On the dramatic increase of *Ditrupa arietina* O.F. Müller (Annelida: Polychaeta) along both the French and the Spanish Catalan Coasts

A. Grémare[a], R. Sardá[b], L. Medernach[a], E. Jordana[a], S. Pinedo[b], J. M. Amourouxa[b], D. Martin[b], C. Nozais[a] and F. Charles[a]

[a] *Observatoire Océanologique de Banyuls, Université Pierre et Marie Curie, UMR CNRS no7621, BP44, F66651 Banyuls-sur-mer cedex, France*

[b] *Centre d'Estudis Avancats de Blanes, CSIC, Camí de Santa Bàrbara s/n, 17300 Blanes, Girona, Spain*

Abstract. The distribution and population structure of the serpulid polychaete *Ditrupa arietina* were assessed along the section of the Mediterranean coast between Barcelona and Montpellier. The study combined: (1) the analysis of the existing historical data referring to the period before the 1970s; (2) the results of impact assessment surveys carried out in the late 1980s and the 1990s; and (3) the results of two surveys carried out in the Bay of Blanes and along the coast between Cape Cerbère and Port-la-Nouvelle during 1996. The results of the surveys carried out in the 1990s show the occurrence of high densities (i.e. >1000 ind m^{-2}) of *Ditrupa arietina* at all the sites sampled. These results can be compared with the few reports of this species before 1970, leading to the conclusion that *D. arietina* has recently increased all along the Catalan coast. *Ditrupa arietina* is preferentially found between 20 and 30 m depth, which mostly corresponds to well-sorted fine sands and muddy sands. Both the results of population monitoring and the heterogeneity of population structure at small spatial scale show that the dynamics of this species is unstable. The observed distribution pattern is therefore interpreted as resulting from a response to both wide-scale environmental parameters (accounting for the dramatic increase of the species at a wide geographical scale), and to local environmental factors (accounting for small-scale heterogeneity in population structure). Analysis of the relationship between sedimentary data and densities of *D. arietina* suggests that this species is highly sensitive to the presence of fine sediments. However, because of the regional importance of the phenomenon, it is concluded that the dramatic increase of *D. arietina* along both the Spanish and the French Catalan coast does not result from sediment instability.

Keywords: *Ditrupa arietina*; serpulid; polychaete; spatial distribution; Gulf of Lions

Introduction

The benthos of the Catalan coast was described by Guille (1971*a*) off France and by Desbruyères *et al*. (1973) off Spain some 25 years ago. The results of these surveys revealed high similarities between the macrofauna associated with these two sections of coast. The recent long-term comparison of the macrobenthos between the 1960s and the 1990s carried out within the soft bottoms of the Bay of Banyuls-sur-mer revealed major changes in the species composition of the three shallowest assemblages, namely: the *Spisula subtruncata* community (well-sorted fine sands), the *Nephtys hombergii* community (muddy sands) and the *Scoloplos armiger* community (sandy muds) (Grémare *et al*., in press). In sandy bottoms, the most important change was linked to the dramatic increase of *Ditrupa arietina* (O.F. Müller), a serpulid polychaete with a calcareous tusk-shaped tube, which was initially absent but can now reach densities up to 3000 ind m^{-2} (Guille, 1971*a*; Grémare *et al*., in press).

In spite of its magnitude, however, the exact significance of this phenomenon remains unclear. The first report of *D. arietina* in the Bay of Banyuls-sur-mer was made by Pruvot (1895) who found this worm within a thin band of coarse sand (20–25 m deep), which disappeared in 1883 following a strong storm. Forty years ago, *D. arietina* was considered by Pérès and Picard (1957) as primarily associated to instable soft substrates. It was thus tempting to attribute its increase to the development of a transient assemblage. However, this hypothesis was not supported by the absence of the other species indicative of sediment instability in the samples collected both within the *S. subtruncata* and the *N. hombergii* communities during 1994 (Grémare *et al*., unpubl.). The assemblages associated with sediment instability are restricted both in time and space. Pérès and Picard (1975) mentioned that their dynamics were so fast that sometimes they 'disappear even before being completely established', whereas they were reported by Picard (1965) as being restricted to small areas (i.e. several submarine canyons located in the Gulf of Marseille). Information on the spatial distribution and the dynamics of *D. arietina* could thus contribute to understanding the changes currently observed within the sandy bottoms of the Bay of Banyuls-sur-mer.

The aims of the present study were to synthesize the results of several already existing studies (i.e. historical data and recent environmental impact assessments) and surveys specifically designed to assess the distribution, population structure and some elements of the dynamics of *D. arietina* along both the French and the Spanish Catalan coasts.

