Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve (Corsica, Northwestern Mediterranean)

Reserve effect
Rocky reefs
Posidonia oceanica seagrass beds
Temporal analysis
Corsica

Effet réserve
Substrat rocheux
Herbiers à Posidonia oceanica
Analyse temporelle
Corse

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ABSTRACT

From July 1988 to September 1992, Scuba divers used a non-destructive sampling method to study the fish communities of rocks and *Posidonia oceanica* seagrass beds, in Scandola Marine Reserve. Sites were established in the integral reserve (protection of the marine environment), in the non-integral reserve (partial protection) and outside the reserve (no protection). Average density and biomass of the sampled population in *P. oceanica* seagrass beds showed no significant difference between the sites in the integral reserve and the others. Only the integrally-protected shallow and deep water zones showed considerably reduced seasonal variations. For rocky substrata, the integral reserve site demonstrated higher density and biomass than the other sites. The impact of seasonal variations on the sampled population was not reduced in this biotope, as in the seagrass beds. Whatever the biotope, the demographic structures of the fish population sampled in the integral reserve and in the other sites were different : the number of large fishes (matured adults) was always the highest. Species diversity was slightly greater in the seagrass bed sites of the integral reserve, but site variations were not significant. This was also true for rocky substrata; in contrast, lesser seasonal differences were recorded in the integral reserve than outside. Three conclusions can be drawn from these pluriannual observations : 1) The reserve effect is real, not just theoretical, and affects the fish population in both rocks and seagrass beds. 2) The two sites studied, the *Posidonia oceanica* seagrass beds and rocky substrata, react very differently to protection which reduces anthropogenic disturbances. These differences may be attributed to the degree of sensitivity of the dominant families (Labridae in the seagrass, Sparidae in rocky substrata) to all disturbances. 3) The reserve effect comprises both a refuge and a buffer effect. The refuge effect is the most traditionally highlighted and is characterized by more large fishes and a greater variety of species and noble fishes (*Dicentrarchus labrax, Sparus aurata, Epinephelus marginatus, Sciaena umbra*). The buffer effect, never shown in previous studies, is characterized by the fact that the impact of seasonal variations on parameters such as density, biomass, and diversity is considerably lessened.

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RÉSUMÉ

Analyse pluriannuelle de l'effet de réserve sur l'ichtyofaune dans la Réserve Naturelle de Scandola (Corse)

Dans la Réserve Naturelle de Scandola, le peuplement de poissons du milieu rocheux et de l'herbier à *Posidonia oceanica* a été échantillonné, en plongée sous-marine, à l'aide d'une méthode non destructive, entre juillet 1988 et septembre 1992. Des stations sont définies dans la réserve intégrale (protection intégrale du milieu marin), dans la réserve non-intégrale (protection partielle) et hors réserve (aucune mesure de protection). Les densités et les biomasses moyennes du peuplement échantillonné ne montrent pas de différences significatives entre la réserve intégrale et les autres stations dans l'herbier à *P. oceanica*. Par contre, leurs variations saisonnières sont considérablement amorties dans la réserve intégrale, en zone superficielle et profonde, alors qu'elles ne le sont pas ailleurs. En milieu rocheux, la station de la réserve intégrale est caractérisée par une densité et une biomasse significativement supérieures à celles calculées pour les autres stations. Leurs variations saisonnières ne sont pas amorties dans ce biotope, comme dans l'herbier. La structure démographique du peuplement échantillonné diffère toujours entre la réserve intégrale et les autres stations, quel que soit le milieu : le pourcentage d'individus de grandes tailles (les adultes arrivés à maturité) y est plus important. La diversité spécifique est légèrement supérieure dans les stations d'herbier de la réserve intégrale, mais les variations entre stations sont faiblement significatives. Il en est de même en milieu rocheux; par contre, les différences enregistrées d'une saison à l'autre sont beaucoup moins marquées dans la réserve intégrale qu'ailleurs. Les conclusions tirées de ce suivi pluriannuel sont au nombre de trois : 1) La notion théorique d'effet de réserve est réelle et se fait sentir, pour le peuplement ichtyologique, dans l'herbier et en milieu rocheux. 2) Les deux milieux étudiés, l'herbier à *Posidonia oceanica* et le milieu rocheux, réagissent très différemment vis-à-vis d'une protection, donc d'une diminution du niveau de perturbation d'origine humaine. Ces différences peuvent être attribuées à une sensibilité différente vis-à-vis d'une perturbation quelconque des familles dominantes (Labridae dans l'herbier, Sparidae sur la roche). 3) L'effet de réserve possède deux composantes, un effet tampon et un effet refuge. L'effet refuge, le plus classiquement décrit dans la littérature se caractérise par la présence d'individus de plus grande taille et par un plus grand nombre d'espèces et de poissons nobles (*Dicentrarchus labrax, Sparus aurata, Epinephelus marginatus, Sciaena umbra*). Une atténuation sensible des fluctuations saisonnières de différents paramètres (densité, biomasse, diversité), jamais mentionnée dans les études précédentes, est décrite et nommée effet tampon.

