Acc. Cont. —
Ameli

Spatio-temporal variability in growth of juvenile sparid fishes from the Mediterranean littoral zone

S. Planes*, E. Macpherson[†], F. Biagi^{†**}, A. Garcia-Rubies[†], J. Harmelin[‡], M. Harmelin-Vivien[‡], J.-Y. Jouvenel*, L. Tunesi[§], L. Vigliola[‡] and R. Galzin*

*EPHE—URA CNRS 1453, Université de Perpignan, 66860 Perpignan, France.

[†]Consejo Superior de Investigaciones Científicas, Centro de Estudios Avanzados de Blanes, Camino de Santa Barbara, E-17300 Blanes, Girona, Spain.

[‡]Dipartimento di Scienze dell'Uomo e dell'Ambiente-DSUA, Università di Pisa, Via A. Volta 6, I-56100 Pisa, Italy.

[§]Centre d'Océanologie de Marseille, Station Marine d'Endoume—URA CNRS 41, F-13288 Marseille Cedex 09, France.

[§]ICRAM, Via L. Respighi 5, I-00197 Roma, Italy.

**Centro Interuniversitario di Biologia Marina ed Ecologia Applicata-CIBM, I-57127 Uvarno, Italy

Populations of three species of juvenile Sparidae (*Diplodus puntazzo*, *Diplodus sargus* and *Diplodus vulgaris*) were sampled at different spatial scales in the north-western Mediterranean Sea over two years to follow growth after settlement. Length–frequency distributions were collected each week for periods of six months following the arrival of off-shore larvae in inshore habitats. Data were collected by underwater visual census along permanent transects.

Growth rate measured as the slope of the linear relationship between mean size and time varied between species. *Diplodus puntazzo* (0.160 mm d⁻¹) and *D. vulgaris* (0.202 mm d⁻¹), which are settling in winter experienced slower growth than *D. sargus* (0.567 mm d⁻¹) which settles in summer. It is concluded that the difference was in part due to water temperature. Analysis of growth rate within each species also revealed significant differences among sites probably related to the currents and the water mass temperatures.

INTRODUCTION

Recruitment usually refers to the input of juveniles to the observed population. The direct link between recruitment patterns and distribution and abundance of adults has been emphasized in several examples (see overview in Sale, 1991; Doherty & Fowler, 1994). Despite the agreement of scientists that recruitment drives adult populations, a major controversy occurs when distinguishing pre-recruitment events (recruitment limitation model) and post-recruitment events (resource limitation and predation models) and which events affect population dynamics most (Jones, 1991; Tolimieri, 1995). Control and regulation of recruitment are terms used to describe the effect of factors, like temperature and feeding activity through processes, like predation and competition. Such regulatory processes can be estimated in the field by measuring mortality rate (for predation) and growth rate (for competition). Assuming that the higher the competition, the lower the growth; estimates could be used to characterize recruitment success and the carrying capacity of a particular site as nursery (Pepin, 1991). As a concomitant idea, growth rates and mortality processes can be viewed as a 'single process' in demographic processes (Cushing, 1975). Growth interacts with mortality as the survival chance of a new recruit increases with increasing size (Tsukamoto et al., 1989). Because of such implications, growth estimates can provide a descriptive parameter of the conditions surrounding a population.

Growth, as the rate at which individuals increase in weight and length, is the demographic parameter that is the most sensitive to environmental conditions (Weatherly & Gill, 1987). The potential of fish to grow (as measured by the rate and the efficiency of food consumption) has been found to depend on whether they have been deprived of food at any stage during their life history (McCormick & Molony, 1992). The analysis of size–frequency distributions has been used to obtain information on growth and mortality of many species (Barry & Tegner, 1989). Growth estimates are calculated from sampling a population at intervals and calculating the mean size of cohorts (groups of individuals of similar size that are assumed to be of a similar age) identified in the size–frequency distribution. Growth can then be estimated from the increase of the mean size of a cohort over time (Grant et al., 1987). Such an analysis requires that recruitment occurs in discrete pulses and that growth rates are high in order that the mean sizes of successive cohorts do not overlap. Nevertheless, size–frequency data are commonly used to estimate growth rates of cohorts between year-classes. Such a procedure can also be applied to estimate growth rates of cohorts within year-classes.

Despite the importance of recruitment processes in the littoral zone of the Mediterranean Sea, previous research concentrated on adult fish communities (e.g. Bell & Harmelin-Vivien, 1982; Bell, 1983; Harmelin, 1987; Garcia-Rubies & Zabala, 1990; Macpherson, 1994; Dufour et al., 1995). Recruitment processes have only recently been surveyed with particular interest in the

habitats of recruits (Harmelin-Vivien et al., 1995; Garcia-Rubies & Macpherson, 1995; Biagi et al., 1997).