Materials and methods

The section of the Mediterranean coast considered during the present study is between Barcelona (Spain) and Palavas-les-Flots (France) (Figure 1). The information gathered corresponds to: (1) the spatial distribution of *D. arietina* (including historical data, original surveys, and several impact assessment studies carried out between 1989 and 1996); and (2) population monitoring.

Spatial distribution

Historical data. On the French Catalan coast, the works of reference for the annelid fauna of the Pyrénées-Orientales are Laubier and Paris (1962), and the initial description of the benthic fauna associated to infralittoral soft substrates carried out by Guille (1971*a*). On the Spanish Catalan coast the main sources of historical data are the work of Desbruyères *et al*. (1973) and the compilation made by Ariño (1987).

Present state. The present distribution of *D. arietina* was assessed through both environmental impact assessment (Palavas-les-Flots, Gruissan, Portbou, Palamós, Maresme) and original (French sandy coast, Banyuls-sur-mer, French rocky coast, Blanes) surveys, based on sampling of 406 stations at nine different sites. Samples were collected using Van Veen grabs. They were sieved and preserved in formalin buffered with seawater. In the laboratory, live specimens of *D. arietina* were sorted and counted. During most of the surveys, tubes were then used for biometrical measurements. Major axis lengths or aperture diameters were measured using automated systems and were then converted into flesh dry weights according to Medernach (1996) or Sardá (unpubl.). At some sites, additional samples of sediment were taken and used for granulometrical analysis, carried out using either a sieve column (1000, 800, 630, 500, 315, 250, 160, 125, 100, 80, 63 and 40 ìm mesh) or a LS particle size counter (Department of Geology of the University of Barcelona). The main characteristics of the methodology used during the different surveys are summarized in Table 1. The effect of depth on both density and biomass per unit of area was assessed by using Kruskal-Wallis ANOVAs based on samples pooled by depth range.

Population monitoring

The density, biomass per unit area and the average individual biomass of *D. arietina* were monitored between June 1994 and 1996 at an 18 m station located within the Bay of Banyuls-sur-mer. During this period, three 0.1 m2 replicated samples were collected by SCUBA divers every other week. The processing procedure was identical to the one used during the survey carried out to assess the spatial distribution of *D. arietina* within the Bay of Banyuls-sur-mer.

The density, biomass per unit area and the average individual biomass of *D. arietina* were monitored between March 1992 and October 1993 at a 15 m deep station located within the Bay of Blanes (Pinedo *et al*., 1996). The sampling periodicity (fortnightly to bimonthly) varied according to years and seasons. All the samples (two replicates) were collected using a 0.06 m2 Van Veen grab. They were then sieved on a 0.5 mm mesh and processed as described in the presentation of the Blanes survey regarding the spatial distribution of *D. arietina*.

Results

Spatial distribution

Historical data. The only references to the presence of *D. arietina* along the section of coast considered during the present study are the works of Pruvot (1895) and Laubier and Paris (1962) for the Bay of Banyuls-sur-mer, and the work of Desbruyères *et al*. (1973) for the Bay of Rosas (Figure 1). According to Laubier and Paris (1962) *D. arietina* was preferentially associated with the *Branchiostoma lanceolatum* coarse sand community, whereas Desbruyères *et al*. (1973) reported it as an associated species (ranked after 10 in the order of dominant species) within the *N. hombergii* community. Quantitative information on the density and biomass of *D. arietina* at these two sites were not available, however, in the Bay of Banyuls-sur-mer during the 1960s, this species was considered as rare by Laubier (pers. comm.).

Present state. Ditrupa arietina was present at all the sites sampled by the authors since 1989 (Table 2). Maximal densities were high for all sites ranging from 645 (French rocky coast) to 11 086 ind m^{-2} (Palamó s), with *Ditrupa arietina* accounting for as much as 79% of total macrofauna (Gruissan). Maximal biomass per unit area ranged from 1238 (French Rocky Coast) to 7196 mg flesh dry wt. m^{-2} (Banyuls-sur-mer). Here again, *D. arietina* represented as much as 79% of total macrofaunal biomass (Gruissan).

When pooling the results of all surveys, *D. arietina* was found between 5 and 40 m depth. However, densities were significantly affected by depth at most sites (Table 2). Figure 2 shows two typical examples of the distribution of *D. arietina*. Both in Banyuls-sur-mer and Blanes, *D. arietina* was absent from the shallowest stations (i.e. down to 9 and 15 m, respectively). Densities were maximal between 20 and 30 m depth. In Banyuls-sur-mer, the distribution was then tightly limited by the 30 m isobath, which corresponds to the appearance of muddy bottoms. This pattern was less marked in Blanes, possibly due to the impact of the Tordera River in the south of the Bay. Proportions of stations with *D. arietina*, average densities and average biomass per unit of area are given in Table 2.

