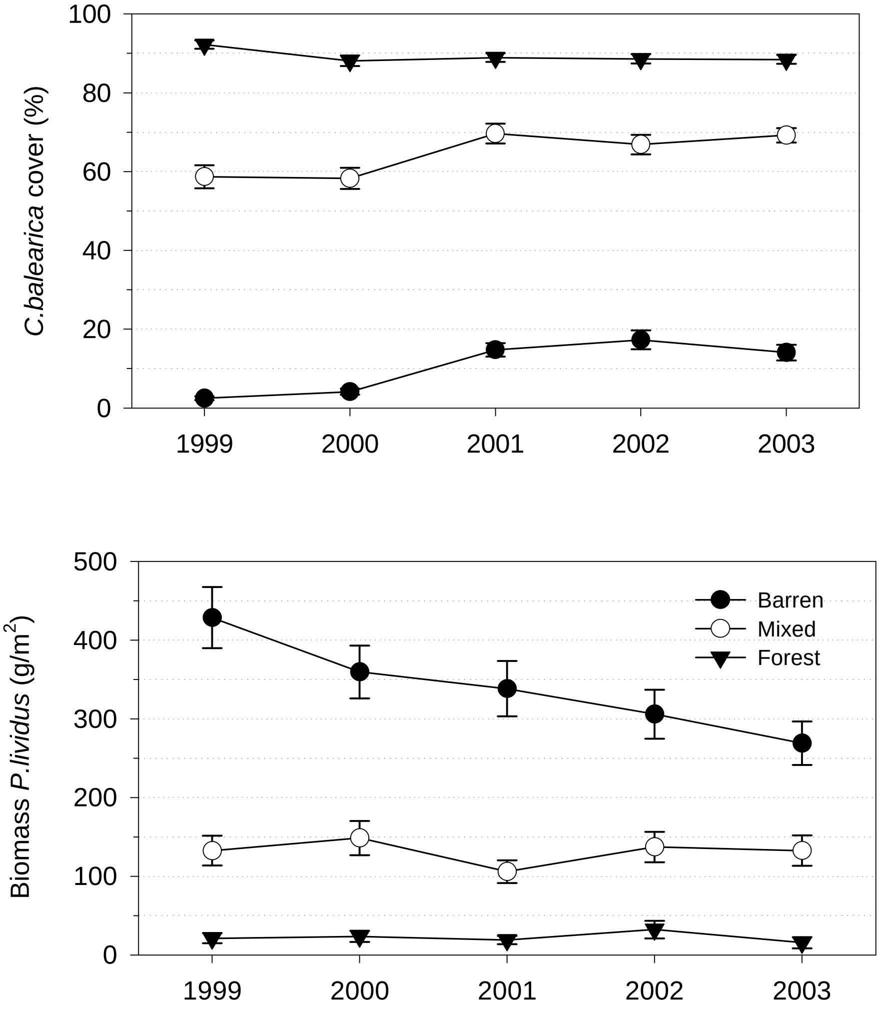


Figure 4- Cystoseira balearica *cover and sea urchins biomass from 1999 to 2003 in the controls without eradication (CWE).*

Table 1- Results of ANOVA comparing Cystoseira balearica *cover and sea urchins biomass over time in the controls without eradication (CWE) on a) barrens, b) mixed communities and c)* Cystoseira balearica *forests.*

a) Barren

Biomass (log x+1)	**df**	**MS**	**F**	**p**
Site	3	1,183	1,727	0,1605
Year	4	2,733	3,988	0,0034
Site x Year	12	0,575	0,840	0,6092
Error	482	0,685		

Cover (Log x+1)	**df**	**MS**	**F**	**p**
Site	3	0,320	1,138	0,3334
Year	4	8,044	28,57	0,0000
Site x Year	12	0,438	1,557	0,1009
Error	471	0,282		

b) Mixed

Biomass (log x+1)	**df**	**MS**	**F**	**p**
Site	3	4,016	6,462	0,0003
Year	4	1,810	2,913	0,0212
Site x Year	12	0,989	1,591	0,0906
Error	475	0,621		

Cover	**df**	**MS**	**F**	**p**
Site	3	1411,938	2,301	0,0764
Year	4	3128,858	5,099	0,0005
Site x Year	12	1460,120	2,380	0,0055
Error	483	613,595		

c) Forests

Biomass (log x+1)	**df**	**MS**	**F**	**p**
Site	3	1,196	4,559	0,0037
Year	4	0,353	1,346	0,2520
Site x Year	12	0,364	1,385	0,1689
Error	477	0,262		

Cover (Log x+1)	**df**	**MS**	**F**	**p**
Site	3	147,018	1,323	0,2662
Year	4	258,470	2,326	0,0556
Site x Year	12	181,490	1,633	0,0793
Error	464	111,124		

Eradication proved to be a very effective way of restoring algal cover. After each annual eradication, algal cover increased progressively, reaching 70% within four years, five times higher than the percentage cover in barrens where eradications were carried out and 0.79 times higher than in forests where eradications were carried out (Figure 5).

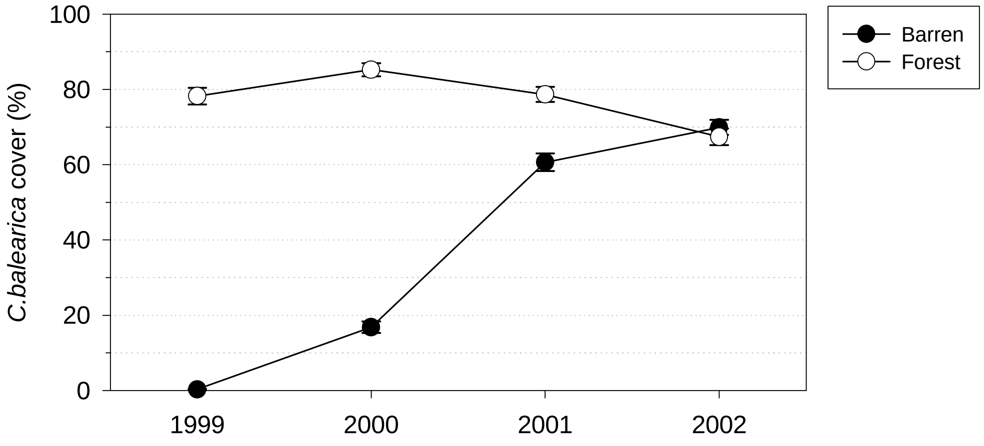


Figure 5- Cystoseira balearica *from 2000 to 2003 in the single eradication (SE) experiment.*

Eradication was also a very effective way of reducing sea urchin biomass. After four years, sea urchin biomass in zones where eradication was carried out represented only 8.16% of the biomass before eradication, and only 10.14% of the biomass in control plots without eradication (Figure 6).

Figure 6- Sea urchins biomass from 2000 to 2003 in the single eradication (SE) experiment.

The structure of sea urchin sizes in the plots where eradication was carried out shows that most sea urchins reached the plots by recruitment and that migration is not a significant factor (Figure 7).

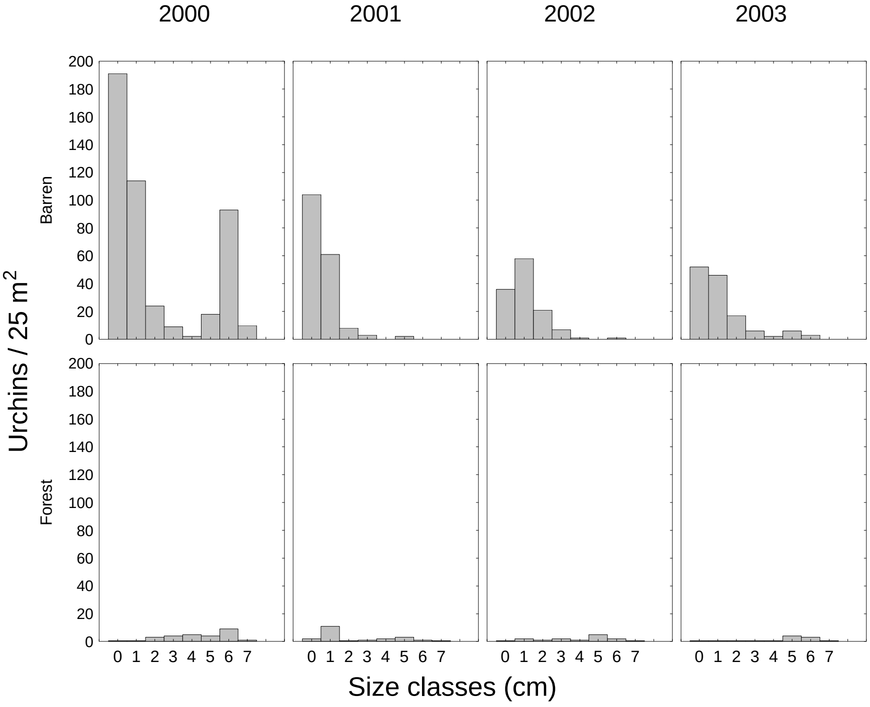


Figure 7- Sea urchins test size frequency from 2000 to 2003 on barren communities and Cystoseira balearica *forests in the single eradication (SE) experiment.*

After three years of recovery, we considered that the communities had overcome the barren threshold: henceforth the evolution of algal cover and sea urchin populations tended towards a greater differentiation between the two communities.

Discussion

This study shows that barren community patches are common in the *Cystoseira balearica* forests of Scandola Marine Reserve. These overgrazed communities affect approximately the 30% of the rocky bottoms between 0 and 10 meters depth.

The results of this study clearly show that the grazing of sea urchins populations is the cause of the formation of barren community patches. The mutual exclusion of algal cover and sea urchin biomass provides correlative evidence (with a very significant negative correlation). The causal nature of this relationship was experimentally proven by manipulating sea urchin densities during eradication exercises. These findings are not new, as a number of different authors (Kempf 1962, Neill and Larkum 1965, Mastaller 1974, Stirn et al. 1974, Torunski 1979, Nédelec 1982, Verlaque et Nédeleck 1983, Vukovic 1982, Zavodnik 1982, Verlaque 1984, 1987, Sala 1996) have likewise concluded that *P. lividus* populations govern the dynamics of cover in *C. balearica* communities.

We found that the relationship between algal cover and sea urchin biomass had a threshold that established the limits of the different states of “barren” and “meadow” at 174 g dry weight of sea urchin biomass or a density of 9.1 individuals/m^2.

These results coincide partially with those of Verlaque (1987), who locates this threshold at densities of 10-20 sea urchins/m^2. We believe that these differences can be explained by the different number of small individuals present caused by variability in recruitment processes. Given that smaller individuals affect algal cover much less than adults do, we believe that a more precise way of describing this threshold is to use the criteria of total biomass.

Despite the fact that the composition of the so-called ‘mixed’ communities (in terms of algal cover and sea urchin biomass) confirms the existence of transitional states between forests and barrens, the scarcity of these states reveals the tension along boundaries (as mentioned by Verlaque 1987, pg. 157). In none of these transitional communities did we find a combination with greater sea urchin biomass than we would expect from the fit of the function in Figure 2 (points located above and to the right of the curve); nevertheless, situations were found in which the algal cover would allow for greater sea urchin biomass then was observed (points to the left and underneath the curve). These deviations indicate that the boundaries are tighter in the direction of the advance of barrens than in the direction of algal cover. Likewise, all the intermediate situations observed correspond to recovery transitions. That is to say, the loss of algal structure can happen very quickly, whereas the recovery of algal cover takes much longer.

In terms of algal cover and sea urchin populations, the structure of the communities in the non-manipulated control plots (CWE) seem to have been characterised by a certain degree of persistence over a period of at least three years. During these three years none of the control plots changed state. Although the CWE plots in areas of barrens did show significant signs of recovery in terms of algal cover and a reduction in sea urchin populations, none actually reached the thresholds established as the limits between the two states.

The feeble dynamics of the situation and the rarity of the intermediate states does tend to reinforce the views of some authors that the communities produced by the interactions between sea urchins and algae are stable alternative states (Leinass and Christie 1999), as in the sense used by Connell and Sousa (1983).

Nevertheless, motives exist that make us believe that algal communities possess a high recovery potential if sea urchin populations decrease. In Scandola we observed no extensive barrens as occur in other regions of the Mediterranean (obs. pers.) and the size of those barrens we observed was small. Assuming that there is a correlation between size and age, we can thus assume that these barrens have only appeared recently and are possibly reversible. On the other hand, given the proximity of forests of *C. balearica* and the observed recovery speeds in algal cover after eradications, we predict that there will be 100% algal cover five years after sea urchin eradication has been carried out. We must also take into account, however, that a recovery of algal cover does not necessarily suppose the immediate return to the structures present in a mature population: according to Verlaque (1987), the recovery of a whole community may take as long as 7-8 years.

The existence of large barrens within the Scandola integral reserve, an area boasting excellent fish populations that has been strictly protected for 25 years, seems to contradict the model proposed by McClanahan and Sala (1997). Furthermore, this fact also casts a serious doubt on the hopes that marine reserves might be used as tools to reverse the advance of barrens.

We still need alternative ideas that, without condemning the general validity of McClanahan and Sala (1997) model, would provide an explications as to why this model is not applicable in Mediterranean marine reserves (Sala et al 1998). A logical extension from the ideas of Volterra-Lotka, the authors who inspired this model, is that the model does not take into account the space nor its heterogeneity. Its predictions may well be applicable to a space under uniform pressure from fishing and predation by fish. At least two reasons, both linked to the lack of spatial heterogeneity in the model, may reveal why it is unable to explain our results: the existence of refuge zones outside the reserve that act as a continual source of sea urchin larvae (and adults), and the existence of refuges against predators within the reserve (Sala et al. 1998). Refuge zones outside reserves are much more extensive than the reserves they surround. Moreover, within reserves, micro-cavities exist (under pebbles and in crevices) that fish predators cannot reach (chapter 5). Lastly, it has been shown that a “size refuge” exists (situated around a diameter of 3 cm without spines), beyond which fish predation is not significant (Sala 1996).

Thus, we can conceive a scenario in which the great variability of settlement sites (chapter 4) available for larvae entering the space from outside enables extraordinary recruitment years to occur, in which the existence of sufficient refuges ensure that predator fish cannot control the cohort of larvae (chapter 5). Thus, enough larvae will reach the refuge size and subsequently be able to provoke the appearance of barrens (Sala et al. 1998); the number of predatory fish may be insufficient to reverse this trend.

The starting point of this work was that if, due to exceptional destabilising factors that we cannot control, there were communities not described by the predictions made by the models, it is still possible to reverse these situations by means of external stimuli such as the elimination of adult sea urchins. A single eradication of adult sea urchins and the subsequent control of recruitment by predator fish would seem to be sufficient to allow communities to revert back towards the predictions made by the models. The rapid recovery of algal cover and the poor recovery of sea urchin populations after a single eradication lend credence to this hypothesis.

If we represent the (temporary) evolution of communities in zones where eradications have been carried out as pathways in the space defined by ‘algal cover-sea urchin biomass’ (Figure 5), we see that the algal cover reached in 2003 was still below that predicted by the curve which best fits the relationship observed between algal cover and sea urchin biomass in natural situations (not manipulated). Nevertheless, algal cover will increase so rapidly that within a mere three years the threshold between forests and barrens will be overcome and in five years algal cover will reach 100%.

Even without more exhaustive analyses of larval recruitment and survival rates, we can affirm that the sea urchin population that has arisen since the eradications is not large enough to generate the barrens observed before the eradications. Although our experiment cannot attribute the control of post-eradication sea urchin populations to predation by fish (because there are no fish-free control zones), this hypothesis seems to be the most plausible way of explaining why the large recruitment episodes that occurred after the eradications in 2000-2001 have not given rise to significant new cohorts of sea urchins.

Moreover, the controls practised in the plots in which the eradication was carried out four years in a row demonstrate that the sea urchin's colonising capacity is limited. We deduce therefore that eradications carried out every five years in a marine reserve whose fish populations have recovered and which has a nearby source of algal communities may be an effective tool for reversing barrens. The effort involved in eradication was small (4 people, two hours). The instigation of such measures would seem to be feasible, above all in marine reserves and other areas possessing exceptional biodiversity (such as Scandola) that are sufficiently near to well preserved algal populations to ensure recolonisation and recovery.

Many studies in other temperate environments have shown that high densities of sea urchins can ensure the presence of barrens for many years (Johnson and Mann 1982, Keats 1991, Simenstad et al. 1978, Duggins 1980, Leinass and Christie 1996). These investigations have demonstrated that sea urchin populations in barrens remain for longer than the life-span of individual adults, thereby proving their persistence (cf. Connell and Sousa 1983). Leinass and Christie (1996) found in kelp forests in Norway that densities of over 10 individuals/m^2 were capable of maintaining barrens, while greater densities were able to eliminate even seasonal species of algae. This effect, moreover, was stronger at greater depth owing to limitations on algal growth. These authors found that after intensive eradications, a breakthrough occurred whenever a species of alga appeared, thereby preventing sea urchin recruitment.

In our case, we have seen how recruitment of sea urchin larvae in barrens is greater than in forests, as other authors have pointed out (e.g. Tegner and Dayton 1977, Ebert 1982, 1983, Cowen 1983, Himmelman et al. 1983, Pearse and Hines 1987, Rowley 1989, 1990). Our eradications may not have totally prevented recruitment, but certainly did enable us to eliminate adult individuals and encourage a recovery of algal communities that should ensure that the barrens revert to forests with high algal cover and low sea urchin recruitment.

The efficiency of these measures in areas with extensive barrens far from algal communities that could act as recovery vectors and/or in areas where fish populations have not recovered is more problematical and has yet to be properly studied.

Although we have a fairly clear idea of the dynamics of sea urchin populations (reproductive effort, settlement rates, post-settlement mortality, predators and growth), there is still an important lack of this type of information regarding algae and, above all, climax species such as members of the genus *Cystoseira*. The individuals of these species tend to be perennial with structural components of slow growth and very limited capacity of propagule dispersal. Although the dynamics of these two groups of organisms are contradictory, we still do not know to what extent they are compatible. We need to know more about the parameters of population dynamics in algal communities, as well as their recruitment, survival, growth, longevity, reproductive and propagule dispersal rates. This information would also allow us to obtain more precise criteria regarding their conservation since it would enable us to predict more precisely the carrying capacity for sea urchins, the return periods for barrens and forests, and the critical size of barrens, beyond which recovery by means of propagules from nearby forests is impossible.

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Chapter 9- General Discussion

There can be no doubt that there is an interrelation between the results of our investigations into the three trophic levels – algae-sea urchins-fish – that this paper is based upon. However, owing to the strict formal structure employed in scientific papers, with an emphasis on independent and self-explicatory chapters, the possibilities of discussing intersecting relationships and connections between different processes – exactly the place the most subtle and interesting of all relationships are to be found - is often lost. Taken individually, the sum of the parts is less than the whole and we run the risk of losing sight of the overall nature of the group of elements we are examining. Thus, I have put special emphasis on this general discussion in which I have allowed myself the licence to jump around from one of the results obtained during the investigations to another in search of more profound and even slightly speculative conclusions.

Question 1: top-down controls or bottom-up controls?

We looked at which processes govern the functioning of rocky Mediterranean infralittoral communities from two extreme standpoints: top-down controls vs. bottom-up controls. In this paper we suggest that both types of processes have a fundamental part to play.

Our results provide a mechanism by which herbivore communities might be able to shift over alternative stable points. In this way we can establish a bridge between Ballesteros' model (1991), conceived essentially on the basis of bottom-up controls, and that of MacClanahan and Sala (1997), which was designed exclusively from a top-down point of view. It is quite possible that the differing applicability of the two models is only a question of temporal and spatial scales: the latter looks to make predictions on a grand scale, while the former has the great virtue of being able to explain the workings of algal communities at a very small scale.

We suggest that any model which aspires to explain satisfactorily the functioning of Mediterranean algal communities will have a greater capacity to predict if it incorporates both types of variables or axes of variation: on the one hand, seasonality as an annual expression of bottom-up controls and, on the other, the structures of consumer populations, especially herbivores, as a manifestation of top-down controls.

Question 2: the relative importance of sea urchins and fish as herbivores

The important effect of sea urchins

By manipulating the populations of herbivores in our enclosures, we were able to confirm that the pressure exercised by a population of sea urchins at similar densities to the densest populations observed in the area (around 16 individuals/m^2, all sizes included) produced significant changes in all the algal populations studied (over 40). Overall there was a loss of algal cover.

In the Medes islands the experiment with sea urchins did not produce any generalised barrens, although within three years the algae communities exposed to this high density of sea urchins did become more dominated by the calcareous alga *Lithophyllum incrustans* and show a loss of total cover. The brunt of the losses were born by large, perennial algae, while ephemeral algae, whose seasonal life-cycle is closely connected to the spring period of proliferation, tended to benefit.

Although in an inverse perspective, the sea urchins effects were even more evident in the eradication experiment in Scandola Marine Reserve. After two years of the sea urchins eradication, the extensive barren communities caused by a dense *P lividus* population (20-25 ind./m^2) begins to change into a *Cystoseiretum* forest.

The effect of fish: unimportant

Unlike the case of sea urchins, the presence of a population of omnivorous fish seems to have little effect - at least directly - on the composition and structure of algal communities (experiments with fish without sea urchins). Likewise, the effect of fish is minimal when the density of sea urchins is maintained artificially constant (comparison of experiments of sea urchins with and without fish).