Populations of three species of Sparidae were sampled: *D. puntazzo*, *D. sargus* and *D. vulgaris*. Because Sparidae species are of economic interest, some studies are already available (Quignard & Man-Wai, 1982, 1983). These focused on growth of juveniles once they enter marine littoral lagoons. Studies of both habitat and growth have shown that sparid juveniles grow relatively quickly from recruitment occurring in discrete pulses. These factors suggest that the analysis of length–frequency distributions may provide reliable information on the growth of sparid juveniles. In the present paper, we use ‘cohort’ to describe groups of fish of a similar size that we have identified in each length–frequency distribution. Growth variation was tested through a multidimensional approach: between species, between sites and between years. In addition, recruitment between protected and unprotected areas was compared.

MATERIALS AND METHODS

Sampling

Assessment of size–frequency of newly recruited sparids was carried out in several stations located in five major sites throughout the north-west Mediterranean Sea (Figure 1) to examine spatial variations at small and large-scales, and over a period of two years (November 1993 to November 1995) to investigate temporal patterns. Initial data on recruitment and habitat (Garcia-Rubies & Macpherson, 1995) recorded the first arrivals of *Diplodus puntazzo* in October, *D. vulgaris* in November and *D. sargus* in May each year. Surveys were conducted to follow growth over a period of six months after settlement. Data were collected by snorkelling in shallow water (<2 m). Each station was visited a minimum of four times each month. Altogether, 21 stations were surveyed with four near Blanes (Spain), three near Banyuls (France), seven near Marseille (France), four near Portofino (Italy) and three around Elba Island (Italy) (Figure 1). Each station consists of a transect parallel to the coast line in a small sheltered bay. Transect length ranged from 27 to 300 m, and juveniles were counted between 0 and 2 m depth. Sites were carefully selected to give a closed recruiting system: a small bay limited by deeper water area with a drop-off. This structure avoids the possibility of migration and previous studies showed that juveniles of these three species were restricted to shallow inshore habitats and did not migrate to deeper water until six months following their arrival (Harmelin-Vivien et al., 1995; Garcia-Rubies & Macpherson, 1995). They are restricted to very shallow water (<2 m) in sites with a gentle slope and coarse sand. Therefore our survey was limited to the first three months after recruitment during which the juveniles are strictly dependent on the shallow habitat. The present study represents 1920 dives with an average of four dives per month during two years at 21 stations.

At the 21 stations, eight sites were selected in marine park areas to test the effect of protection on recruitment. Only sites in France and Spain included sites within protected areas, with three stations in Blanes, two stations in Banyuls and three stations in Marseille. Similar stations within

marine protected areas could not be selected in Italy (Portofino and Elba Island) due to the lack of administrative marine park status when the survey started.

All individuals belonged to the 0+ cohort. Smaller juveniles recorded (<10 mm total length, TL) were just settling from the ocean as they were still post-larval stage, whereas the largest individuals taken into account in this study were 60–80 mm long. Abundance and the size of individuals were recorded for each species. Observed size, *in situ*, was recorded in 11 classes starting at 5 mm up to more than 70 mm (5–10, 11–15, 16–20, 21–25, 26–30, 31–35, 36–40, 41–50, 51–60, 61–70, >71 mm TL) using shapes drawn on underwater plastic boards. This standardized protocol was designed to avoid variation between observers. In addition, all observers underwent an initial training to standardize underwater counts and size estimate methodology. Final data were reduced to a mean TL of species surveyed for each sampling time. Mean TL values were calculated from abundance and size range of individuals using the median of the size range, over the four successive counts performed in each station each time.

Underwater surveys show the existence of two *D. vulgaris* cohorts within the same year arriving at a one month interval at some sites (Blanes and Marseille). The density of the two cohorts was always very different with one consisting of numerous individuals and the other consisting of fewer individuals (the first one). When such situations occurred, we reported only data concerning the most abundant cohort and separated it from the other cohort all along the survey.

Statistical analysis

Several growth models were tested for each species; linear ($y=a+bx$), exponential ($y=a \times \exp(b \times x)$) and logistic ($y=a/\exp(b-c \times x)$). Some models fitted one species and not others and we chose the linear model, which was suitable for all species (>90% of the variation was explained for all growth data sets), in order to compare the growth rates between species. For each count, time (t) and mean total length (TL) were used to fit the model:

$$TL_t = b \times t + a \quad (1)$$

where: b, growth rate in mm d^{-1} (slope of linear model); t, time in days; TL_t , predicted mean total length at time t in mm; a, intercept corresponding to the predicted mean total length at zero time. From 126 growth curves expected from the sampling, only 110 could be used as ten growth curves could not be significantly computed due to missing sampling dates.