However, caution should be taken when comparing these parameters among stations because differences may partly result from heterogeneity either in the range of sampled depths or in the sampling effort with depth. The relationship between granulometry and density is presented Figure 3 for the Banyuls-sur-mer (a), the Blanes (b), the Portbou (c) and the Palamós (d) surveys. Both in Banyuls-sur-mer and Palamós, *D. arietina* appeared very sensitive to increasing concentrations of fines, and rather tolerant for the presence of coarse and heterogeneous sediments. In the Bay of Blanes, *D. arietina* was often absent from the stations presenting the coarsest and the most heterogeneous sediments. The relationship obtained in the Portbou cove was difficult to interpret because most of the sampled stations presented similar granulometries.

The ranges of average individual biomass recorded at different stations of a given site are given in Table 2. Except for the French rocky coast where there were only two stations with *D. arietina*, the variability among stations was always high, indicating heterogeneity in population structure among stations. This result was further supported by the comparison of size frequency histograms associated with several stations of the Bay of Banyuls-sur-mer, which were all sampled during January 1996 (Figure 4). Size frequency histograms were either unimodal (and composed of small or large worms) or bimodal depending on stations. The unimodal histograms exclusively composed of large individuals seemed preferentially associated to the stations located between 10 and 20 m depth explaining the generally lower densities compared to those located between 20 and 30 m depth (see Figure 2).

Population monitoring

Banyuls-sur-mer. The monitoring of *D. arietina* in the Bay of Banyuls-sur-mer began following a period of high recruitment. Density was maximal during June 1994 (20 000 ind

m^{-2}) and then continuously dropped to a value of 100 ind m^{-2} during May 1996 (Figure 5). Biomass per unit area increased from 3.92 to 13.69 g flesh dry wt. m^{-2} between June 1994 and July 1995, and then decreased to represent only 0.04 g flesh dry wt. m^{-2} by the end of May 1996. Mean individual dry weight was low (i.e. about 0.2 mg flesh dry wt. ind^{-1}) during the beginning of the period under study and then increased to 2.2 mg flesh dry wt. ind^{-1} (June 1995) before remaining fairly constant during the second year.

Blanes. Density (4133 ind m^{-2}) and biomass per unit area (0.683 g flesh dry wt. m^{-2}) were maximal during May 1992 [Figure 5(b)] comprising mainly small newly recruited worms (average individual of 0.02 mg flesh dry wt.). During July and August, the presence of *D. arietina* became almost negligible. This was probably due to the location of the station just in front of the mouth of the Tordera River. Indeed, extremely high rainfalls (317 l m^{-2}, Cebrian *et al.*, 1996) took place during June and July 1992, and river runoff was consequently very high washing out the bed platform sediment of the station (Sardá, pers. obs.). After the recovery of the population, density diminished steadily to 0 ind m^{-2} between January and March 1993. By that time, individual dry weight had increased reaching 1.8 mg during the end of December 1992. A second peak in density (775 ind m^{-2}) occurred during May 1993. It was mainly composed of small, newly recruited individuals (average individual dry weight of 0.01 mg flesh dry wt.). Densities then dropped to 0 ind. m^{-2} by the middle of June 1993.

Discussion

The geographical range of the increase of Ditrupa arietina

Ditrupa arietina has a boreal to subtropical distribution and has been reported in the eastern Atlantic from Iceland to Senegal and in the Mediterranean (Fauvel & Rullier, 1959; Picard, 1965; Glémarec, 1973; Montbet, 1978; Gambi & Giangrande, 1985; Ten Hove & Smith, 1990; Gambi & Jerace, 1997). However, the occurrence of high densities such as those found during the present study has not been previously reported. In the Mediterranean, the highest reported percentage of dominance was only 10% (Gambi & Giangrande, 1985), which can be compared with the 79% that we found during the Gruissan survey.

High densities of *D. arietina* within the infralittoral soft bottoms of the Gulf of Lions were first recorded in Banyuls-sur-mer during the summer of 1994 (Grémare *et al.*, in press).