The indirect role of fish on algal populations via predation on sea urchins depends to a large extent on their capacity to control sea urchin populations.

Nevertheless, the presence of fish did cause the predicted trophic cascade in the abundance of a number of algal species, of which some can turn out to be quantitatively very important in community structures (e.g. *Corallina elongata*). Given that we maintained the biomass of sea urchins artificially constant during the experiments, the effect of fish must be explained in terms of their role as behavioural inhibitors rather than as predators. This effect may be related to the feeble natural mobility of sea urchins and may be explained by the changes induced in the sea urchins' grazing habits by the presence of fish. If, as we noted in chapter 6, when fish are present sea urchins leave their hiding places under rocks or in crevices less frequently, then this behaviour will benefit the more photophilous algae living on the top of blocks (far from sea urchin refuges), but be detrimental to the more shade-loving species that prefer the vertical walls of blocks more easily accessed by sea urchins.

Question 3. The importance of floristic composition and functional groups

The role of the composition of the community

The differences in the response in algal cover to high levels of herbivores (basically sea urchins) in the experiments in the Medes Islands (no barrens) and in Scandola (extensive barrens) seems to suggest that the floristic composition of the community has an important role in the process and, more specifically, in the different susceptibility of each species of algae to grazing by sea urchins. At Scandola, we dealt with a presumably mature community dominated by *Cystoseira balearica* (chapter 8), a perennial arborescent species (albeit with important seasonal fluctuations in its biomass) that is corticate and possesses a very specialised histology, unable to disperse vegetatively and has with the attributes of species from climax phases of succession (Littler and Littler 1980).

In the Medes Islands the algal biomass is shared out between a much more varied pool of species, amongst which the perennial species are just a small fraction. Much of the cover corresponds to ephemeral species, which produce a discrete peak in biomass, generally synchronised with the period of greatest production at the end of spring. This reduction in the length of the biomass cycle to a short period of around a month, during which many species proliferate more or less in synchronised fashion, may be a way of escaping pressure from herbivores by means of a satiation strategy (Littler and Littler 1980).

We believe that this is the mechanism which explains how the top-down and bottom-up processes interact: the perennial algae, better adapted to oligotrophic situations, will be selected by a bottom-up control, are more sensible to pressure from herbivores than seasonally growing algae with no limitations imposed by nutrients that are eliminated by a top-down control. Thus, herbivore pressure as much as production conditions may determine what type of algal strategies we will find in a given community.

The failure of conventional functional groups

Whenever we have ignored interspecific variability and looked for regularities in algal responses and have tried to test the usefulness of grouping sea urchins into the functional groups (see footnote) proposed by Littler and Littler (1980) or by Steneck and Dethier (1994), we have failed to find the homogenous response patterns that these authors have described.

Footnote : Functional groups

(*) A number of factors – spatial and temporal variability in the composition and structure of algal communities, the variable response of different types of algae to different biotic and abiotic factors, and, globally speaking, the variation in responses of algal communities according to their specific composition – have obliged ecologists to try to group algae into simplified categories that follow patterns in algal responses to the interactions and factors being studied (herbivores, light gradients, nutrients, physical stress, and so forth).

The first attempts tried to find a relationship between the form and productivity of algae (Odum et al. 1958, Kanwisher 1966, Little 1979). At the same time it was noticed that the life-histories of certain species of algae were connected, which then led to the realisation that the composition of life-forms – that is to say, the incorporation of the life-history of the species that form a community – could provide clues to the environmental conditions of a particular habitat (Ketada and Satomi 1975). Subsequently, Little and Littler (1980) developed a model of functional forms in which they described two extreme forms (for example, opportunistic forms and late forms in a successional process) as successional strategies that included criteria regarding form, production and resistance to perturbations (including from herbivores).

These strategy-based attempts allow us to compare different environments using the same criteria. For example, Steneck and Dethier (1994) carried out a comparative study between three different biogeographical regions in which they studied the effects of productivity and grazing by herbivores on the structure of algal communities. They used morphological criteria to develop a model that associated evolutionary strategies in response to production and resistance to herbivores.

In our case, the failure to find data that fitted in with the most universally recognised functional groups can be explained in part by the particular characteristics of the algae and the algal communities of the Mediterranean. Unlike other temperate regions, dominated by fields of kelp, Mediterranean algal communities are miniaturised and there is no great range in sizes such as those used as a basis for the groupings discussed earlier. The group criteria selected by Steneck and Dethier (1994) do not take into account the seasonality of the life cycle when, as we have seen, this is a very important factor in the response of algae to production factors such as the presence of herbivores. Neither do these authors consider the morphological or histological characteristics that provide better protection against grazing by sea urchins, which can be described as being akin to the destruction wrought by a bulldozer. Thus, we believe that for markedly seasonal seas such as the Mediterranean we must explore new functional groupings that, if we incorporate criteria regarding seasonality and morphological adaptations aimed at being able to survive grazing by herbivores, will be better placed to provide more accurate predictions.

It is debatable whether the algal populations of the Medes Islands marine reserve, which seem to enjoy greater productivity and trophic dynamism, are in more of a pioneer successional phase and are better adapted to living to dense populations of sea urchins than the algal populations in Scandola, which seem to be proliferating in a more oligotrophic environment and may be in successional phases that are closer to the climax. Later on in this discussion we will propose a working hypothesis on the evolution of western Mediterranean algal communities in light of anthropic changes and the role that sea urchins may be playing in these changes.

Question 4. What controls the demographic dynamics of sea urchin populations?

Within the triangular relationship ‘algae-sea urchins-fish’, sea urchins have proved to have a key role, not only because they are in a central position within the interaction (on the one hand, they predate on algae, while on the other are controlled by predatory fish), but also because when abundant their grazing pressure alters the structure of the whole community. Given that the key to understanding how these systems work lies in the number and biomass of the sea urchins, is fundamental to understand the processes that regulate the structure and dynamics of sea urchin populations. Leaving aside migratory movements for a moment, from a perspective of the maintenance of small populations the question can be reduced to the antagonism between settlement and recruitment as a destabilising process, and the mortality caused by predators operating as a controlling process.

Mobility

All the evidence gathered during our study, in both the Medes Islands and the Scandola reserve, from the enclosures, from the eradication experiments and from the experiments designed to measure mobility point to the conclusion that the sea urchin *Paracentrotus lividus* is a very sedentary species. Its poor mobility is evident at all the temporal levels we studied: day-night, weekly, seasonally, pluri-annual and ontogenetically. Immobile by day, during their nocturnal activity they do not move on average more than 20 cm from their preferred refuge site. This faithfulness to a refuge also means that over a whole week these sea urchins on average do not move more than 1.3 m from their refuges. This pattern of sedentary behaviour is repeated throughout the year and not even storms and seasonal changes in physical conditions seem capable of provoking large-scale movements. On an ontogenetic scale, there must be a certain degree of movement from the under side of stones and under adult sea urchins where they live during the settlement phase to the crevices which are used as refuge by adults. Even so, these displacements only consist of movements of a few metres. It is important to understand that the sea urchin *Paracentrotus lividus* completes its life cycle in an area which is very near to where the pelagic larva first settle (see below).

These results provide us with much valuable information since, surprisingly, the mobility of *P. lividus* has so far been little studied (Barnes and Crook 2001). Difficult to measure, the importance of these movements has often been underestimated in demographic studies, largely through ignorance rather than through irrelevance. We must not forget that, if these movements exist, they may mask or confuse the true role of the other two demographic processes involved: mortality through predation and the settlement-recruitment relationship. The fact that the populations of *P. lividus* we have studied seem to be all but immobile at all periods of their life cycles is a great advantage that simplifies any study of this species, which is otherwise very variable in all its other attributes. Thanks to its sedentary nature, we have been able to reliably demonstrate the important role of the other two processes (settlement-recruitment and mortality), as we discuss below.

Settlement

Our study has enabled us to gain an overall vision of the very spatially and temporally heterogeneous settlement pattern of *Paracentrotus lividus*. The confrontation between this heterogeneity and the homogeneity found in adult populations suggests that there is no relation between the density of reproductive parent populations and settlement patterns. Thus, in order to examine the ecology of the sea urchin *Paracentrotus lividus* it would seem reasonable to begin with the concept of open populations as proposed by the defenders of the so-called 'supply-side ecology' (see review by Menge 2000). We have seen that the number of settled individuals may vary through various orders of magnitude from one year to another, and that settlement occurs in a spatially very heterogeneous pattern, probably as a result of the high heterogeneous distribution of larvae in plankton. Our results indicate that sea urchins do not choose a settlement spot, but rather that physical factors such as coastline topography, and in particular, orientation and exposure to currents, are the determining factors in settlement patterns. Thus, we found no difference in the settlement potential in the Medes marine reserve and the unprotected area. The only stable pattern we found was that of decreasing levels of settlement with depth, which also coincides with adult distribution patterns.

We believe that settlement is a passive process that depends largely on the water mass that is transporting the larvae: a good metaphor would be of a "shower of larvae". A future model that aims to predict larval distribution might find inspiration in meteorological rainfall-prediction models. If, moreover, we take into account bathymetry, an even more graphic comparison would be with snowfall patterns on a range of mountains: the quantity of snow that falls will vary from year to year and from place to place, depending on wind direction. However, despite these variations, snow will always fall above a certain altitude because below that level the snow will melt.

Sea urchins have a very high reproductive capacity. Moreover, given their relatively long planktonic phase and the lack of observable active mechanisms of larval retention, we are forced to conclude that the dispersion capacity of the larvae is great (up to hundreds of kilometres). Although studies into genetic fluxes that would determine this question are lacking, this great capacity for dispersal allows us to rule out the existence of genetically isolated populations, and to predict a large degree of interconnectivity between different geographical zones.

These results are very important if we are to analyse the role of settlement in the control of sea urchin populations in marine reserves. The capacity to disperse over large distances makes mass arrival by larvae possible, even in zones where the density of adults is low. Thus, even if greater numbers of fish in reserves could control sea urchins densities (see below), a sudden arrival of a large quantity of larvae could negate this control mechanism. We cannot expect that sea urchin populations in a marine reserve, be they large or small, be completely closed: rather, they are continually exposed to the arrival of larvae from peripheral zones where the overfishing of sea urchin predators has led to greater abundance of reproductive adults.

In conclusion, the great spatial scope of larval dispersion and the great variety in observed settlement patterns at all scales (position and year) in *P. lividus,* as well as the strong sedentary nature of settled individuals confirms the **potential** of this process (settlement-recruitment) as a destabilising factor in sea urchin populations.

Mortality through predation in post-settlement phases

We have also derived clear support from our experiments for an antagonistic process: the regulatory role that trophic models attribute to mortality through predation (especially in marine reserves). Despite the significant destabilizing potential suggested by settlement patterns, in chapter 7 we saw that adult populations are very homogeneous and relatively stable over long periods of time. Bearing in mind the feeble mobility of the species, these results can only be explained if we assume that mortality plays a significant role in the control of fluxes of new recruits by acting as a filter that determines the size of adult populations.

The importance of predation by fish in mortality rates of *Paracentrotus lividus* is not a new concept and has been studied by various experiments that have concentrated on predation on large sea urchins (>3 cm diameter; but see Sala 1997). On the other hand, mortality in post-settlement juvenile phases has been relatively little studied (López et al. 1995). This lacuna is significant since predation on juveniles may be an important factor in the control of sea urchin populations (Sala et al. 1998). At least, this is what the analysis of population size structures suggests (chapter 7) when it reveals that the highest mortality rates occur in post-settlement phases. Our experimental work confirms that, as occurs in most benthic animals, highest mortality rates through predation in *P. lividus* are found in post-settlement phases in a range of between 0.2 (the size they reach on settlement) and 1 cm. Tethering experiments carried out on individuals within these size ranges have given consumption levels which are much greater than observed by Sala and Zabala (1996) in large sea urchins (>3 cm diameter).

Previous investigations concentrating on large sea urchins have identified, firstly, the white seabream (*Diplodus sargus*) and, secondary, the spiny starfish (*Marthasterias glacialis*) as the main predators of sea urchins (Sala 1997, Dance 1987). However, our results show that other species of fish that have previously not been considered as being such significant predators may also play a very important role owing to their abundance and their ability to control juvenile phases.

We have been able to observe a clear relationship between prey size and the size and nature of predators. When sea urchins are smallest during the earliest phases, small Labridae such as Mediterranean rainbow wrasse (*Coris julis*) and ornate wrasse (*Thalassoma pavo*) are the commonest of up to six species of predator. Once the sea urchins reach a diameter of over 0.5 cm (after about six months of life), small Labridae can no longer prey on them and larger Labridae such as brown wrasse (*Labrus merula*) and Sparidae such as white seabream (*Diplodus sargus*) and common two-banded seabream (*D. vulgaris*) become the main predators.

The correlation between sea urchin size and the minimum size of their predators confirms the ability of sea urchins to use size as a mechanism against predation (Sala 1996, 1997). Thus, fish size will determine the refuge size beyond which the sea urchins will no longer be predated on. Given that in Medes marine reserve the size and number of fish are greater (including the small Labridae), sea urchins face a greater risk of being devoured by a predator. On the other hand, in fished areas, fish are smaller and so sea urchins will reach their refuge size earlier and be susceptible for less time to being eaten by small Labridae.

These results reinforce the often underestimated effect that recreational fishing can have on sea urchin populations and, incidentally, on the conservation of infralittoral communities (Sala 1997). Experimental evidence exists that the size structure of populations of the Mediterranean rainbow wrasse (*Coris julis*), the main controlling fish of sea urchins in the post-settlement phase, is greatly influenced by pressure from recreational fishing (Harmelin and Vachet 1995).

Nevertheless, we should take into account the fact that, aside from the fish, there are also a significant number of crustaceans that can consume a considerable part of these settled individuals. This type of predation may also vary from a marine reserve to a unprotected area: in areas with lots of fish, invertebrates tend to be less numerous (Sala 1997b) and so predation by crustaceans on the sea urchins will be less significant. This effect works in the opposite direction from the effects described thus far, and in a protected area this type of predation will be less frequent, thereby favouring the sea urchins.

The experimental results dealing separately with the effects of settlement (chapter 4) and predation (chapter 5) provide powerful evidence for their potential for regulating sea urchin populations. Given that that both processes have antagonistic effects, when they act simultaneously on the same population the effects of one have to be subtracted from those of the other. In this situation, it is obviously important to decide which process dominates the other. The long series of sea urchin censuses carried out in the Medes Islands reserve and on the nearby unprotected coastline shows that there are significant interannual oscillations in the sizes of individuals that, in the absence of notable migratory movements, can only be interpreted as a consequence of recruitment pulses.

Nevertheless, we have demonstrated that these oscillations are due exclusively to changes in the class of sea urchins that have just settled, whereas, on the other hand, the sizes of adult individuals remain fairly stable. This means that the effects of predation on post-settlement classes of sea urchins quickly cancels out the effect of variability in settlement. Proof of this is the lack of significant correlation between the size of the first class at time 0 and the size of the higher classes during subsequent years: the demographic signal introduced by cohorts produced by extraordinarily high levels of recruitment does not follow through into the adult population. Thus, predation acts a stabiliser in sea urchin populations since it counteracts any large-scale entrance of recruits.

The role of marine reserves in the control of sea urchins is not clear yet. Deterministic models describe two situations with opposed recruitment and predation patterns for protected and unprotected zones. Protected zones should have lower populations of sea urchins due to lower levels of settlement and greater predation. On the other hand, in overfished areas populations of sea urchins will be kept high by the significant entry of recruits and low predation levels that are incapable of controlling these entries.

However, we have observed exceptions to these models. There is evidence that barrens occur in marine reserves and that well developed algal communities appear in areas where fish density is very low.

In the Medes Islands marine reserve, where fish density is one of the highest in the Mediterranean and only small overgrazed areas exist, sea urchins densities are higher than in *Cystoseira* forests in Scandola. Long-term population studies in sea urchins here have enabled us to observe that densities of adult sea urchins do not differ appreciably between protected and unprotected areas: in the latter, the poor populations of fish still seem to be able to control sea urchin populations. However, if we look closely, herein lies the most important difference; that the oscillations in the densities of sea urchins on the unprotected coastline are much more pronounced than within the marine reserve, a fact suggesting that the control capacity of the fish is reaching its limit.

We must also take into account the fact that in the Medes Islands and other marine reserves with high densities of predator fish, the majority of sea urchins are hidden and thus have smaller home ranges and less overall effect on the community as a whole (Sala 1996; chapter 2 and 3). This fact demonstrates that we should not only consider the density of sea urchins in itself, given that the ecological effects of their presence will vary according to their mobility (Sala et al. 1998).

Another piece of evidence regarding the failure of deterministic models comes from Scandola, where in a zone with high fish density, areas of barrens exist alongside *Cystoseira balearica* forests. These patches can be caused, in part, by migratory fronts of sea urchins. However, the low mobility of sea urchins shown in experiments and the fact that these patches are isolated do not lend any support to this hypothesis. Although we have not yet fully investigated this phenomenon, the most probable origin of these barrens are significant peaks in recruitment followed by episodes of low post-settlement mortality. Thus, it seems that in some marine reserves, despite higher fish densities, predator fish cannot control the demography of sea urchin populations, although they are able to affect their effects by a behavioural way.

Question 5: Why are the predictions made by trophic models not fulfilled in marine reserves?

What could be the cause of the differences between predictions made by trophic models (e.g., MacClanahan and Sala 1997) and our empirical observations?

At different points in our investigations we have found mechanisms that could explain why sea urchins are not controlled by fish in marine reserves. All have one thing in common, which could be summarised under the generic name of “role of the space”. All the trophic models mentioned are based on the logic of the predator-prey models of Lotka (1925) and Volterra (1926), whose principal weakness, so often recognised (Margalef 1974), is to ignore the fact that interactions take place within an essentially heterogeneous space with defined dimensions. These models, inspired by physical models of the ‘Law of mass action’ type, would probably be adequate for describing the interaction of species at a very large scale in the absence of significant physical barriers. However, in the case of interactions of the type ‘fish-sea urchins-algae’, the heterogeneity of the space should be analysed on at least three scales:

1– at a scale of kilometres, the inequalities between the ***dispersal capacity of sea urchin larvae*** and the size of the reserves.

2– at a scale of tens of metres, the ***random patterns of both settlement*** of sea urchins and topography, and the ***patchiness in the distribution of benthic*** communities and fish.

3– at a scale of centimetres, for the existence of crevices and spaces under boulders that act as ***refuges*** for sea urchins.

1 – The dispersal capacity of the larvae does not correspond to the size of the reserves

One of the reasons that explain the inadequacy of trophic models which predict a cascade effect may be the unresolved problem of scale. The spatial scale in which larval dispersion works is much wider than the scale at which the control processes (predation) operate in marine reserves.

Sea urchin ‘birth’ dynamics cannot be considered to be subordinated to the control that, according to the logic contained in the Volterra-Lotka models, predators exercise on the parent population, since its long planktonic phase allows larvae to enter the reserve from outside. Thus, the Medes islands act as a larval sink and probably receive more larvae from the mainland – the unprotected nearby coastline - than are produced by sea urchin populations in the reserve themselves.

2 – The random settlement of sea urchins and topography and patchiness in the distribution of benthic and fish communities.

Experiments with artificial collectors have demonstrated the random settlement pattern of sea urchins larvae. Bays and closed zones where eddies occur and plankton is retained are favourable points for receiving large quantities of larvae: as we have pointed out before, this occurs regardless of the size of local populations. Because of the highly limited mobility of post-settled sea urchins , settlement patterns must be closely related to the final position of the sea urchins.

Moreover, the distribution of Mediterranean infralittoral communities is very patchy at a scale of tens of metres (Garrabou 1997). Despite their mobility, fish populations are sensitive to benthic patchiness and show patchy distributions on their own. In the Scandola reserve, plots covered by dense forests of *Cystoseira* always have lower density of recruits than barrens. These results suggest that the fauna associated with well-constituted algae forests may operate as a first filter acting on settlement (before the fish come into action).

3- Refuges

The micro-topography of the substratum which allows the young sea urchins to find refuges during the critical post-settlement period seems to be the most important scale at which heterogeneity may be relevant in explaining the discrepancies between predictions made by models and field observations. The roughness of the rock surfaces and the existence of crevices and/or small blocks with interstitial spaces are the keys that enable urchins to escape predation, even in the Medes Islands with its dense fish populations. In addition to roughness, we have shown experimentally that algal cover can also significantly attenuate the effects of predation.

If we also take into account the behavioural responses of sea urchins, we will be able to build up a more complete picture of the importance of refuges.

We have seen that the home range of sea urchins is significantly reduced in the presence of predators. The behavioural inhibition of grazing activity by fish is, along with direct predation, another form of control (trait-mediated indirect interactions; Trussel et al., Werner and Peacor 2003, Bruno et al. 2003) that will prevent extensive grazing by sea urchins and will limit their growth and reproductive potential without actually affecting their numbers.

Nevertheless, we should remember that a high availability of refuges will lead to a greater density of sea urchins that, despite smaller home ranges, will still be capable of denuding a whole community of algae (as we have observed in some areas of the Medes Islands).

Question 6: Barrens and algal forests: are they stable states?