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INTRODUCTION

The overall objective of protected areas is to preserve genetic resources and to protect endangered species (Brekel, 1979 *in* Kennedy, 1990; Salm, 1984 *a*). In a more restricted economic environment, they maintain the profitable yields of regional fishing (Bell, 1992) and increasingly attract tourists (Savina and White, 1986; Boudouresque, 1990). The concept of preserving marine areas has been very slow to develop, despite the usefulness of these zones in terms of protection and conservation of fauna and flora (Randall, 1982). This is possibly due to the recent underwater penetration of man, the difficulties inherent in carrying out non-destructive studies on site (Bell, 1983) and the complexity of legal factors (Kennedy, 1990). The development of protected marine areas is often based on untested theories rather than on technical field data (Salm, 1984 b), and biological studies are scarce and recent : Russ and Alcala (1989) and Samoilys (1988) in tropical zones, Bell (1983), Buxton and Smale (1989), Cole *et al.* (1990) and Bennett and Attwood (1991) in temperate zones. Fish population studies are the most frequent, but several works have dealt with the analysis of the impact of these reserves on invertebrate species : Moreno *et al.* (1984; 1986) and McClanahan (1989) for gastropods; Cole *et al.* (1990) for echinoids and shellfish. In the Mediterranean, there are even fewer studies available. After Bell's (1983) initial survey in Banyuls, no further work was done until 1988, when a research programme was initiated in Corsica, in the Scandola Natural Reserve (Francour; 1989), and in Spain in the Medes Islands marine reserve (Garcia-Rubies and Zabala, 1990). Most studies, both in the Mediterranean and elsewhere, deal with hard substrata (rock, coral reefs). Only Francour (1989; 1991) has studied the marine phanerogam grassbeds (*Posidonia oceanica*).

As with all biological phenomena, the reserve effect has two components : spatial and temporal. The spatial factor involves the possible differences between protected and unprotected zones. The definition of the reserve effect, traditionally recognized in various studies, is based on the knowledge of these differences (Russ and Alcala, 1989; Garcia-Rubies and Zabala, 1990; Francour 1991).

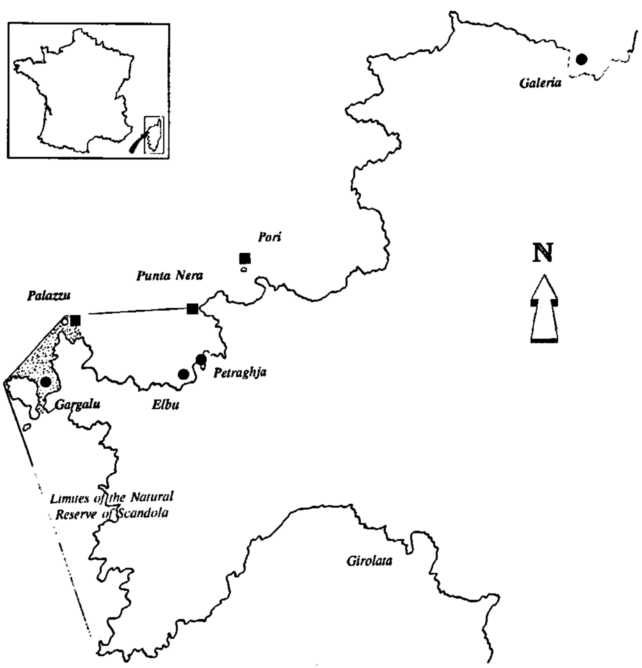

Figure 1

Location of the stations in the Scandola natural reserve (Corsica, northern-occidental Mediterranean): meadow = ●; rock substrate = ■; integral reserve = grey.

However, this reserve effect could vary throughout the year like any biological factor, according to an annual or pluriannual cycle. At present, only Moreno *et al.* (1986) and Bennett and Attwood (1991) have done a pluriannual study of a reserve, respectively for a gastropod species (Chile, 5 years) and for fishes (South Africa, 4.5 years).