They have also been observed during all the recent surveys of the present study. Maximal densities at each site were always greater than 1000 ind m^{-2} and reached values up to 11 000 ind m^{-2} (Palamós). These figures are exceptionally high for the Mediterranean sea, which is largely oligotrophic and where macrobenthos abundance is usually low (Guille, 1971*a*). This present state is to be compared with the two reports as an accessory or even an accidental species regarding the Bay of Palamó s and the Bay of Banyuls-sur-mer before 1970. In spite of evident differences between sampling efforts among periods, the magnitude of density changes (i.e. only a few individuals per metre square before and during the 1970s *vs* several thousand individuals per square meter during the 1990s) shows that the importance of *D. arietina* as a component of the coastal benthic macrofauna in this portion of the Gulf of Lions has drastically increased. While high densities were found at all recently sampled sites, the presence of *D. arietina* was not restricted to solely those sites, since high densities (up to 2730 ind m^{-2}) have also been found: (1) along the section of the Spanish Catalan coast south from Barcelona (Sardá, 1986); and (2) in front of the Sète Harbour during an environmental impact assessment study carried out by the Institut d'Aménagement Régional de l'Environnement during May 1993 (Dutrieux, pers. comm.). This suggests that the increase of *D. arietina* occurred all along the Spanish and the French Catalan coasts. This process is at least of regional importance and it should be pointed out that its whole geographical range is not known yet.

The constant presence of this species at all of the sites sampled during the present study could also suggest that this phenomenon is stable and well synchronized over the whole studied area. The analysis of population dynamics and population structure, however, shows that this is not the case.

Temporal stability and spatial heterogeneity

The results of the two monitoring surveys suggest that the population dynamics of *D. arietina* is not stable. In Banyuls-sur-mer, density steadily declined between May 1992 and May 1994. This pattern is thus consistent with the fact that the dynamics within the Bay mostly resulted from a strong recruitment during 1994, followed by a low (or even a total absence of) recruitment during both 1995 and 1996. This instability was even more pronounced in the Bay of Blanes where, probably due to exceptional precipitation, the population crashed between the two recruitments observed during 1992 and 1993.

Such a lack of stability in population dynamics is further supported by the analysis of population structure at small spatial scale. The background for this analysis is provided by the main characteristics of the life history and the population dynamics of *D. arietina* as studied at a selected site (Medernach, 1996; Medernach & Grémare, in press). In the Bay of Blanes, sharp increases in densities always took place during spring, which strongly suggests that *D. arietina* reproduces once a year. This conclusion is supported by the direct observations of newly recruited individuals in the sediment-traps moored above the Banyuls-sur-mer monitoring station between 1992 and 1996 (Medernach, 1996). This allows for the interpretation of size-frequency histograms in terms of cohorts. Medernach and Grémare (in press) followed size frequency histograms based on samples collected every other week at the Banyuls-sur-mer monitoring station between June 1994 and June 1996. These authors concluded to the existence of a yearly reproduction with a 2-year lifespan. The population structures recorded during the present study at different sites along both the Spanish and the French coasts were very heterogeneous even at small spatial scales.

Both unimodal and bimodal size frequency histograms were, for example, simultaneously present samples from the Bay of Banyuls-sur-mer and along the French sandy coast. This pattern is consistent with the existence of a 2-year lifespan with recruitment failures for some given years. It shows that at small spatial scale, the population dynamics of this species is highly dependent on local environmental factors. Such instability has important consequences for the interpretation of the authors' distribution data. As the different surveys composing the present study took place between 1989 and 1996, and because of the existence of a 2-year lifespan, the occurrence of high densities of *D. arietina* at all the stations considered during the present study does not necessarily imply that high densities of *D. arietina* were simultaneously present at all these sites. These results may also reflect the occurrence of several patches, each presenting its own dynamics in conjunction with environmental factors.

Factors controlling the distribution

The exact limits of the bathymetric distribution of *D. arietina* are difficult to determine given the occurrence of empty tubes (Zibrowius, 1968; Ten Hove & Smith, 1990; Ben-Eliahu & Fiege, 1996). According to the literature, *D. arietina* is present at depths ranging from 0 to 150m (Bellan, 1959; Fauvel & Rullier, 1959; San Martín, 1984; Gambi & Giangrande, 1985; Ten Hove & Smith, 1990) or even 200 m (Picard, 1965; Zibrowius, 1968; Glémarec, 1969, 1973; Ben-Eliahu & Fiege, 1996). However, those studies dealt with low density populations.

The authors' results clearly show that the distribution of *D. arietina* is affected by depth. *Ditrupa arietina* was rarely found at stations less than 10 m in depth, whereas, in most cases the distribution of this species was limited by the 30 m isobath (as shown, for example, the results of the survey regarding the Bay of Banyuls-sur-mer). Except for the Palavas-les-Flots survey (maximal density at a 35.2 m deep station), maximal densities were always found at stations between 20 and 30 m depth. This pattern is consistent with observations carried out in the Gulf of Policastro (Salerno, Italy) (Gambi & Giangrande, 1985; Gambi & Jerace, 1997). The deeper distribution of *D. arietina* off Palavas-les-Flots can also be related to observations carried out in the Messina area (Gambi & Jerace, 1997).