Although our experimental manipulation of sea urchin densities in the Medes Islands were unable to generate extensive barrens, in the Scandola marine reserve (Corsica), the effects of sea urchins on algal communities were much more noticeable and we found evident barrens along this coastline in between the dense forests of *Cystoseira balearica.* We estimated that up to 30% of the potential area of distribution of *C. balearica* is currently covered by barrens. Eradication experiments have shown that sea urchin biomass is the factor which governs the transition between forests and barrens.

The algal cover in forests is very high and the density and recruitment of sea urchins are both very low. On the other hand, in the barrens high densities of sea urchins have completely denuded the *Cystoseira* forests and there is, moreover, a high level of recruitment that maintains adult populations. The experimental controls carried out between 1998 and 2003 have shown that, despite high densities of predator fish, the two communities and their boundaries remain constant over large periods of time. The observed dynamics and the persistence of boundaries between the two types of community fit well with the model proposed by Ballesteros of the organisation of Mediterranean algal communities (Ballesteros 1994): the stable co-existence of different types of community under the same environmental conditions is possible. In this case, the herbivorous sea urchins provide the mechanism for transition between communities.

According to Ballesteros' model, these two stable states may alternate trough time. Although in our case we do not know the causes of changes, we do have evidence to suggest that the barrens and forests may well alternate, since we have observed barrens being recolonised, as well as small and expanding barrens in the middle of forests. On the one hand, the change from meadow to white patch would seem to be the result of a combination of an exceptional period of settlement and low levels of predation. On the other hand, the opposite change – from white patch to meadow – in theory will be caused by high mortality in sea urchins leading to a move towards mature forests. Although they are not very frequent, massive sea urchin mortality does sometimes occur, be it due to disease or strong storms (Boudouresque et al. 1980, Azzolina 1983). Eradication experiments have shown that the disappearance of sea urchins will lead to a relatively quick (three years) recovery of *Cystoseira balearica* forests.

It is harder to answer the question regarding the dynamics between these two supposedly stable states: is this a reversible cyclical process operating on a stable and manageable scale?, or are we going to have to confront an irreversible increase in the extension of barrens? The answer probably lies in the temporal and spatial scales at which the problem is tackled. Sea urchins have a very rapid demographic dynamic (high reproductive capacity, quick growth and short average generation length), long-distance spatial dispersal capacity (from tens to hundreds of kilometres), and high grazing rates, all of which translates into a great capacity for the transformation of algal communities. Algae belonging to the genus *Cystoseira*, for example, have slow demographic dynamics: their perennial tissues grow slowly, they live for a long time, they presumably have low reproductive capacity and, in what is probably the most important difference, their propagules have very limited dispersal capacities (perhaps just metres or tens of metres).

In a system in which the barrens are small (1 – 100 m) and where algae can recolonise via propagules, the two communities may alternate. However, if the barrens become too big, they may reach a critical size beyond which *Cystoseira* cannot recolonise by sexual dispersion.

Question 7: Strategic algal groups and the development of barrens

It is worth analysing why, if experimental conditions in terms of fish density (high biomass) and sea urchins (16-20 individuals/m^2) were more or less the same, extensive barrens occurred in Scandola but not in the enclosures in the Medes islands. Possibly the answer lies in the nature of the species that constitute the respective algal communities and in their resilience to grazing disturbance. It should be pointed out that algal communities in Scandola are dominated by an erect perennial alga (*Cystoseira balearica*), whereas the algal community on the Medes Islands are constituted by a greater variety of erect or filamentous ephemeral algae.

In reality, forests and barrens are merely two extreme stages in a more complex successional series that, albeit very distinctive, are in fact quite exceptional in the Mediterranean today. Verlaque (1987) defined at least one other type of community dominated by erect, seasonal and short-lived species that forms an intermediate stage between these two communities. These erect species, dominant in the Medes islands, take advantage of pulsations in nutrient availability and thus have markedly seasonal cycles.

From the point of view of life strategies, these species belong to a group of algae that Littler and Littler (1980) defined as opportunists. They are typically short-lived, fast-growing rapid colonisers and have simple forms and a high calorific content. Opportunist algae may use their rapid growth, undoubtedly greater than the biomass lost to predation, as an escape route from predators. They also synchronise with other species so that growth takes place during a short period, thereby offering an excessive amount of vegetal biomass (what Littler and Littler call escape by satiation). Thanks to these attributes, these species seem adapted to survive relatively high herbivore grazing pressure in seasonal environments where they can take advantage of nutrient and light peaks to grow quickly. This type of intermediate community may not represent a climax situation, but will still have a certain structural and specific complexity that is much greater than that of the barrens.

Looking from this point of view, barrens, intermediate communities and *Cystoseira* forests correspond to three successional levels with different tolerances to herbivore grazing. If we compare this situation with the model for terrestrial vegetation developed by Grime (1977), these three types of community could correspond to the three strategies defined by this author (Verlaque 1987, also reached this conclusion). Firstly, we have the ***Competitive Strategy*** (C) which would correspond to the *Cystoseira* forests, since they represent the final successional stage and are made up of long-lived species that compete and dominate under stable conditions. Secondly, the species present in barrens are ***Stress tolerant*** (S), since they are adapted to constant pressure from herbivores and in these particular conditions are favoured despite the presence of other, competitively superior species. Thirdly, the intermediate stages will correspond to the ***Ruderal strategy*** (R) that is present in pre-climax successional stages dominated by erect species of a certain complexity that are less competitive but more resistant to herbivores than *Cystoseira* species are.

Despite being totally insufficient for tracing successional sequences, the evolution of the enclosures - in which sea urchin numbers were manipulated for almost three years - did show some tendencies of changing dominance in algal strategies that were completely in line with Grime's successional model. Thus, we have observed that a moderate density of sea urchins provokes a substitution of species of the type C by those of type R that, despite their structural complexity and specific variety, are better adapted to greater herbivore pressure. High densities of sea urchins favoured a proliferation of incrusting algae of the type S at the expense of types C and R. The opposite occurred in enclosures with no sea urchins, where the frequency of C-type species increased in detriment of S-type species.

Question 8: How can we combine all these results in a coherent context?

It is tempting to try and arrange all these fragmentary results in a single, coherent context. We are looking in the different areas studied (Medes Islands and Scandola; we could, however add other areas for which we also possess data such as Port-Cros, Balearic Islands, Cabo de Palos, and so forth) for a general model that will enable us to explain the differences observed in the outcome of 'algae-sea urchins-fish' interactions on the basis of the processes analysed in our work rather than on the basis of differences associated with geographical distance. Here I find that there is a temporal dimension missing that as yet we have not analysed: the part played by recent ***history*** in the current state of these communities.

The lack of historical work or palaeo-ecological descriptors that deal with the infralittoral ecosystems of the Mediterranean means that we have to speculate as to what these communities were like in the recent past (Sala 2004).

Despite all the difficulties, sufficient evidence exists – albeit rather disperse – to suggest that the algae of the genus *Cystoseira* were more widespread in the 20th century than they are now. In the few phytosociological investigations carried out before the invention of the scuba diving, some authors (Sauvageau 1912, Feldmann 1936, Gros 1978) described the algal communities at Banyuls de la Marenda, including more than 10 *Cystoseira* species described as common. These authors described the community of *Cystoseira spinosa* as dominant on all the rocky bottoms around this locality. According to a recent investigation (Tibaut and Ballesteros in prep), only 5 species of *Cystoseira* species still remain in the locality and the once extensive communities of *C. spinosa* have completely disappeared. We suspect that sea urchins have played a significant (although possibly not exclusive) role in this regression.

More precise evidence comes from the Port-Cros Natural Park in France, where, during the 1970s, an increase in the number of sea urchins led to the elimination of the local populations of *Cystoseira* cf. *caespitosa* (Augier and Boudouresque 1975). Between 1982 and 1983 there were high levels of mortality amongst sea urchins that left populations at similar levels to the 1970s (Azzolina 1983). Despite this decline in sea urchins (from which numbers have not yet recovered; unpublished pers. obs.), populations of *C. caespitosa* have not yet recovered, probably because of a lack of a focus of dispersion.

Other evidence suggests that there was a widespread disappearance of *Cystoseira* forests throughout the Mediterranean (Giaccone 1971, Katzmann 1974, Gros 1978, Augier and Boudouresque 1967, 1970a,b, 1976, Mastaller 1974, Zabodnik 1977, Torunsky 1979, Verlaque and Nédelech 1983) during the 1970s and subsequent years coinciding with unchecked episodes of sea urchin proliferation.

Even more speculative is the affirmation that anthropic activities may have played a significant role in the recent regression of Mediterranean populations of *Cystoseira*. A number of different mechanisms could explain this disappearance and in at least one (and possibly more) cases sea urchins are involved.

Some authors (e.g. Sala et al. 1998, Sala 2004) maintain that, during the last 500 years there has been an increase in fishing in the Mediterranean (as along all coastlines) that has led to declines in littoral predatory fish populations and, owing to the cascade effect, a subsequent increase in sea urchin populations (Sala et al. 1998). This increase in sea urchins will have led to a degradation in *Cystoseira* communities and a move towards barrens or intermediate communities, in which seasonal species or species adapted to herbivore pressure dominate.

On the other hand, the increase in the human population around the Mediterranean coastline has caused an increase in organic contamination (sewage, agricultural fertilisers, etc.). This pollution may have acted as fertiliser in coastal waters in the Mediterranean and provoked changes in different ways in algae-sea urchin interactions (Sala et al. 1998).

Sea urchins may increase their fitness if waters become eutrophic: the amount of material ingested increases, be it due to the greater nutritional content of algae they consume (Hemmi and Jormalainen 2002), to direct absorption of the particles of organic material that fall as sediment on the algae, or by direct absorption (Régis 1977). By ingesting more organic material the sea urchins can grow more, produce more gametes and survive longer as adults. Increased eutrophication leads to a greater productivity of phytoplankton and thus better feeding and survival conditions for planktonic larvae (López et al. 1995) and, in turn, increased recruitment and higher densities of sea urchins. Moreover, if feeding conditions are better, sea urchins have to move less and thus avoid the dangers that moving presupposes.

However, greater nutrient levels may also play a significant role in the substitution of perennial algae by competitively superior seasonal algae. Perennial algae are better equipped in oligotrophic environments since they possess mechanisms to survive during seasons in which nutrient availability is limited (storage organs, growth pauses, etc.). Seasonal algae, on the other hand, function as opportunists and grow above all during spring, the time of year when the combination of light and nutrient availability is greatest: when environmental conditions are not favourable, they are unable to survive. When there is an increase in the availability of nutrients, however, competitive relationships between the two type of algae change and favour seasonal species of algae.

In conclusion, our hypothesis is that the different combinations of ‘algal communities-sea urchin populations-fish populations’ observable in various localities in the western Mediterranean today can be explained as different phases in a successional process in which anthropic activities such as overfishing and organic contamination play a key role. This role can be described as that of a historical axis, whereas regional climatic and trophic conditions (bottom-up) represent another principal axis. The size of sea urchin populations, whilst not being independent of either the first or second axes, can be thought of as a third axis that brings together the immediate structural force of the top-down factors.

In this model **Cystoseira forests** with low densities of sea urchins represent a climax community in regionally oligotrophic coasts (such as those of the Mediterranean islands) unaffected by organic contamination or overfishing. A good example of this community can be found in the Scandola Natural reserve in Corsica.

The **intermediate communities** made up of erect or mat-forming seasonal species represent a secondary successional state that has appeared in response to historical episodes of sea urchin proliferation and the disappearance of *Cystoseira* communities in regionally more eutrophic zones (continental coasts near river mouths), and/or overfished zones. Examples of these intermediate communities are common all along the Catalan coast and in the south of France and even in the marine reserves of the area (Medes Islands, Port-Cros).

Barren communities represent the most extreme case of disturbance and successional regression in algal communities and are a response to a current episode of sea urchin proliferation caused by a combination of overfishing and organic contamination or by just overfishing. This may occur in all the oceanographic regions of the Mediterranean, although tend to be more common in oligotrophical regions (central Mediterranean islands and southern coastline) subject to a history of overfishing.

The **existence of a geographical gradient of these successional conditions** can be predicted in the axis which runs from the continental coastlines enriched by river mouths and densely populated since antiquity, to the Mediterranean islands untouched by continental pollutants and traditionally all but uninhabited (for example, Cabrera).

These axes represent, moreover, **a historical sequence** - at the moment irreversible – in which the last few enclaves of *Cystoseira* forests are being damaged by expanding sea urchin populations benefiting from both their ability to disperse and the favourable modification of production (bottom-up) and trophic conditions (top-down) caused by anthropic action.

The **Medes Islands,** which might constitute an **exception** where this regional successional process could be inverted, have neither the capacity to control sea urchin populations (problems of scale and the existence of refuges) or the ability to achieve natural recolonisation by algae of the genus *Cystoseira* owing to the excessive distance from potential dispersal foci.

Question 9: How can our findings be applied to the management of Mediterranean infralittoral communities?

As a result of the combined effects of overfishing and anthropic contamination, ruderal communities dominated by seasonal algae, as opposed to barrens or forests, may currently be the dominant communities in the Mediterranean. *Cystoseira* forests are an endangered relic that are only present in the least populated areas (tipically islands) where both organic pollution and fishing are weaker. Given that *Cystoseira* forests, the most mature and best structured communities, harbour the greatest biodiversity, their conservation and recovery should be a priority in the management of the Mediterranean littoral. All those protected areas that still contain extensive communities dominated by species of the genus *Cystoseira*, have a special responsibility to promote in some way the recovery of these communities.

The lessons that we can derive from our work may be a positive step towards achieving this objective.

Thus, if we look back at the predictions of the deterministic models such as that produced by MacClanahan and Sala (1997), we may conclude that we should not expect them to work on the small scale of a marine reserve or on a temporal scale as short as that of a single scientific survey. Rather, they work best for a model on a meso-scale (or, for example, for the whole of the western Mediterranean basin) with a sufficiently broad temporal scale (at least a number of decades). At the scale of a marine reserve, we should not forget that despite recoveries in fish populations, the existence of refuges, trophic conditions (natural or anthropic) and the disproportion between the dispersal scales of the sea urchins and the size of the reserve all work against controlling sea urchin populations. The attempts to eradicate sea urchins in the Scandola reserve show that a quick reversion to original communities is possible if there is a nearby focus of algal recolonisation and if fish populations have recovered. Although we have not yet studied the effort needed to control sea urchin populations, the persistence of the positive results of a single eradication programme carried out four years ago makes us think that the techniques of sea urchin removal should be applied to more extensive areas if neighbouring populations are not too dense and do not represent a potential source of continual larval invasions. This recommendation is especially directed at the protected areas that still harbour valuable algal populations and show signs of the appearance of barrens.

Future research

This study has answered some questions, but also originated many new ones. The following are some of the most important in order to understand the organization of the Mediterranean rocky infralittoral.

Define functional groups by integrating criteria based on morphology, seasonality and resistance to herbivores

To understand better the response of herbivores within a seasonal framework and to be able to compare the effects at different biogeographical scales possessing different specific compositions we must be able to group species into functional groups defined by criteria based on morphology, seasonality and resistance to herbivores. Following the model proposed by Littler and Littler (1980), we should try and distinguish between different species or groups of species within limits ranging from opportunists to terminal successional states in order to try and see what effects herbivores have. The problem that we have to overcome is how to establish the criteria for groupings that will be applicable to other communities and will respond in the same way to different factors (herbivores and seasonality) that control them. At the moment, the most widely accepted functional groups (for example, Littler and Littler 1984, Steneck and Dethier 1995) do not seem to be well adapted to Mediterranean communities. Thus, if we accept that the main factors to take into account are herbivore pressure and seasonality, we must find a grouping that makes morphological criteria compatible with seasonal and life-cycle criteria. The most promising way forward may well be that of mixing

Grime's response-to-aggression criteria, morphological criteria such as those proposed by Steneck, and Ballesteros' seasonality criteria. In this way, groupings could be established in different types of community that respond in the same way to herbivore pressure and to bottom-up controls in production.

The dynamics of algal populations

We have quite a good idea of the dynamics of sea urchin populations, although we do not have all the relevant information for algae and, in particular, for climax species. Thus, we do not yet know much about recruitment rates, longevity, reproductive effort and propagule dispersal in the majority of species of algae.

Just as in managed woodland in terrestrial systems, this knowledge would allow us to evolve more precise criteria regarding conservation, since we could produce dynamic population models for the most characteristic algal species, predict the sea urchin carrying-capacity for each system, the critical size for barrens and even return periods.

The restoration of algal communities: the possibility of transplantation

It is essential that we find out more about the dispersal capacity of algae of the genus *Cystoseira* in order to evaluate the possibilities of restoring the forests of these species once they have been lost. There have been a number of attempts at this type of restoration and sea urchin eradication programmes must be seen as another way of preventing the destruction of algal colonies. Other attempts have been made to transplant plants that will act as a source of propagules to recolonise recently denuded areas. Although the debate as to what extent we should intervene in this process is still open, these first attempts are a starting point for designing action that will prevent the destruction of *Cystoseira* colonies and stimulate the recolonisation of barrens.

Competition between algae as a result of grazing by herbivores

The majority of studies into grazing that have been carried out so far have dealt with the effects of herbivores on single species of algae or on functional groups. However, we have noted that the competitive interaction between grazed species could play an important role in the specific composition of the community, above all if there are predators such as fish present, which will affect differentially, attacking some species of algae and not others. Thus, the interactions between grazing, as well as the competitive relationships between different species of algae (or functional groups), are subjects that thus far have been little studied; more knowledge of these fields would allow us to fine tune our models to a greater accuracy.

The effects of eutrophication

The role of eutrophication in the substitution of algal communities may be more significant than it appears at first sight since, as we have commented already, it may lead to the substitution of climax species by ruderal species. A simile can be drawn with tropical environments where, aside from the effects of sea urchins and overfishing, the importance of nutrients in the substitution of hermatypic corals by algae has been noted. Our hypothesis is still to be tested experimentally and there is a need to examine the correlation between the substitution of algal communities and eutrophication gradients throughout the Mediterranean.

The role played by eutrophication may vary according to local characteristics and in the Medes Islands, for example, various factors may have led to increased levels of eutrophication. On the one hand, increased population and tourism means greater amounts of sewage, while the proximity of the mouth of the river Ter, just a few kilometres from the islands, implies an significant input of continental eutrophic water into the sea in the area. Furthermore, the breeding colony of seagulls on the islands acts as a considerable source of material: the gulls feed away from the islands and all the organic material they eat ends up in the reserve in the form of excrements or carcasses that fall into the water. If we take into account the fact that the gulls are changing their feeding habitats and are consuming more and more human waste (rubbish tips, fishing waste, etc.), then this is another way in which humans are indirectly causing the eutrophication of the seas. We must find out to what extent the presence of the gulls affects the algal communities and the sea urchins in the area.

Population dynamics in sea urchins: is there a limit to recruitment?

During this work we have become well aware of the great potential that sea urchins possess for producing gametes. Notwithstanding, there are some areas in the Mediterranean where sea urchin densities are still low: these areas coincide in general with oligotrophic regions. Hypothetically, regions may exist in which a lack of resources limits the recruitment of sea urchins: in this case sea urchin populations would be controlled by recruitment levels. Thus, it is imperative that we investigate the reproduction, settlement and recruitment patterns in areas that are too isolated to be colonised by larvae from other populations.

The genetics of sea urchin populations

The dispersal of larvae and the interconnection of populations must be studied at genetic level. Although their great dispersal capacity in theory should lead to fairly homogeneous populations, studies of *Strongylocentrotus franciscanus* and *S. purpuratus* (Edmans et al. 1996 Moberg and Burton 2000) show that a certain structure does exist in the genetic make up of local populations, a discovery that suggests that under certain conditions sea urchin populations could maintain geographic heterogeneity.

Variability in settlement patterns at larger temporal and geographical scales

We have seen that at local scale settlement patterns exhibit great temporal and spatial variation. However, these observations have led to a series of questions that must be answered if we are to have a wider vision of the dynamics of sea urchin populations. For example, what factors act on an annual basis on sea urchin settlement patterns? We have accrued information regarding settlement on a local scale but not on a wider scale, and so we should aim to repeat settlement experiments in various parts of the Mediterranean (or at least in the northwest of the Mediterranean Basin) to test whether the heterogeneous pattern on a scale between tens and hundreds of metres is repeated on a meso-scale (kilometres to hundreds of kilometres). It would be very interesting to analyse the correlation between macro-scale data on settlement and environmental parameters and existing data on adult population densities.

Trait-mediated indirect interactions

Recent studies on terrestrial systems have brought to light how herbivore escape behaviour when confronted with carnivores can reduce grazing pressure as much as direct predation on herbivores does. Although there is some evidence of escape behaviour in sea urchins (taking refuge in crevices , etc.), no work has yet quantified its effects on algal communities. In our experiments we have observed how in the presence of fish sea urchins have less effect on some species of algae which have a certain importance in defining the composition of a community (for example, *Corallina elongata*), a fact that could be interpreted as an initial indicator of the importance of escape behaviour. We suggest that the significance of these effects, both quantitatively and qualitatively, be tested for different communities.

