



Littoral fish assemblages

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Abstract

Visual counts in summer of 2009 in the Medes-Montgrí (NW Mediterranean) at 5 and 10m deep, evidenced a significant decrease in the mean species richness, abundance and total biomass of littoral fish assemblages when compared to counts from previous years (1999, 2002, 2005). The most conspicuous effects were: 1) a decrease of the abundance and biomass of *Chromis chromis*, *Coris Julis* and *Diplodus sargus*, and 2) a decrease of biomass, but not of the total abundance, which was counterbalanced by a very high recruitment after the storm in *Serranus cabrilla*, *Symphodus tinca* and small *Symphodus spp.*, in general. The rest of the studied species experienced no significant alteration after the storm.

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**Impact of 2008 Sant Esteve's storm on littoral rocky reef fish assemblages in
Medes Islands Marine Protected Area and the coast of Montgrí (NW
Mediterranean)**

By

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Resumen

Recuentos visuales realizados el verano de 2009 en Medes-Montgrí (Mediterráneo NO) a 5 y 10m de profundidad, pusieron en evidencia una disminución significativa de los valores medios de riqueza específica, abundancia y biomasa total en comunidades de peces litorales al compararlos con recuentos de 1999, 2002 y 2005. Los efectos más conspicuos fueron: 1) una disminución en la abundancia y la biomasa de *Chromis chromis*, *Coris Julis* y *Diplodus sargus*, y 2) una disminución de la biomasa pero no de la abundancia total, contrarrestado por un reclutamiento muy superior tras la tormenta de *Serranus cabrilla*, *Symphodus tinca* y de pequeños *Symphodus* spp., en general. El resto de especies estudiadas no mostraron ninguna alteración significativa tras la tormenta.

Abstract

Visual counts in summer of 2009 in the Medes-Montgrí (NW Mediterranean) at 5 and 10m deep, evidenced a significant decrease in the mean species richness, abundance and total biomass of littoral fish assemblages when compared to counts from previous years (1999, 2002, 2005). The most conspicuous effects were: 1) a decrease of the abundance and biomass of *Chromis chromis*, *Coris Julis* and *Diplodus sargus*, and 2) a decrease of biomass, but not of the total abundance, which was counterbalanced by a very high recruitment after the storm in *Serranus cabrilla*, *Symphodus tinca* and small *Symphodus* spp., in general. The rest of the studied species experienced no significant alteration after the storm.

Introduction

Coastal fishes on sublittoral rocky substrate form a relatively diverse assemblage in the Mediterranean. The spatial distribution of these fish in the first 50 m of depth is mostly due to a vertical gradient characterized by a continuum in which some species

gradually replace other, with a few species showing a wide distribution in depth (Garcia-Rubies 1993). The maximum diversity is reached at about 10m deep in the area of the Costa Brava (NW Mediterranean) according to Garcia-Rubies (1999). Other environmental factors that modulate the qualitative and quantitative composition of the

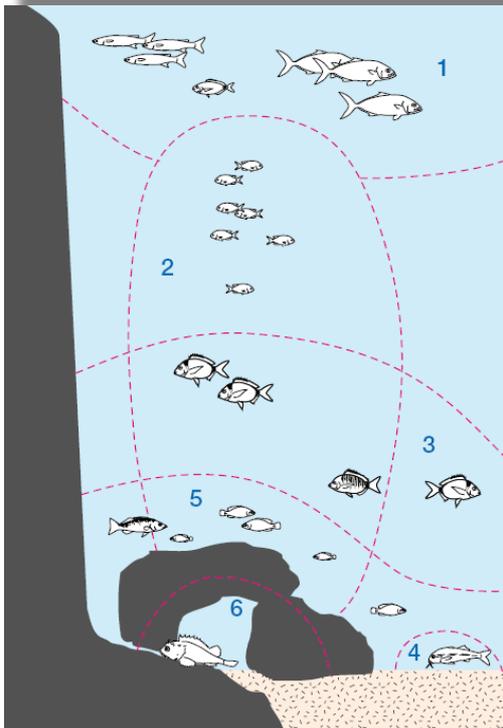


Figure 1. The 6 spatial categories of Mediterranean littoral fish on rocky substrate according the position in the water column and their connection to the seabed (after Harmelin, 1987, redrawn by Corbera in Garcia-Rubies, 1997)

assemblage are the complexity of the bottom or rugosity, (*sensu* Lukchurst & Lukchurst, 1978) and seasonality.

Regarding the distribution in the water column, 6 spatial categories were established by Harmelin (1987), ranging from category 1, which consists of nektonic fish that move freely in the water column with little contact with the bottom, up to category 6, which assembles benthic species, with short horizontal and vertical displacements, never far away from the bottom in which they take permanent or temporary shelter (Figure 1).

The traditional exploitation of the Mediterranean Sea has seriously affected the assemblage of coastal fish in areas open to fishing, so littoral rocky reef fish assemblage is very different to that seen in marine protected areas or marine reserves where fishing is strictly prohibited. The differences between protected and unprotected areas go beyond mere qualitative or quantitative variations. Effective recovery of predatory fish produce cascading effects that affect the entire coastal benthic assemblage, being the ratio between fish, seaweed and urchins the best known and studied of these effects (Guidetti, 2006; Guidetti & Sala 2007).

Most studies conducted so far on this assemblage deal on the distribution (Garcia-Rubies 1993), the effect of protection (Bell, 1983; Garcia-Rubies & Zabala, 1990; Francour, 1991; Garcia-Charton & Pérez Ruzafa, 1999), and their associated ecological effects, but also the settlement and the recruitment (Garcia-Rubies & Macpherson, 1995) have been studied in detail. Until now no study has looked to check the possible impact of a severe storm on Mediterranean littoral rocky fish assemblage, although it has been demonstrated that wave action can condition the success of nesting in some species (Raventós 2004, 2006). This lack of information about the impact of severe storms may be due to the rarity and the unpredictability of such extreme events that makes it difficult

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to collect appropriate data (Adams, 2001).

In tropical coral reef communities, where cyclones and hurricanes tend to be more frequent, the effects of these

(Walsh, 1983; Fenner, 1991, Adams & Ebersole, 2004) but habitat shifts after the storm have been observed (Kaufman, 1993) and the main changes in fish assemblage have been

Table 1. List of species of the fish found dead on the beach of l'Estartit (Weitzmann, obs pers.) after the storm, habitat and spatial category of the rocky reef species (**: very abundant; * abundant; 1: one specimen observed).

Species	Habitat	Category
<i>Anthias anthias</i> **	Rocky bottoms	2
<i>Apogon imberbis</i> *	Rocky bottoms	6
<i>Apterichthys anguiformis</i> (1)	Demersal soft bottom	
<i>Boops boops</i>	Rocky bottoms	1
<i>Cepola rubescens</i> (1)	Demersal soft bottom	
<i>Chromis chromis</i> *	Rocky bottoms	2
<i>Coris julis</i>	Rocky bottoms	5
<i>Diplodus sargus</i>	Rocky bottoms	3
<i>Epinephelus marginatus</i>	Rocky bottoms	5
<i>Hippocampus ramulosus</i> (1)	Rocky bottoms	6
<i>Merluccius merluccius</i>	Demersal soft bottom	
<i>Oblada menlanura</i>	Rocky bottoms	1
<i>Pagellus erythrinus</i>	Demersal soft bottom	
<i>Serranus cabrilla</i>	Rocky bottoms	5
<i>Spicara smaris</i> (1)	Rocky bottoms	1
<i>Squalus blainvillei</i> (1)	Demersal soft bottom	
<i>Cyprinus carpio</i> *	Fresh water	
<i>Scardinius erythrophthalmus</i> *	Fresh Water	
<i>Rutilus rutilus</i> *	Fresh water	

disturbances have been documented in a series of works. Storms are considered among the main sources of disturbances on coral reef fish assemblages (Jones & Syms, 1998; Syms & Jones, 2000), but their effects showed a large degree of variation, depending on the violence of the storm and the biological features of the different species. High fish mortality directly provoked by wave action was rarely reported (Pfeffer & Tribble, 1985, but see Robins, 1957) and direct mortality does not seem extremely important in many cases

documented to be mostly related to changes in habitat composition as a result of the loss of living coral cover (Kaufman, 1983; Fenner, 1991; Aronson et al., 1991). Mobile fish species are often less affected than sedentary species (Bortone, 1976; Walsh, 1983), and the spatial distribution of sedentary species may be changed (Woodley et al., 1981). After Adams (2001) there is insufficient information on the extent to which hurricanes impact fish assemblages on coral reef fishes.



Figure 2. Location of the sampling zones inside the Medes Islands Marine Protected Area (R; top) and in the unprotected coast of Montgrí (NR; bottom).

On December 28, 2008 a violent easterly storm affected mainly the northern part of the Catalan coast.

After the storm, thousands of fish of various species (Table 1) were found dead on the beach of l'Estartit and on

others also, showing that the impact had been large. Mobile species such as *Anthias anthias* and *Chromis chromis* were the most abundant of marine fish species on the beach and both species belonged to the spatial category 2. More sedentary fishes belonging to category 5, after Harmelin (1987) were also found on the beach, including labridae (mainly *Coris julis*) and Serranidae (mainly *Serranus cabrilla*, but also some specimens of *Epinephelus marginatus*). Only two species of the most bottom-related species (category 6, after Harmelin, 1987), were found on the beach. Apparently the impact of the storm was not homogeneous across the whole fish assemblage, and, interestingly, the strictly benthic species were not among the most affected. In order to ascertain if the apparently important impact of the storm on littoral fish assemblages was evident *in situ*, during the summer of 2009 several visual counts of littoral fish were carried out in the protected area of the Medes Islands and in the unprotected coast of Montgrí at shallow depths (5 and 10m). These records were compared with previous data that were collected during the summer of the years 1999, 2002 and 2005.

Study sites and sampling method

The study was carried out in the Medes Islands Marine Protected Area and in the neighbouring unprotected coast of El Montgrí (Figure 2) during the years 1999, 2002 and 2005

(before the storm) and 2009 (after the storm). Two zones at two depths (5 and 10 m) were sampled inside (Freuetó) and outside the Marine Protected Area (Illa del Dui-Falaguer). Both zones were totally exposed to the easterly winds. We therefore chose a third reference zone inside the MPA (Meda Petita) that was partially sheltered from the easterly winds (Figure 2); however, finally it was not included in the analysis because there were only data from 1999 and 2009.