Sediment granulometry correlates tightly with depth. The high densities of *D. arietina* reported during the present study were thus found both for well-sorted fine sands (*S. subtruncata* community) and for muddy sands (*N. hombergii* community). The relationship linking sediment granulometry and observed density of *D. arietina* within the Bay of Banyuls-sur-mer and the area of Palamó s shows that this species can be found at high densities within a wide variety of coarse sediments, whereas the transition of high densities to the absence of *D. arietina* is very steep in the presence of increasing proportions of fines. On the other hand, the same analysis carried out in the Bay of Blanes allows further the assessment of the limits of tolerance of *D. arietina* to coarse and heterogeneous substrates. These results are consistent with those of Glémarec (1969) who considered that *D. arietina* was characteristic of the presence of a coarse component in sandy bottoms. This may also explain the presence of this species in gravels (Laubier & Paris, 1962; Picard, 1965).

There are several lines of evidence suggesting that changes in abundance of adult populations of *D. arietina* are regulated by post-settlement processes. First, significant settlement was observed in the sediment traps moored in the Bay of Banyuls-sur-mer during the springs of 1994 and 1995 whereas no effective recruitment took place on the bottom during these 2 years (Medernach, 1996). Second, a very high settlement was recorded (i.e. up to 20 000 ind m^{-2}) in the Bay of Banyuls-sur-mer during the spring of 1997. Very high mortality during early stages, resulted in no effective recruitment (Grémare, pers. obs.). Changes in adult density thus do not correlate with either larval supply or settlement rates but are rather controlled by post-settlement processes. How could this be related to sediment granulometry? On present evidence the dependence of *D. arietina* on coarse substrates appears to be linked to the presence of a mucous tube in young postmetamorphic juveniles, since the tube is anchored onto sediment grains. According to this hypothesis, too many fines may preclude efficient anchoring from taking place and thus contribute to reduce recruitment.

More generally, the possible causes driving recent faunal changes (including the increase of *D. arientina*) in the Gulf of Lions have been discussed in detail by Grémare *et al*., in press. Based on: (1) the direct comparison of sediment granulometry between the 1960s and the 1990s; (2) the granulometrical affinities of the species having featured the greatest changes in density during this last quarter of century; and (3) the frequency of easterly storms, these authors concluded to the effect of a modification of sediment granulometry (i.e. diminution of fines). The results of the present study support these observations in the sense that they confirm the dependence of *D. arietina* upon coarse substrates. Moreover, the authors results show that the increase of *D. arietina* occurred at least over a regional scale, which precludes the effect of sediment instability, and is consistent with the action of easterly storms on sediment granulometry.

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TABLE 1. Main characteristics of the different surveys carried out to assess the spatial distribution of *Ditrupa arietina* along the Catalan coast

Location	Date	*N*	S (m^2)	R	RD (m)	MS (mm)	Biometry	Granulometry	Environmental issue
Palavas-les-Flôts	Spring 1991 and February 1993	63	0·1	1 or 2	2–46·5	1	—	—	Sludge output
Gruissan	April 1995	10	0·1	—	23·5–26·5	1	—	—	Waste treatment plant
French sandy coast	January 1996	52	0·1	2	10–40	1	MA	—	Distribution of *D. arietina*
Banyuls-sur-mer	January 1996	78	0·1	2	4–32	1	MA	SI	Distribution of *D. arietina*
French rocky coast	January 1996	34	0·1	2	7–44	1	MA	—	Distribution of *D. arietina*
Portbou	November 1995	22	0·06	—	7–20	1	A	SI	Harbour development
Palamós	June 1995	23	0·06	—	5–30	0·5	A	SI	Sludge output
Blanes	July 1996	37	0·06	—	8–30	1	A	PC	Distribution of *D. arietina*
Marèsme	May 1989	87	0·12	—	5–25	1	—	—	Beach nourishment

N, number of sampled stations; *S*, sampled surface; R, number of replicates per station; RD, range of sampled depths; MS, mesh size; Biometry (A, aperture; MA, major axis); Granulometry (PC, particle counter; SI, sieves).

TABLE 2. Main characteristics of the populations of *Ditrupa arietina* at the different sampled sites.