Growth variation was analysed through a multi-dimensional approach: among species, among sites and between years. Because the growth rate data (b in the linear model) were not normally distributed (χ^2 -test with a normal distribution, $P>0.05$) and because of non-homogeneity of the variance (Bartlett test, $P>0.05$) despite using several transformations. Spatio-temporal variations in growth were assessed using a non parametric three-factors analysis of variance (Zar, 1984, p. 249). This procedure is an extension of the Kruskal–Wallis test which uses the rank of each value. The three factors were: species (*D. puntazzo*, *D. sargus* and *D. vulgaris*), sites

Figure 1. Map of the north-western Mediterranean Sea showing the five sites sampled and details and numbers of stations surveyed. Marine protected areas are circled with a dashed line. Stations are denoted with P for protected area sites and UP for unprotected area sites.

(Blanes, Perpignan, Marseille, Portofino and Elba) and year (recruitment in 1994 and 1995). *Post hoc* tests (Newman–Keuls) were performed on ranks to identify which variables differed significantly (Zar, 1984, p. 190). The significance levels for multiple tests were adjusted using the sequential Bonferroni technique (Rice, 1989).

In addition, the effect of protection was tested separately because some sites did not have any marine protected areas (Italy). The same procedures as used previously and a non parametric four-factors analysis of variance was performed with species (*D. puntazzo*, *D. sargus* and *D. vulgaris*), sites (Blanes, Perpignan and Marseille), year (recruitment in 1994 and 1995) and protection (protected and unprotected areas) (Zar, 1984, p. 234).

RESULTS

Out of the 110 growth curves fitted, only one was not significant with $r^2=0.494$ (*Diplodus puntazzo*, MA2UP in 1994 from Marseille). This data set was removed from subsequent analyses. All other linear fits were significant and out of the 109 coefficients of determination, 107 were greater than 0.8. The number of observations varied from 4 to 33. Such high variability in the number of observations was not correlated to linear fits to the growth model and resulted mainly from poor weather conditions (during winter sampling) which limited access to some stations (mainly those in protected areas).

The growth rate 'b' (slope of linear model) varied from 0.080 mm d⁻¹ for *D. puntazzo* in Marseille (MA6P in 1994) to 1.010 mm d⁻¹ for *D. sargus* in Portofino (PO3UP in 1994). An overview of mean growth rate shows variation with *D. sargus* showing higher values (0.567 mm d⁻¹) than *D. vulgaris* (0.202 mm d⁻¹) and *D. puntazzo* (0.160 mm d⁻¹). Within each species there is also a consistent growth pattern between years with the average growth during 1994 higher than that of 1995 (Appendix 1). Analysis of range (minimal–maximal growth rate) within species and between years and sites shows that growth of juveniles of *D. sargus* varies much more (0.631 mm d⁻¹) than that of *D. puntazzo* (0.226 mm d⁻¹) and *D. vulgaris* (0.272 mm d⁻¹). However, once ranges were standardized to mean growth rate of juveniles, it appears that *D. sargus* exhibits a lower variability (108% of the mean growth) than *D. puntazzo* (140%) and *D. vulgaris* (136%).

Spatio-temporal variations

Non parametric three-factors analysis of variance shows that more than 70% of the variance in growth

resulted from difference between species ($H=588.17$; $P<0.001$) (Table 1). This pattern in growth was the same for the two years surveyed as the species–years factor was not significant ($H=3.73$; $P>0.05$). Variance between sites was also significant and accounts for 7% of the total variance ($H=59.79$; $P<0.001$). When combined with species (species–sites factor), it represented 7% of the total variance indicating that sites where faster growth occurred are different from one species to another ($H=55.00$; $P<0.001$). Two other sources (sites×years and species×sites×years) were significant ($P<0.01$) but accounted for only 2% of the total variance respectively. These interactions indicate that good conditions for growth, resulting from a dynamic environment, are highly variable from one species to another, from one site to another and from year to year. Nevertheless, no significant difference was found between years when species and sites are mixed ($H=1.21$, $P>0.05$). Finally, only 9.6% of the total variance could not be explained. Such a low value in analysis of biological processes resulted from the type of analysis used which computed variance from rank values and not from raw data.