This paper presents the results of a long-term study (1988 to 1992) in the Corsican Natural Reserve of Scandola. Data collected throughout this period have been used to analyze the temporal factors of the reserve effect and to define the nature of the biological impact of a protected marine area for rocky substrata and seagrass bed. Finally, recommendations have been made for the implementation and maintenance of marine reserves.

MATERIAL AND METHODS

The data presented herein are the results of eight surveys undertaken in the Scandola Marine Reserve (Corsica, Northwestern Mediterranean; Fig. 1) between 1988 and 1992 (three during the cold season : February 1990, March 1991, and March 1992, and five during the warm season : July 1988, August 1989, July 1990, August 1991, and September 1992). Two biotopes have been sampled : *Posidonia oceanica* seagrass beds and rocky substrata. In the beds, two bathymetric strata have been studied : the shallow zone, less than 10 m deep, and the deep-water zone, between 10 and 20 m in depth. Rocky substrata have been only studied between 0 and 10m depth.

Seven stations (Fig. 1) have been selected within the integral reserve (integral protection of the marine environment, Gargalu, Palazzu), the non-integral reserve (partially protected, Elbu, Petraghja, Punta Nera) and unprotected zones (external to the reserve, Galeria, Pori). Disturbances recorded in these stations, graded from 1 (minimum) to 4 (maximum), are mainly caused by tourism (all stations), fishing, both professional (non-integral and unprotected reserves) and amateur (external to the reserve only : angling and underwater fishing), and passing boats (all zones). Scuba diving is prohibited throughout the reserve waters (integral or not) and the only form of diving allowed is skin-diving. The degree of disturbance is minimal in the integral reserve (Gargalu and Palazzu) and maximal outside the reserve (Pori and Galeria). In the non-integral reserve, rugosity is greater at Petraghja station (as described by Luckhurst and Luckhurst, 1978) than at the neighbouring Elbu station. This complex structure discourages anchoring by boats and the level of

Posidonia oceanica seagrass beds		**Rocky substrata**
Labridae		**Moronidae**
Coris julis	*Labrus* spp.*	*Dicentrarchus labrax*
Symphodus cinereus	*Symphodus doderleini*	**Muligidae**
Symphodus mediterraneus	*Symphodus melanocercus*	
Symphodus ocellatus	*Symphodus roissali*	**Sciaenidae**
Symphodus rostratus	*Symphodus tinca*	*Sciaena umbra*
Mugilidae		**Sparidae**
Mullidae		*Dentex dentex*
Mullus surmuletus		*Diplodus puntazzo*
		Diplodus sargus
Serradinae		*Diplodus vulgaris*
Serranus cabrilla	*Serranus scriba*	*Sarpa salpa*
Sparidae		*Sparus aurata*
		Spondyliosoma cantharus
Diplodus annularis	*Sarpa salpa*	
Spondyliosoma cantharus		

* *Labrus merula and Labrus viridis*

Table 1

List of the fish species sampled in the Posidonia oceanica *seagrass beds and on rocky substrata.*

	dp	N	Density	CV	Biomass	CV
Ga	4	140	3.84 (3.12)	81.2	43.04 (127.71)	296.7
Pe	2	140	5.64 (3.86)	68.4	87.04 (73.80)	84.8
ES	3	140	4.08 (3.27)	80.1	61.15 (94.12)	153.9
GS*	2	140	4.84 (3.24)	66.9	91.10 (99.12)	108.8
ED	2	124	2.81 (2.51)	89.3	87.95 (399.15)	453.8
GD*	1	124	2.89 (1.80)	62.3	61.56 (78.89)	128.1

** = integral reserve; G = Gargalu; E = Elbu; S = Shallow (< 10 m); d = deep (> 10 m); Pe = Petraghja; Ga = Galeria; dp = degree of perturbation (1 = minimum, 4 = maximum); N = number of censuses; CV = coefficient of variation (100* standard deviation-mean).*

Table 2

Total fish density (number of individuals/10 m², standard deviation in brackets) and biomass (grams of wet weight/10 m²), for the different stations sampled in Posidonia aceanica *seagrass beds.*

disturbances is therefore lower than at Elbu. The non-integral station studied in rocky substrata (Punta Nera) is near the limits of the reserve (Fig. 1). Nevertheless, it is the only station which has a morphology and structural complexity similar to Palazzu or Pori.