Rocky bottoms in all zones were characterised by large ($\emptyset > 2\text{m}$) or medium sized ($1 < \emptyset < 2\text{m}$) rocky boulders with a high degree of substrate complexity or 'rugosity' (*sensu* Luckhurst & Luckhurst, 1978). Sampling was always conducted during summertime (from August to September) in order to avoid seasonal differences among years. Interannual differences in littoral Mediterranean rocky fish communities can be mainly explained by differences in annual recruitment of several species that usually settle and recruit from late spring to early summer (Garcia-Rubies & Macpherson, 1995). Therefore, the abundance of young of the year (YOY) can greatly alter the total abundance of several species from year to year.

Sampling was carried out by scuba diving over 50 x 5 m (250 m²) transects haphazardly placed in the two zones at 5 and 10 m depth. All fish in each transect were identified, counted, and their size estimated with $\pm 2\text{cm}$ accuracy. This sampling method can be used to make a good estimate of the density and size of most necto-

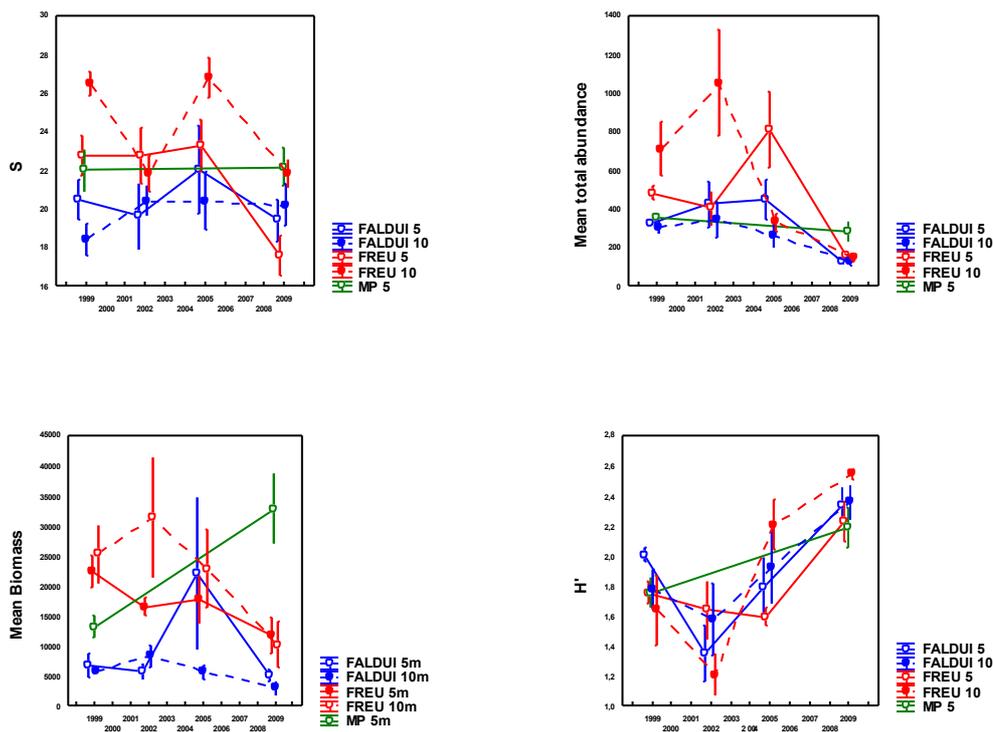


Figure 3. Interannual variations of mean number of species (S), mean abundance (number of ind. 250 m⁻²), mean biomass (g 250m⁻²) and specific diversity (H') at the three zones (FD: Falaguer-Dui; FR: Feuetó; MP: Meda Petita) at 5 and 10m deep.

benthic species; however, the abundances of small crypto-benthic species (i.e. blennidae and gobidae) are somewhat underestimated (Harmelin-Vivien et al., 1985). A total of 84 transects was sampled on different days in August and at the beginning of September.

Data treatment

Fish density and abundance were converted into biomass using the length-weight transformation equations found in the literature (Morey et al., 2001) or in Fishbase (www.fishbase.com). If these equations were not available for a given species, the length-weight relationship was taken from

taxonomically and morphologically very similar species. Abundance and biomass are not redundant parameters of the fish assemblage: the number of individuals gives more importance to species represented by many small individuals, while biomass gives more importance to the species represented by a few large individuals (Bohnsack, 1983).

At the assemblage level, principal component analyses (PCO) (PRIMER ©) were applied to the previously transformed abundance and biomass data of the species ($x' = \sqrt{x}$; $x' = \text{Log}(x+1)$ respectively). Variations in the synthetic descriptors of the assemblage, such as the number of species per transect (S), Shannon-Weaner, abundance, biomass and

diversity (H') were compared by a three way analysis of variance (ANOVA) in which the predictors 'zone', 'depth' and 'year' were taken as fixed, orthogonal factors. From the results of the multivariate analysis we selected certain species to be treated at a population level. Variations were tested by means of an analysis of variance (ANOVA) following the same design as described above. In order to meet the assumptions of normality, independence of means and variances, and homogeneity of variances, data were transformed if necessary using the square root ($x' = \sqrt{x}$) or the logarithm ($x' = \log(x + 1)$) of the original data. If the transformed data

did not meet the requirements of the ANOVA, the analyses were carried out anyway on original data but taking a higher threshold of significance ($p < 0.01$ instead of $p < 0.05$) in order to prevent type I errors (Underwood, 1997).

Results

Littoral rocky fish assemblage structure

Up to 55 species belonging to 18 families were observed during the study (Annex 1). The total number of species did not greatly vary among years (48 in 1999; 48 in 2002; 45 in 2005 and 46 in 2009) or zones, since

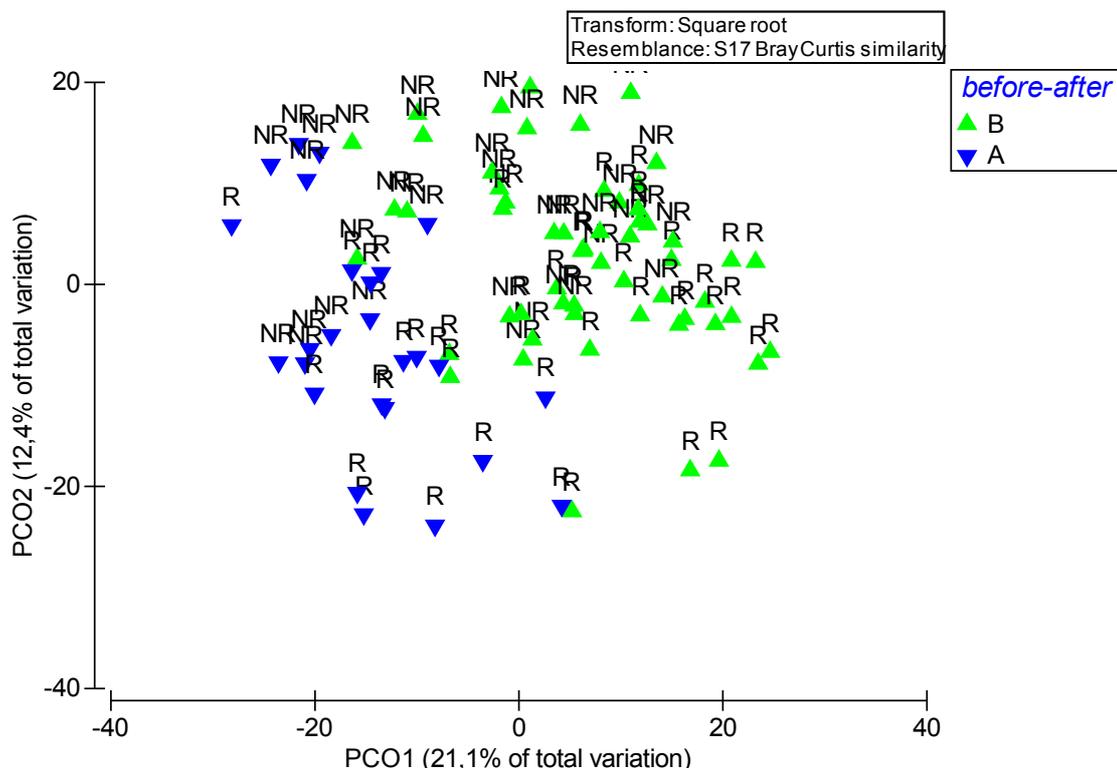


Figure 4. Results of the principal coordinate analysis with the two first axis of variation (Blue triangles: after the storm; green triangles: before the storm; R: samples from MPA; NR: samples from non-protected area).

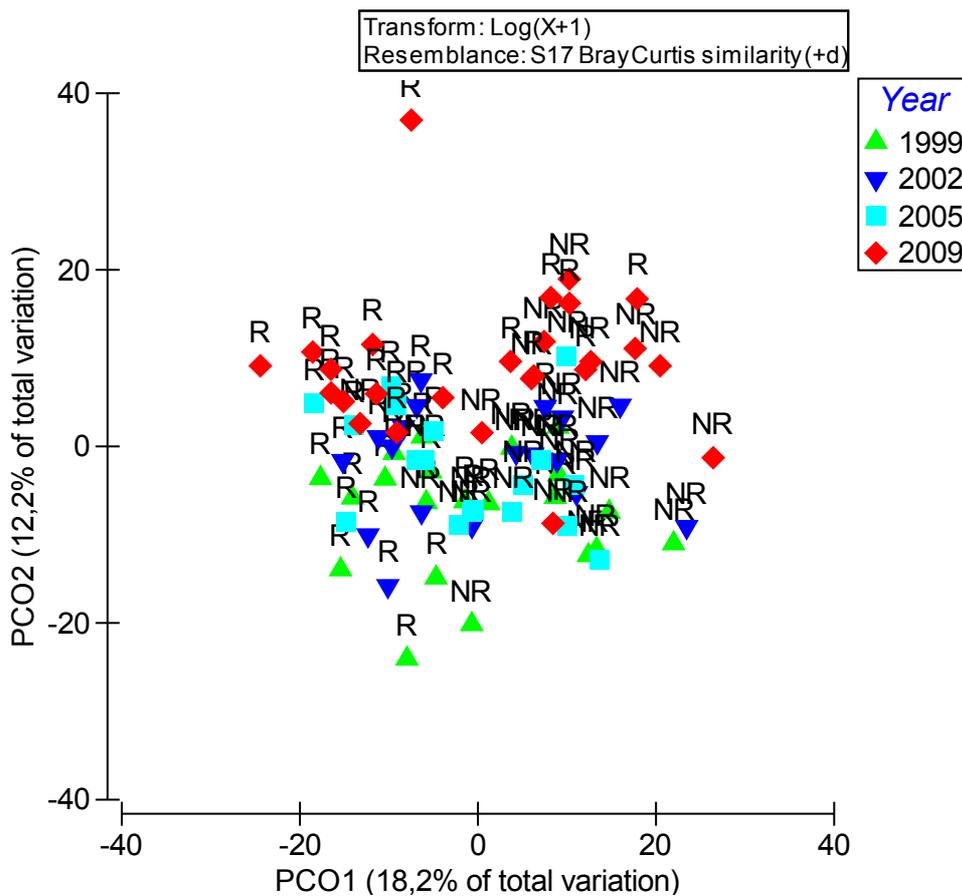


Figure 5. Two first axis of variation of the PCO analysis showing variations of species biomasses (R: samples from MPA; NR: samples from non protected area).