Newman–Keuls tests on pairwise comparisons within each single factor (species or sites or years) show that all three species grow significantly differently with *D. sargus* showing higher mean rank (92.21), *D. puntazzo* exhibiting the lower rank (29.81) and *D. vulgaris* in intermediate position (44.75). Probabilities of the three comparisons were about 10⁻⁴. This result fits with initial observations made directly on growth rate values where *D. sargus* was found to have a higher growth rate (0.567 mm d⁻¹) than *D. vulgaris* (0.202 mm d⁻¹) and *D. puntazzo* (0.160 mm d⁻¹). Similar Newman–Keuls tests were performed on sites and showed two groups: one at Marseille (46.55), Banyuls (48.08) and Blanes (54.56) with lower rank values than the other group at Portofino (62.11) and Elba Island (66.65). However, direct comparison of growth rate data show that Marseille conserves its position with lower growth (0.249 mm d⁻¹), the other sites showing the following order: 0.305 mm d⁻¹ for Elba Island; 0.336 mm d⁻¹ for Banyuls; 0.360 mm d⁻¹ for Portofino; and 0.367 mm d⁻¹ for Blanes. This different conclusion could result from the significant interaction effects. Finally, there is no significant difference between the 1994 and 1995 surveys ($P=0.23$) despite a large decrease (18%) of growth between 1994 (0.617 mm d⁻¹) and 1995 (0.509 mm d⁻¹) in *D. sargus* and a smaller decrease in *D. puntazzo* (4%) and *D. vulgaris* (9%).

Table 1. Non-parametric three-factors analysis of variance on growth rate b.

Source	Sums of Squares	df	H	% of variance
Species	73477.9	2	588.17***	71.1
Sites	7469.9	4	59.79***	7.2
Years	151.5	1	1.21 ^{ns}	0.1
Species×sites	6870.6	8	55.00***	6.7
Species×years	465.8	2	3.73 ^{ns}	0.5
Sites×years	2072.2	4	16.59**	2.0
Species×sites×years	2903.7	8	23.24**	2.8
Residuals	9869.2	79		9.6

df, degrees of freedom for χ^2 -test; ^{ns}, $P>0.05$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

Table 2. Non-parametric four-factors analysis of variance on growth rate *b*. This analysis was computed only on sites Blanes, Banyuls and Marseille where both protected and unprotected areas were followed (Portofino and Elba omitted).

Source	Sums of squares	df	H
Protection	281.7	1	0.11 ^{ns}
Protection×species	81.6	2	0.03 ^{ns}
Protection×sites	12.0	2	0.00 ^{ns}
Protection×years	37.8	1	0.01 ^{ns}
Protection×species×sites	n.d.	n.d.	n.d.
Protection×species×years	65.9	2	0.03 ^{ns}
Protection×sites×years	59.7	2	0.02 ^{ns}
Protection×species×sites×years	n.d.	n.d.	n.d.
Residuals	2545.7		

df, degrees of freedom for χ^2 -test; ^{ns}, $P > 0.05$; n.d., no data (not computed).

Effect of protection level

The effect of protection was tested by itself and combined within species, sites and years (Table 2). None of the sources tested were significant, demonstrating that there is no effect of site protection on the growth of juveniles.

DISCUSSION

Growth of juveniles of *Diplodus* appears to vary significantly between species and sites. A major characteristic of fish growth is its flexibility. The same species may show very different patterns of growth in different environments (Cushing, 1975). Although the flexibility of fish growth means that individuals of the same species may show different growth patterns, there is also a degree of heritability in growth patterns (Purdom, 1979). The heritability gives the contribution of genetic factors, relative to environmental factors, to the variation shown by a phenotypic trait (such as growth). Heritability can take values from 0 (no genetic effect) to 1 (no environmental effect). Heritability for growth of juveniles has been shown to be low (–0.1) in experiments with Atlantic salmon and/or rainbow trout (Gjerde, 1986). This suggests that growth of fish is mainly controlled by environmental conditions and that differences in growth observed between *Diplodus* spp. are mainly due to exogenous factors. In our studies, the growth rate of *D. sargus* varied from 0.385 to 1.010 mm d^{–1} during the same period between different sites. Such a range of 262% shows that environmental conditions account for a high degree in the variation of growth rate. External factors affecting growth, are mainly food and temperature. In some environments, oxygen and salinity may be controlling factors as well. Our results have shown that *D. puntazzo* and *D. vulgaris* which settled in October and November respectively exhibited lower growth than *D. sargus*, settling in May. In the north-western Mediterranean Sea, water temperature shows its maximum in July and/or August (21–23°C) and decreases until its minimum in February (11–13°C). Consequently, juveniles of both *D. puntazzo* and *D. vulgaris* arrive during the cold water season which will limit their growth, while juveniles of *D. sargus* which arrive in May, during the warm water season, will grow faster (Pepin, 1991; Polo et al., 1991). In addition, zooplankton abundance decreases during the winter season in the north-western Mediterranean Sea and is also a factor limiting the growth of