Location	Pres (%)	MDens (ind m^{-2})	ADens (ind m^{-2})	RDepth (m)	MBiom (mg dry wt. m^{-2})	ABiom (mg dry wt. m^{-2})	RIndBiom (mg dry wt. ind^{-1})	Effect of depth	
								Dens	Biom
Palavas-les-Flots	6	6040	125	15–40	1588	—	—	—	—
Gruissan	40	3327	664	24–26·5	1177	—	—	No	—
French sandy coast	38	2680	332	10–30	2844	408	0·47–2·95	Yes	Yes
Banyuls-sur-mer	60	3550	491	9–30	7196	990	0·47–3·37	Yes	Yes
French rocky coast	6	645	33	26–27	1238	61	1·80–1·92	Yes	Yes
Portbou	95	5901	597	6–20	4831	536	0·35–1·57	Yes	Yes
Palamós	61	11 086	1181	15–30	6415	474	0·07–0·76	Yes	Yes
Blanes	41	2717	206	15–33	3621	241	0·18–2·42	Yes	Yes
Marèsme	42	1584	56	5–25	—	—	—	—	—

ABiom, average biomass per unit area; ADens, average density per unit area; Biom, biomass per unit area; Dens, density; MBiom, maximal biomass per unit area; MDens, maximal density per unit area; Pres, proportion of the sampled stations with *Ditrupa arietina*; RDepth, range of depth; RIndBiom, range of individual biomass.

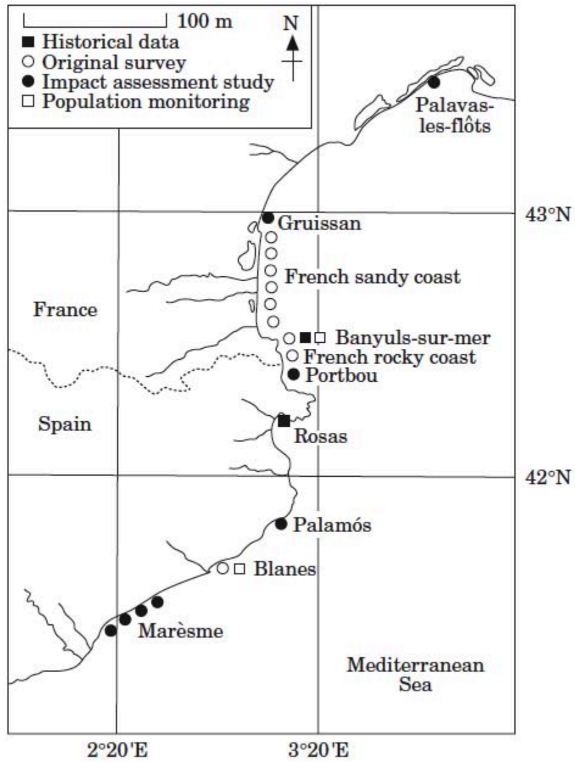

FIGURE 1. Map of the study area showing the exact location of the impact assessment studies, the historical, the original and the monitoring surveys.

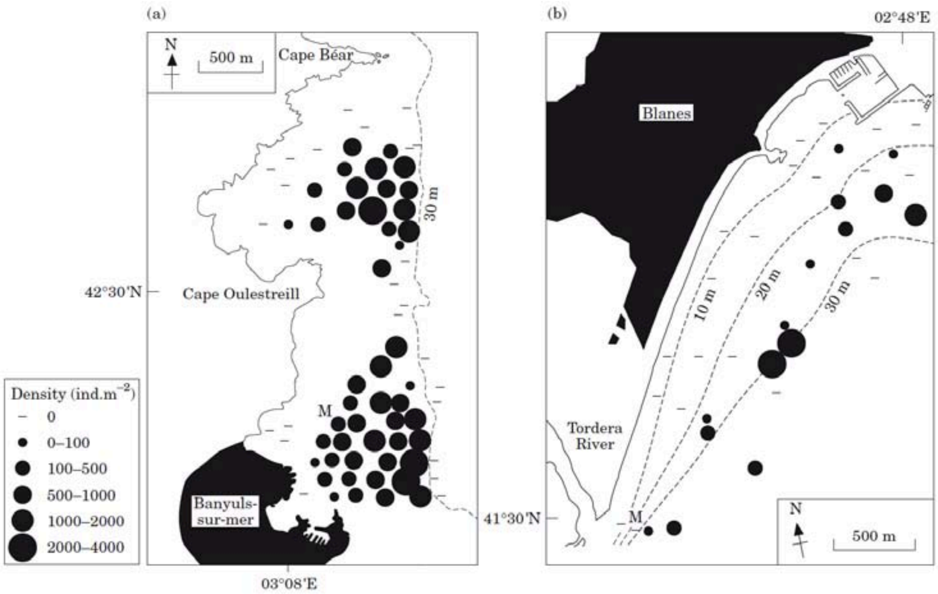

FIGURE 2. Map showing the density (ind m^{-2}) of *Ditrupa arietina* within (a) the Bay of Banyuls-sur-mer (January 1996) and (b) the Bay of Blanes (July 1996).