most of species were frequent in the samples. Although the total number of species did not show great differences among years, the results of the analysis of variance of the mean number of species showed significant effects for factors 'zone' and 'year' (Annex 2). The first indicates that mean species richness is higher inside the marine reserve than in the unprotected zone, as expected from previous results (Garcia-Rubies & Zabala, 1990; Garcia-Rubies, 1997). The second indicates that the mean number of species differed between years, and the *post hoc* test demonstrated that it decreased

significantly in 2009 compared to earlier years. There was a significant interaction between 'zone' and 'depth', which implies that the mean number of species was higher at 10 m deep inside the MPA, but very similar at the two depths in the unprotected zone. There was also a significant interaction between 'zone' and 'year', showing that the decrease in the mean number of species is more noticeable inside the protected area from 2005 (before the storm) to 2009 (after the storm). No such decrease in mean number of species was observed in the partially sheltered zone of Meda Xica from 1999 to 2009 (Figure 3).

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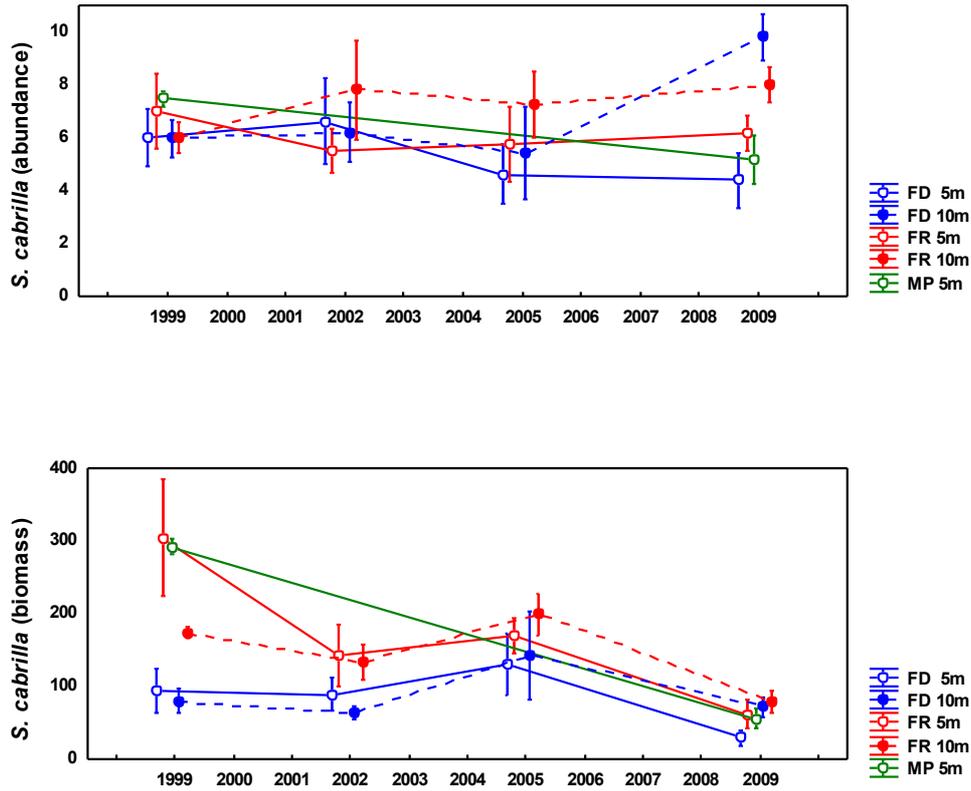


Figure 6. Influence of zone, depth and year on mean (\pm se) abundance (top) and biomass (bottom) values of *Serranus cabrilla* (FD: Falaguera-Dui, unprotected zone; FR: Freuetó, inside the MPA; MP: Mede Petita, inside the MPA).

Large differences in mean total abundance were observed between zones and years, with a significant interaction between 'depth' and 'year' that could be because there was a slight increase at 5m depth in mean abundance from 2002 to 2005 before the decline observed between 2005 and 2009. At 10 m depth, however, a decrease in mean abundance from 2002 to 2005 preceded the drop from 2005 to 2009. Mean total biomass also declined sharply in 2009 compared to previous years, which was the only significant result of the ANOVA. *Post-hoc* tests demonstrated that both the mean total abundance and mean total biomass significantly decreased in 2009 (1999= 2002= 2005> 2009).

The ANOVAs carried out on mean diversity showed similar clear cut results: only differences among years were significant and *post-hoc* tests revealed that in spite of other minor variations (in 2002 the mean diversity was lower than in 1999), the mean diversity values obtained in 2009 were significantly higher than the mean values of the rest of the years. Specific diversity H' correlated well with the evenness (J), indicating that changes observed in diversity depended more on the fluctuations in the abundance of a few dominant species than qualitative changes in the number of species per sample. Therefore, the significant increases in diversity and evenness were a

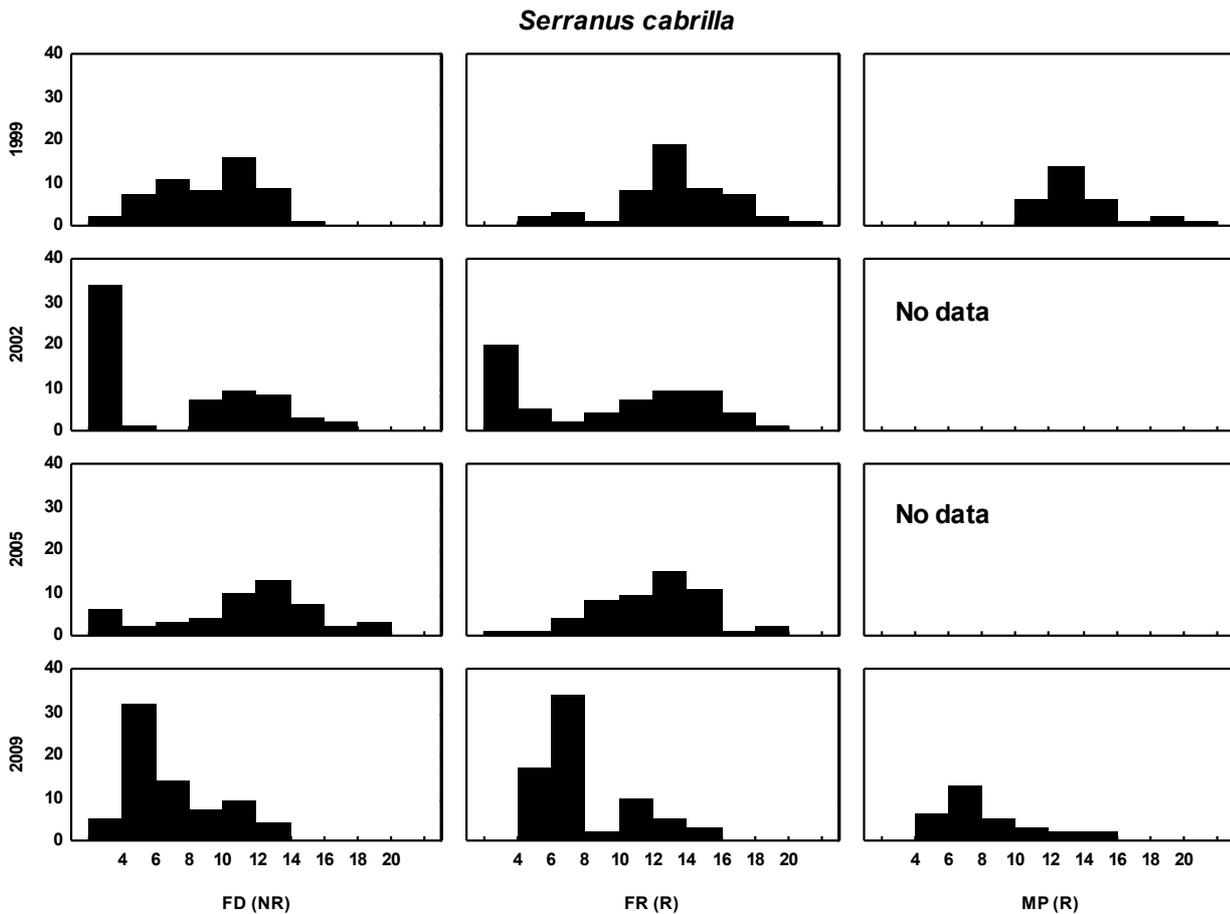


Figure 7. Length frequency distributions (size class TL= 2cm) of *Serranus cabrilla* according the different zones and years. It can be seen that young fishes, mostly YOYs, were dominant in 2009 even in the MPA zones (FD: Falaguer-Dui, unprotected zone NR; FR: Freuetó, inside the MPA, R; MP: Meda Petita, inside the MPA, R).

response to significant downsizing of some quantitatively dominant species. The increase in diversity and evenness was also evident in the partially sheltered zone of Meda Xica in 2009 compared with the mean values obtained in 1999 (Figure 3).