D. puntazzo and *D. vulgaris* which feed on zooplankton (Kentouri & Divanach, 1982). Species recruiting during winter time also show a higher growth rate range between years (136 and 140% of the mean growth) than *D. sargus* which arrives in late spring (108%). Such a large difference suggests that environmental conditions are more variable in winter than in summer. It also suggests that juveniles of *D. puntazzo* and *D. vulgaris* may have a higher potential to increase their growth as most values represent a low level due to cold water temperature and limited food availability. Growth rate values of *D. sargus* observed in our study (0.567 mm d^{–1}) are similar to those estimated from aquaculture experiments (0.530 mm d^{–1}; Kentouri et al., 1980) or in a coastal lagoon along the north-western Mediterranean (0.518 mm d^{–1}; Quignard & Man Wai, 1982). Nevertheless, wild growth showed higher values than aquaculture growth despite the feeding *ad libitum* and maintenance at a constant 20°C water temperature in aquaculture. Such a comparison suggests that aquaculture processes did not optimize all parameters and that parameters other than temperature and food and, such as competition in limited space of aquaculture tanks, may affect growth.

Variation in growth among regional areas also explained a significant part of the total variance. An analysis using rank transformed data, detected two groups, with higher growth rates in the Italian sites (Portofino and Elba Island) and lower ones in the French and Spanish sites (Marseille, Banyuls and Blanes). The analysis on rank transformed data decreases the variance, reduces the range of raw data and consequently decreases the weight of extreme values. Because of such effects our results give a general pattern. This pattern may be related to the current affecting the area. Both Elba Island and Portofino (located along the western coast of Italy) are affected by warm currents flowing from Sicily and the south Mediterranean Sea (Castelbon, 1972), while Marseille, Banyuls and Blanes are affected by the Liguro–Provençal current which flows from east to west and drives colder water (Millot, 1987). Moreover, the last three sites are exposed to frequent northerly winds in winter which induce local upwellings and bring cold deep water to the surface. These winds are less frequent in Italy. The high range of growth rates observed in *D. puntazzo* and *D. vulgaris* is definitively related to the fact that these two species are recruiting during winter in opposition to *D. sargus*. In addition, the absence of significant differences of growth rate distribution between 1994

and 1995 enforces the idea that seasonal variations, which are mainly driven by temperature shifts in temperate climate, have a greater effect on growth rate than inter-annual variations. As no analysis of plankton was undertaken during the survey, it was not possible to identify which factor was primarily responsible for the high variance of growth rate in winter (i.e. temperature or food availability).

The absence of effect of fishing limitation on the growth of juveniles has implications for the management of marine protected areas. Up to now, the main effect described in protected areas in the Mediterranean Sea is to concentrate large fish (Bell, 1983; Garcia-Rubies & Zabala, 1990; Dufour et al., 1995; Harmelin et al., 1995) and protect large species sensitive to spear-fishing and line fishing. The results suggest that juvenile sparids do not compete with adults for habitat because they recruit in very shallow water, 1–2 m deep along the coast line and consequently the increase of adult density in a protected area does not affect juvenile growth.

We gratefully acknowledge the assistance of all volunteers; with special reference to P. Francour, S. Gambaccini, L. Le Direach, L. Mariani, M. Mori, H. Vacchi and M. Zazzeta. This study was supported by grants from the European Community (DG XIV, MED 92/007), the Italian National Programme (MURST) and PNDR-France GLOBEC (French National Programme on the Determinants of Recruitment).