Only the 18 most common and conspicuous species have been sampled in the *Posidonia oceanica* meadow and 10 species in rocky substrata (Tab. 1). As Miniconi *et al.* (1990) listed 125 species in the Scandola reserve, the term «fish population» as used hereafter refers to the sampled fauna, not to total fauna (Harmelin-Vivien and Francour, 1992). The abundance and size-class structure of the fish populations have been estimated using the underwater visual techniques described in Harmelin-Vivien *et al.* (1985). This sampling method is well adapted to protected marine areas (Bell, 1983). Fishes were counted along 20 m long and 2 m wide transects (40 m²) in the *P. oceanica* meadow or, in rocky substrata, on randomly selected circular areas of 10 to 15 m in diameter, depending on the visibility. A minimum of twenty replicates have been conducted within each site. Abundance data have been recorded for small, medium and large individuals of each fish species. Each size class has been defined as one third of the maximum recorded total length of each species, given by Bauchot and Pras (1980). Individual mean weight has been calculated for each of the three size classes using the length/weight relationships according to the literature (Harmelin-Vivien and Francour, 1992). The biomass (grams of wet weight, WW, per 10 m²) of visually estimated fish populations has been calculated by multiplying the individual mean weight of a given size class by its population density within the transect or the circular point.

The differences between sampling periods have been sought using the non-parametric Kruskal-Wallis test. The non-parametric Newman-Keuls-Student (NKS) comparison procedure has then been used to establish between which sampling periods the means were different. For each station, the density or biomass variations during the sampling period (eight surveys) have been estimated using the coefficient of variation (CV = 100*s.d./mean) calculated per given station. The diversity of the sampled population has been evaluated using the Shannon index, calculated on base-2 logarithms.

Density

	Ga	Pe	ES	GS	ED
GD		*		*	
ED	*	*	*	*	
GS	*		*		
ES		*			
Pe	*				

Biomass

	Ga	Pe	ES	GS	ED
GD	*	*		*	
ED		*		*	
GS	*		*		
ES	*	*			
Pe	*				

Figure 2

Pictorial representation of the results of NKS test on total density and biomass of the sampled population for the seagrass bed stations.
** = denotes significant difference (p<0.05) between two samples; Ga = Galeria; Pe = Petraghja; E = Elbu; G = Gargalu; S = shallow; D = deep.*

RESULTS

Relative abundance

A total of 140 and 124 censuses have been made in the seagrass bed, respectively for the shallow and the deep stations. The mean density and biomass of the sampled population are summarized in Table 2. The Kruskal-Wallis test shows highly significant differences in density or biomass of the total population (Tab. 3). In the reserve, for the total *P. oceanica* seagrass population, the deep sites density and biomass differed significantly from the shallow-station values (NKS's test, Fig. 2), except for the mean biomass at Elbu. In the shallow zones of grassbed, the mean density and biomass of the Gargalu population were higher than outside the reserve (Galeria) and than in the non-integral reserve (Elbu). In contrast, Gargalu and

Station	Average rank density	average rank biomass
Galeria	388.65	287.15
Petraghja	519.01	524.37
Elbu shallow	401.57	370.17
Gargalu shallow*	483.94	501.09
Elbu deep	287.56	339.15
Gargalu deep*	323.66	396.71
H- statistic	96.72	109.19
p	0	0

** = integral reserve.*

Table 3

Results of non parametric Kruskal-Wallis test on total density and biomass of the sampled population for the different stations of Posidonia oceanica *beds.*

	Labridae	Serranidae	Sparidae
Mean Density			
Galeria	2.75 (2.79)	0.06 (0.13)	0.17 (0.32)
Petraghja	2.82 (2.35)	0.11 (0.17)	0.23 (0.28)
Elbu	2.41 (2.88)	0.11 (0.15)	0.22 (0.38)
Gargalu*	2.66 (2.10)	0.22 (0.24)	0.22 (0.31)
Kruskal-Wallis test			
Galeria	283.59	272.32	248.36
Petraghja	299.01	271.98	301.02
Elbu	243.03	280.73	284.71
Gargalu*	296.37	341.97	287.91
H-statistic	10.77	48.26	9.84
p	0.01	0	0.02

** = integral reserve.*

Table 4

Density (140 censuses; number of individuals/10 m², standard deviation in brackets) of Labridae (size classes S and M), Serranidae (M, L) and Sparidae (M, L) for the shallow stations of Posidonia oceanica *seagrass beds. Results of non-parametric Kruskal-Wallis test (average rank).*

Petraghja (station of the non-integral reserve with highly complex structure) did not show significant difference in density and biomass (Fig. 2).