Species distribution

The results of the principal coordinate analysis based on the square root transformed abundances of the species defined two main axes: The first axis segregates the samples according to the years in which they

were taken and explains just over 21% of the total variance. On this axis, samples from 2009 were clearly segregated from those of the rest of the years, which tended to be notably more congregated on this factor. The second axis explained 12% of the total variance and mainly separated the samples from the MPA, with negative values, from those of the unprotected coast, with positive values (Figure 4). *Chromis chromis*, *Coris julis*, *Diplodus sargus*, *Thalassoma pavo* and *Symphodus tinca* had high correlations with the first factor because they were more abundant in

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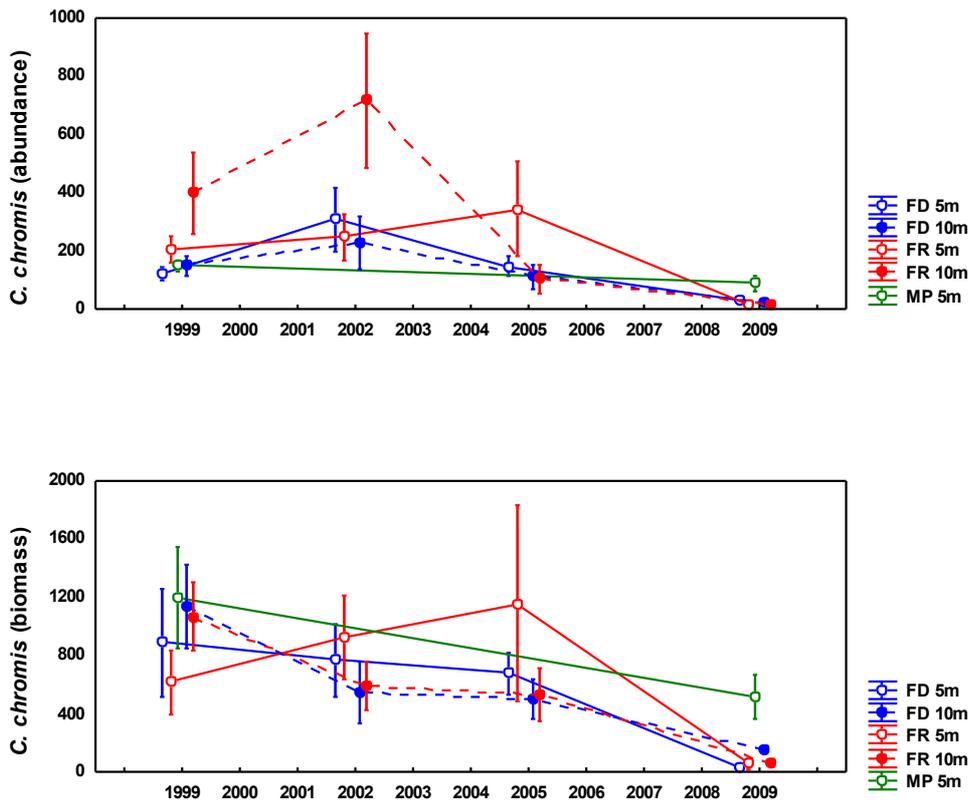


Figure 8. Variations among zones, depths and years on mean (\pm se) abundance (top) and biomass (bottom) values of *Chromis chromis* (FD: Falaguer-Dui, unprotected zone; FR: Freuetó, inside the MPA; MP: Mede Petita, inside the MPA).

the early years of monitoring, while *Serranus scriba* and *Epinephelus marginatus* were positively correlated with the second axis, attributed to protection, and negatively correlated with the first axis, showing that their abundance has increased in recent years. *S. tinca* and *D. sargus* had a marked negative correlation with the two first axes, which shows that they were more abundant inside the marine reserve, but their abundance decreased in the last years of monitoring.

Similar results were obtained when the PCO analysis was repeated on biomass data (log transformed), although the separation between

samples from the protected and unprotected zones was clearer than in the analysis of abundances (Figure 5). In this case, the first axis could be clearly attributed to the protection level, while the second axis was related to interannual variations (18.2 and 12.2% of total variation, respectively). It is worth noting that there were some samples from the MPA in 2009 among the cloud of points that mainly corresponded to the unprotected area. *Symphodus mediterraneus*, *S. tinca*, *S. doderleini*, *Chromis chromis*, *Diplodus sargus*, *Spodyliosoma cantharus*, *Diplodus vulgaris*, *Symphodus ocellatus*, *Gobius* spp. and *Serranus cabrilla* were negatively correlated with the second

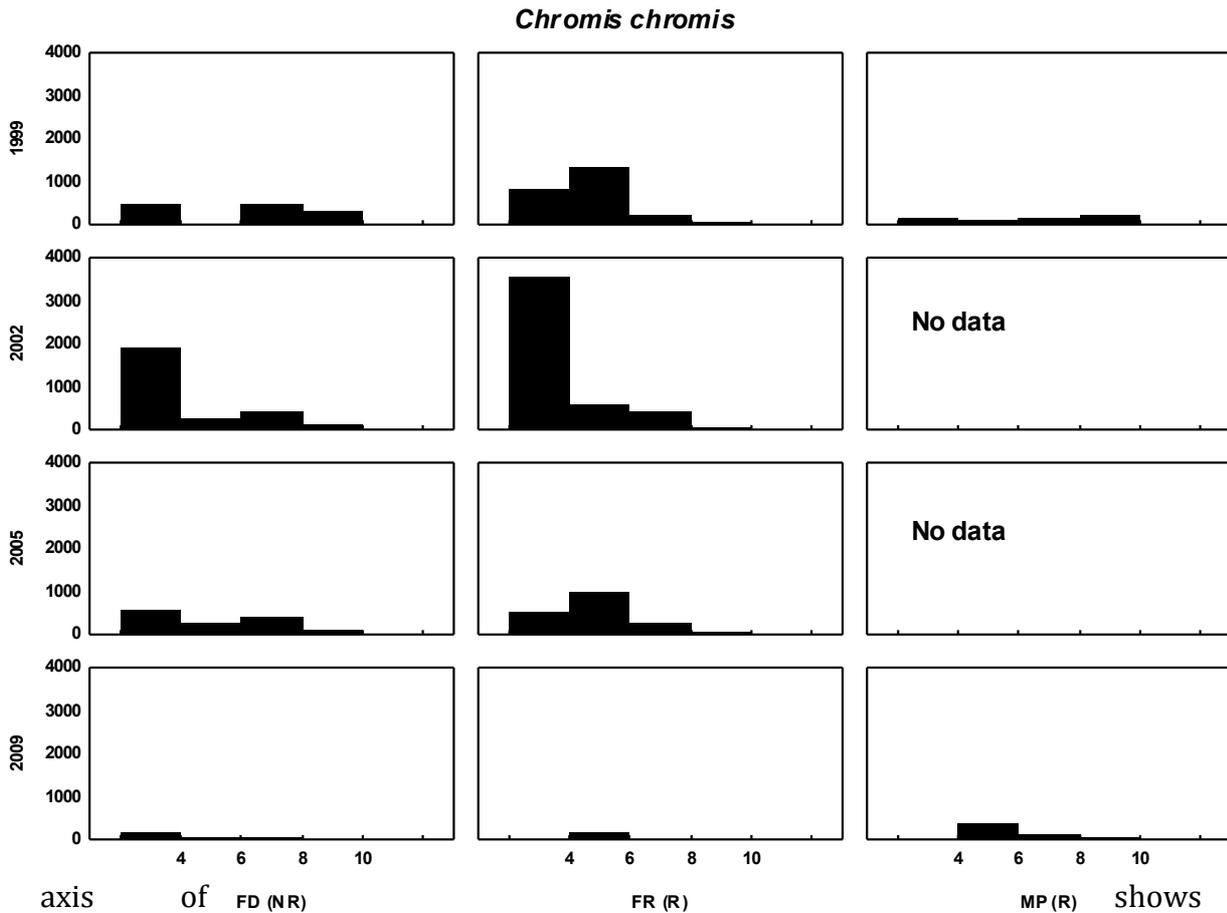


Figure 9. Length frequency distributions (size class TL= 2cm) of *Chromis chromis* in the different zones and years. It can be observed that even the YOYs (TL≤ 4cm) suffered a severe reduction in 2009 (FD: Falaguer-Dui, unprotected zone NR; FR: Freuetó, inside the MPA, R; MP: Meda Petita, inside the MPA, R).

variation. *Diplodus puntazzo*, *E. marginatus*, *Sarpa salpa* and *Labrus merula*, with high negative correlations with the first axis, showed higher biomasses inside the protected area, especially during the last years of the study. Biomasses of *Diplodus cervinus*, *D. sargus*, *Symphodus tinca*, *Coris julis* and *Serranus cabrilla* were higher during the first years of monitoring inside the MPA. *Apogon imberbis* and *Gobius* spp, were negatively correlated with the second axis and showed no correlation with the second axis. This

that the biomass of these species tended to decrease in recent years independently of the protection status, since neither species is commercially valuable.

Fish populations

Both mean abundance and mean biomass were analysed with ANOVAs for the species that seemed to be more affected by the storm according to the results obtained in the PCO analyses.

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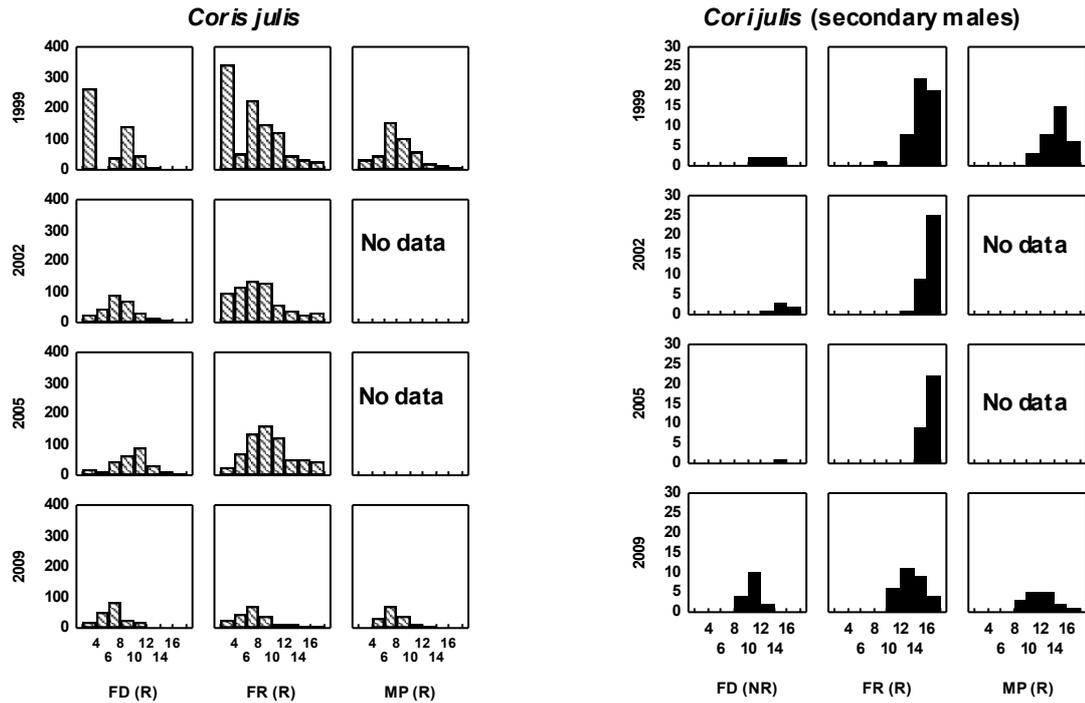


Figure 11. Size frequency distributions (size class TL= 2cm) of the whole population of *Coris julis* (left) and of the secondary terminal males (right). The rarefaction of the biggest specimens was noticeable in 2009 after the storm, including the secondary males (FD: Falaguer-Dui, unprotected zone NR; FR: Freuetó, inside the MPA, R; MP: Meda Petita, inside the MPA, R).