REFERENCES

- Barry, J.P. & Tegner, M.J., 1989. Inferring demographic processes from size–frequency distributions: simple models indicate specific patterns of growth and mortality. *Fishery Bulletin. National Oceanic and Atmospheric Administration, Washington, DC*, **88**, 13–19.
- Bell, J.D., 1983. Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean Sea. *Journal for Applied Ecology*, **20**, 357–369.
- Bell, J.D. & Harmelin-Vivien, M.L., 1982. Fish fauna of French Mediterranean *Posidonia oceanica* seagrass meadows. I. Community structure. *Tethys*, **104**, 337–347.
- Biagi, F., Gambaccini, S. & Zazzetta, M., 1997. Insediamento e microhabitat di specie ittiche nella fascia costiera toscana. *Bolotin Marino de Mediterraneo*, **4**, 195–203.
- Castelbon, C., 1972. Etude de la circulation des masses d'eau dans le Golfe de Marseille. *Tethys*, **4**, 269–312.
- Cushing, D.H., 1975. *Marine ecology and fisheries*. Cambridge: Cambridge University Press.
- Doherty, P.J. & Fowler, T., 1994. An empirical test of recruitment limitation in a coral reef fish. *Science, New York*, **263**, 935–939.
- Dufour, V., Jovenel, J.-Y. & Galzin, R., 1995. Study of a Mediterranean reef fish assemblage. Comparisons of population distributions between depths in the protected and unprotected areas over one decade. *Aquatic Living Resources*, **8**, 17–25.
- García-Rubies, A. & Macpherson, E., 1995. Substrate use and temporal pattern of recruitment in juveniles fishes of the Mediterranean littoral. *Marine Biology*, **124**, 35–42.
- García-Rubies, A. & Zabala, M., 1990. Effect of total fishing prohibition on the rocky fish assemblages of Medes Island marine reserve NW Mediterranean. *Scienza Marina*, **544**, 317–328.
- Gjerde, B., 1986. Growth and reproduction in fish and shellfish. *Aquaculture*, **57**, 37–55.
- Grant, A., Morgan, P.J. & Olive, P.J.W., 1987. Use made in marine ecology of methods for estimating demographic parameters from size/frequency data. *Marine Biology*, **95**, 201–208.
- Harmelin, J.G., 1987. Structure et variabilité de l'ichtyofaune d'une zone rocheuse protégée en Méditerranée, Parc National de Port-Cros, France. *Marine Ecology*, **83**, 263–284.
- Harmelin, J.G., Bachet, F. & Garcia, F., 1995. Mediterranean marine reserves: fish indices as a test of protection efficiency. *Marine Ecology*, **16**, 233–250.
- Harmelin-Vivien, M.L., Harmelin, J.G. & Leboulleux, V., 1995. Microhabitat requirement for settlement of juvenile sparid fishes on Mediterranean rocky shores. *Hydrobiologia*, **300/301**, 309–320.
- Jones, G.P., 1991. Post-recruitment processes in the ecology of coral reef fish population: a multifactorial perspective. In *The ecology of fishes on coral reefs* (ed. P.F. Sale), pp. 294–327. San Diego: Academic Press.
- Kentouri, M. & Divanach, P., 1982. Différences et similitudes dans la genèse des comportements locomoteurs et trophiques des stades prélarvaires de *Sparus aurata*, *Diplodus vulgaris* et *sargus*. *Aquaculture*, **27**, 355–376.
- Kentouri, M., Divanach, P. & Cantou, M., 1980. Données préliminaires sur le comportement, la croissance et la survie du sar *Diplodus sargus* L. en élevage. *Etudes et Revues du Conseil Général des Pêches en Méditerranée*, **57**, 33–51.
- Macpherson, E., 1994. Substrate utilisation in a Mediterranean littoral fish community. *Marine Ecology Progress Series*, **114**, 211–218.
- McCormick, M.I. & Molony, B.W., 1992. Effects of feeding history on the growth characteristics of a fish at settlement. *Marine Biology*, **114**, 165–173.
- Millot, C., 1987. Circulation in the western Mediterranean Sea. *Oceanologica Acta*, **10**, 143–149.
- Pepin, P., 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 503–518.
- Polo, A., Yuféra, M. & Pascual, A., 1991. Effects of temperature on egg and larval development of *Sparus aurata* L. *Aquaculture*, **92**, 367–375.
- Purdum, C.E., 1979. Genetics of growth and reproduction in teleosts. *Symposium of the Zoological Society of London*, **44**, 207–217.
- Quignard, J.P. & Man-Wai, R., 1982. Croissance linéaire et pondérale des jeunes *Diplodus sargus* O+ (Pisces Osteichthyes Sparidae) des étangs languedociens de Mauguio et du Prevost. *Revue des Travaux de l'Institut des Pêches Maritimes*, **45**, 253–269.
- Quignard, J.P. & Man-Wai, R., 1983. Relation taille-poids et coefficient de condition de *Diplodus sargus* O+ et O++ de deux étangs palavasiens: Prévost et Mauguio. *Cybiurn*, **7**, 31–41.
- Rice, W.R., 1989. Analysing tables of statistical tests. *Evolution*, **43**, 223–225.
- Sale, P.F., 1991. Reef fish communities: open non-equilibria systems. In *The ecology of fishes on coral reefs* (ed. P.F. Sale), pp. 564–596. San Diego: Academic Press.
- Tolimieri, P., 1995. Effects of microhabitats characteristics on the settlement of a coral reef fish at two spatial scales. *Oecologia*, **102**, 52–63.
- Tsukamoto, K., Kuwada, H., Hirokawa, J., Oya, M., Sekiya, S., Fujimoto, H. & Imaizumi, K., 1989. Size-dependent mortality of red sea bream, *Pagrus major*, juveniles realised with fluorescent otolith-tags in News Bay. *Japanese Journal on Fish Biology*, **35**, 59–69.
- Weatherly, A.H. & Gill, H.S., 1987. *The biology of fish growth*. London: Academic Press.
- Zar, J.H., 1984. *Biostatistical analysis*, 2nd ed. Englewood Cliffs, New Jersey: Prentice-Hall.