Labridae

	Ga	Pe	ES
GS			*
ES		*	
Pe			

Serranidae

	Ga	Pe	ES
GS	*	*	*
ES	*		
Pe			

Sparidae

	Ga	Pe	ES
GS			
ES			
Pe	*		

Figure 3

Pictorial representation of the results of NKS test on density of the three main families for the shallow stations of seagrass bed.
** = denotes significant difference (p<0.05) between two samples; Ga = Galeria; Pe = Petraghja; ES = Elbu shallow; GS = Gargalu shallow.*

The coefficients of variation (CV) have been calculated with the mean seasonal values of density and biomass. Both CV were weaker in Gargalu (shallow and deep zones) and Petraghja than in the other stations (Tab. 2). A low value of CV corresponds to a weak difference between the sampling dates. Therefore, the seasonal variations were less marked in the integral reserve and in the station of the non-integral reserve with a highly complex structure than outside. In the meadow, seasonal variations were thus dampened in the three low-disturbance stations (degree of perturbation {≤ 2).

The three most abundant families in the seagrass were Labridae, Serranidae and Sparidae. The Labridae (small- and medium-size classes) can be preyed on by ichthyophagous fish, such as the Serranidae (mainly medium- and large-size classes). Numerous target species for fishermen belong to Sparidae. The relative abundance (density data) of the main families have been thus compared between sites only for two size classes (S and M for the Labridae, and M and L for the Serranidae and the Sparidae). To reduce the depth effect (see above), further family analyses have been conducted only on the shallow stations. In the shallow zones of grassbed, variance analysis of the mean relative abundance of Labridae showed significant differences between sites (Tab. 4, Fig. 3). The density of Elbu station is lower than that of the Gargalu and Petraghja stations. The mean density outside the reserve (Galeria) was important but did not differ significantly from the integral reserve data. The mean density of Serranidae was highest in the integral reserve and weakest in Galeria, outside the reserve. The density of Sparidae was similar in the integral and the non-integral reserve stations. Only Galeria density differed from Petraghja's.

The mean density and biomass of the total population of rocky substrata are summarized in table 5. The results of NKS tests, which were used to determine significant differences between the stations, are summarized in figure 4. The mean density and biomass were higher in

Station	dp	N	Density	Biomass	CVD	CVB
Mean (s.d.)						
Pori	4	121	0.31 (0.43)	97.70 (209.77)	138.7	214.7
Punta Nera	3	117	0.15 (0.29)	45.54 (81.95)	193.3	179.9
Palazzu*	2	134	0.96 (1.58)	333.73 (668.79)	164.6	200.4
Kruskal-Wallis test						
Pori	–	–	179.29	173.15	–	–
Punta Nera	–	–	127.84	121.17	–	–
Palazzu*	–	–	244.23	255.60	–	–
H- statistic	–	–	76.02	100.97		
p	–	–	0	0	–	–

** = integral reserve; dp = degree of perturbation (1 = minimum, 4 = maximum); N = number of censuses; CVD, CVB = coefficient of variation for density and biomass.*

Table 5

Density (number of individuals/10 m², standard deviation in brackets) and biomass data (grams of wet weight/10 m²) for the stations of rocky substrata. Results of non parametric Kruskal-Wallis test (average rank).

	Pori	P. Nera
Palazzu	*	*
Punta Nera	*	

Figure 4

Pictorial representation of the results of NKS test on total density and biomass of the sampled population for the stations on rocky substrata.
** = denotes significant difference (p<0.05) between two samples.*

Palazzu (integral reserve) than outside. But surprisingly, mean values were lower in Punta Nera (non-integral reserve) than in Pori, the outside reserve station. The Punta Nera station is situated near the limits of the non-integral reserve (Fig. 1). Amateur fishermen are more numerous around the reserve than at Pori during summer (F. Finelli, personal communication). Thus, this difference could be due to higher fishing pressure at Punta Nera than at Pori. In the three stations, the seasonal variations were important according to the high values of CV (Tab. 5).

In relative abundance, the outside-inside integral reserve ratio was 1 to 4.1 for rocky substrata and 1 to 1.1 for shallow seagrass beds. The impact of the integral reserve on the relative abundance of fishes was more marked on rocky substrata than on *P. oceanica* beds. On the other hand, the seasonal variations of relative abundance were dampened in the seagrass bed but not in rocky substrata.