Applications for conservation

Aside from the simple knowledge of the workings of infralittoral systems from a naturalistic point of view, we should not lose sight of the use of this type of research in the management and conservation of these systems. We believe, as mentioned above, that the debate regarding whether we should intervene or not in marine ecosystems has still to be fully solved. In favour of the non-interventionist stance is the general lack of knowledge we have about the functioning of these systems. Nevertheless, we should try and begin to develop lines of work that will mitigate the undesired side-effects of anthropic action such as (probably) the proliferation of barrens and the subsequent loss of diversity. If we conclude that the man’s actions are causing this damage and that it must then be avoided or corrected, we must then have appropriate policies ready to be implemented. In the field of the restoration of submarine habitats there is a vast experimental field of work as yet untouched waiting to be tackled.

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Resum.

Dins el ventall d’especialitats en que s’acostuma a dividir l’ecologia, aquesta tesi s’enquadra en l’anomenada “ecologia de comunitats” (Diamond i Case 1986). Amb més precisió, el meu treball ha estat dedicat a investigar el grau en que les relacions tròfiques entre els organismes que formen una xarxa tròfica arriben a governar l’estructura i dinàmica de la comunitat que formen. L’aproximació es experimental i tot el treball s’ha realitzat al camp, basat en el que hom anomena “experiments naturals” amb les seves virtuts i inconvenients. L’ecosistema triat ha estat el bentos marí litoral, i en concret les comunitats de l’infralitoral rocós. Es tracta d’un marc de treball favorable, ja que aquest escenari ha produït algunes de les contribucions més importants a l’ecologia de comunitats, sobretot en el que fa al desenvolupament de la seva vessant experimental (revisat per Castilla 2000).

A causa d’aquests treballs precedents, una part dels objectius del meu treball no és estrictament novedosa, ja que han estat molt estudiats en altres mars (veure Castilla 2000 per a una revisió). Paradoxalment tractant-se del mar que ha estat el bressol de les ciències naturals (Aristòtil, cap el 350 a.C.) i de la invenció de l’escafandre autònom per Gagnan i Cousteau el 1944, la Mediterrània ha quedat en gran mesura fora de l’àrea on han tingut lloc els avenços de l’ecologia bentònica experimental. Tot i que confiem en l’universalitat de les descobertes més sòlides de l’ecologia de comunitats bentòniques, mai serà una precaució excessiva per al ecòlegs copsar la forma en que les particularitats regionals (la Mediterrània es un mar en molts sentits singular; Margalef 1985) modelen aquests principis generals.

A més, almenys en una part sí que les experiències d’ecologia bentònica mediterrànies participen de la més disputada actualitat, i és en el paper que hom pot esperar que realitzin les Reserves Marines o Àrees Marines Protegides (MPA’s) com eines de gestió racional d’uns ecosistemes massa castigats per l’acció humana. En aquest sentit el meu treball comparteix amb molts altres que es realitzen actualment el tret d’utilitzar les Reserves Marines com un dels tractaments experimentals estudiats i, per comparació amb el que succeeix a les zones properes no protegides, tracta d’esbrinar els seus efectes.

Per acabar de focalitzar el tema objecte de la meva tesi només cal afegir que el sistema estudiat és el que relaciona tròficament les algues macroscòpiques, com principals productors primaris del fito-bentos, amb els seus herbívors, que al bentos litoral mediterràni es poden simbolitzar en una espècie de garota de mar (*Paracentrotus lividus*) i un peix (*Sarpa salpa*), i amb el gremi de peixos omnívors entre els que es compten opcionals pasturadors d'algues i depredadors de les garotes herbívores. L'estudi aborda les interaccions entre tots els elements d'una comunitat complexa, i no només d'algunes espècies selectes, encara que, pel seu paper central, la garota *Paracentrotus lividus* ha concentrat més esforços que la resta. Al llarg de la memòria i per simplificar, parlarem sovint d'aquest "triangle" algues-garotes-peixos, que es descriu amb més detalls en l'Annex 1.

Crec que l'interès d'aquest treball pot ser doble. Més enllà del coneixement que pot aportar a l'Ecologia de comunitats l'estudi experimental de les interaccions d'una comunitat complexa en condicions naturals, els resultats tenen un clar interès aplicat per a la gestió dels litorals i per a la biologia de la conservació. És sabut que altes densitat de garotes poden provocar la regressió de les comunitats algals i una forta pèrdua de diversitat (que pot ser comparada als efectes de la desertització sobre la biodiversitat dels ecosistemes forestals). Estudiant experimentalment els mecanismes que regulen aquestes interaccions busquem aportar criteris vàlids per a la gestió. Un tema d'especial interès ha estat esbrinar quin paper han pogut jugar canvis d'origen antròpic, com els derivats de l'eutrofització o de la sobre-pesca, en la proliferació de les garotes i la regressió de les comunitats algals.

El marc teòric: Models tròfics en ecologia

Les causes (o els factors) que governen l'estructura i dinàmica dels ecosistemes han estat un dels temes recurrents de l'Ecologia de comunitats. Quan aquest tema s'ha plantejat des de la perspectiva del flux d'energia i les interaccions tròfiques, històricament s'han enfrontat dues línies (només en principi oposades): en essència, uns autors sostenen que els control de l'estructura i dinàmica de les comunitats esta determinat des de dalt de les cadenes tròfiques (top-down), pel control que n'exerceixen els depredadors, mentre que d'altres sostenen que tot el sistema està controlat des de baix (bottom-up) per les entrades d'energia.

Models de control TOP-DOWN

El de Hairston et al. (1960) és possiblement el treball seminal de la línia de pensament que defensa una regulació de les comunitats basada en el control dels depredadors. Aquest model explica que la Terra és verda, és a dir que la vegetació domina (en biomassa) a la majoria dels ecosistemes, perquè els carnívors limiten l'abundància dels herbívors; i aquest control redueix la pressió d'herbivoria, permetent el desenvolupament de les comunitats vegetals. En suma, prediu que són les interaccions entre els diferents nivells tròfics les que determinen la composició i abundància de les comunitats vegetals: els carnívors estarien regulats per processos de competència i els herbívors i plantes per depredació.

Models BOTTOM-UP

De seguida es va avivar la polèmica amb els defensors d'un model totalment oposat. Molts autors (i.e. White 1978, Hairston i Price 1992) sostenien que són les variacions en l'entrada d'energia al sistema, a partir dels productors primaris, i les posteriors limitacions termodinàmiques en les transferències d'energia al llarg de la xarxa tròfica, els factors que regulen la biomassa que pot sustentar cada nivell tròfic i, per tant, les que controlen l'estructura i dinàmica de l'ecosistema. En resum, el control ve de baix cap a dalt, limitat per la productivitat.

Models mixtes

L'oposició dels dos models com alternatives excloents va donar pas a visions més flexibles. En conseqüència, el model bàsic de Hairston i col·laboradors va ser modificat posteriorment per Fretwell (1977) i va ser formulat matemàticament per Oksanen et al., (1981), per tal d'incloure-hi les limitacions per baix. Aquest model mixt (Explotation Ecosystem Hypothesis) admet que la disponibilitat de recursos podia determinar el nombre de nivells tròfics. Com, fidel a les hipòtesis de “top-down” (control pels depredadors) aquest model prediu una alternança en la dominància de la vegetació o dels herbívors segons el nombre de nivells tròfics, en definitiva l'estructura de les comunitats estarà determinada per la productivitat del sistema.

Altres autors, reconeixent de que ambdós processos actuen simultàniament, varen desenvolupar la “Bottom up – Top Down hypothesis” (Mc Queen et al. 1986, 1989, De Melo et al. 1992), en la que suggereixen que els processos botom-up (competència) són més forts i dominen en els nivells baixos de les xarxes tròfiques i els processos top-down (depredacio) són els que dominen als nivells més alts.

A partir de treballs experimentals, Menge i Sutherland (1976, 1987) i Menge i Olson (1990) implementaren aquest model en el terreny de l'ecologia bentònica. Hi introduïren les pertorbacions físiques i varen descriure com variava la importància dels processos que regulen les comunitats al llarg de gradients ambientals.

Cascades tròfiques: evidències del control "top-down"

Una extensió lògica de la hipòtesi de Hairston et al., (1960) de control de la comunitat per la depredació, és la transmissió d'una ona d'efectes de dalt cap a baix al llarg de qualsevol xarxa que tingui tres o més nivells tròfics. La ona es manifestaria en la correlació positiva entre les biomasses de dos nivells tròfics no contigus sinó separats per un entremig, amb el que la correlació seria negativa (dit de forma simplista, en la correlació positiva entre els nivells que ocupen respectivament posició parella o senar a la xarxa tròfica). És el que es va anomenar la cascada tròfica i que de manera molt intuïtiva s'explica pel vell aforisme que diu "enemic de enemic, amic". En un estil més formal, la Cascada tròfica es defineix com la propagació de mutualismes indirectes entre nivells tròfics no adjacents en una xarxa tròfica (Schoener 1993, Menge 1995).

L'existència de cascades tròfiques constituiria la evidència més observable del control top-down de les comunitats. En conseqüència, els ecòlegs es varen interessar per la demostració experimental de l'existència de cascades a diversos ecosistemes, sense que aquestes recerques hagi donat el consens esperat. Les primeres evidències provenen dels sistemes bentònics intermareals amb els treballs de Paine (1966, 1974). Als sistemes limnètics, els experiments d'exclusió de peixos en la cadena peixos-zooplancton-fitoplancton varen donar moltes evidències d'aquestes cascades tròfiques tant en llacs, (Carpenter et al. 1985, 1987, Leibold et al. 1997, Power et al. 1985, Brett and Goldmann 1997) com en rius (Power 1990, 1992, Rosemond et al. 1993) o basses temporals (Cochran-Stafira and von Ende 1998, Hulbert and Mulla 1981).

Posteriorment s'han descrit efectes de cascades en sistemes terrestres a nivell de ocells-insectes-plantes (Atlegrim 1989, Marquis i Whelan 1994), Aranyes-insectes-plantes (Schmith et al 1997, 2000, Carter i Rypstra 1995), llangardaixos - insectes -

plantes (Chase 1998), llops-ants-abets (McLaren i Peterson 1994), nematodes parassits-orugues-arbustos (Strong et al. 1996).

Malgrat totes aquestes evidències, no s'ha demostrat que les cascades tròfiques sigui un fenomen universal. Alguns autors sostenen que es produeixen en sistemes molt concrets, molt productius, amb baixa riquesa específica i unes connexions tròfiques molt lineals i amb una baixa heterogeneïtat espacial (Strong 1992, Polis i Strong 1996, Persson 1999). Altres autors han suggerit els mecanismes que podrien compensar o eliminar aquestes cascades, entre els quals destaca el paper de la omnivoria (Dihel 1993, Agrawal 2003).

Cascades tròfiques en sistemes marins

Les relacions tròfiques entre coralls o algues bentòniques, les garotes que són els principals herbívors i els depredadors de les garotes (és a dir, el sistema algues-garotes-peixos objecte d'aquest estudi) han proveït algunes de les millors evidències de cascada tròfica als sistemes marins. Com quedarà pales al llarg de la memòria, l'explicació cal buscar-la en el paper singular de les garotes que són uns potents herbívors capaços de modificar completament les comunitats algals, i que, alhora, estan controlades pels seus depredadors.

L'estudi d'aquestes relacions ha constituït una línia clàssica en ecologia marina (reviews: Laurence 1975, Lawrence i Sammarco 1975, Schiel i Foster 1986, Sala et al. 1998, Pinnegar et al. 2000). La problemàtica es començà a debatre durant els anys 70 en els mars temperats de EEUU, on proliferacions de garotes denudaren grans extensions de boscos de macroalgues, transformant-les en comunitats dominades per algues calcaries incrustants (Lawrence 1975, Bernstein et al. 1981). Aquest canvi de comunitat comportava una gran pèrdua estructural i de diversitat, ja que, a més dels mateixos kelp, la fauna i flora associada també desapareixia.

Es va identificar la desaparició dels depredadors (lludrigues marines) com la causa de la proliferació de garotes. Degut a que les garotes estaven controlades pels seus depredadors, la caça excessiva de llùdrigues va fer augmentat les poblacions de garotes, incrementant així la pressió d'herbivoria sobre les comunitats algals.

Treballs procedents d'altres mars temperats han demostrat que, amb petites variacions, aquests mecanismes funcionaven de manera molt similar amb diversos tipus de depredadors de les garotes, com llúdrigues (Estes i Palmisano 1974, Estes at al. 1978, Estes at al. 1998, Breen et al. 1982, Duggins 1988), peixos (Sala 1996, 1998, Tegner i Dayton 2000, Shears i Babcock 2002 2003) o llagostes (Mann i Breen 1972, Mann 1977). També tenen un funcionament similar als mars tropicals amb peixos com depredadors, garotes i coralls hermatípics com productors primaris (McClanahan i Mutiga 1989).

Models quantitatius i el paper de l'home

Les prediccions dels models tròfics "top-down", i en concret, els efectes de les cascades tròfiques, adquireixen una gran rellevància vista la importància de l'home com depredador culminal de tots els ecosistemes litorals (Vitousek et al 1996, Jackson i Sala 2001, Jackson et al. 2001).

A fi de predir els efectes de l'activitat antròpica i proveir criteris de gestió costera, s'han desenvolupat models deterministes quantitatius basats en les hipòtesis de control "top-down" i en la lògica del model depredador-presa de Lotka-Volterra (Margalef 1974). Aquests models (McClanahan 1992, McClanahan i Sala 1997) prediuen diferents estats terminals en l'estructura i dinàmica de les comunitats algals en funció de l'activitat humana, que, per efectes en cascada, controla l'abundància de depredadors que poden exercir el control dels herbívors. En els extrems, perfilen dos estats oposats : 1) sistemes no sobrepescats, amb abundants depredadors que controlen les garotes, i exhibeixen comunitats algals ben desenvolupades; i 2) sistemes sobrepescats amb altes densitats de garotes i comunitats algals de sobrepastura, dominades per algues calcàries incrustants i altres espècies efímeres.

A més de descriure aquests dos estats terminals, aquests models prediuen les condicions que propicien el pas d'un estat a un altre: l'augment de la pressió de pesca provoca la desaparició de depredadors i produeix una degradació de les comunitats algals a través de l'augment dels herbívors; i a l'inversa, la creació d'àrees protegides que possibiliten una recuperació dels depredadors, permetria el control de les garotes i el pas de zones sobrepasturades a comunitats algals ben desenvolupades.

Perspectiva i reptes a l'inici d'aquesta tesi

Tot i la gran quantitat de treballs que s'han realitzat sobre aquest sistema d'interaccions al Mediterrani, encara ens manca informació per a tenir una visió complerta del funcionament d'aquestes comunitats. Aquesta tesi s'ha focalitzat en els punts que, des del meu punt de vista, restaven menys explorats:

1) Incompliment de les prediccions dels models tròfics en el Mediterrani:

En molts indrets del Mediterrani, durant els anys 60-70, va haver un augment considerable de les poblacions de garotes, que denudaren la cobertura de comunitats algals, dominades majoritàriament per espècies del gènere *Cystoseira* (Giaccone 1971, Katzmann 1974, Gros 1978, Augier i Boudouresque 1967, 1970a,b, 1976, Mastaller 1974, Zabodnik 1977, Torunsky 1979, Verlaque i Nédelech 1983).

Com hem vist en l'apartat anterior (Annex 1), els models tròfics que descriuen la dinàmica de les comunitats algals al Mediterrani (McClanahan i Sala 1997) ja prediuen aquesta transformació. L'atribueixen a una reducció dràstica en la densitat dels peixos deguda a la sobrepesca, que permetria un gran desenvolupament de les poblacions de garotes.

Però els mateixos models també prediuen que una recuperació de les poblacions de depredadors pot invertir aquest procés. Es a dir, que en llocs com les reserves marines on les comunitats de peixos estan ben desenvolupades, aquests últims podran controlar les poblacions de garotes i retornar els blancalls a l'estat de comunitats ben desenvolupades.

Tanmateix, existeixen nombroses evidències de una vulneració d'aquestes prediccions. D'una part, l'aparició i extensió de blancalls en zones amb altes densitats de peixos com a les reserves marines; s'en poden trobar exemples a tots els espais protegits de la Mediterrània, des dels més antics com el Parc Nacional de Port-Cros (Var, França), la Reserva de Banyuls-Cerbère (França), alguns punts de l'espai protegit de les Illes Medes (Catalunya), o la Reserva Natural de Scandola, a Còrsega (veure el capítol 8), fins a espais de més recent creació, com la Reserva Marina de Ustica (Sicilia), el Parc Nacional de Cabrera (Illes Balears), la Reserva Marina de Cabo de Palos-Islas Hormigas (Murcia), o el Parc Marí internacional de las Bouches de Bonifacio (Corcega-Serdenya). Tampoc són rars els exemples de zones fortament pescades i tanmateix proveïdes de comunitats algals molt ben desenvolupades.

En definitiva, les prediccions d’aquests models, no acaben d’ajustar-se a la realitat de la Mediterrània NW. En el millor dels casos hem d’acceptar que existeixen altres factors no considerats en els models que juguen un paper decisiu per a entendre la composició i dinàmica de les comunitats algals (Sala et al. 1998). Un repte important de la meva tesi ha estat explorar aquests factors.

2) Limitacions metodològiques dels treballs experimentals precedents

Tot i que la major part de les interaccions tròfiques objecte d’aquest estudi ja han estat investigades experimentalment als ecosistemes mediterranis, el disseny simplificat, o excessivament breu dels experiments fa sospitar que alguns dels resultats obtinguts podrien ser diferents a escales espaials i temporals mes grans.

Alguns dels problemes dels protocols experimentals emprats en el passat són:

1) Mida excessivament reduïda de les gàbies i tancats utilitzats en la manipulació de les densitats de depredadors i preses, que poden produir artefactes; entre els més freqüents es troben, l’efecte de refugi per als invertebrats, o d’acumulació de sediments (detallat a Kennely 1991).

2) Dissenys experimental anteriors no van analitzar l’efecte relatiu dels peixos i les garotes; aquesta exigència també es troba condicionada, encara que indirectament, a l’ús de tancats de grans dimensions com els que es fan necessaris per a controlar les densitats de peixos i de garotes conjuntament.

3) S’estudia la resposta de les algues a l’herbivoria en sistemes d’interaccions simplificades espècie-espècie, o a nivell de **grups funcionals** (erectes-turfs-blancalls), però rarament a nivell de tota la comunitat algal. Això és degut a la gran diversitat fitobentònica mediterrània que fa del monitoreig de les algues a nivell de comunitat un aspecte no ben resolt (però veure Sala i Boudouresque 1997). Tanmateix, no podem oblidar les relacions de competència entre les algues, que poden acabar donant respostes molt diferents a les resultants del simple efecte dels herbívors. Això es farà més patent sempre que els herbívors siguin selectius. Alterant les relacions de competència entre les diferents espècies d’algues, els herbívors poden produir a nivell de comunitat efectes de facilitació (com el mostrat per Sala i Boudouresque 1997) o de inhibició que serien insospitables en experiments simplificats d’efectes d’herbivoria entre parells d’espècies.

4) L’estacionalitat, que altera la composició i la dinàmica de la comunitat, i la relació entre les espècies d’algues, no pot ser aïllada adequadament de l’efecte dels herbívors. La interacció entre herbivoria i estacionalitat pot resultar en un emmascarament o un reforçament dels efectes dels herbívors.

5) La durada de previs experiments fou breu i no van poder integrar les oscil·lacions estacionals ni tendències de canvi a llarg terme.

El punt de partida del meu treball va ser la tesi que Enric Sala va desenvolupar en aquest mateix lloc (Illes Medes) i en el mateix ambient (comunitat infralitoral entre 5 i 10 m de fondària) (Sala 1996). Tot i que el treball de Sala va constituir una contribució fonamental per a entendre el funcionament d’aquest ecosistema, el seu disseny acusava alguna de les limitacions referides més amunt al temps que plantejava aspectes nous que calia investigar de forma experimental o canviant les escales d’experimentació.

En aquest treball he volgut abordar un disseny experimental a escales espaials de 10-100s m^2 i durant 3 anys, amb la idea de esbrinar quins són els factors que podrien ser responsables de les desviacions de la resposta predita pels models tròfics precedents. Per a això, he instal·lat **tancats de grans dimensions** a la Reserva Marina de les Illes Medes per controlar les densitats de peixos i de garotes, i he fet un **seguiment a nivell pluriespecífic** de les comunitats algals naturals in situ al llarg de tres cicles de producció, per tal d’ integrar l’efecte de l’estacionalitat i veure efectes sinèrgics que els estudis a petita escala poden emmascarar. En especial m’he proposat determinar experimentalment els efectes que tenen **per separat i conjuntament les garotes i els peixos** sobre les comunitats algals. Per últim, he posat l’èmfasi en els mecanismes que controlen la dinàmica de les poblacions de garotes, com l’assentament, la depredació i les migracions, i en especial els processos que regulen les poblacions dels juvenils.

Objectius i resultats principals:

Les interaccions entre els organismes d’una comunitat situats a més de dos nivells tròfics diferents, tot i constituir un tot indestriable, presenten vàries perspectives superposades, i el seu estudi ha de ser desglossat en diferents objectius concrets que inevitablement s’han de presentar de forma seqüencial.

Aquest treball està estructurat des de baix cap a dalt, seguint l'ordre que ens marca la situació de les diferents organismes en la xarxa tròfica. Així, l'estructura i el cicle de producció de les algues i la seva interacció amb els herbívors serà el primer que tractarem. Desprès abordarem la dinàmica poblacional de les garotes, identificades com els principals herbívors. I dintre dels factors que controlen aquesta dinàmica estudiarem la mortalitat de garotes induïda pels peixos carnívors i la capacitat de l'home de revertir les relacions entre herbívors i algues fomentant la recuperació de les poblacions de peixos o eradicant directament les garotes.