Submitted 16 May 1997. Accepted 5 January 1998.

Appendix 1. Growth rate ($b \pm 95\%$ confidence interval) computed each year from a linear model for each station. Stations with *P* indicate protected area sites and UP non protected area sites. Between brackets are indicated respectively, the number of observations used in the linear model which corresponds to the number of times a site was sampled, followed by the r^2 coefficient of determination of the linear model used and its significance.

	<i>Diplodus puntazzo</i>		<i>Diplodus sargus</i>		<i>Diplodus vulgaris</i>	
	1994	1995	1994	1995	1994	1995
Blanes (Spain)						
GI1UP	0.157 $\pm$ 0.017 (27, 0.938*)	0.167 $\pm$ 0.016 (33, 0.935*)	0.806 $\pm$ 0.112 (15, 0.953*)	0.670 $\pm$ 0.098 (19, 0.934*)	0.172 $\pm$ 0.029 (22, 0.885*)	0.211 $\pm$ 0.042 (28, 0.902*)
GI2P	0.121 $\pm$ 0.025 (13, 0.911*)	0.148 $\pm$ 0.022 (19, 0.921*)	0.553 $\pm$ 0.066 (11, 0.979*)	0.487 $\pm$ 0.096 (11, 0.937*)	nd	nd
GI3UP	nd	nd	nd	nd	nd	nd
GI4P	0.114 $\pm$ 0.017 (14, 0.950*)	0.125 $\pm$ 0.018 (18, 0.931*)	0.810 $\pm$ 0.139 (12, 0.945*)	0.594 $\pm$ 0.093 (13, 0.953*)	nd	nd
Banyuls (France)						
BA1P	0.140 $\pm$ 0.017 (17, 0.963*)	0.115 $\pm$ 0.025 (19, 0.857*)	0.789 $\pm$ 0.093 (11, 0.976*)	0.604 $\pm$ 0.130 (10, 0.935*)	0.091 $\pm$ 0.016 (17, 0.923*)	0.166 $\pm$ 0.022 (14, 0.957*)
BA2P	0.163 $\pm$ 0.022 (18, 0.970*)	0.130 $\pm$ 0.019 (20, 0.917*)	0.816 $\pm$ 0.090 (12, 0.976*)	0.563 $\pm$ 0.101 (12, 0.939*)	0.128 $\pm$ 0.029 (18, 0.863*)	0.178 $\pm$ 0.030 (14, 0.934*)
BA3UP	0.158 $\pm$ 0.033 (21, 0.870*)	0.110 $\pm$ 0.018 (23, 0.889*)	0.794 $\pm$ 0.078 (13, 0.979*)	0.760 $\pm$ 0.068 (11, 0.990*)	0.138 $\pm$ 0.019 (21, 0.933*)	0.201 $\pm$ 0.036 (18, 0.906*)
Marseilles (France)						
MA1UP	0.128 $\pm$ 0.089 (11, 0.676*)	0.187 $\pm$ 0.027 (6, 0.989*)	0.396 $\pm$ 0.072 (14, 0.932*)	0.461 $\pm$ 0.067 (17, 0.940*)	nd	0.200 $\pm$ 0.023 (9, 0.984*)
MA2UP	0.210 $\pm$ 0.046 (18, 0.943*)	0.144 $\pm$ 0.023 (15, 0.932*)	0.385 $\pm$ 0.084 (13, 0.914*)	0.419 $\pm$ 0.037 (14, 0.982*)	nd	0.236 $\pm$ 0.041 (10, 0.957*)
MA3UP	0.110 $\pm$ 0.041 (8, 0.910*)	0.130 $\pm$ 0.013 (18, 0.969*)	0.437 $\pm$ 0.086 (12, 0.937*)	0.451 $\pm$ 0.047 (16, 0.972*)	0.281 $\pm$ 0.064 (10, 0.940*)	0.183 $\pm$ 0.025 (12, 0.965*)