Demographic pattern

The percentage of large-size individuals in the *Posidonia oceanica* meadow was not always the highest in the integral reserve, during the warm season (Tab. 6), but it was always higher during the winter than during the summer, in the integral reserve and at Petraghja, the highly complex station. On average and after eight missions a higher average percentage of large individuals has been recorded at Gargalu (8.1 %, shallow and 7.8 %, deep) and at Petraghja (7.2 %) than elsewhere (6.9 % to 4.1 %). In the same way, the biomass : density ratio was calculated

	S88	S89	W90	S90	W91	S91	W92	S92
***Posidonia oceanica* seagrass beds**								
Gargalu shallow*	6.7	5.7	8.6	6.0	15.5	5.7	12.3	4.3
Gargalu deep*	4.2	6.7	6.9	17.0	7.0	5.6	6.9	–
Elbu shallow	4.4	3.6	2.0	7.3	4.8	4.8	3.1	6.0
Elbu deep	8.7	11.4	5.2	5.9	2.2	8.6	6.9	–
Petraghja	–	6.3	6.6	8.7	16.5	4.4	3.7	4.3
Galeria	4.4	6.0	1.6	7.0	3.7	4.3	2.1	4.1
Rocky substrata								
Palazzu*	44.8	50.6	26.2	30.7	29.6	3.9	7.8	–
Punta Nera	42.1	6.9	7.7	9.0	14.5	8.4	10.4	–
Pori	–	4.1	55.3	26.6	11.6	9.6	7.3	–

*– : station not sampled; * = integral reserve.*

Table 6

Percentage of large size individuals for the different stations of seagrass beds and rocky substrata. These percentages are calculed from the number of individuals.

	Seagrass		Rocky substrata	
	N	Mean (s.d.)	N	Mean (s.d.)
Biomass to density ratio				
Outside Reserve (OR)	140	12.8 (38.3)	121	220.7 (303.9)
Non-integral Reserve (NIR)	404	20.2 (33.2)	117	193.1 (333.7)
Integral Reserve (IR)	264	22.2 (26.9)	134	334.7 (401.0)
Kruskal-Wallis test				
Outside Reserve	–	286.29	–	154.29
Non-integral Reserve	–	412.10	–	130.35
Integral Reserve	–	455.55	–	203.56
H-statistic	–	48.98	–	35.31
p	–	<0.001	–	<0.001
NKS's test	–	OR<NIR=IR	–	OR=NIR<IR

Table 7

Biomass to density ratio for the sampled population in the seagrass bed and the rocky substrata. Results of non-parametric Kruskal-Wallis test (average rank) and results of the NKS's test.

for the total population sampled. This ratio corresponds to the mean individual weight of a fish. It differed significantly between the inside and outside of the integral reserve (Tab. 7).

On rocky substrata (Tab. 6), for both density and biomass, the results were markedly different from those found in the meadow. The percentage of large individuals was always higher during the warm season in the integral reserve than outside. During the cold season, no clear trend was observed from year to year, in opposition to observations made during the warm season. In March 1992, percentages did not differ between all stations; the percentage was particularly low at Palazzu. In March 1990, the maximum value was obtained at Pori, outside the reserve. On average, a higher percentage of large-size individuals was recorded at Palazzu (33.4 %) than outside the integral reserve (14.1 % at Punta Nera and 19.1 % at Pori). The biomass : density ratio differed significantly between the integral reserve and the other stations (non-integral reserve and outside the reserve; Tab. 7).

Diversity

The diversity index (Tab. 8) used in the *Posidonia oceanica* meadow did not permit the individualization of stations or periods, in terms of density and biomass. On the other hand, the calculation of an average index for the entire sampling period (mean of 7 or 8 indices), at constant depth, showed the Shannon index to be higher in the integral reserve than in the non-integral reserve or outside the reserve. In the non-integral reserve, specific diversity was the highest in the highly complex station (Petraghja).