1- Control "top-down" o "botom-up" de les comunitats algals de l'infralitoral mediterrani, o l'efecte dels herbívors sobre les comunitats algals en un marc estacional

Les comunitats algals Mediterrànies s'han estudiat tradicionalment des de dues perspectives que fins al moment s'han tractat com problemàtiques independents. Per una part, molts especialistes de l'ecologia de les algues mediterrànies (veure Ballesteros 1991, 1992, Sant 2003 i treballs allí referenciats) estudien l'estructura i dinàmica de les comunitats algals en relació amb les limitacions fisiològiques que imposa el medi, es a dir, assumint un control "per baix" de les comunitats. Per altra banda, els models tròfics deterministes (com el de Maclanahan i Sala 1997) pretenen explicar el control de les comunitats algals "per dalt", com el resultat de les relacions biòtiques de depredació dels nivells tròfics superiors.

Però aquesta separació representa una simplificació excessiva (explicable per les limitades capacitats experimentals) de la realitat, que reclamaria estudiar l'estructura i dinàmica de les comunitats algals considerant alhora les dues perspectives (seguint el precedent de Verlaque (1987). De fet, el més probable és que aquests dos tipus de factors actuïn simultàniament, i és esperable que no siguin independents, sinó que hi hagi algun tipus de interacció, de forma que uns processos modulin els altres. Per exemple, l'efecte conjunt de les condicions climàtiques (variables a les diferents èpoques de l'any), de les diferents estratègies de les algues (perennes, estacionals, oportunistes), dels diferents tipus d'herbívors, o de la naturalesa omnívora del gremi de peixos donarà respostes que possiblement no es detectarien en experiments en els que cadascun d'aquests factors s'analitzes independentment.

Per a respondre a aquestes qüestions, vàrem plantejar un experiment que permetés:

1-integrar i discriminar l’efecte de les garotes i dels peixos herbívors,

2- integrar i discriminar l’efecte del gremi de peixos omnívors, com a herbívors i com a depredadors de les garotes,

3- englobar i analitzar porcions representatives de les comunitats algals i evitar els “efectes de paret”, el que suposava augmentar l’escala espacial dels tancats,

4- distingir l’efecte dels herbívors de les variacions estacionals intrínseques de les comunitats algals, el que demandava allargar l’experiment durant un període de temps suficientment llarg (plurianual).

El **segon capítol** de la tesi presenta els resultats d’aquest experiment d’avaluar simultàniament l’efecte de l’herbivoria (“top-down”) i l’efecte de les condicions climàtiques (“bottom-up”) sobre la dinàmica i l’estructura de les comunitats algals. Aquest experiment va exigir un gran esforç ja que durant quasi 2 anys i mig, que és l’interval que separa tres fases de producció consecutives (un període suficientment llarg com per a integrar l’estacionalitat dins els efectes dels herbívors), vàrem tancar amb xarxes verticals tres petites cales de la Reserva Marina de les Illes Medes, de forma que els peixos no hi poguessin accedir; dins i fora de cada tancat vàrem manipular densitats de garotes i vàrem realitzar controls mensuals de les comunitats algals “in situ” considerant les més de 40 espècies que podien ser monitoritzades visualment. Degut a l’esforç que implica i per la multiplicitat dels factors estudiats, aquest capítol constitueix la part central d’aquesta tesi.

La majoria d’algues varen mostrar un marcat pic anual de biomassa a la primavera, i un mínim a l’hivern, seguint el patró estacional de disponibilitat de nutrients i llum. Estudis previs indiquen que els pics de biomassa algal estàn seguits per una major bioassa d’epifauna invertebrada invertebrats. Aquests resultats indiquen un imnportant control dels processos que limiten la producció (i.e. bottom-up).

Les garotes varen reduïr considerablement la biomassa total d’algues, eliminant-ne la majoria, tot i que afavoreixen, mitjançant un procés de facilitació, espècies oportunistes i calcàries incrustants, indicant així un control pels nivells tròfics superiors (i.e. top-down).

La presència de peixos va tenir efectes diversos. Per una part, com a herbívors, el seu efecte sobre les algues va ser significativament menor que el de les garotes. Però la presència de peixos depredadors va provocar que l'efecte de les garotes fos menor, probablement per un efecte de inhibició comportamental.

Els anàlisis multivariants ens indicaren que la interacció entre les variacions estacionsals de la disponibilitat de nutrients i llum i l'efecte de la herbivoria induïen a la formació de quatre tipus de comunitats algals. En un espai multivariant, les comunitats algals amb i sense garotes, es movien en direccions oposades. Tot i aquesta tendència, totes les comunitats mostraven una oscil·lació que responia als cicles estacionals, dins de la trajectoria successional general.

Aquests resultats ens mostren que les comunitats infralitorals rocoses del Mediterrani estàn determinades per la interacció entre el control que exerceixen els nivells tròfics superiors i les limitacions ambientals en la producció de les algues: els processos top-down marquen una trajectoria successional en les comunitats algals, mentre que el control bottom-up produeix fluctuacions en la trajectoria successional marcada pels processos bottom-up.

Degut a l'exigència de no alterar les condicions dels tancats durant les tres temporades que va durar l'experiment, el capítol precedent abordava l'estudi de les algues mitjançant censos visuals que no permeten estimar ni la producció ni les pèrdues de biomassa a causa dels herbívors. Per tal d'obtenir mesures quantitatives de l'evolució de la biomassa i estimes de les taxes d'herbivoria vaig aprofitar el desplegament dels tractaments experimentals anteriors per a realitzar un experiment complementari basat en superfícies artificials sobre les que es poden trasplantar i manipular quantitats mesurables de certes espècies d'algues. Aquest experiment dedicat a quantificar l'efecte de les garotes i dels peixos herbívors i omnívors per separat, i també conjuntament, es va restringir a unes poques espècies degut a les restriccions metodològiques, i és objecte del **capítol 3.**

En aquest experiment es va comprovar un cop més que les garotes causaven el major efecte sobre les algues. L'efecte dels peixos com a herbívors va ser molt més moderat, tot i que més important del que cabria esperar, ja que en tots els casos varen causar una reducció de la biomassa. Sorprenentment l'efecte de les garotes i dels peixos no va ser additiu, sinó que va ser menor que el de les garotes soles, ja que la presència dels peixos va inhibir el seu efecte. Aquests resultats mostren un cop més l'efecte dràstic de les garotes i dóna més importància a l'efecte dels peixos en consumir algues. A més, ens mostren un efecte de facilitació en el que la presència de peixos depredador inhibeix l'efecte de les garotes per un comportament escapatori, fet que s'hauria de tenir en compte a l'hora de modelitzar el funcionament d'aquestes comunitats.

2- Processos que regulen les poblacions del principal herbívor, la garota *Paracentrotus lividus*

Degut a que les garotes del gènere *Paracentrotus lividus* estan considerades com el principal herbívors bentònic de l'infralitoral rocòs mediterrani, entendre la dinàmica de les seves poblacions és fonamental per entendre la dinàmica de tot el sistema. Les poblacions de garotes, com la majoria d'espècies, estan regulades pels processos de reclutament, mortalitat i migració. Tot i que els patrons generals d'aquests processos ja han estat llargament estudiats, encara hi ha factors (com per exemple l'espai i els refugis) l'efecte dels quals no controlem i/o encara no han estat adequadament considerats en els models, que podrien provocar els desajusts observats entre els models i la realitat. Hem fet un èmfasi especial en els processos que es produeixen en les primeres fases de la vida bentònica de les garotes (quan medeixen menys de 2 cm de diàmetre d'esquelet sense pues), ja que és l'aspecte menys estudiat de l'ecologia d'aquests animals i tenim raons per a sospitar que poden jugar un paper cabdal en la regulació de les seves poblacions.

Així, hem fet una sèrie d'experiments per a entendre millor els processos d'assentament (Capítol 4), la mortalitat per depredació en la fase de post-assentament (Capítol 5) i l'abast dels desplaçaments i les pautes de comportament lligatdes al moviment (Capítol 6). Per últim i com a complement als experiments anteriors, hem analitzat l'evolució durant una sèrie temporal llarga (12 anys) de la mida de dues poblacions de garotes (capítol 7).

2.1- Variabilitat en l'assentament:

En el **capítol 4** fem una descripció de les pautes temporals i espacials d'**assentament** de *Paracentrotus lividus* en el marc de una reserva marina i una zona no protegida.

Durant el seu cicle, les garotes tenen una fase planctònica de dispersió molt llarga que els permet colonitzar zones molt allunyades dels reproductors. Durant aquesta fase planctònica, les larves estan sotmeses a una sèrie de factors (disponibilitat d'aliment, mortalitat, dispersió passiva per corrents, eddies etc.) que poden provocar una arribada molt desigual al benthos. En conseqüència, l'assentament pot actuar com a factor desestabilitzador de les poblacions de garotes, ja que una forta variabilitat en la magnitud de l'assentament, pot provocar canvis en la dinàmica de les poblacions de garotes adultes. Per una banda, una limitació de l'arribada de larves pot limitar la renovació de les poblacions adultes (Underwood Fairweather 1989); però també s'ha suggerit que pulsos important d'assentament poden produir un augment en les densitats dels adults i provocar episodis de sobrepastura (Watanabe i Harrold 1991). Per altra banda, un patró d'assentament espacialment heterogeni pot provocar una forta heterogeneïtat en la distribució espacial de les poblacions de garotes adultes en una zona determinada.

Mitjançant col·lectors artificials que permeten estimar la força de l'assentament, hem fet un seguiment d'aquest procés en tres punts de la reserva marina al llarg de tres anys amb la finalitat de estudiar la seva variabilitat interanual. A més, altres dos experiments ens han permès determinar la variabilitat en les pautes espacials d'assentament, en el pla horitzontal i en l'eix batimètric respectivament.

L'assentament es va produir en un sol pic anual durant 3 setmanes entre Maig i Juny, i la variació interanual en la potència de l'assentament va ser de més de dos ordres de magnitud. Es va poder observar una elevada variabilitat en el patró espacial de l'assentament a una escala de desenes de metres. Ni el tipus de substrat, ni la major abundància de peixos depredadors, ni la densitat de les poblacions adultes no varen mostrar cap correlació amb la densitat d'assentats. No obstant, es va trobar una correlació amb el grau d'exposició a les onades i als corrents, indicant així que els processos físics són molt importants en determinar les pautes d'assentament de *Paracentrotus lividus*. El patró d'assentament en fondària va mostrar també un patró molt clar, essent més important a menys fondària (5 m). La forta heterogeneïtat espacio-temporal en l'assentament de *P.lividus*, i el desacoblament amb les poblacions adultes suggereix que la importància de l'assentament en determinar l'abundància de les poblacions adultes depèn d'altres factors difícilment predibles.

2.2- Paper de la depredació i dels refugis.

En el **capítol 5** estudiem el control que pot exercir sobre les poblacions de garotes la **depredació** dels individus més joves (post-assentats) per part dels peixos.

La depredació s'ha descrit com el factor de control més important per a les poblacions de garotes (Sala i Zabala 1996). Degut a la gran variabilitat en l'assentament de les garotes, només un control per part dels seus depredadors pot atenuar aquestes fortes entrades de reclutes. Es considera que els principals depredadors de *Paracentrotus lividus* són els peixos, i més concretament els espàrids *Diplodus sargus* per a les talles de més de 1 cm i petits làbrids, com *Coris julis,* per als juvenils (Sala 1997).

Però a més, la disponibilitat de refugis juga un paper important, i pot interaccionar tant amb la mida de les garotes com amb la dels seus depredadors.

Si tenim en compte que la major mortalitat de garotes es produeix durant el període de post-assentament (que segurament representa el cul d'ampolla de les poblacions), l'impacte demogràfic d'aquesta mortalitat poden ser quantitativament molt més important que la depredació en la fase d'adults, tot i que la pèrdua en termes de biomassa sigui insignificant.

Determinar quines són les espècies de peixos implicades en la depredació durant el període de post-asentament i la seva importància relativa, així com la relació de talles entre les garotes i els seus depredadors afecta aquesta interacció i com pot ser modulada per la disponibilitat de refugis (i.e. la complexitat estructural del substrat) és indispensable per a comprendre qui controla la dinàmica de les poblacions de garotes. L'interès és fa obvi en termes de gestió, si tenim en compte que l'impacte dels diferents tipus de pesca varia per a cada espècie de peix.

Les estimes més realistes de l'impacte de la depredació sobre les poblacions de garotes s'han basat en experiments de tethering, realitzats en condicions que encara resulten simplificacions excessives de la realitat i que poden exagerar la importància d'aquest factor. De fet, hi ha factors com la heterogeneïtat espacial o la disponibilitat de refugis que poden alterar, rebaixant-les, les taxes de mortalitat obtingudes en aquests experiments. Un fet que complica la consideració dels refugis és que els seus efectes també poden ser dependents de la talla, tant de les garotes com dels depredadors. Sospitem que tot i el seu caràcter secundari, aquests factors que modulen "indirectament" la mortalitat de garotes, podrien ser responsables de les discrepàncies observades amb les prediccions dels models; com per exemple, les elevades densitats de garotes a les Reserves Marines en zones amb abundància de peixos, o la heterogeneïtat en les densitats de les poblacions de garotes a zones homogèniament exposades a altes (Reserves) o febles densitats de peixos (costes no protegides).

El capítol 5 presenta diferents experiments que inclouen refugis i la talla de les garotes. L'efecte del refugi ha estat estudiat mitjançant substrats naturals amb un grau creixent de rugositat. A partir d'experiments amb garotes de talles diferents, en un rang que va de 2 fins a 10 mm de diàmetre de closca, hem determinat la relació específica i de talla entre les garotes i els seus depredadors.

Per a determinar l'efecte de la pesca i de les Reserves sobre la força de la depredació, hem fet estudis experimentals comparant la força de depredació dins i fora de la reserva.

La força de depredació sobre els juvenils de *P.lividus* va ser major amb densitats més elevades de peixos depredadors, i menor amb una complexitat estructural més elevada, tot i que la protecció proporcionada per la complexitat estructural disminueix amb la talla de les garotes. La depredació sobre les talles menors va ser produïda principalment per petits labrids, pincipalment *Coris julis* mentre que les talles majors varen ser consumides principalment per *Diplodus sargus.* aquests resultats mostren uns efectes en cascada produïts per la prohibició de la pesca en les reserves marines, i evidencien l'alt paper potencial dels petits peixos en el control de les poblacions de *P.ividus*.

2.3- Comportament i magnitud dels desplaçaments

En el **capítol 6** hem tractat de determinar a grans trets les pautes comportamentals de *Paracentrotus lividus* pel que fa al seu home-range, **desplaçaments** estacionals i moviments migratoris.

Tot i que són animals quasi sèssils o de poca mobilitat, els desplaçaments de les garotes, ja sigui com a resposta a la manca de recursos o a altres factors que no controlem (Palacin et al. 1997, Barnes i Crook 2001) poden alterar profundament l'estructura de les seves poblacions. Segons la seva magnitud i sentit, aquests moviments podrien contribuir a regularitzar (moviments denso-dependents de redistribució dels recursos) o a desestabilitzar (fronts migratoris) les densitats, i de retruc a evitar o promoure l'aparició de blancalls.

Per altra banda, i a més petita escala, el comportament escapatori de les garotes front a la pressió dels depredadors pot alterar el seu efecte d'herbivoria sobre les algues. S'ha constatat que les garotes eviten els depredadors amagant-se en esquerdes o sota les pedres o sota els adults reduint així el seu home range, i per tant, la superfície pasturada (Sala 1996, Sala i Zabala 1996). L'interès dels ecòlegs en aquests "trait mediated indirect interactions" (Abrahms et al. 1996) ha augmentat en els darrers anys des que hom ha trobat efectes de facilitació tant en sistemes terrestres (e.g. Schmitz et al. 1997) com limnètics (e.g. Turner et al. 2000) o marins intermareals (e.g. Trussell et al. 2003) de forma que la presència de depredadors provoca una disminució de l'activitat dels herbívors que pot ser tan important per als productors primaris com la pròpia depredació (reviewed by Werner i Peacor 2003).

Sorprenentment per la seva importància, els desplaçaments de *Paracentrotus lividus* han estat molt poc estudiats (Palacín et al. 1997, Shepherd i Boudouresque 1979; revisat a Boudouresque i Verlaque 2002), i, ni la seva mobilitat ni la seva resposta comportamental front als depredadors, no han estat tingudes en compte (en els models) a l'hora de integrar els factors que afecten a la dinàmica de les comunitats algals. Pel que fa a la meva tesi, mesurar l'abast dels desplaçaments resultava clau perquè, segons la seva magnitud, podien relativitzar la transcendència dels resultats obtinguts en els altres experiments. És a dir, que fins que no s'estableixi amb precisió l'abast dels patrons de mobilitat d'aquesta espècie no es podrà apreciar la importància real de l'assentament o de la depredació en la regulació de les poblacions de garotes.

Al capítol 6 presentem una sèrie d'experiments destinats a omplir aquesta llacuna. Mitjançant marques que ens permeten individualitzar i referenciar espacialment els individus, hem determinat els patrons de moviment de les garotes. Un experiment plantejat a l'escala circadiana, que engloba l'alternança dels períodes de repòs (dia) i activitat (nit), ens ha permès establir el seu home range. Hem repetit l'experiència dins i fora de la reserva per demostrar que la presència dels depredadors provoca un "trait mediated effect" sobre el home range d'aquests herbívors. Paral·lelament, un segon experiment ha permès fer un estudi de la seva capacitat de migració a mig termini (mesos).

Durant els tres mesos d'estudi la distància total recorreguda va ser de 380 cm de mitja, i no es varen distanciar més de 150 cm al voltant de la posició inicial, movent-se de forma atzarosa. P.*lividus* es va mostrar més actiu durant la nit, i els desplaçaments varen ser més importants a fora de la reserva. La distància mitja recorreguda durant el dia va ser de 50 cm. Aquests resultats estan d'acord amb els d'altres autors que mostren un paper poc important de les migracions en determinar l'estructura de les poblacions adultes. No obstant, aquests resultats evidencien el paper dels peixos depredadors en determinar els moviments de les garotes, afavorint indirectament les comunitats algals.

2.4.- Evolució real de les poblacions: assentament vs depredació

Els experiments presentats als capítols precedents varen produir resultats molt concloents: d'una banda varen confirmar la poca importància dels desplaçaments, el que simplifica molt la comprensió i modelització de la dinàmica de les garotes; i d'altra banda, varen mostrar que tant la variabilitat de l'assentament com la força de depredació dels peixos sobre les joves garotes post-assentades eren poderosos factors capaços, almenys potencialment, de desestabilitzar i de controlar, respectivament, la dinàmica de les poblacions de garotes.

Tot i així aquests experiments no estaven en condicions de resoldre el dilema de qui controla la dinàmica demogràfica de les garotes. La raó és evident: si, per una part, assentament i depredació produeixen efectes antagònics, els d'un han de prevaler sobre els de l'altre; però per altra part, com els experiments tractaven cada problema separadament no permeten fer un diagnòstic sobre quin seria el balanç. Manipular simultàniament la magnitud de l'assentament i de la depredació en un experiment controlat em va semblar extremadament difícil. A més, experiments realitzats a tan curt termini poden emmascarar efectes que es produeixin a una escala espacial i temporal més àmplia. Sembla clar, doncs, que només una anàlisi a llarg termini dels patrons i fluctuacions en poblacions naturals sotmeses a l'acció simultània de tots els factors ens permetrà determinar la importància real dels processos estudiats en la dinàmica de les poblacions de garotes.

Per a testar si els models deterministes tenen força de predicció quan anticipen el control de les garotes pels depredadors, o si té més pes la component de desestabilització de l'assentament o dels refugis que sembla evidenciar-se als nostres experiments, hem analitzat al **capítol 6** els resultats d'un **seguiment a llarg termini** (12 anys) **de la mida i l'estructura de talles de les poblacions de garotes** de dins i fora de la reserva Marina de les Illes Medes. Aquest estudi forma part del programa de monitoreig del patrimoni d'aquesta reserva marina, i està dissenyat per a determinar les variacions en l'abundància i estructura de les poblacions de garotes. En fer-se dins i fora de la reserva permet analitzar l'efecte de la depredació i l'efecte de la pesca; en fer-se en dos habitats diferents de rugositat molt contrastada permet analitzar alhora el paper dels refugis; i en analitzar una sèrie llarga d'anys, amb assentaments de mida molt variable permet analitzar simultàniament l'efecte de la variabilitat de l'assentament.

La imatge que ens proporciona tota la sèrie temporal sobre el paper jugat per les mesures de protecció (contrast AMP- no AMP) és confusa, principalment per la seva forta variabilitat. Sembla que són les variacions en el reclutament les que tenen un pes molt important en la variabilitat: tots els canvis que s'han produït en les poblacions de garotes al llarg dels anys han estat continuació de fortes entrades de reclutes. Tanmateix observem diferències en l'efecte produït: fora de la AMP, els canvis provocats per arribades de reclutes són molt marcats; en canvi, dins la AMP aquests pics deguts al reclutament resulten més modulats. Aquesta diferència semblaria suggerir que, si bé la més gran biomassa de peixos de la AMP no pot contrarestar totalment els efectes desestabilitzadors de les arribades massives de larves, sí produeix un cert efecte regulador en suavitzar les oscil·lacions que se'n deriven.