Only the species that were frequent enough to provide reliable data to be analysed were taken into account. Significant results showing differences in abundance or biomass between 2009 and the rest of the years, or any interaction between 'year' and other factors, were considered to be due to the storm. Mean total abundance and biomass are shown in Annex I and Annex II.

Serranus cabrilla

As shown in former works (Garcia-Rubies, 1999), *S. cabrilla* was significantly more abundant at 10 m than at 5 m deep (Figure 6), but there were no significant differences in mean densities between the protected

and unprotected zones. No significant differences were observed between years, although the mean density increased in the unprotected zone at 10 m deep from 2005 to 2009 (Annex 3). The *S. cabrilla* density appeared to be rather untouched by the storm, but the results were quite different when the mean biomasses were analysed. In fact, significant differences can be observed between zones (*post hoc* test: Freu > Dui) and years, and the mean biomass of 2009 is significantly lower than the rest of the years (*post hoc* tests: 1999= 2002= 2005 > 2009). Moreover, the decrease in the mean biomass from 2005 to 2009 seems to

have affected both zones in a very similar way (Figure 6), which suggests

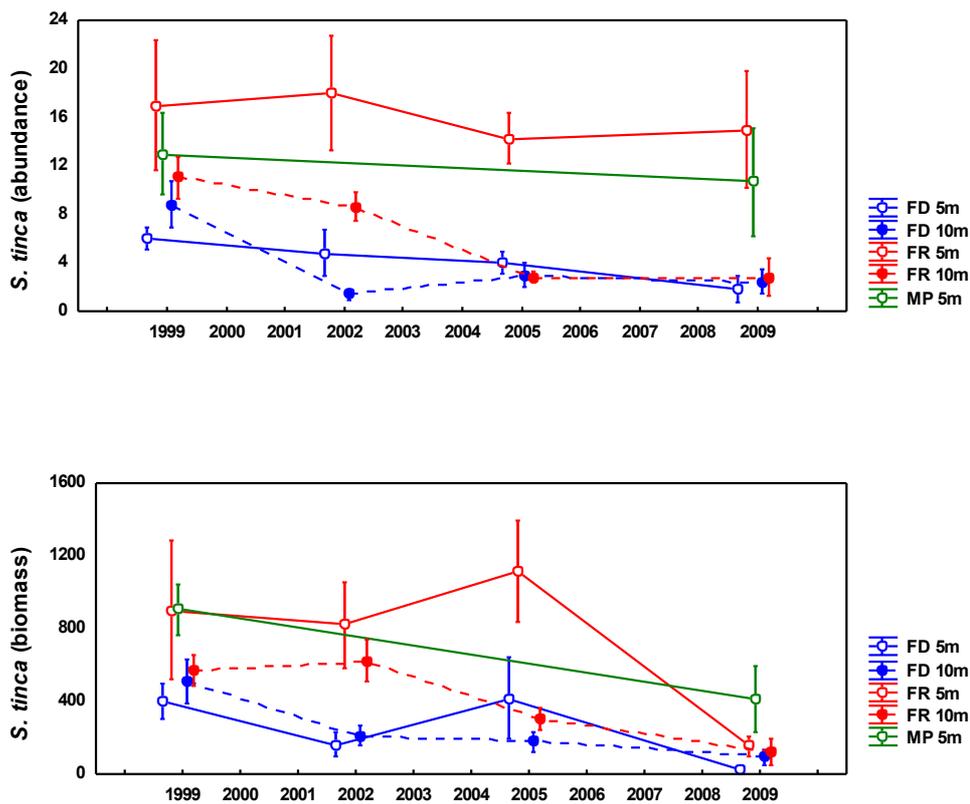


Figure 12. Variations of mean (\pm se) abundance (top) and biomass (bottom) of *Symphodus tinca* according to the zone, depth and year (FD: Falaguer-Dui, unprotected zone; FR: Freuetó, inside the MPA; MP: Mede Petita, inside the MPA).

that something on a large spatial scale (exceeding the narrow limits of the reserve) has seriously affected both the protected and unprotected subpopulations.

Looking at the annual size distributions, we can see that most of the 'adult' (all specimens older than 1 year) population disappeared in 2009 in both zones, and the young of the year (YOYs, TL < 8cm) were the dominant size-class (Figure 7). Although densities were maintained after the storm due to extremely good recruitment in 2009, the small size of the individuals meant the biomass decreased.

Chromis chromis

C. chromis is one of the most abundant littoral rocky reef fish species in the NW Mediterranean. It is a planktophagous, gregarious and small sized species that normally moves in the water column during the day and takes shelter at the bottom during the night (category 2, after Harmelin, 1985). Its quantitative variations from count to count are generally so pronounced that they lead to enormous variance. This is why in many quantitative studies on littoral fish fauna this species is not taken into

account although it represents one of the most quantitatively important components of the infralittoral rocky fish assemblage.

According to the results of the ANOVAs on mean abundance and biomass (Annex 4), this species was greatly affected by the storm (Figure 8), as suggested by initial observations. The results of the ANOVAs were almost identical and quite unambiguous in both cases: the only significant results were due to differences among years, and *post-hoc* tests demonstrated that 1999= 2002= 2005 > 2009. Such drastic results could only be explained by a massive disappearance of most of the 'adult' population, along with extremely low recruitment (Figure 9), probably due to a very low reproduction output during the breeding season of 2009.

Coris julis

This small nekto-benthic species is one of the most abundant of Mediterranean rocky fish fauna. Despite its small size and its limited commercial value, *C. julis* is actively caught by local sport fishermen, especially during summer. Being a hermaphrodite protogynous species, the main effects of exploitation can be seen in terminal males, which are far more aggressive than females and primary males, and usually attack baited hooks more frequently than the rest of the population. Therefore, older and consequently bigger males can be seen inside the marine reserve,

proving that sex change is socially inhibited by the presence of dominant males (Garcia-Rubies, 1999). This is why differences in both the abundances and biomass were significant between zones (Annex 5), and values were higher inside the marine reserve (*post hoc* tests: $R > NR$). In spite of this, there has been a progressive decrease in annual mean densities and mean biomasses in both zones since 1999 due to unknown causes (maybe low recruitment rates, as suggested in the figure). However, *post hoc* paired tests revealed that there were significant reductions in 2009 after the storm compared to the rest of years of monitoring in both the abundance (1999> 2002= 2005> 2009) and biomass (1999= 2002= 2005> 2009). There was also a significant interaction between 'year' and 'depth' when mean biomasses were compared due to the higher mean biomass value observed in 2005 inside the protected area at 5m deep (Figure 10).

This gives the impression that the whole population was affected by the storm, as the individuals older than 1 year were severely reduced, and there was also limited recruitment in 2009 (Figure 11), as was the case of *Chromis chromis*. Moreover, even the large terminal males decreased in size after the storm (Figure 10).

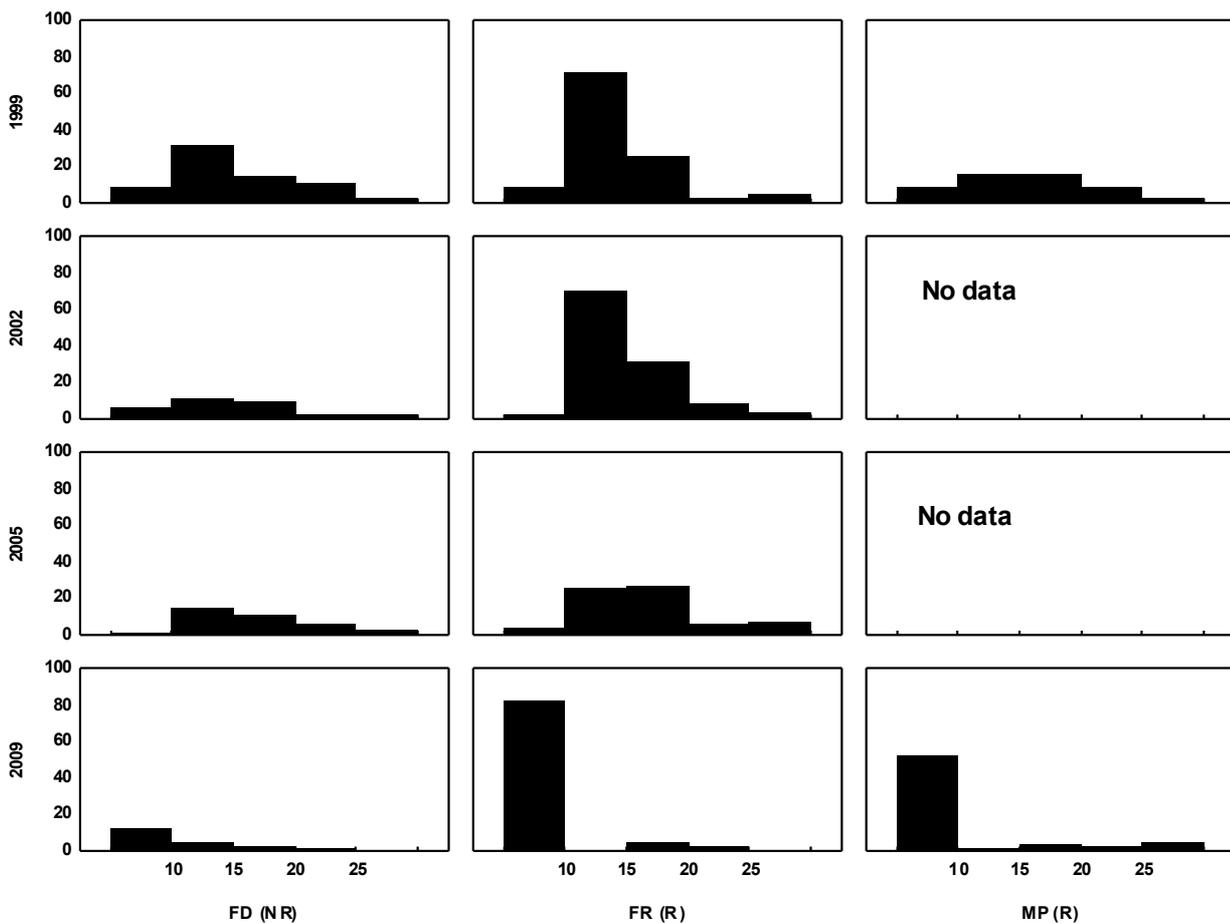


Figure 13. Annual size frequency distributions of *Symphodus tinca* (size class TL= 5cm) at the three sampling zones. The preponderance of YOYs (TL \leq 10cm) is nearly absolute in FR and MP. (FD: Falaguer-Dui, unprotected zone NR; FR: Freuetó, inside the MPA, R; MP: Meda Petita, inside the MPA, R).