On rocky substrata (Tab. 8), specific diversity was calculated on biomass values, due to the extremely low density values recorded in some cases. In most cases, diversity decreased from Palazzu to Pori, from the integral reserve to the station outside the reserve, with some exceptions, however, *e. g.* March 1990. A characteristic trend has been observed : diversity indices calculated at

	S88	S89	W90	S90	W91	S91	W92	S92	Mean D	Mean B
Posidonia oceanica **seagrass beds (SHD/SHB)**										
Gargalu shallow*	3.79/3.47	2.29/3.25	2.01/2.52	2.76/2.88	2.15/2.51	2.83/3.02	2.44/2.57	3.54/3.39	2.73	2.95
Gargalu deep*	3.68/3.64	2.57/2.91	2.31/2.78	2.88/2.09	1.68/2.14	2.42/2.47	2.43/2.00	–	2.57	2.57
Elbu shallow	3.01/2.38	1.55/3.22	2.24/2.79	2.91/2.47	1.63/2.46	2.67/2.55	2.70/2.86	2.81/3.09	2.44	2.75
Elbu deep	3.98/3.31	2.03/1.61	2.51/2.54	2.32/2.57	2.06/2.19	2.55/2.27	2.23/2.34	–	2.53	2.40
Petraghja	–	1.63/2.95	2.41/2.40	2.86/3.19	2.24/2.57	3.15/3.02	2.73/2.71	2.54/3.31	2.51	2.88
Galeria	3.33/3.02	1.51/2.66	1.61/2.24	2.79/1.79	1.19/2.04	1.70/2.91	1.17/1.55	2.84/2.98	2.02	2.40
Rocky substrata (SHB)										
Palazzu*	1.92	1.97	1.60	2.09	1.66	2.09	1.85	–	–	1.88
Punta Nera	1.82	1.71	2.79	1.47	1.11	1.11	1.06	–	–	1.58
Pori	–	1.59	0.92	2.13	n.c.	1.73	1.35	–	–	154

*Mean D, B: mean of the Shannon index for density or biomass; – : station not sampled; n.c.: not calculed; * = integral reserve.*

Table 8

Specific diversity (Shannon index, logarithm base 2) calculed from density (seagrass beds only: SHD) and from biomass (seagrass beds and rocky substrata (SHB) for the different stations.

Palazzu were relatively comparable between seasons with a drop in winter. However, at Punta Nera and Pori, the diversity index fluctuated from season to season.

DISCUSSION

The two studied environments, *Posidonia oceanica* seagrass bed and rocky substrata, react quite differently to protection, and thereby to the reduction of human-induced disturbances. Density and biomass data alone did not highlight the difference between the integral reserve and the other zones of the seagrass bed. Whereas in rocky substrata, data clearly demonstrated higher values in the integral reserve and supply an adequate separation criterion between protected and unprotected zones as emphasized in the literature (Bell, 1983; Buxton and Smale, 1989; Cole *et al.*, 1990). This apparent contradiction could be caused by non-compliance with protection regulations in the integral reserve. Samoilys (1988), in coral reefs of Kenya, established that species richness was highest in marine parks, but fish abundances (underwater censuses) were not greater in the marine parks than in unprotected sites. She supposed that this could be due to illegal forms of disturbances in protected zones (fishing with explosives, for example). These disturbances outweigh the effects of protective management on fish communities. At Scandola, it is not possible to exclude the pressure of illegal fishing in meadows of the integral reserve (F. Finelli, personal communication). However, this illegal activity is relatively limited in time (three months) and does not outweigh the reserve effect. I suggest the following explanations of this apparent contradiction in the reserve effect for both biotopes :

1) Different dominant families in the two biotopes (the necto-benthic Labridae in the meadows and the more mobile Sparidae in rocky substrata) and different fishing effort according to the species (Sparidae are preferred to Labridae by amateur and professional fishermen) : the fishing pressure exerted outside the reserve is therefore greater in rocky substrata than in the meadows.

2) The presence of predators on rocky substrata of the integral reserve whose feeding habits bring them to prey occasionally in meadows. They could then exert greater pressure in the meadow of the integral reserve than outside. The presence of a greater number of high-level predators in the reserves than outside has important consequences on the environment dynamic (McClanahan, 1989; Russ and Alcala, 1989). Absence or low numbers of high-level predators outside the reserve are synonymous with increasing numbers of preys.

As observed by Frontier and Pichod-Viale (1991) and Buxton (1993), populations skewed towards juveniles would result from over-exploitation (removal of reproductive adults) and in the first stage, this leads to increased production and perhaps biomass. However, gradual disappearance of big fish could be an insurmountable obstacle to reproduction in some hermaphrodite fish families (Randall, 1982; Buxton, 1993). The main families of Mediterranean coastal zones (Labridae, Serranidae and Sparidae) are protogynous or protandrous hermaphrodites; partial disappearance of one of the two sexes could hamper successful reproduction.