L'únic factor que sembla establir una pauta persistent en el comportament temporal de les garotes és la topografia. La diferència entre els fons de blocs (densitat elevada, talla mitjana petita) i les parets verticals (densitat menor, talla mitjana més gran) no ha variat cap any, mostrant així una forta estabilitat.

3- Aplicació dels resultats a la gestió

Finalment, el **capítol 8** aborda l'**aplicació** de les prediccions dels models tròfics a la gestió d'un espai litoral protegit.

La localitat seleccionada va ser la Reserva Marina d'Scandola (Còrsega), on entre els fons infralitorals dominats per boscos madurs de l'alga perenne *Cystoseira balearica,* vàrem poder observar l'existència de blancalls extensos. Les condicions especials d'aquests blancalls (amb altes densitats de garotes) que formaven fronteres molt estrictes al costat de boscos ben desenvolupats (quasi desproveïts de garotes) en una reserva marina on els peixos són abundants, ens va semblar que oferien el marc adequat per a avaluar experimentalment les prediccions dels models tròfics sobre un possible retorn de blancalls cap a boscos ben formats. Així, en aquell capítol presentem els resultats d'un experiment d'eradicació de garotes, dissenyat per a testar si una disminució sobtada de les poblacions de garotes adultes pot ser capaç de forçar el retorn dels blancalls a boscos de *C.balearica*. El resultat d'aquest test pot ser important per als gestors d'espais protegits que tindrien en les eradicacions de garotes una eina útil per a combatre la proliferació dels blancalls. Al mateix temps, aquest experiment continuat durant tres anys ha permès indagar la persistència i quins eren els mecanismes que mantenen els blancalls.

Els resultats d'aquest estudi mostren clarament que a les comunitats de *C. balearica* de la Reserva Natural de Scandola els blancalls són un fenomen freqüent que pot afectar a quasi una tercera part de la superfície rocosa entre 0 i 10 metres de fondària. Així mateix, els resultats de l'estudi confirmen clarament que la causa d'aquests blancalls és l'herbivoria de les poblacions de la garota *P.lividus*. L'exclusió mútua de les distribucions de la cobertura algal i de la biomassa de garotes aporta una evidència correlacional (amb una correlació negativa fortament significativa). La funció que descriu la relació entre la cobertura i la biomassa de garotes presenta un umbral que estableix els límits de l'estat "blancall" i de l'estat "bosc". Aquest límit es situa en 174 gPS de biomassa de garotes o una densitat de 9,1 individus per m2.

La ràpida recuperació de la cobertura algal i la feble recuperació de les poblacions de garotes desprès de la erradicació puntual dona suport a la hipòtesi de que una eradicació puntual de les garotes adultes i el posterior control del reclutament per part dels peixos semblaria suficients per permetre una reversió de les comunitats cap a les predites pels models.

4. Posant totes les peces juntes: Nou marc conceptual i propostes de recerca futura

La memòria acaba amb un apartat prou voluminós per a constituir-ne un capítol més; però, a diferència dels anteriors, aquest no aborda un objectiu de recerca concret sinó que planteja una **discussió general** dels resultats obtinguts als capítols anteriors, tractats conjuntament e intentant explicar-los en un marc global coherent.

Aquesta lectura transversal no pot ser més oportuna ja que la rigidesa formal de la literatura científica (a la que estan abocats els diferents capítols de la tesi) impedeix fer referències creuades a temes que, tot i haver estat tractats sectorialment per imposicions experimentals, estan en realitat profundament inter-connectats. En la meva opinió, és en aquestes relacions creuades on rau el principal interès del treball i on s'amaguen els seus resultats més originals. Per això, m'he permès la llibertat de presentar la discussió amb una visió més especulativa que la rigorosa aproximació experimental dels capítols anteriors, ja que un treball de recerca com aquest, a més de descriure i de testar les hipòtesis plantejades, hauria de servir per identificar quins forats deixa i generar noves hipòtesis, que haurien de ser explorades en un futur. La proposta pretén explicar les diferencies entre els escenaris que hem anat trobant a diferents localitats de la Mediterrània NW afegint la consideració d'un eix històric o succesional (en el que pesa molt l'acció de l'home) als dos eixos principals que han constituït el tema de debat de tota la memòria: les condicions de producció ("bottom-up") i la pressió dels depredadors ("top-down"). El caràcter especulatiu de la proposta es justifica per l'absència de dades paleoecològiques o d'ecologia històrica mediterrània que donin suport a la relació entre la suposada regressió generalitzada de les comunitats dominades per algues del gènere *Cystoseira*, l'avenç de les poblacions de garotes i l'activitat humana. La discussió acaba amb una llista dels temes de recerca que, des del meu punt de vista, resultaria prioritari explorar en el futur.

Discussió

Els resultats de les recerques realitzades a cadascun dels tres nivells tròfics que han polaritzat l'organització de la memòria, algues-garotes-peixos, estan innegablement inter-relacionats. Però, per l'estructura formal de presentació dels treballs científics en capítols que forçosament han de ser autònoms i auto-explicatius, es perd la possibilitat de discutir les relacions transversals i les connexions entre els diferents processos i nivells, que és sovint on s'amaguen les relacions més subtils i les més interessants. Agafades així d'una en una, la suma de les parts no fa el tot i correm el risc, en definitiva, de perdre la visió de conjunt. Per aquesta raó he realitzat aquesta discussió general on em permeto la llicència de saltar d'un a altre dels resultats obtinguts al llarg del treball, buscant les conclusions més profundes i, per què no, també un xic especulatives.

Questió 1: controls top-down o controls bottom-up

Començant pels aspectes més generals, abordàvem la qüestió de quins processos governen el funcionament de les comunitats infralitorals rocoses mediterrànies des de dues postures extremes: controls de dalt a baix (top-down) contra controls de baix a dalt (bottom-up). Aquest treball suggereix que tots dos tipus de processos juguen un paper fonamental.

Amb l'herbivoria, els resultats d'aquest estudi proveeixen un mecanisme pel qual les comunitats podrien saltar punts estables. D'aquesta manera s'estableix un pont entre el model de Ballesteros (1991), bàsicament concebut des de la perspectiva de controls "bottom-up" i el de McClanahan i Sala (1997), dissenyat des d'una perspectiva exclusivament "top-down". Possiblement el que separa l'aplicabilitat d'un i l'altre és una questió d'escales espacials i temporals, buscant el darrer prediccions a escala molt gran, quan el primer té la virtut de poder explicar el funcionament de les comunitats algals a escala molt petita.

Nosaltres proposem que qualsevol model que aspiri a explicar satisfactòriament el funcionament de les comunitats algals mediterrànies, tindrà més gran capacitat predictiva si incorpora els dos criteris o eixos de variació: la estacionalitat, com expressió anual dels controls "bottom-up" i l'estructura de les poblacions de consumidors, especialment dels herbívors, com manifestació dels processos "top-down".

Questió 2. Importància relativa de garotes i peixos com herbívors

L'Efecte de les garotes és molt important

Manipulant les densitats dels herbívors dins els tancats, hem pogut confirmar que la pressió d'una població de garotes de densitat semblant a les més denses que havíem observat a la zona (al voltant de 16 individus/m2, totes les talles compreses), produeix canvis significatius en les poblacions de totes les espècies d'algues considerades (més de 40). En general, el sentit del canvi és una pèrdua de cobertura.

Als experiments de les Illes Medes, els tractaments amb garotes no varen ser capaços de provocar l'aparició de blancalls generalitzats. Però al cap de tres anys, les comunitats d'algues exposades a aquesta densitat de garotes experimentaven un desplaçament cap a la predominància de l'alga calcària *Lithophyllum incrustans* i la pèrdua de cobertura total. Aquest desplaçament es feia en perjudici de les algues perennes de gran port i en benefici d'algues efímeres, de cicle de vida estacional estretament relacionades al període de proliferació de primavera.

Encara que plantejat en els termes inversos, l'efecte de les garotes va resultar encara més evident a l'experiment d'eradicació de la Reserva Natural de Scandola. Els extensos blancalls que va provocar l'aparició d'una densa població de *P.lividus* (20- 25 individus per m2) varen començar a recuperar-se ostensiblement al cap de dos anys de la total eradicació de les garotes.

L'efecte dels peixos és poc important

En contrast, la presència d'una població omnívora de peixos sembla tenir poca importància en la composició i l'estructura de la població d'algues, almenys per la seva acció directa sobre les algues com herbívors (tractaments amb peixos sense garotes). També sembla menyspreable el seu efecte directe en presència de garotes quan la densitat de garotes es manté artificialment constant (comparació dels tractaments de garotes amb i sense peixos).

El paper indirecte dels peixos sobre les poblacions d'algues per la via de la depredació de garotes dependrà en gran part de la seva capacitat per a controlar les poblacions de garotes.

Tanmateix, la presència dels peixos va mostrar ser capaç de produir la facilitació o la cascada tròfica predita sobre la abundància d'algunes espècies d'algues concretes, algunes de les quals poden ser molt importants quantitativament en l'estructura de la comunitat (e.g. *Corallina elongata*). Com en aquests experiments vàrem mantenir artificialment constant la biomassa de garotes, l'efecte dels peixos ha de ser explicat no en termes de depredació, sinò com una inhibició de base comportamental. L'efecte pot estar relacionat amb la feble mobilitat natural de les garotes i pot ser explicat pels canvis induïts en el camp de pastura de les garotes per la presència dels peixos. Si, com s'observava al capítol 6, en presència de peixos les garotes surten menys de sota els blocs o des de les esquerdes que els serveixen de refugi, aquest comportament beneficiarà a les algues més fotòfil·les que proliferen als cims superiors dels blocs (allunyats dels refugis), i perjudicarà a les més ombrívoles que prefereixen les parets verticals dels blocs a on les garotes tenen més fàcil accés.

Questió 3. Importància de la composició florística i grups funcionals

Paper de la composició de la comunitat

Les diferències en la resposta de la cobertura d'algues a elevades densitats d'herbívors (bàsicament garotes) als experiments de les Illes Medes (no blancalls) i de Scandola (blancalls extensius) sembla suggerir un paper important de la composició florística de la comunitat en el resultat final del procés; i més concretament, de la diferent susceptibilitat de cada espècie d'alga a la herbivoria per garotes. A Scandola, es tractava d'una comunitat presumptament molt madura, dominada per *Cystoseira balearica* (Capítol 8), una espècie d'alga perenne (encara que amb fortes oscil·lacions estacionals de la biomassa), arborescent, corticada i amb forta especialització histològica, incapaç per a la dispersió vegetativa i amb tots els atributs de les espècies de fases climàciques de la successió (Littler i Littler 1980).

A les Illes Medes, la biomassa algal està repartida entre un "pool" molt més variat d'espècies, entre les que les perennes no representen més que una fracció menor. Molta de la cobertura correspon a espècies efímeres que produeixen un pic discret de biomassa, per a la majoria d'elles sincronitzat al voltant del període de màxima productivitat de final de primavera. Reduir la durada del cicle de biomassa a un curt període (al voltant d'un mes) en el que proliferen moltes espècies d'algues de forma més o menys sincrònica pot ser una forma d'escapar a la pressió dels herbívors en el temps per una estratègia de saciament (Littler i Littler 1980).

Pensem que aquest és el mecanisme que explica com els processos "top-down" interaccionen amb els processos "bottom-up": les algues perennes, més adaptades a la situació d'oligotròfia i que serien seleccionades per un control "per baix", són més sensibles a la pressió d'herbivoria que les algues que tenen creixements estacionals, no limitat pels nutrients, i són eliminades per un control "per dalt". Així, la pressió d'herbivoria pot determinar tant com les condicions de producció quin tipus d'estratègies d'algues ens trobarem en una comunitat.

Fallida dels grups funcionals convencionals

Quan, a despit de la variabilitat inter-específica i buscant regularitats en les respostes de les algues, hem provat la utilitat d'agrupar-les en grups funcionals (veure peu de pàgina) com els propugnats per Littler i Littler (1980) o els de Steneck i Dethier (1994) no hem trobat els patrons de resposta homogenis que descriuen aquests autors.

La no adequació al nostre cas dels grups funcionals més reconeguts universalment es pot explicar, en part, per les particulars característiques de les algues i les comunitats algals de la Mediterrània. Contràriament a la resta de regions temperades, on dominen els boscos de "kelps", les comunitats algals mediterrànies estan miniaturitzades i no existeix l'ampli ventall de talles en que es basen les agrupacions precedents. Per altra banda en els criteris d'agrupació seleccionats per Steneck i Dethier (1994) no es considera l'estacionalitat en el cicle vital quan, com ja hem vist, aquesta té molta importància en la resposta de l'alga tant als factors de producció com als herbívors.

Peu de pàgina: Grups funcionals.

(*) Degut a la variabilitat espacial i temporal en la composició i estructura de les comunitats algals, degut a la resposta variable dels diferents tipus d'algues al l'efecte de qualsevol factor biòtic o abiòtic, i en resum, degut a la variabilitat en la resposta de la comunitat algal segons la seva composició específica, els ecòlegs han hagut de fer categories entre les algues per a simplificar i trobar regularitats en les seves respostes al conjunt de interaccions i factors que estudien (herbivoria, gradients de llum, nutrients, stress físic...).

Les primeres aproximacions es feren per a determinar una relació entre la forma i la productivitat de les algues (Odum et al. 1958, Kanwisher 1966, Littler 1979). Es va veure que també la life-history estava relacionada, i es va determinar que la composició de "life-forms" (i.e. la incorporació de la life-history de les espècies que formen una comunitat) podia donar pistes de quines eren les condicions ambientals d'un habitat determinat (Katada i Satomi 1975). Més endavant, Littler i Littler (1980) ja varen desenvolupar un model de "formes funcionals" en el que es descrivien dos formes extremes (i.e. formes oportunistes i formes tardanes de la succesió), com a estratègies successionals, en les que incorporava criteris de forma, producció i resistència a les agressions, incloent els herbívors.

Aquesta aproximació en estratègies han permès comparar diferents ambients sota els mateixos criteris. Per exemple, Steneck i Dethier (1994) fan un estudi comparatiu entre tres regions biogeogràfiques diferents en les que estudien els efectes de la productivitat i la herbivoria en l'estructura de les comunitats algals. Així, desenvolupen un model en el que associen estratègies evolutives en resposta a la producció i a la resistència als herbívors utilitzant criteris morfològics.

Tampoc es consideren les característiques morfològiques i histològiques que brindarien millor protecció contra la forma de pasturar de les garotes, que s'assembla al pas d'un bulldozer. Es per això que creiem que per als mars marcadament estacionals, com és el cas del Mediterrani, cal explorar noves agrupacions funcionals. Els nous grups funcionals aconseguirien major poder predictiu si incorporessin criteris d'estratègia estacional i d'adaptacios morfològiques per a suportar la pressió dels herbívors.

Es podria discutir si les poblacions algals de la Reserva de les Illes Medes, que semblen representar una situació de més productivitat i dinamisme tròfic, estan en una fase succesional més pionera i estan millor adaptades a conviure amb denses poblacions de garotes que les poblacions algals de Scandola, que semblen proliferar en una situació més oligotròfica i poden representar fases succesionals més climàciques. Més endavant d'aquesta discussió proposarem una hipòtesi de treball sobre l'evolució de les comunitats a la Mediterrània occidental com a conseqüència dels canvis antròpics i del paper que les garotes poden estar jugant en aquests canvis.

Questió 4. Que controla la dinàmica demogràfica de les garotes ?

Dins del triangle de relacions algues-garotes-peixos, les garotes han demostrat tenir un paper clau, no només perquè es troben a la posició central de la interacció (per una part depreden sobre les algues i alhora són controlades pels peixos depredadors), sinò perquè, quan es troben en gran nombre, la seva pressió de pastura acaba alterant tota la comunitat. Com la clau rau en el seu nombre i biomassa per a comprendre el funcionament d'aquests sistemes, és fonamental entendre els processos que regulen l'estructura i la dinàmica de les poblacions de garotes. Deixant de banda els moviments migratoris i des de la perspectiva de mantenir poblacions petites, la qüestió es redueix a l'antagonisme entre l'assentament-reclutament, com procés desestabilitzador, i la mortalitat afavorida pels depredadors, com procés controlador.

Mobilitat

Totes les evidències recollides al llarg d'aquest treball, tant a les Illes Medes com a la Reserva de Scandola, als tancats, als experiments d'erradicació i als experiments dissenyats específicament per a mesurar la seva mobilitat apunten en la mateixa direcció: la garota *Paracentrotus lividus* és una espècie molt sedentària. La feble mobilitat d'aquesta espècie és evident a totes les escales temporals estudiades: dia-nit, setmanal, estacional, plurianual i ontogenètica. Immòbil durant el dia, la seva activitat nocturna no l'allunya més de 20 cm en mitjana del refugi preferit. Aquesta tendència de retorn a un refugi preferent fa que els moviments a l'escala d'una setmana no els allunyin en mitjana més de 1.3 m. Aquesta pauta de sedentarietat es repeteix al llarg de l'any sense que ni els temporals ni els canvis estacionals en les condicions físiques de la columna d'aigua semblin capaços de provocar desplaçaments de llarg abast. A escala ontogenètica deu existir un cert desplaçament des de les cares inferiors dels còdols i de sota les garotes adultes on habiten durant la fase de post-assentament fins a les esquerdes que els serveixen de refugi durant l'època adulta. Però aquests moderats desplaçaments han de situar-se en l'escala d'uns pocs metres. Així, hem de veure la garota *Paracentrotus lividus* com una espècie que desenvolupa tot el seu cicle vital molt a prop (metres) del lloc on es va assentar (veure a continuació) la larva pelàgica.

Aquests resultats aporten una informació molt valuosa ja que, sorprenentment, la mobilitat de *P.lividus* havia estat molt poc estudiada (Barnes i Crook 2001). Difícils de mesurar, sovint la importància dels desplaçaments és infravalorada en els estudis demogràfics més per desconeixement que perquè siguin realment irrellevants. Però no podem oblidar que, en el cas d'existir, aquests desplaçaments poden emmascarar o confondre el veritable paper dels altres dos processos demogràfics implicats: la mortalitat per depredació i l'assentament-reclutament. Que les poblacions de *P.lividus* estudiades siguin realment molt poc mòbils a totes les escales del seu cicle vital és interpretat aquí com un gran avantatge que simplifica l'estudi d'una espècie que és en tota la resta d'atributs molt variable. Gràcies a la seva sedentarietat, l'important paper dels altres dos processos (l'assentament-reclutament i la mortalitat) ha pogut ser demostrat amb tota garantia, tal com es discuteix a continuació.

Assentament

Aquest estudi ha permès obtenir una visió del patró d'assentament de *Paracentrotus lividus*, on es mostra una gran heterogeneïtat espacial i temporal. La confrontació d'aquest patró heterogeni amb l'homogeneïtat de les poblacions adultes ens suggereix que no hi ha cap relació entre la densitat de les poblacions reproductores parentals i el patró d'assentament. Per tant, en abordar l'ecologia de la garota *Paracentrotus lividus* sembla recomanable la perspectiva de poblacions obertes propugnada pels defensors de l'anomenada "supply-side ecology" (veure revisió de Menge 2000). Hem vist que el nombre d'individus assentats pot variar entre ordres de magnitud d'un any per l'altre, i que l'assentament mostra un patró espacial molt heterogeni, probablement reflex de una distribució molt heterogènia de les larves en el plàncton. Els nostres resultats ens indiquen que les garotes no seleccionen el lloc de l'assentament, sinó que factors físics com la topografia de la costa, en particular la orientació i la exposició a les corrents, tenen un paper determinant en la pauta d'assentament. Així, no vàrem trobar cap diferència en la potència de l'assentament entre la reserva marina i la zona no protegida.

L'únic patró estable que hem trobat és una distribució decreixent de l'assentament en fondària, que coincideix amb la distribució de les poblacions adultes.

Crec que l'assentament és un procés tan passiu, i que depèn tant de la massa d'aigua que transporta les larves, que la imatge que més li escau és la d'una "pluja de larves". Un futur model que pretengui predir la distribució de les larves podria trobar útil inspirar-se en els models meteorològics de predicció de les precipitacions. Si a més tenim present el patró batimètric, seria encara més gràfic fer un símil amb el patró de nevades d'una serralada, en que la quantitat de neu que cau en un lloc determinat varia cada any, i també d'un lloc per l'altre, depenent de la direcció d'on venen els fronts. Tot i aquesta variabilitat, sempre caurà neu a partir de certa alçada, ja que a partir de certa altitud la neu es fon.

Les garotes tenen un potencial reproductor molt alt. A més, degut a que tenen una fase planctònica relativament llarga i que no s'observen mecanismes actius de retenció larvària, hem de concloure que la seva capacitat de dispersió ha de ser molt gran (desenes a centenars de kilòmetres). Tot i que falten estudis de flux genètic per determinar-ho, aquesta alta capacitat de dispersió ens permet descartar l'existència d'aïllament entre les poblacions, i pronosticar una connexió molt gran entre les diferents zones geogràfiques.