Symphodus tinca and smaller *Symphodus* spp.

In spite of significant differences among years, the mean density of *S. tinca* seemed to be less altered by the storm than densities of other species (Figure 12; Annex 6). In fact, *post hoc* paired tests revealed that 1999=2002 > 2005=2009. Densities inside the MPA were significantly higher than in the unprotected zone; however, this species was more abundant at 5 m than at 10 m inside the marine reserve, while in the

unprotected area mean densities among depths were quite similar (Figure 12). This is why there was a statistically significant interaction between the factors 'zone' and 'depth' for the mean density of *S. tinca*. The results of the analysis carried out on mean biomass were similar but much clearer in that the *post-hoc* comparisons demonstrated unambiguously that 1999=2002=2005 > 2009. This result implies that the population size structure was in all probability altered by the storm (Figure 13). As previously observed in

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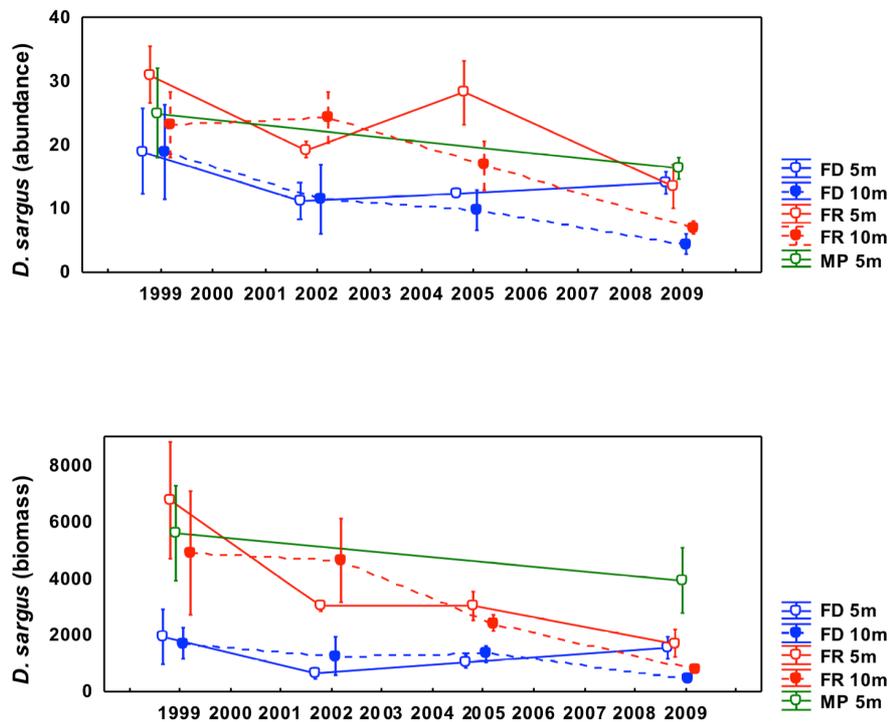


Figure 14. Interannual variations of mean (\pm se) abundance (top) and biomass (bottom) of *Diplodus sargus* in each zone and depth (FD: Falaguer-Dui, unprotected zone; FR: Freuetó, inside the MPA; MP: Mede Petita, inside the MPA).

other species, most of the medium and large specimens vanished from the population after the storm, although mean abundances were maintained to some extent by an unusually high recruitment in 2009. Similar results were obtained for the majority of the species of the genus *Symphodus* (*S. doderleini*, *S. mediterraneus*, *S. melanocercus*, *S. ocellatus*, and *S. roissali*), as well as some other species (Annex 7)

Diplodus sargus

Since *D. sargus* is a target species it was significantly more abundant

inside the protected area, as expected (Annex 8). However, the lowest values of mean density and biomass inside the protected area since 1999 were obtained in 2009, which reduced most of the previous differences with the unprotected area. The decrease in mean density seems to be due to the impact of the storm (post hoc tests: 1999= 2002= 2005 > 2009), as there was a sharp decline from 2005 to 2009 (Figure 13), while the mean biomass showed a more lineal decrease from 1999 to 2009 (Figure 13) inside the marine reserve. The storm seems to have affected the whole population of *D. sargus*, since

differences in size distribution were not evident between 2005 and 2009, although a decrease in large and medium sized fish was apparent compared to earlier years (Figure 14). Since YOYs of this species were still segregated in nursery areas from the habitat of the adult population during the summer (Garcia-Rubies & Macpherson, 1995; Macpherson, 1999) it was impossible to calculate the annual recruitment strength of the adult population.

Discussion and conclusions

This work is an opportunistic study of the impacts of a catastrophic disturbance, and therefore the experimental design is far from perfect. However, strong circumstantial evidence shows that the disturbance to the rocky fish assemblage was quite destructive. It affected a large number of species, which showed a wide range of responses to the disturbance. While some species did not demonstrate any apparent effect, others were practically wiped out in shallow waters up to a depth of 10 m.

At the assemblage level, one of the most perceptible effects was the significant decrease in mean species richness per count, independent of the area and the depth, expressed as a generalised rarefaction of the frequency of occurrence of some species. Significant increases in mean diversity and evenness were also observed after the storm, which implies that the abundance of

quantitatively dominant species seriously decreased. This result is consistent with the so-called intermediate disturbance hypothesis (Connell, 1978). Although the mean number of species in the partially sheltered zone of Meda Xica remained unaltered, increases in diversity and evenness were also observed in this area due to the severe decrease in the most abundant species.

Although mobile fish species often seem to be less affected than sedentary benthic species in coral reef fish communities after a hurricane (Turpin & Bortone, 2002; Pfeffer et al., 1983), in this case there was no significant effect on small benthic fish (which were underestimated due to the sampling method). However, littoral species that spend most of their time in the water column (category 2, according to Harmelin, 1985) were adversely affected to a greater extent than sedentary benthic species. In fact, the mean abundance and biomass of *Chromis chromis* were greatly reduced by the storm, and the differences compared to those of the previous years were of a lower order of magnitude. Similar results were obtained for a similar species (*Chromis cyanea*) on the most exposed fringing reefs of Cozumel after Hurricane Gilbert in 1988 (Fenner, 1991), and also by Rodríguez & Claro Madruga (2009) after Hurricane Ike in Camagüey (Cuba), although it was less affected in more sheltered areas. Kaufman (1983) also observed the lack of foraging aggregations of planktivorous species, such as *C.*

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cyanea, 4 or 5m above the reef in Discovery Bay (Jamaica) after Hurricane Allen. Cheal et al. (2002) detected a drastic decrease in *Chromis weberi* and other pomacentrid fish species on Hastings Reef (Great Barrier Reef, Australia) after a severe but short cyclone. Pomacentrids were the only family showing no evident recovery (Halford, et al., 2004). *Chromis chromis* usually swims in the water column during the day and shelters in bottom crevices at dusk. It inhabits shallow waters and its density tends to decrease with depth. At around 30m deep (on the Costa Brava, according to Garcia-Rubies,

1997) *Chromis chromis* is replaced by *Anthias anthias*. *A. anthias* is also a planktivore species that moves in the water column near the bottom, and was one of the most abundant in number among the dead fish that appeared on the beach of l'Estartit after the storm, along with *Chromis chromis*. *A. anthias* is known by the popular name of *temporaler* (literally 'storm fish', in Catalan) in the area, precisely because it is washed up dead on beaches after the most severe storms. Although *A. anthias* was not included in this report as there were no recent counts at 30m or more (the most recent samples of this species

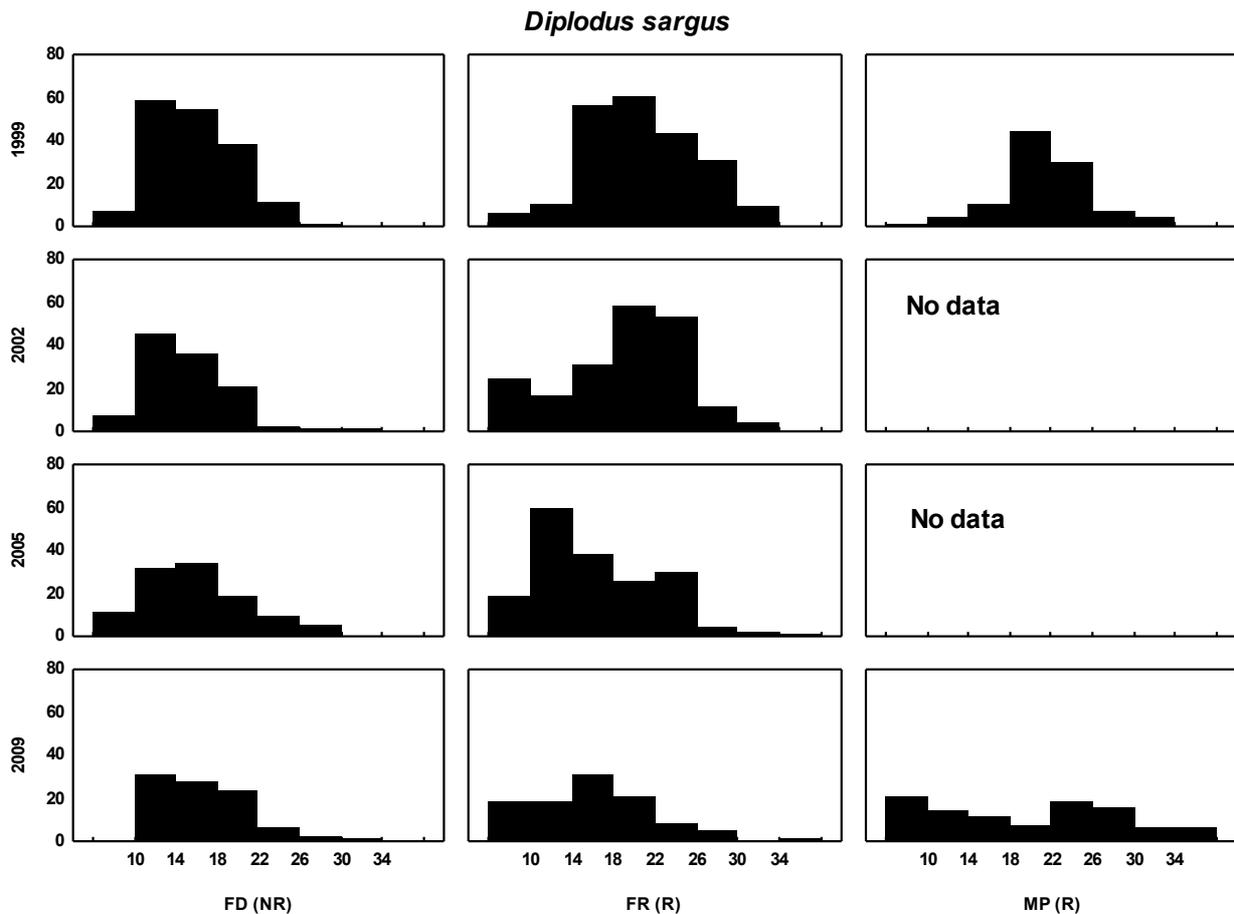


Figure 15. Annual size frequency distributions of *Diplodus sargus* (size class TL= 2cm) in the different sampling zones.