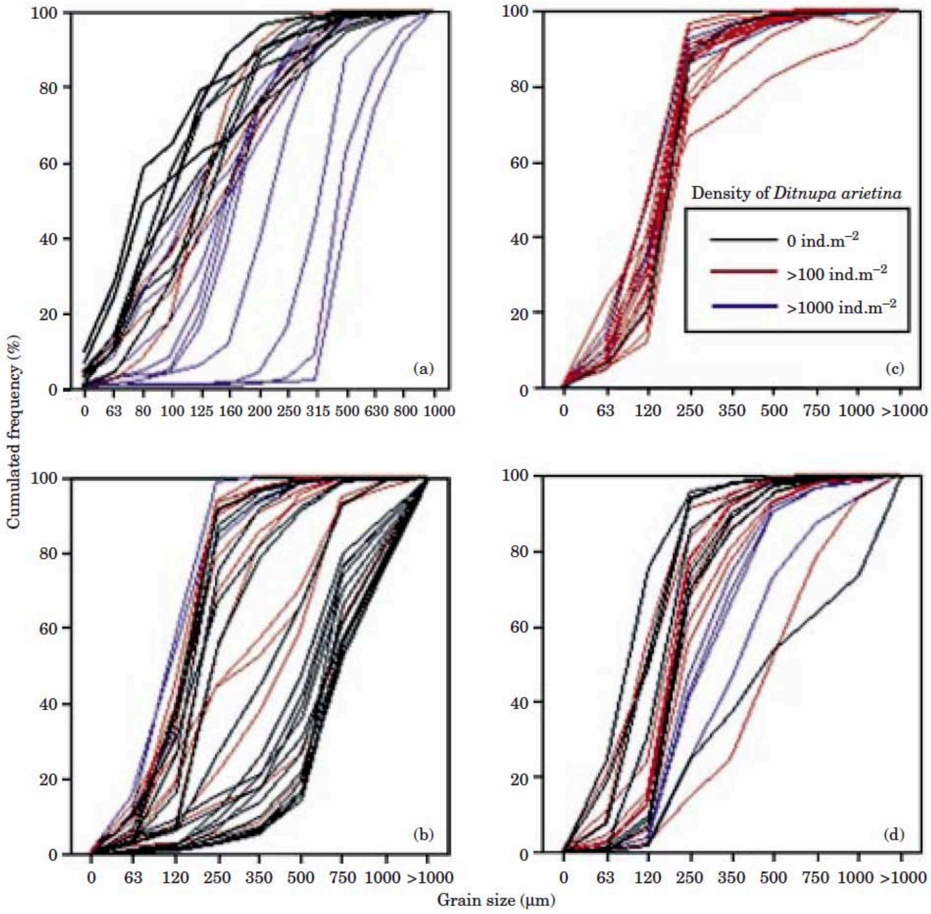

FIGURE 3. Relationship linking the sediment granulometry and the density of *Ditrupa arietina*. (a) Bay of Banyuls-sur-mer; (b) Bay of Blanes; (c) Portbou cove; (d) Palamós.

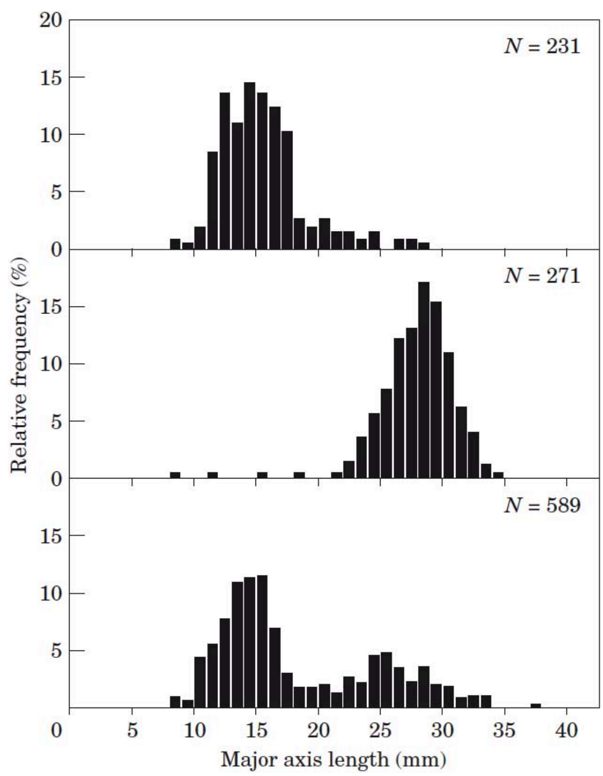

FIGURE 4. *Ditrupa arietina*. Examples of size frequency histograms observed at three stations located within the Bay of Banyuls-sur-mer and sampled during January 1996.