This study has evidenced a refuge effect of protected zones, particularly characterized by the presence of large individuals, which are the most sensitive to fishing pressure (amateur or professional). This refuge effect stands out more clearly in rocky substrata than in the grassbeds. More thorough analysis of the specific components of existing populations (not restricted to the sampled population) also revealed the presence of rare or rarely encountered species in the most protected zones (sea-bass, *Dicentrarchus labrax*, sea-beam, *Sparus aurata*, brown-meagre, *Sciaena umbra* and dusky-grouper *Epinephelus marginatus* : Francour, 1989; 1991), also observed by Garcia-Rubies and Zabala (1990) at the Medes Islands (Spain, natural reserve) and Chauvet and Francour (1990) in Port-Cros (France, National Park). This refuge effect, with the presence of large individuals and species vulnerable to fishing, is one of the characteristics most often described in the definition of a reserve effect (for review see Russ and Alcala, 1989). Most authors agree that the size of individuals in the protected zones is greater than outside, both for fish (Bell, 1983; Samoilys, 1988; Buxton and Smale, 1989; Cole *et al.*, 1990) and invertebrates (Moreno *et al.*, 1986; Cole *et al.*, 1990).

Authors have most often described the impact of a reserve as that of a refuge effect. Through pluriannual analysis of this impact, this study can highlight a second feature, the buffer effect, characterized by markedly reduced seasonal variations in several parameters (density, biomass, diversity). The refuge effect corresponds to the spatial dimension of the phenomenon, whereas the buffer effect corresponds to its temporal dimension.

Both refuge and buffer effects probably act jointly in a given substratum, but one may be predominant. In rocky substrata, the refuge effect is the only one clearly pointed out by the data; adversely, in meadows the buffer effect is strongest. It is possible that the natural complexity of rocky substrata, their rugosity, enhances the controlling factor of recruitment, thus minimizing the importance of predation and competition as controlling factors. As classically accepted in the literature on *Posidonia* seagrass beds, if larval recruitment is supposed to be the main controlling factor of fish populations, the annual and pluriannual abundance variation cycles could be partly explained by massive, seasonal arrivals of larvae, submitted to existing conditions. In the reserves, this general pattern is completed by the presence of high-level predators, more abundant than outside. Moreover, competition between individuals (highest specific richness) could be another reinforcing factor. Both factors contribute to dampening seasonal and pluriannual abundance variations, thus defining the buffer effect.

Moreno *et al.* (1986) have called these interspecific competition levels the cascade effect. In the reserve of Scandola, results recorded with Labridae (prey for predators such as Serranidae, less abundant in the reserve than outside) seem to reinforce this idea and could correspond to the existence of this cascade effect, a third component of the reserve effect. Work performed in the reserve at Scandola on macrozoobenthos and phytobenthos also corroborates this theory (Boudouresque *et al.*, 1992).

More thorough analysis of the buffer effect and its consequences on low-disturbance environments such as reserves would be of interest. The dynamics of the ichthyofauna of the *P. oceanica* seagrass beds as they are classically described (Harmelin-Vivien, 1983; Francour, 1990) could be modified by anthropic factors. A wider, more appropriate picture could perhaps be obtained by studying very low-level disturbance environments. Moreno *et al.* (1986) suggest that the unusual aspect of the intertidal community they are working on in Chile results from the protection offered by a reserve. That is not often observed where the human influence occurs.

Furthermore, it is also interesting to emphasize that the disturbance types have different consequences on the effects themselves. So-called selective disturbances, such as traditional fishing, damage the refuge effect essentially, whereas the non-selective disturbances (anchoring, pollution) often alter or damage the environment (Munro *et al.*, 1987; Russ and Alcala, 1989) and modify the buffer effect.

Several recommendations could be made on the basis of these first conclusions, before a protected marine area is developed and managed.

1) For biological success in a reserve, there must be a sufficiently complex structure, *i.e.* different substrata within the protected area, such as seagrass beds, rocky substrata in the Mediterranean (overall complexity) and each must have its own complexity (internal complexity) in the form of shelters, patches of cobbles or boulders for example.

2) It is important that disturbance levels should be maintained as low as possible in the protected zone. To obtain the maximum reserve effect, it is necessary to limit the selective and non-selective disturbances which alter the components of the reserve effect.

3) Finally, the peculiarities of each individual species or family require a fairly long operational time before the initial beneficial effects of the reserve set in, and before the complex interactions between the faunal and floral components could be established or restored.

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