Aquests resultats prenen una gran importància quan es tracta de jutjar el paper de l'assentament en el control de les poblacions de garotes a les reserves marines. Una capacitat de dispersió a llarga distància permet arribades massives de larves arreu, inclòs en zones on les densitats d'adults són molt baixes. Això fa pensar que encara que una major densitat de peixos a les reserves pogués controlar les densitats de garotes (fet que es comenta més endavant), una arribada atzarosa de gran quantitat de larves independent de les poblacions adultes podria invalidar els efectes d'aquest control.

Així, no podem esperar que les poblacions de una reserva marina sigui gran o petita romanguin tancades, sinó que es trobaran contínuament exposades a l'arribada de larves des de zones perifèriques, on la sobrepesca dels seus depredadors pronostica més abundància de reproductors.

En resum, el gran abast espacial de la dispersió larvària i l'elevada variabilitat observada en l'assentament a totes les escales (entre llocs i entre anys) en *P. lividus*, junt a la forta sedentarietat dels individus post-assentats, confirmen el ***potencial*** d'aquest procés (assentament-reclutament) com a factor desestabilitzador de les poblacions de garotes.

Mortalitat per depredació de les fases post-assentades

Tanmateix, dels nostres resultats experimentals també se'n deriva un clar suport per al procés antagònic: el paper regulador que els models tròfics atribueixen a la mortalitat per depredació (especialment a les Reserves marines). Tot i l'important potencial desestabilitzador que ens ha mostrat el patró d'assentament, hem vist al capítol 7 que les poblacions adultes són molt homogènies i relativament estables al llarg d'una llarga sèrie temporal. Tenint present la feble mobilitat de l'espècie, aquests resultats només poden ser explicats assumint que la mortalitat ha de tenir un paper molt eficaç en el control d'aquests pulsos d'entrada de reclutes, actuant de filtre i determinant la mida de les poblacions adultes.

La importància de la depredació per peixos en la mortalitat de *Paracentrotus lividus* no és un resultat nou ja que ha estat objecte de diferents treballs experimentals, que, tanmateix, s'han centrat a en la depredació de garotes grans (>3 cm de diàmetre; però veure Sala 1997). En contrast, la mortalitat de las fases juvenils post-assentament ha estat un tema relativament poc estudiat (Lopez et al. 1995). L'oblit no deixa de ser significatiu ja que el procés de depredació en les talles petites pot tenir una gran importància en el control de les poblacions de garotes (Sala et al. 1998); almenys això és el que suggereix l'anàlisi de l'estructura de talles de les poblacions (capítol 7) que evidencia que és en les fases de post-assentament on es produeix la major mortalitat. El nostre treball experimental confirma que, com succeeix a la majoria d'animals bentònics, la major mortalitat de *P.lividus* per depredació es produeix en fases de post assentament, en un rang de entre 0.2 (talla que arriben al fons) i 1 cm. Els experiments de "tethering" realitzats amb individus d'aquestes talles han brindat unes taxes de consum molt superiors a les observades per Sala i Zabala (1996) en garotes grans (> 3 cm de diàmetre).

Els treballs precedents, dedicats a la depredació de garotes adultes, havien identificat el sargs (*Diplodus sargus*) i secundàriament les estrelles de mar (*Marthasterias glacialis*) com els principals depredadors (Sala 1997, Dance 1987), i *Coris julis* per a les talles petites (Sala 1997). Els nostres resultats ens indiquen que la depredació en les talles petites per *Coris julis* i altres espècies de peixos que fins al moment no es consideraven claus com a depredadors de garotes, poden tenir un paper molt important per la seva abundància i la seva capacitat de control de les fases juvenils.

Hem pogut observar una clara relació entre la talla de les preses i la talla i naturalesa especifica dels depredadors. En les fases inicials, quan les garotes són més petites, els petits làbrids (*p.e. Coris julis, Thalassoma pavo*) són els més importants d'entre un espectre de depredadors d'almenys 6 espècies. Quan les garotes assoleixen un diàmetre superior a 0,5 cm (i tenen una edat de aproximadament mig any), els petits làbrids ja no poden depredar sobre elles i els làbrids de talla gran (L*abrus merula*) i els espàrids (*Diplodus sargus, D.vulgaris*) passen a ser els principals depredadors.

La correlació entre les talles de les garotes i les talles mínimes dels seus depredadors confirma l'existència d'un refugi contra la depredació en la talla de les garotes (Sala 1996, 1997). Així, la talla dels peixos determinarà la talla refugi (a partir de la qual ja no poden ser depredades) de les garotes. Com a les reserves marines, les talles (a més del nombre) dels peixos, inclòs dels petits làbrids, són més grans, les garotes s'enfronten a un risc més gran de ser depredades. Per contra, en les zones pescades les talles dels peixos són més petites, i això farà que les garotes assoleixin la talla refugi abans, reduint així el temps en que són susceptibles de ser menjades pels petits làbrids.

Aquests mateixos resultats també reforcen la importància, sovint menyspreada, que la pesca esportiva pot tenir en el control de les poblacions de garotes i, de retruc, en la conservació de les comunitats infralitorals (Sala 1997). Hi ha evidències experimentals que l'estructura de talles de les poblacions de *Coris julis*, el principal peix controlador de les garotes en les fases de post-assentament, es troba molt condicionada per la pressió de pesca esportiva (Harmelin i Bachet 1995).

No obstant, hem de tenir en compte que, a més dels peixos hi ha una fracció important de crustacis que poden depredar una fracció molt important d'aquests post-assentats. Aquesta depredació també pot ser diferencial entre una reserva i una zona no protegida: en les zones amb molts peixos els invertebrats són menys nombrosos (Sala

1997b), i per tant la depredació de depredació dels crustacis sobre les garotes hauria de ser menor. Aquest efecte actuaria en contra del descrit fins ara, ja que en zones de reserva aquest tipus de depredació seria menor, afavorint les garotes. Aquest tipus de mortalitat, per tant, podria atenuar el patró de mortalitat determinat per la presència de peixos.

Els resultats experimentals de tractar per separat l'efecte de l'assentament (capítol 4) i la depredació (capítol 5) aporten evidències molt contundents del seu potencial en la regulació de les poblacions de garotes. Però com ambdós processos tenen efectes antagònics, en actuar simultàniament sobre les mateixes poblacions, s'han de restar; en aquestes condicions, resultava evident l'interès de decidir quin domina sobre l'altre.

La llarga sèrie temporal de censos de la població de garotes de la Reserva de les Illes Medes i de la costa propera no protegida mostra l'existència de fortes oscil·lacions inter-anuals en la mida poblacional que, en absència de moviments migratoris importants, només podrien ser interpretats com la conseqüència de polsos de reclutament. Tanmateix, hem demostrat que les oscil·lacions són degudes exclusivament a canvis en la densitat de les classes just assentades; en canvi, la mida de la població de les classes adultes roman força estable. Això significa que l'efecte de la depredació sobre les classes post-assentades anul·la ràpidament l'efecte de la variabilitat en l'assentament. N'és una prova la manca de correlacions significatives entre la mida de la primera classe en el temps 0 i la mida de les classes superiors en els anys següents, mostrant que la senyal demogràfica introduïda per les cohorts resultants d'un reclutament extraordinari no pot ser seguida en la població adulta. Així, la depredació actua com a paper estabilitzador de les poblacions de garotes, ja que contraresta l'entrada massiva de reclutes.

El paper de les Reserves Marines en aquest control no resulta molt contrastat. Els models deterministes descriuen dues situacions amb patrons de reclutament i depredació oposats per a les zones protegides i no protegides. Les zones protegides haurien de tenir poblacions de garotes menys denses, mantingudes per un assentament menor, i una força de depredació major. Contràriament, a les zones sobrepescades, les poblacions de garotes es mantindrien molt elevades degut a una forta entrada de reclutes i a una pressió de depredació incapaç de controlar aquestes entrades.

Però hem observat que hi ha excepcions a aquests models. Hi ha evidències de blancalls dins de reserves marines i comunitats algals ben desenvolupades en zones on la densitat de peixos és molt baixa.

A la reserva marina de les Illes Medes, on la densitat de peixos és de les més elevades del Mediterrani, les densitats de garotes són encara superiors a les trobades en els boscos de *Cystoseira* de Scandola; i hi trobem petites zones sobrepasturades. El seguiment a llarg termini de les poblacions de garotes ens ha permès observar que finalment les densitats de garotes adultes no es diferencien entre la zona protegida i la no protegida, on les migrades poblacions de peixos també demostren ser capaces de controlar-les. Però, i en aquest matís rau la diferència més important, les oscil·lacions de la densitat de garotes a la costa no protegida són molt més acusades que a la Reserva, suggerint que la capacitat de control dels peixos es troba prop del límit.

Hem de tenir en compte, però, que a les Medes i a altres reserves marines amb alta densitat de peixos depredadors, la majoria de garotes estan amagades, reduint així el seu home range i, per tant, el seu efecte sobre les comunitats (Sala 1996; capítol 2 i 3). Aquest fet demostra que no només s’ha de considerar la densitat de garotes per si sola, ja que els efectes ecològics poden ser molt diferents depenent de la seva mobilitat (Sala et al. 1998).

Una altra prova de l’incompliment dels models deterministes la tenim a la reserva de Scandola, on en una zona amb alta densitat de peixos hi ha comunitats de blancall al costat de boscos de *Cystoseira balearica*.

La formació d’aquestes taques pot ser deguda, per una part, a fronts migratoris de garotes. Però la baixa mobilitat que han mostrat les garotes en els experiments, i el fet que aquestes taques estiguin aïllades, no suporten aquesta hipòtesis. Tot i que no ho hem investigat, la hipòtesis més probable de la formació d’aquests blancalls és que es produeixen importants pics de reclutament, seguits de episodis de poca mortalitat post-assentament.

Així, sembla que a algunes Reserves Marines tot i que hi ha més densitat de peixos, aquests finalment no poden controlar la demografia de les poblacions de garotes, però sí els seus efectes via comportamental.

Questió 5: Per qué no s’acompleixen les prediccions dels models tròfics sobre les Reserves?

Quines poden ser les causes dels desajusts entre les prediccions dels models tròfics (p.e. McClanahan i Sala 1997) i les observacions empíriques?

A diferents parts del meu treball he trobat mecanismes que podrien explicar que les garotes escapin al control dels peixos a les Reserves Marines. Tots ells tenen un element en comú que aquí podríem resumir sota el títol genèric del “paper de l’espai”. Els models tròfics al.ludits, basats com estan en la lògica dels models de depredador-presa de Lotka (1925) i Volterra (1926), tenen l’inconvenient molts cops assenyalat (Margalef 1974) d’ignorar que les interaccions ocorren en un espai de dimensions definides i essencialment heterogeni. Aquests models inspirats en els models físics de “llei d’acció de masses” serien probablement adequats per descriure les interaccions d’espècies a molt gran escala i sense barreres físiques importants. Pel contrari, en el cas de les interaccions entre peixos- garotes – algues el paper creador d’heterogeneïtats de l’espai és evident almenys a tres nivells:

1.- a escales de km en la desigualtat entre la ***capacitat dispersiva de les larves*** de les garotes i la mida de les Reserves;

2.- a escala de desenes de metres en el ***capriciós patró d’assentament*** de les garotes i la topografia i ***patchiness en la distribució de les comunitats bentòniques*** i els peixos; i,

3.- a escala de decímetres, en l’existència d’esquerdes i espais sota els blocs que actuen de ***refugis***.

1- Desfasament entre la capacitat dispersiva de les larves i la mida de les Reserves

La dinàmica de “naixements” de les garotes no pot considerar-se supeditada al control que, en la lògica dels models Volterra-Lotka, els depredadors han d’exercir sobre la població parental, ja que la llarga fase planctònica de les larves permet que arribin larves de poblacions de fora de la reserva. Així, les reserves actuen com a sumiders de larves, ja que probablement reben més larves de garotes des del “mainland” que constitueixen les costes immediates no protegides, de les que produeixen les poblacions de la propia reserva.

2- Capriciós patró d’assentament de les garotes i la topografia i patchiness en la distribució de les comunitats bentòniques i els peixos

Els experiments amb col·lectors de larves han demostrat el capriciós pattern d’assentament de les garotes. Les badies i zones tancades on es produeixen “eddies” i retenció de plancton són punts favorables per a rebre grans quantitats de larves, un cop més independents de la mida de les poblacions parentals locals; ates que la mobilitat posterior és molt reduida, el patró d’assentament sembla tenir consequències molt notables en la densitat final de les garotes.

A més, la distribució de les comunitats infralitorals mediterrànies té un fort patchiness a escala de decenes de metres (Garrabou 1997). Malgrat la seva mobilitat, les poblacions de peixos són sensibles al patchiness bentònic. A la Reserva de Scandola, les parcel·les cobertes per un dens bosc de *Cystoseira* mostren sempre una densitat molt petita de reclutes, el que suggereix que la fauna associada als boscos d’algues ben constituïts, pot actuar com un primer filtre de l’assentament (abans de l’entrada en acció dels peixos); als blancalls, pel contrari, el nombre de reclutes és sempre superior.

3- Refugis.

Però de totes les escales a les que la heterogeneïtat de l’espai pot ser rellevant, la micro-topologia del substrat que permet (o no) trobar refugis a les joves garotes durant l’època crítica del post-assentament, és el factor més important per explicar les discrepàncies entre les prediccions dels models i les observacions. La rugositat del fons i l’existència d’esquerdes i/o de petits blocs amb espais intersticials, és la clau de que les garotes puguin escapar a la depredació fins i tot a les Reserves amb poblacions més denses de peixos (p.e. les Medes). A més de la rugositat, hem provat experimentalment que la cobertura de les algues pot atenuar molt la força de depredació.

Si, a més, tenim en compte les respostes comportamentals de les garotes tindrem una visió més complerta de la importància dels refugis.

Hem vist que el ”home-range” de les garotes queda sensiblement reduït per la presència de depredadors. La inhibició comportamental de l’activitat de pastura de les garotes pels peixos seria una forma de control alternatiu (trait mediated indirect interactions; Trussel et al., Werner i Peacor 2003, Bruno et al. 2003) a la depredació directa, que impediria una pastura extensiva per part de les garotes i limitaria el seu creixement i el seu potencial reproductor sense afectar al seu nombre.

Tanmateix, cal considerar que una alta disponibilitat de refugis permetrà una densitat més elevada de garotes que, tot i que tinguin un “home-range” més petit, seran capaces de denudar tota la comunitat d’algues (com hem observat en alguns punts de les Illes Medes) .

Questió 6 Blancalls-boscos d’algues, son dos estats estables ?

Si els experiments de manipulacions de la densitat de garotes a les Illes Medes no varen ser capaces de generar l’aparició d’àrees extensives de blancall, a la Reserva Marina de Scandola (Còrsega) l’efecte de les garotes sobre les comunitats algals és més notori i al seu infralitoral trobem nítides taques de blancalls intercalats enmig dels densos boscos de *Cystoseira balearica.* Les nostres estimes suggereixen que un 30 % de l’àrea potencial de distribució dels bosquets de *C.balearica* són actualment blancall; els experiments d’eradicació han demostrat que la biomassa de garotes és el factor que governa la transició entre els boscos i els blancalls.

En els boscos la cobertura algal és molt alta i la densitat i el reclutament de garotes són molt baixos. En els blancalls per contra, densitats molt elevades de garotes han denudat completament les boscos de *Cystoseira*; a més, hi ha un reclutament molt elevat que manté les poblacions adultes.

Els controls experimentals realitzats entre 1998 i 2003 han demostrat que, malgrat les densitats elevades de peixos depredadors les dues comunitats i les seves fronteres es mantenen sense grans canvis al llarg del temps.

La dinàmica contrastada i la persistència de les fronteres entre els dos tipus de comunitat encaixaria dins el model proposat per Ballesteros per a explicar l’organització de les comunitats algals mediterrànies (Ballesteros 1991), que considera possible la coexistència estable de diferents tipus de comunitat sota les mateixes condicions ambientals. En aquest cas, l’herbivoria de les garotes proporcionaria el mecanisme per al desplaçament entre comunitats. A més, hem vist que els patrons d’assentament de garotes, més aviat contraintuitius (elevats als blancalls i baixos als boscos) poden proporcionar el mecanisme que actuï de feed-back positiu a l’hora de mantenir aquestes comunitats.

Segons el model de Ballesteros, aquests dos estats estables es poden anar alternant al llarg del temps. En el nostre cas, tot i que no coneixem les causes dels canvis, tenim evidències de que els blancalls i boscos poden alternar-se, ja que hem vist zones de blancall recuperant-se i zones de petites taques de blancall en expansió al mig de boscos.

Per una part, el pas de boscos a blancalls sembla que seria una conseqüència de la combinació d'un assentament extraordinari i una baixa taxa de depredació. Per altra banda, el pas contrari hauria d'estar causat per una mortalitat massiva de les garotes que desencadenessin el salt cap als boscos desenvolupats. Encara que no són un fet freqüent, no falten exemples a la bibliografia de mortalitats massives per malalties o per temporals (Boudouresque et al. 1980, Azzolina 1983). Els experiments d'eradicació varen permetre constatar que una desaparició de les garotes permetia una recuperació relativament ràpida (3 anys) dels boscos de *Cystoseira balearica*.

Més difícil de respondre és la qüestió de si la dinàmica entre aquests dos suposats punts estables respon a un procés cíclic reversible i a una escala adequada estable, o si ens trobem enfront d'un procés irreversible d'augment de l'extensió dels blancalls. Probablement, la clau rau en l'escala temporal i espacial a la que s'observi el problema. Les garotes tenen una dinàmica demogràfica molt ràpida (alta capacitat de reproducció, creixement ràpid, temps mig de generació curt), una capacitat dispersiva de llarg abast espacial (desenes a centenars de km) i unes taxes de pastura elevades que signifiquen una alta capacitat de transformar les comunitats algals. Les algues del gènere *Cystoseira*, en canvi, exhibeixen una dinàmica lenta, ja que tenen un creixement lent dels teixits perennes, gran longevitat i (presumiblement) baixa taxa de reproducció; i, el que presumiblement representa al diferència més important, una molt limitada capacitat de dispersió dels propàguls (metres, desenes de metres?).

En un sistema on els blancalls són de mides petites (1m-100m) i les algues poden recolonitzar-los via propàguls, l'alternança d'aquestes comunitats es pot mantenir. Però si els blancalls esdevenen massa grans, aleshores poden assolir una mida crítica a partir de la qual ja no seria possible una recolonització per les cystoseires via dispersió sexual.

Questió 7 Grups estratègics algals i desenvolupament de blancalls

Val la pena analitzar per que, si les condicions experimentals eren més o menys semblants en quant a la densitat de peixos (molta biomassa) i de garotes (16 – 20 ind/m2), a la Reserva de Scandola es produeixen blancalls extensos i als tancats de les Illes Medes no. Potser la clau radica en la naturalesa de les espècies que composen les respectives comunitats algals i en la seva resiliència a la pertorbació que suposa la herbivoria. Recordem que a Scandola la comunitat es troba dominada per una alga perenne erecta (*Cystoseira balearica*) mentre que a les Illes Medes la comunitat està constituïda per un ventall més variat d'algues efímeres erectes o filamentoses.

De fet, els blancalls i els boscos no són més que dos estadis extrems d'una sèrie successional més complexa, que, si bé són molt característics, a nivell de Mediterrani actualment són més aviat excepcionals. Verlaque (1987) va definir almenys un altre tipus de comunitat dominada per espècies erectes estacionals de vida curta, que formaven un estadi intermig entre les dues comunitats. Aquestes espècies erectes, les que dominen a les Illes Medes, tenen cicles estacionals marcats aprofitant els pulsos de disponibilitat de nutrients.

Des del punt de vista de les estratègies de vida correspondrien al grup d'algues que Littler i Littler (1980) varen anomenar espècies oportunistes. Es caracteritzen per ser ràpids colonitzadors, de vida curta, formes simples amb alt contingut calòric i creixement ràpid; les algues oportunistes poden tenir un escapament de la depredació gràcies al seu ràpid creixement, sense dubte més alt que la pèrdua per depredació, i sincronitzat amb el d'altres espècies al voltant d'un període curt en el que l'oferta de biomassa vegetal és excessiva (el que Littler i Littler anomenen escapament per saciament). Gràcies a aquests atributs, aquestes espècies semblen adaptades a suportar una pressió d'herbivoria relativament alta en ambients estacionals, on aprofiten els pics de nutrients i llum per a fer el creixement fort. Aquest tipus de comunitat intermitja, tot i no representar una situació climàcica, pot mantenir una certa complexitat estructural i específica, en qualsevol cas molt més elevada que les dels blancalls.

Des d'aquesta perspectiva, els blancalls, comunitats intermitges i boscos de *Cystoseira* correspondrien a tres nivells successionals amb diferent tolerància a la pressió d'herbivoria.

Si els comparem amb el model desenvolupat per a vegetació terrestre per Grime (1977), aquest tres tipus de comunitats podrien correspondre a cada una de les estratègies definides per aquell autor (a unes conclusions semblants va arribar ho diu també Verlaque 1987): la ***Competitive Strategy*** **(C)** a la que serien assimilables les *Cystoseira*, ja que representen l'estadi successional final amb espècies longeves, que dominarien competitivament en les condicions més estables; les espècies presents als blancalls correspondrien a les ***Stress tolerants*** **(S)**, ja que són espècies que estan adaptades a una pressió constant dels herbívors, i en aquelles condicions són afavorides respecte a altres espècies competitivament superiors; els estadis intermitjos serien assimilables a la ***Ruderal strategy (R)*** que es troben en estadis successionals anteriors als climàcics i estan dominats per espècies erectes amb certa complexitat, menys competitives però més resistents als herbívors que les *Cystoseira*.