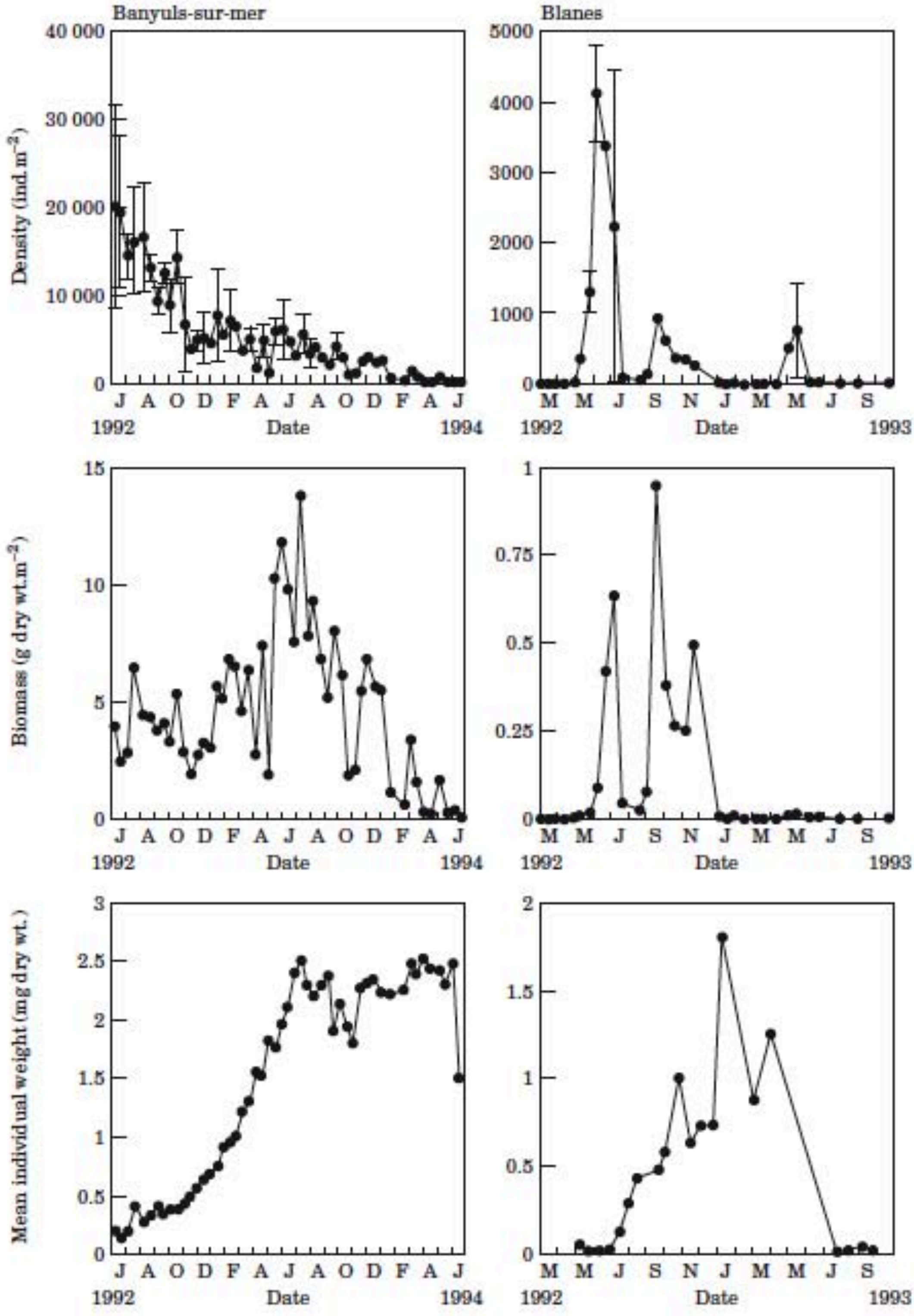

FIGURE 5. Temporal changes in density, biomass per unit of area and average individual dry weight during the monitoring surveys carried out within the Bays of Banyuls-sur-mer (1992–1994) (left hand panels) and Blanes (1992–1993) (right hand panels).