were from nearly 20 years ago; Garcia-Rubies, 1997), it is quite apparent that this small, coastal, free-swimming, planktivore species (defined by Harmelin (1985) as belonging to category 2 out of a rank from 1 to 6 in relation to the bottom) was greatly impacted by the storm.

The *Coris julis* population was also very affected by the storm in a quite similar way. Apparently, a severe decrease in large and medium specimens combined with limited recruitment led to a large decrease in abundance. This species has had recruitment difficulties during recent years (2002, 2005 and 2009), and therefore the decrease cannot be clearly attributed directly to the storm. It should also be noted that sex reversal could have been accelerated after the storm due to the extensive disappearance of large dominant terminal males. *Diplodus sargus* also showed a significant decrease in mean abundance and biomass but mainly inside the protected zone, where densities were higher.

However, drastic decreases in abundance have not been a general rule for all the species presumably affected by the storm. *Serranus cabrilla*, for instance, and also several *Symphodus* species, lost many large and medium sized specimens but also had enhanced recruitment, and thus the YOY were the most important segment of the population in 2009. In the case of *Serranus cabrilla*, the recruitment success could be related to the severe rarefaction of large individuals in shallow waters. There is

some correlational evidence of density dependence, which suggests that adults prevent recruitment in already saturated populations inside protected areas (Garcia-Rubies, 1997). Despite the losses, the reproduction output of *S. cabrilla* was assured by a large pool of mature individuals living deeper on bottoms that were not so drastically affected by the wave strength.

In many other species (e.g. genus *Symphodus*), recruitment also seemed to be enhanced after the storm without any apparent explanation. It can be argued that the storm seriously depleted the possible predators acting against the settlers or the nests (all *Symphodus* are nesting species with a short planktonic larval phase, Raventós, 2006). In any case, it seems that the few mature specimens that survived the storm successfully reproduced, since there is no relationship between the adult population and the number of YOYs (Raventós, 2009). Bohnsack (1983) obtained similar results after a massive fish kill in Big Pine Key (Florida) due to a period of extremely cold conditions. According to this author, high recruitment of juveniles occurred following this disturbance presumably due to reduced competition, predation, or a combination of both (Bohnsack, 1983). There is evidence that recruitment to artificial reefs is lower in reefs already occupied by fish than to empty reefs (Russell et al., 1974; Talbot et al., 1978). Anyway, the possibility of a fast recovery after a

catastrophic event could be greater among fish that have a short larval period (e.g. genus *Symphodus*), even if the total number of individuals able to reproduce has been dramatically decreased by the disturbance. This is not the case of *Chromis chromis* and *Coris julis*, which have significantly longer larval periods.

According to Kaufman (1983), coral reef fish species that share a common mode of life respond in a similar way to the storm. This seems to be perfectly true for *C. chromis* and *A. anthias*, and even for most *Symphodus* species, but there were some notable exceptions. In fact not all the similar species seem to have been affected in the same way, even among very similar, congeneric species. For instance, while the *Serranus cabrilla* population decreased greatly, the similar sympatric species *Serranus scriba* did not appear to diminish at all in spite of having a shallower distribution than *S. cabrilla* (Garcia-Rubies, 1991). Not only did the analyses not show any significant effects on the *S. scriba* population, but also this species, which is now quite abundant in this area, was not seen among the numerous dead fish found on the nearby beach (Table 1). Its shallower distribution could mean that *S. scriba* is better adapted than *Serranus cabrilla* to enduring rougher hydrodynamic conditions without significant losses.

All the results presented here deal with immediate mortality due to the turbulence of the storm. In coral reefs, hurricanes can impact fish in two

ways: directly or indirectly (Jones and Syms, 1998). Direct impacts are the result of strong currents and/or waves that sweep fish from their habitat or injure them so that they die or are more susceptible to predation (e.g., Woodley et al., 1981; Lassig, 1983). Indirect mortality due to hurricanes is caused by habitat changes resulting from damage to coral (Kaufman, 1983; Fenner, 1991; Aronson et al., 1991; Aronson, 1993). Unlike in coral reefs, where long term secondary mortality of fish associated with live coral could be important and long-lasting due to a loss of substrate complexity (Garpe et al., 2006), the rocky bottoms in the study area were not destroyed or their complexity modified by the storm. Rocky boulders were moved or overturned and most sessile coverage was removed by erosion or abrasion. This could imply problems of food availability for some species or changes in the trophic structure of the fish assemblage (Kaufman, 1983). In any case, long-term mortality in rocky reef fish due to changes in habitat or food availability, or any other long-term effects can only be properly understood when multiple year trends are included, which requires continuous monitoring rather than sporadic or single-time sampling (Adams, 2001). However, the results obtained in this study suggest that fish populations will recover fairly quickly because the fish that were most damaged are short-living and fast growing species. Many species also had enhanced recruitment. However, the evolution of the species that

suffered heavy losses and did not have improved recruitment will be longer and somewhat more hazardous.

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Annex 1. List of species and families present in the study area with data of presence (+) or absence in each zone, depth and year (FD5 and FD10: Falaguer-Dui at 5m and 10m deep; FR5 and FR10: Freuetó at 5 and 10m deep; MP5= Meda Petita at 5m deep).

Family	Species	FD5	FD5	FD6	FD7	FD10	FD10	FD10	FD10	FR5	FR5	FR5	FR5	FR10	FR10	FR10	FR10	MP5	MP5
		99	02	05	09	99	02	05	09	99	02	05	09	99	02	05	09	99	09
Muraenidae	<i>Muraena helena</i>		+																+
Gadidae	<i>Phycis phycis</i>							+					+			+	+		
Serranidae	<i>Dicentrarchus labrax</i>											+			+				+
Serranidae	<i>Epinephelus marginatus</i>												+	+	+	+	+		+
Serranidae	<i>Serranus cabrilla</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Serranidae	<i>Serranus scriba</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Apogonidae	<i>Apogon imberbis</i>	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	
Carangidae	<i>Seriola dumerilii</i>														+				
Sciaenidae	<i>Sciaena umbra</i>		+								+	+	+	+	+		+		
Mullidae	<i>Mullus surmuletus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sparidae	<i>Boops boops</i>	+			+					+			+	+		+	+	+	+
Sparidae	<i>Dentex dentex</i>	+				+	+			+				+	+	+		+	
Sparidae	<i>Diplodus annularis</i>	+	+	+		+	+	+	+	+				+			+	+	+
Sparidae	<i>Diplodus cervinus</i>	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sparidae	<i>Diplodus puntazzo</i>		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sparidae	<i>Diplodus sargus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sparidae	<i>Diplodus vulgaris</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sparidae	<i>Oblada melanura</i>	+	+	+	+	+		+	+	+	+	+	+	+	+	+		+	+
Sparidae	<i>Pagrus pagrus</i>																		+
Sparidae	<i>Sarpa salpa</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sparidae	<i>Sparus aurata</i>	+		+	+			+	+		+	+	+	+	+			+	+
Sparidae	<i>Spondylisoma cantharus</i>	+	+	+	+	+	+	+	+	+	+			+	+	+			
Centracanthidae	<i>Spicara maena</i>									+					+	+			
Pomacentridae	<i>Chromis chromis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Labridae	<i>Coris julis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Labridae	<i>Ctenolabrus rupestris</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Labridae	<i>Labrus merula</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Labridae	<i>Labrus mixtus</i>						+	+							+	+	+		
Labridae	<i>Labrus viridis</i>			+	+		+	+	+	+	+	+	+		+	+	+	+	+
Labridae	<i>Symphodus cinereus</i>																		+
Labridae	<i>Symphodus doderleini</i>	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+
Labridae	<i>Symphodus mediterraneus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Labridae	<i>Symphodus ocellatus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Labridae	<i>Symphodus roissali</i>	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+
Labridae	<i>Symphodus rostratus</i>		+	+	+	+		+	+	+	+	+		+		+	+	+	+
Labridae	<i>Symphodus tinca</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Labridae	<i>Symphodus melanocercus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Labridae	<i>Thalassoma pavo</i>	+	+			+	+			+	+		+	+	+	+		+	
Mugilidae	<i>Chelon labrosus</i>	+	+	+	+	+	+			+	+	+	+	+	+	+		+	+
Gobiidae	<i>Gobius bucchichi</i>	+			+													+	+
Gobiidae	<i>Gobius cruentatus</i>							+							+				
Gobiidae	<i>Gobius geniporus</i>	+	+					+				+							
Gobiidae	<i>Gobius vittatus</i>													+		+	+		
Gobiidae	<i>Gobius xanthocephalus</i>	+	+	+		+	+	+						+	+	+	+		
Blennidae	<i>Parablennius gattoruggine</i>	+	+				+							+		+	+	+	
Blennidae	<i>Parablennius pilicornis</i>	+		+	+			+	+	+		+	+	+	+	+		+	+
Blennidae	<i>Parablennius rouxi</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Blennidae	<i>Parablennius zvorimiri</i>	+			+								+						
Tripterygiidae	<i>Tripterygion delaisi</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Tripterygiidae	<i>Tripterygion melanocercus</i>			+				+	+	+	+		+		+		+		
Tripterygiidae	<i>Tripterygion tripteronotus</i>									+									
Scorpaenidae	<i>Scorpaena maderensis</i>						+								+				
Scorpaenidae	<i>Scorpaena notata</i>	+		+	+	+			+				+			+		+	
Scorpaenidae	<i>Scorpaena porcus</i>		+	+	+		+	+	+	+						+	+		
Scorpaenidae	<i>Scorpaena scrofa</i>	+					+		+		+			+		+	+		+

Annex 2 . Summary of the results of the ANOVAs comparing mean values of specific richness (S), abundance (sqrt transformed), biomass (log transformed) and specific diversity (H') (significant probabilities in bold; see the text for explanations about interactions among factors).