Encara que totalment insuficient per a traçar seqüències succesionals, l'evolució dels tancats amb densitats de garotes manipulades durant quasi tres anys va mostrar unes tendències de desplaçament de la dominància de les estrategies algals completament congruent amb aquest model succesional.

Així, veiem que una densitat moderada de garotes provocava una substitució d'espècies C a espècies R, que, tot i tenir una complexitat estructural i específica força complexa, estan adaptades a una pressió d'herbivoria major. Una densitat de garotes elevada afavoria la proliferació d'algues incrustants S a costa de les C i R. La situació contrària s'observava en els tancats desproveïts de garotes, on la feqüència d'espècies C augmentava a costa de les S.

Questió 8 Com posar tots aquests resultats en un context coherent?

Resulta temptador intentar col·locar tots aquests resultats fragmentaris en un context coherent. Busquem un model general que permeti explicar les diferències observades en la sortida de les interaccions algues-garotes-peixos als diferents llocs estudiats (Medes, Scandola, però podríem afegir altres zones conegudes de les que tenim dades com Port-Cros, Balears, Cabo de Palos, etc.) no en base a les diferències associades a la distància geogràfica sinó en clau dels processos analitzats en el meu treball. En aquest punt es troba a faltar una dimensió temporal que encara no he considerat: el component que té la ***història*** recent en l'estat actual d'aquestes comunitats.

La manca de treballs històrics i de decriptors paleo-ecològics als ecosistemes infralitorals mediterranis obliga a especular sobre com eren aquestes comunitats en un passat recent (Sala 2004).

Malgrat les dificultats existeixen prous evidències disperses per a proposar que la distribució de les espècies d'algues del gènere *Cystoseira* era a mitjans del segle XX molt més extensa del que és ara. En un dels rars treballs fito-sociològics realitzats abans de l'arribada de l'escafandre autònom alguns autors (Sauvageau 1912, Feldmann 1937, Gros 1978) descriuen les comunitats algals de Banyuls de la Marenda i descriu com comuns un mínim de 10 espècies de *Cystoseira*. Aquest autor descriu la comunitat de *Cystoseira spinosa* com la dominant a tot el llarg del circalitoral rocós d'aquesta localitat. En una prospecció ralitzada recentment (Thibaut i Ballesteros in prep), només persisteixen en l'actualitat 5 espècies de *Cystoseira* i l'abans extensa comunitat de *C.spinosa* ha desaparegut totalment. Sospitem que les garotes han jugat un paper molt important, encara que probablement no exclusiu en aquesta regressió.

Una evidència més clara prové del Parc Nacional de Port-Cros (França): durant els anys 70 hi va haver un augment de garotes que va eliminar les poblacions de *Cystoseira* cf. *caespitosa* (Verlaque 1987); posteriorment, entre els anys 1982 i 1983 va haver una mortalitat molt important de garotes que va deixar les densitats semblants als nivells inicials (Azzolina 1983). Tot i el descens de les densitats de garotes (del que encara no s'han recuperat; dades pròpies inèdites), no hi ha hagut una recuperació de les poblacions de *C.caespitosa*, probablement degut a la falta de focus de dispersió.

Altres evidències suggereixen que hi ha hagut una desaparició a gran escala dels boscos de *Cystoseira* a tot el Mediterrani, i que va tenir lloc durant els anys 70 i següents, coincidint amb episodis de proliferació desmesurada de les garotes (Giaccone 1971, Katzmann 1974, Gros 1978, Augier i Boudouresque 1967, 1970a,b, 1976, Mastaller 1974, Zabodnik 1977, Torunsky 1979, Verlaque i Nédelech 1983).

En una afirmació encara més especulativa, hi ha la sospita que les activitats antròpiques han jugat un paper rellevant en la regressió recent de les *Cystoseira* mediterrànies. Hi ha diferents mecanismes que podrien explicar aquesta relació i almenys en un d'ells (però possiblement en més d'un) es veuen involucrades les garotes.

Tal com sostenen alguns autors (Sala et al. 1998, Sala 2004), durant els darrers 500 anys hi ha hagut un augment de l'esforç de pesca a la Mediterrània (com a totes les costes del món) que ha fet disminuir la densitat de peixos depredadors litorals i, per efectes en cascada, ha provocat un augment de les poblacions de garotes (Sala et al. 1998). Aquest augment de les garotes hauria causat una degradació de les comunitats de *Cystoseiretum* cap a unes comunitats de blancall (algunes) o cap a comunitats intermitges, en que dominen les espècies estacionals i/o adaptades a la pressió dels herbívors.

Per altra banda, l'augment de la població al voltant de la costa mediterrània ha comportat un augment de la contaminació orgànica (clavegueres, fertilitzants pels conreus..etc). Aquesta contaminació pot haver actuat com adob per a les aigües litorals del Mediterrani, causant així canvis en la interacció algues-garotes per diferents vies (Sala et al. 1998).

Per una banda les garotes poden augmentar la seva fitness com a conseqüència de una eutrofització, augmentant la seva ingesta ja sigui per una major qualitat nutricional de les algues (Hemmi i Jormalainen 2002), per una absorció directa de la matèria orgànica particulada que sedimenta sobre les algues, o per absorció directa (Régis 1977). La major ingesta de matèria orgànica els permet un major creixement, una major producció de gàmetes i una major supervivència en l'estadi d'adults. L'eutròfia es tradueix en un augment de la productivitat del fitoplancton, i per tant de les condicions d'alimentació i supervivència de les larves planctòniques (Lopez et al. 1995), causant així un major reclutament i finalment una major densitat de garotes. A més, si tenen major disponibilitat d'aliment s'han de moure menys, reduint així els possibles efectes mediats pel comportament.

Però els nutrients també poden tenir un paper important en la substitució de les algues perennes per les algues estacionals via competència. Per una part, les algues perennes són competitivament superiors en ambient oligotròfics, ja que tenen mecanismes per a suportar les èpoques en que la disponibilitat de nutrients és limitant (òrgans de reserva, aturen el creixement, etc.). Les algues estacionals, en canvi, actuen com a oportunistes, ja que creixen sobretot durant la primavera, el moment en que la combinació de llum i disponibilitat de nutrients és màxima, i quan les condicions els són desfavorables no poden viure. Però si es produeix un augment de la disponibilitat de nutrients, les relacions de competència entre les algues perennes i les estacionals es pot alterar en favor de les espècies estacionals.

En resum, la hipòtesi sostinguda aquí és que les diferents combinacions de comunitats algals- poblacions de garotes- poblacions de peixos que es poden observar a diferents localitats de la Mediterrània occidental actual poden explicar-se com diferents fases d'un procés successional en què les activitats antròpiques, via la sobrepesca i la contaminació orgànica juguen un paper fonamental. Aquest paper pot resumir-se en un eix històric. Les condicions climàtiques i tròfiques (bottom-up) regionals representen un altre eix principal. La magnitud de les poblacions de garotes, no essent un eix independent del primer ni del segon, representen el tercer eix que resumeix la força estructuradora immediata dels factors "top-down".

En aquest model, **els boscos de *Cystoseira*** amb molt feble densitat de garotes representen la condició climàcica de costes regionalment oligotròfiques (com les de les Illes Mediterrànies) i no afectades per contaminació orgànica ni sobrepesca. Un exemple d'aquesta situació serien les comunitats infalitorals de la Reserva Natural de Scandola (Còrcega).

Les **comunitats intermitges** constituides per algues erectes o cespitoses però de cicle estacional constitueixen un estat succesional secundari de resposta a episodis històrics de proliferació de garotes i desaparició de les comunitats de *Cystoseira*, en zones regionalment més eutròfiques (costes continentals prop de rius), eutrofitzades per acció antròpica i/o sobrepescades. Els exemples d'aquesta situació són molt abundants tot al llarg de les costes catalanes i del sud de França, i inclouen la majoria de les seves Reserves (Illes Medes, Port-Cros).

Les **comunitats de blancalls** representen el cas més extrem de pertorbació i regressió successional de les comunitats algals i responen a un episodi vigent de proliferació de garotes per una suma de sobrepesca i contaminació orgànica o per simple sobrepesca. Es poden donar en totes les condicions oceanogràfiques de la Mediterrània però són més probables a les regions oligotròfiques (illes de la Mediterrània Central i costes meridionals) sotmeses a un procés històric de sobrepesca.

Es pot predir **l'existència d'un gradient** geogràfic d'aquestes condicions succesionals en l'eix que va des de les costes continentals enriquides per les desembocadures dels rius i densament poblades des d'antic cap a les illes de la

Mediterrània desproveïdes d'aports continentals i històricament poc habitades (p.e. Cabrera).

Aquests eixos representen a més **una seqüència històrica**, de moment irreversible, en que els darrers enclavaments posseïdors de boscos de *Cystoseira* estan rebent l'atac d'unes poblacions de garotes en expansió gràcies a la seva elevada capacitat dispersiva i a la modificació favorable de les condicions de producció (bottom-up) i de control tròfic (top-down) propiciades per l'home.

Les **Reserves Marines**, que constituirien les condicions d'**excepció** on aquest procés de regressió succesional podria revertir-se no tenen la capacitat de controlar les poblacions de garotes (per problemes d'escala i per l'existència de refugis) ni d'aconseguir un retorn natural de les poblacions de les algues del gènere *Cystoseira* degut a la distància excessiva dels focus potencials de dispersió.

Questió 9 Quines poden ser les aplicacions d'aquest treball a la gestió de les comunitats infralitorals mediterrànies ?

Així, les comunitats "ruderals" dominades per algues estacionals, que no són ni blancalls ni boscos, poden ser actualment les comunitats dominants al Mediterrani, com a conseqüència dels efectes conjunts de la sobrepesca i la contaminació de l'home. Per la seva banda, els boscos de *Cystoseira* són una relíquia en perill d'extinció, presents només en les zones menys poblades, amb menys aports organics (illes) i menys pescades. Com els boscos de Cystoseira representen les comunitats més madures i estructurades i més riques en biodiversitat, conservar i recuperar aquestes comunitats pot ser un objectiu prioritari en els criteris de gestió del litoral mediterrani. Les Reserves Marines, i en especial aquelles que conserven comunitats extenses dominades per algues del gènere *Cystoseira*, concentren una bona part de la responsabilitat en aquesta recuperació.

Les lliçons que podem treure d'aquest treball poden contribuir positivament a la consecució d'aquest objectiu.

Així, si revisem les prediccions dels models deterministes com el de McClanahan i Sala (1997), podem concloure que no és esperable que funcionin a la petita escala d'una Reserva Marina o d'un periode de temps tan curt com el d'un estudi científic, però segueixen constituint un punt de referència útil per a un model de mesoescala (o per a tota la conca W de la Mediterrània) i d'una escala temporal prou ampla (almenys de desenes d'anys). A l'escala més petita de les Reserves, no hem d'oblidar que tot i la recuperació de les poblacions de peixos, l'existència de refugis, les condicions tròfiques (naturals o modificades per l'home), i la desproporció entre les escales de dispersió de les garotes i les mides de la reserva juguen en contra del control de les poblacions de garotes. Els experiments d'eradicació de garotes realitzats a la Reserva de Scandola proven que es pot obtenir una reversió ràpida de les comunitats sempre que els focus de recolonització algal es trobin propers i que les poblacions de peixos ja estiguin recuperades. Encara que no hem fet un estudi de l'esforç necessari, la persistència dels efectes d'una eradicació puntual al cap de quatre anys fa pensar que la tècnica mereix ser aplicada a àrees extenses sempre que les poblacions veïnes no siguin tan denses que provoquin una continuada invasió larvària. Aquest consell és especialment dirigit a les Reserves Marines i àrees protegides que allotgin un patrimoni algal valuós i mostrin símptomes d'aparició de blancalls.

Futures recerques:

Per últim, tot i que ha ajudat a resoldre algunes qüestions, crec que la principal utilitat d'aquest estudi ha estat la d'obrir noves preguntes que haurien de ser investigades per a aprofundir en el coneixement del funcionament i la dinàmica de les comunitats infralitorals. El que segueix és una llista dels temes que semblen prioritàris:

Definir grups funcionals integrant criteris morfològics, estacionals i de resistència a l'herbivoria

Per a entendre millor la resposta dels herbívors dins un marc estacional, i poder comparar els efectes a escales biogeogràfiques on varií la composició específica, hauríem de poder agrupar les espècies en grups funcionals amb criteris morfològics, successionals i de resposta als herbívors. Seguint el model de Littler i Littler (1980), hauríem de poder distingir les diferents espècies o grups d'espècies dins un rang de oportunistes fins a estadis successionals terminals per a testar l'efecte dels herbívors. El problema que se'ns ha plantejat és com trobar els criteris per fer agrupacions que es puguin aplicar en altres comunitats i responguin de la mateixa forma als diferents factors (herbívors i estacionalitat) que les controlen. Com els grups funcionals més acceptats (p.e. Littler i Littler,1984, Steneck i Dethier,1995) no semblen adaptar-se bé a les comunitats mediterrànies i acceptant que els factors principals són la pressió d'herbivoria i la pròpia estacionalitat, caldrà trobar una agrupació que integrin els criteris morfològics amb els purament estacionals, o de cicle de vida. Així, el camí més prometedor serà barrejar els criteris de resposta a les agressions de Grime, criteris morfologics com els de Steneck i la resposta a l'estacionalitat de Ballesteros. D'aquesta forma es podrien fer agrupacions en diferents tipus de comunitat, però que responguessin de la mateixa forma a la pressió dels herbívors i als controls per baix de la producció.

Dinàmica de les poblacions d'algues

Tenim una idea bastant precisa de la dinàmica de les poblacions de garotes però no tenim tota aquesta informació per a les algues, i concretament per a les espècies climàciques. Així, encara no sabem quin és la taxa de reclutament, la supervivència, el creixement, la longevitat, l'esforç reproductor i la dispersió dels propàguls de la majoria de les espècies d'algues.

Igual que es fa en sistemes terrestres on es gestiona el bosc, amb aquests coneixements, es poden tenir criteris més precisos per a la seva conservació, ja que es podria modelitzar la dinàmica poblacional de les espècies d'algues més representatives, predir la capacitat de càrrega de garotes en un sistema, la mida crítica dels blancalls i els períodes de retorn. Aquesta informació seria útil per a prevenir episodis de sobrepastura i conservar els punts calents de la biodiversitat infralitoral.

Restauració de comunitats algals: potencialitat dels trasplantaments

En especial resulta prioritari el coneixement de les capacitats dispersives de les algues del gènere *Cystoseira*, per tal d'avaluar les possibilitats de recuperació dels seus boscos una vegada denudats. Hi ha varis antecedents d'actuacions d'aquest tipus. Per una part, els programes d'eradicació de garotes permeten una prevenció de la desforestació. Però també hi ha iniciatives per a la recuperació mitjançant trasplantaments, ja sigui d'individus directament fixats, o d'individus reproductors amb la finalitat que actuïn com a font de propàguls per a repoblar via reclutament zones denudades.

Tot i que és necessari encara un debat més exhaustiu de fins a quin punt l'home ha d'intervenir en aquests processos, aquests antecedents haurien de servir de punt de partida per a dissenyar actuacions de prevenció de la deforestació dels boscos de *Cystoseira* i de reforestació dels blancalls.

Competència entre algues com a conseqüència de la herbivoria

La majoria de treballs que s'han fet sobre herbivoria han tractat l'efecte dels herbívors sobre espècies d'algues individuals o sobre grups funcionals. Però hem vist que la interacció competitiva entre les espècies pasturades pot tenir un paper important en la composició específica de la comunitat; i més si hi ha depredadors, com els peixos, que actuen de manera diferencial sobre algunes espècies concretes però no sobre altres. Així, les interaccions entre la herbivoria i les relacions de competència entre espècies d'algues (o grups funcionals) és un camp encara força inexplorat que ens pot permetre afinar més els models.

Efectes de l'eutrofització

L'efecte de la eutrofització en la substitució de les comunitats algals, podria tenir més importància del que sembla ja que, com hem comentat, pot influir en la substitució d'espècies climàciques per espècies ruderals. Fent un símil en ambients tropicals, s'ha vist que més enllà de l'efecte de les garotes i la sobrepesca, els nutrients han contribuït de forma important a la substitució de coralls hermatípics per algues. Aquesta hipòtesi hauria de testar-se experimentalment, però també s'hauria de testar correlacionalment seguint gradients de eutrofia al llarg del Mediterrani.

Aquesta via d'eutròfia, podria ser més o menys important segons les característiques locals. Concretament a les Illes Medes, aquest pot haver estat un efecte que ha afecta per varies vies. Per una part, l'augment de la població i el turisme ha fet augmentar les aigues residuals. A més, la desembocadura del riu Ter, a escassos kilòmetres de les Illes Medes, produeix un aport molt important d'aigua continental eutrofitzada.

Per altra banda, la colònia de gavians actua com a un sumider de matèria ja que s'alimenten fora de la reserva i tota la matèria orgànica que mengen va a parar dins la reserva (ja sigui per excrements o per els cadàvers que cauen cada any a l'aigua). Si tenim en compte que els gavians han canviat els seus habits alimenticis aprofitant les deixalles humanes (abocadors, descartes de pesca...) l'home esta influint indirectament a una eutrofització de la zona per aquesta via. Caldria comprovar, per tant, com els gavians influencien les comunitats algals i les garotes d'aquesta àrea.

Dinàmica poblacional de garotes: Hi ha limitació en el reclutament?

En aquest treball ens ha quedat una imatge força clara del gran potencial de producció de gàmetes de les garotes. No obstant, existeixen zones de la Mediterrània on la densitat de les garotes és encara molt baixa. En general, aquestes zones coincideixen amb regions oligotròfiques. Hipotèticament poden existir regions on hi hagi una limitació en els recursos i conseqüentment una disminució en el reclutament de garotes, fent que les poblacions de garotes puguin estar limitades pel reclutament. S'hauria de veure en aquestes zones aïllades, on no poden arribar larves de poblacions foranies quins són els patrons de reproducció, assentament i reclutament de les poblacions adultes.

Genètica de poblacions de garotes

La dispersió de les larves i la interconnexió de poblacions s'hauria d'estudiar a nivell genètic. Tot i la gran dispersió que en teoria permet una homogeneització de les poblacions, estudis amb *S. franciscanus* i *S. purpuratus* (Edmands et al. 1996, Moberg i Burton 2000) demostren l'existència de certa estructura genètica en les poblacions locals, suggerint que es podrien donar circumstàncies en que les poblacions de garotes mantinguin una heterogeneïtat geogràfica.

Variabilitat en l'assentament a més gran escala temporal i geogràfica.

Hem vist que a nivell local, els patrons d'assentament tenen una variabilitat temporal i espacial mot important. Però aquest patró ha obert diverses preguntes que s'haurien de respondre per a tenir una visió més àmplia de la dinàmica de les poblacions de garotes. Per una part, quins factors afecten a la potència de l'assentament d'un any per l'altre? Per altra banda, hem obtingut informació del patró d'assentament a escala local, però desconeixem com es comporta a una escala més àmplia. Caldria repetir experiments de assentament en diversos punts del Mediterrani (o almenys a nivell de conca NW) per a testar si el patró heterogeni de desenes a centenars de metres es repeteix a mesoescala (Km a 100's Km). Seria molt interessant analitzar la correlació entre les dades d'assentament obtingudes a gran escala i paràmetres ambientals o amb les dades ja existents de densitats de poblacions adultes.

Trait mediated Indirect Interactions

Recents estudis en sistemes terrestres han posat de manifest que els efectes mediats pel comportament escapatori dels herbívors en front als depredadors poden produir una reducció de l'efecte de l'herbivoria inclòs tant important com els mateixos efectes derivats de la depredació.

Tot i que hi ha evidències del comportament escapatori de les garotes (es refugien en esquerdes etc.) encara no hi ha cap treball que hagi quantificat aquest efecte en la comunitat algal. En els nostres experiments hem vist com l’efecte de les garotes en presència de peixos era menor sobre algunes espècies que tenien certa importància a l’hora d’explicar la composició de la comunitat (p.e. *Corallina elongata*), fet que es pot interpretar com un primer indici d’aquest efecte. Suggereixo testar la importància d’aquests efectes tant a nivell quantitatiu com a nivell qualitatiu, i en diferents tipus de comunitats.

Aplicacions per a la conservació

A més del coneixement naturalístic del funcionament dels sistemes infralitorals, no s’ha de perdre la perspectiva de una recerca aplicada a la gestió i conservació d’aquests sistemes. Crec que, com ja he dit, encara s’ha de fomentar el debat sobre la conveniència d’intervenir o no en els ecosistemes marins. A favor del principi de no intervenció juga la falta generalitzada de coneixement que tenim sobre el seu funcionament. No obstant, caldria començar a pensar en actuacions que mitiguessin els efectes no desitjats causats per l’home, com probablement ho és la proliferació de blancalls, amb la corresponent pèrdua de diversitat. Si concloem que aquest efecte és causat per l’home i que s’ha d’evitar o corregir, aleshores haurem de tenir preparades les actuacions adequades. En el terreny de la restauració subaquàtica s’obre davant nostre un vast camp experimental enterament a descobrir.