MA4UP	0.088 $\pm$ 0.022 (11, 0.839*)	0.140 $\pm$ 0.013 (22, 0.966*)	0.439 $\pm$ 0.059 (19, 0.940*)	0.417 $\pm$ 0.048 (17, 0.962*)	0.151 $\pm$ 0.032 (11, 0.865*)	0.192 $\pm$ 0.026 (11, 0.971*)
MA5P	0.171 $\pm$ 0.046 (9, 0.964*)	0.146 $\pm$ 0.025 (10, 0.961*)	0.424 $\pm$ 0.075 (10, 0.963*)	0.396 $\pm$ 0.059 (8, 0.984*)	0.180 $\pm$ 0.031 (6, 0.944*)	0.150 $\pm$ 0.042 (11, 0.930*)
MA6P	0.080 $\pm$ 0.027 (8, 0.657*)	0.118 $\pm$ 0.072 (4, 0.961*)	0.501 $\pm$ 0.059 (9, 0.987*)	nd	0.128 $\pm$ 0.050 (12, 0.815*)	nd
MA7P	0.125 $\pm$ 0.126 (6, 0.494 ns)	0.146 $\pm$ 0.035 (6, 0.972*)	0.472 $\pm$ 0.069 (9, 0.979*)	nd	0.157 $\pm$ 0.031 (9, 0.954*)	nd
Portofino (Italy)						
PO1UP	0.188 $\pm$ 0.031 (15, 0.930*)	0.180 $\pm$ 0.022 (18, 0.953*)	0.624 $\pm$ 0.175 (10, 0.895*)	0.646 $\pm$ 0.097 (10, 0.968*)	0.246 $\pm$ 0.044 (11, 0.946*)	0.232 $\pm$ 0.063 (9, 0.931*)
PO2UP	0.157 $\pm$ 0.021 (20, 0.932*)	0.199 $\pm$ 0.027 (19, 0.936*)	0.635 $\pm$ 0.121 (10, 0.949*)	0.495 $\pm$ 0.112 (16, 0.834*)	0.249 $\pm$ 0.052 (12, 0.929*)	0.210 $\pm$ 0.038 (11, 0.952*)
PO3UP	0.180 $\pm$ 0.034 (11, 0.943*)	0.179 $\pm$ 0.025 (21, 0.930*)	1.010 $\pm$ 0.364 (8, 0.937*)	0.477 $\pm$ 0.184 (9, 0.844*)	0.225 $\pm$ 0.048 (7, 0.967*)	0.196 $\pm$ 0.069 (11, 0.823*)
PO4UP	0.232 $\pm$ 0.093 (6, 0.924*)	0.188 $\pm$ 0.015 (19, 0.976*)	0.949 $\pm$ 0.229 (11, 0.958*)	0.379 $\pm$ 0.039 (15, 0.972*)	0.363 $\pm$ 0.042 (4, 0.999*)	0.208 $\pm$ 0.037 (12, 0.949*)
Elba Island (Italy)						
EL1UP	0.219 $\pm$ 0.038 (15, 0.923*)	0.206 $\pm$ 0.024 (12, 0.973*)	0.459 $\pm$ 0.078 (15, 0.932*)	0.471 $\pm$ 0.070 (13, 0.963*)	0.312 $\pm$ 0.061 (11, 0.936*)	0.168 $\pm$ 0.031 (8, 0.968*)
EL2UP	0.306 $\pm$ 0.079 (12, 0.897*)	0.193 $\pm$ 0.022 (25, 0.933*)	0.549 $\pm$ 0.082 (21, 0.936*)	0.450 $\pm$ 0.043 (18, 0.973*)	0.295 $\pm$ 0.045 (13, 0.955*)	0.186 $\pm$ 0.042 (20, 0.847*)
EL3UP	0.186 $\pm$ 0.054 (13, 0.856*)	0.155 $\pm$ 0.019 (18, 0.950*)	0.486 $\pm$ 0.089 (13, 0.945*)	0.427 $\pm$ 0.066 (16, 0.943*)	0.266 $\pm$ 0.048 (12, 0.940*)	0.149 $\pm$ 0.034 (13, 0.897*)
Means (/species/years)	0.162	0.155	0.617	0.509	0.211	0.192
Means (/species)	0.160		0.567		0.202	

*, $P < 0.05$; ns, $P > 0.05$; nd, no data.