Abundance									
Source of variation	df	SS	MS	F	p	SS	MS	F	P
Zone	1	142,083	142,083	19,500	0,000	862346,08	862346,08	16,018	0,000
Depth	1	20,160	20,160	2,767	0,102	2108,23	2108,23	0,039	0,844
Year	3	113,846	37,949	5,208	0,003	1905634,98	635211,66	11,799	0,000
Z*D	1	45,360	45,360	6,225	0,015	131105,93	131105,93	2,435	0,124
Z*Y	3	71,194	23,731	3,257	0,028	281317,65	93772,55	1,742	0,168
D*Y	3	16,709	5,570	0,764	0,519	917613,57	305871,19	5,681	0,002
Z*D*Y	3	40,181	13,394	1,838	0,150	653053,38	217684,46	4,043	0,011
Error	58	422,600	7,286			3122555,00	53837,16		
Total	74	34496,000				19315426,00			

Biomass									
H'									
Source of variation	df	SS	MS	F	p	SS	MS	F	P
Zone	1	21,193	21,193	52,986	0,000	0,028	0,028	0,229	0,634
Depth	1	0,229	0,229	0,573	0,452	0,080	0,080	0,661	0,420
Year	3	8,882	2,961	7,402	0,000	8,490	2,830	23,310	0,000
Z*D	1	0,736	0,736	1,839	0,180	0,017	0,017	0,141	0,708
Z*Y	3	0,860	0,287	0,717	0,546	0,160	0,053	0,439	0,726
D*Y	3	2,294	0,765	1,912	0,138	0,848	0,283	2,329	0,084
Z*D*Y	3	0,784	0,261	0,653	0,584	0,868	0,289	2,383	0,079
Error	58	23,198	0,400			7,041	0,121		
Total	74	6212,147				277,556			

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Annex 3. ANOVA comparing mean values of abundance and biomass (sqrt transformed) of *Serranus cabrilla* between zones, depths and years, and *post-hoc* tests results (significant probabilities are in bold).

a) Abundance						b) Biomass				
Source of variation	df	SS	MS	F	P	SS	MS	F	P	
Zone	1	5,786	5,786	0,846	0,361	187,127	187,127	22,020	0,000	
Depth	1	30,903	30,903	4,520	0,038	0,009	0,009	0,001	0,975	
Year	3	17,914	5,971	0,873	0,460	288,859	96,286	11,330	0,000	
Z*D	1	0,411	0,411	0,060	0,807	3,928	3,928	0,462	0,499	
Z*Y	3	5,956	1,985	0,290	0,832	52,630	17,543	2,064	0,115	
D*Y	3	40,628	13,543	1,981	0,127	51,068	17,023	2,003	0,124	
Z*D*Y	3	25,817	8,606	1,259	0,297	14,148	4,716	0,555	0,647	
Error	58	396,500	6,836			492,890	8,498			
Total	74	3579,000				8737,377				

<i>Post-hoc</i>				<i>Post-hoc</i>					
Depth	5m	10m		Zone	FD	FR			
Mean	5,7	7,1		Mean	8,8	11,7			
10m	0,032			FR	0,000				
				Year	1999	2002	2005	2009	
				Mean	11,9	9,9	12,0	7,4	
				1999					
				2002	0,207				
				2005	0,999	0,140			
				2009	0,000	0,046	0,000		

Annex 4. Summary of the results of the ANOVAs comparing mean values of abundance and biomass (both sqrt transformed) of *Chromis chromis* between zones, depths and years, and *post-hoc* tests results (significant probabilities are in bold).

a) Abundance						b) Biomass				
Source of variation	df	SS	MS	F	P	SS	MS	F	P	
Zone	1	0,011	0,011	0,008	0,930	4,175	4,175	0,046	0,832	
Depth	1	0,001	0,001	0,001	0,980	0,054	0,054	0,001	0,981	
Year	3	95,568	31,856	22,334	0,000	5090,190	1.696,730	18,529	0,000	
Z*D	1	0,129	0,129	0,091	0,765	15,890	15,890	0,174	0,679	
Z*Y	3	7,346	2,449	1,717	0,174	79,786	26,595	0,290	0,832	
D*Y	3	9,254	3,085	2,163	0,102	642,301	214,100	2,338	0,083	
Z*D*Y	3	3,996	1,332	0,934	0,430	47,365	15,788	0,172	0,915	
Error	58	82,729	1,426			5.311,232	91,573			
Total	74	1622,694				43.281,548				
Post-hoc						Post-hoc				
Year	1999	2002	2005	2009		Year	1999	2002	2005	2009
Mean	5,2	5,4	4,6	2,6		Mean	28,8	24,8	23,9	7,5
	1999						1999			
	2002	0,932					2002	0,618		
	2005	0,520	0,188				2005	0,444	0,991	
	2009	0,000	0,000	0,000			2009	0,000	0,000	0,000

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Annex 5. Results of the ANOVAs on mean abundance and biomass of *Coris julis* (both log transformed) between zones, depths and years, and results of *post-hoc* paired tests. See in the text the explanations of interactions among factors.

a) Abundance						b) Biomass				
Source of variation	df	SS	MS	F	P	SS	MS	F	p	
Zone	1	7,576	7,576	30,814	0,000	20,162	20,162	56,346	0,000	
Depth	1	0,039	0,039	0,157	0,693	0,203	0,203	0,567	0,454	
Year	3	15,987	5,329	21,675	0,000	24,240	8,080	22,581	0,000	
Z*D	1	0,020	0,020	0,083	0,775	0,000	0,000	0,000	1,000	
Z*Y	3	1,981	0,660	2,685	0,055	1,058	0,353	0,985	0,406	
D*Y	3	1,806	0,602	2,448	0,073	3,065	1,022	2,855	0,045	
Z*D*Y	3	1,155	0,385	1,566	0,207	1,346	0,449	1,254	0,299	
Error	58	14,260	0,246			20,754	0,358			
Total	74	1030,765				2385,834				

<i>Post-hoc</i>				<i>Post-hoc</i>			
Zone	FD	FR		Zone	FD	FR	
Mean	3,4	4,0		Mean	5,1	6,1	
FD				FD			
FR	0,000			FR	0,000		

Year	1999	2002	2005	2009	Year	1999	2002	2005	2009
Mean	4,3	3,7	3,7	3,0	Mean	6,0	5,7	6,1	4,7
1999					1999				
2002	0,002				2002	0,385			
2005	0,002	0,999			2005	0,923	0,111		
2009	0,000	0,001	0,001		2009	0,000	0,000	0,000	

Annex 6. Results of the ANOVAs on mean abundance and biomass of *Symphodus tinca* (both log transformed) between zones, depths and years, and results of *post-hoc* paired tests. (significant probabilities in bold; see in the text the explanations of interactions among factors).

a) Abundance						b) Biomass			
Source of variation	df	SS	MS	F	P	SS	MS	F	P
Zone	1	29,715	29,715	35,507	0,000	1192,35	1192,352	23,170	0,000
Depth	1	13,224	13,224	15,801	0,000	165,91	165,911	3,224	0,078
Year	3	17,526	5,842	6,981	0,000	2691,37	897,122	17,433	0,000
Z*D	1	10,079	10,079	12,044	0,001	246,47	246,467	4,789	0,033
Z*Y	3	3,974	1,325	1,583	0,203	342,41	114,135	2,218	0,096
D*Y	3	3,239	1,080	1,290	0,286	345,16	115,054	2,236	0,094
Z*D*Y	3	3,001	1,000	1,195	0,320	10,50	3,501	0,068	0,977
Error	58	48,540	0,837			2984,71	51,461		
Total	74	539,000				28889,66			

Post-hoc				Post-hoc			
Zone	FD	FR		Zone	FD	FR	
Mean	1,8	3,0		Mean	13,3	20,9	
	FD				FD		
	FR	0,000			FR	0,000	
Depth	5m	10m		Year	1999	2002	2005
Mean	2,8	2,0		Mean	23,2	18,6	19,5
	5m				1999		
	10m	0,001			2002	0,252	
					2005	0,457	0,978
Year	1999	2002	2005	2009	0,000	0,000	0,000
Mean	3,1	2,4	2,2	1,8			
	1999						
	2002	0,102					
	2005	0,020	0,899				
	2009	0,001	0,176	0,555			

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Annex 7. Results of the ANOVAs on mean abundance (sqrt transformed) and biomass (log transformed) of *Diplodus sargus* between zones, depths and years, and results of *post-hoc* paired tests (significant probabilities in bold).

a) Abundance						b) Biomass				
Source of variation	df	SS	MS	F	P	SS	MS	F	P	
Zone	1	18,933	18,933	14,396	0,000	20,881	20,881	11,143	0,001	
Depth	1	6,947	6,947	5,282	0,025	0,443	0,443	0,237	0,629	
Year	3	28,994	9,665	7,349	0,000	24,426	8,142	4,345	0,008	
Z*D	1	0,064	0,064	0,048	0,827	0,615	0,615	0,328	0,569	
Z*Y	3	5,222	1,741	1,324	0,275	6,503	2,168	1,157	0,334	
D*Y	3	5,538	1,846	1,404	0,251	3,202	1,067	0,570	0,637	
Z*D*Y	3	3,037	1,012	0,770	0,516	8,289	2,763	1,475	0,231	
Error	58	76,280	1,315			108,680	1,874			
Total	74	1182,000				3907,021				

Post-hoc				Post-hoc				
Zone	FD	FR		Zone	FD	FR		
Mean	3,3	4,3		Mean	6,6	7,6		
	FD				FD			
	FR	0,001			FR	0,003		
Depth	5m	10m		Year	1999	2002	2005	2009
Mean	4,0	3,5		Mean	7,8	7,2	7,4	6,3
	5m				1999			
	10m	0,035			2002	0,593		
					2005	0,817	0,979	
					2009	0,011	0,174	0,086
Year	1999	2002	2005	2009				
Mean	4,6	3,8	3,8	2,9				
	1999							
	2002	0,263						
	2005	0,256	1,000					
	2009	0,000	0,049	0,060				

