FORAMINIFERAL COLONIZATION ON ARTIFICIAL SEAGRASS LEAVES

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ABSTRACT

Colonization of seagrass leaves was studied using artificial ribbon-like substrates. The study was carried out in a seagrass (*Posidonia oceanica* (L.) Delile) meadow off the Medes Islands (NW Mediterranean). Artificial leaves of different colors and textures were immersed at two depths (5 and 13 m), and retrieved after 3 and 6 months; epiphytic foraminifera were identified and counted, and the results were compared with those obtained from natural leaves. Although some differences were found in the colonization of the various types of artificial leaf (e.g., smooth, green leaves with float bladder had the highest number of individuals and species) ANOVA and cluster analyses revealed that the type of substrate did not significantly affect the colonization by foraminifera; the main sources of variability were mainly seasonality and, to a minor extent, water depth. Thus, the dominant species were the same in both natural and artificial leaves. The calcareous perforated shells and the trochospiral morphotype were the most abundant, and the dominant biological types were groups B and C, i.e., temporarily or permanently mobile species.

INTRODUCTION

Foraminifera can be found in most marine habitats, both planktonic and benthic, and, within the benthos, they live in a large variety of substrata or as epibionts. Seagrasses are known to host rich and diverse animal assemblages, playing an essential role in sustaining a very high biodiversity in shallow marine areas (Larkum and Den Hartog, 1989). Although foraminifera are among the most abundant organisms inhabiting such seagrass meadows, little is known about this group compared to others (e.g., algae, mollusks, fishes). Several works have investigated the specific composition of the foraminiferan assemblage in seagrass meadows (see, Boltovskoy, 1965; Blanc-Vernet, 1969; Buzas and Severin, 1993; Langer, 1993; Fujita and Hallock, 1999); however, ecological aspects remain poorly understood. Among them, one which seems crucial is the interaction between the foraminifera and the organic substrate they colonize, i.e., the seagrass leaves. Seagrass leaves are substrates with specific features, including physical instability (movement by waves and currents), relatively short life-span (between a few weeks and several months, depending on the species) and basal growth (inducing a leaf age gradient from young at the base to old at the apex). Moreover, the organic nature of this substrate results in potential biological interactions with the epibiota. Hence, the epifaunal community,

and especially the foraminiferan assemblage, should reflect complex interactions between a (potentially) selective colonization and losses caused by water movement or fragmentation of the leaf.

To examine the colonization process and the controls exerted by the substrate properties on the foraminiferan assemblage, we performed an experiment using artificial substrates. The use of artificial substrates is widespread in marine biology (e.g., Niell, 1979; Sebens, 1985) and some features of colonization by benthic foraminifera have been assessed through this approach (Buzas, 1993; Kitazato, 1996; Schaefer and others, 1996). However, the use of artificial seagrass leaves to elucidate the dynamics of epiphytic communities is far less common (e.g., Inglis, 1994; Liu & Loneragan, 1997), and has never, as far as we are aware, been used in the study of foraminiferan communities.

The aim of the present work is to study some features of foraminiferan populations that live as epiphytes on seagrass leaves, their dependence on the properties of the substrate, and their variability with depth. To do so, we have performed an experimental study based on the colonization by foraminifera of different artificial substrates simulating leaves of the Mediterranean seagrass *Posidonia oceanica* (L.) Delile, and the results have been compared to those obtained on natural leaves. This exploratory attempt should be considered as a preliminary approach to better understand the main sources of variability, and as a pilot study aimed to help in the design of future works.

METHODOLOGY

STUDY AREA

The study was conducted in the Medes Islands Natural Reserve, at 42° N and 3°13′E, (NE Spain, Western Mediterranean, Fig. 1), a relatively small archipelago where a *P. oceanica* meadow occurs, from 4–5 to 14–20 m (bathymetric range), in its southwestern portion. The sediment ranges from fine to coarse sand and has a relatively high organic content (about 4%, see López, 1993). Water temperature varies seasonally between 12.5° and 23 °C on average, with only minor variation within the bathymetric range of the seagrass distribution.

The seagrass meadow is protected by the islands from strong N and NW winds; however, the area is unprotected from eastern storms, relatively rare between January and June, but inducing heavy swells in the meadow area, and totally open to SE-S and SW winds, which are less strong but more frequent. More details about this seagrass meadow can be found in Alcoverro (1995), and references cited therein.

EXPERIMENTAL DESIGN

Shoots of artificial seagrass leaves were prepared, in an attempt to reproduce the shape of *P. oceanica* shoots at this time of the year (i.e., six leaves 35 cm long and 1.5 cm

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TABLE 1. Characteristics of the samples analyzed. Artificial shoots: GSN (green smooth without float); GSF (green smooth with float); GRN (green rough without float) and BRN (brown rough without float). Natural leaves (N).

Acronym	Characteristics				
	Color	Texture	Float blader	Depth	Date of colletion
Artificial leaves					
GSN5/3	green	smooth	no	5 m	March
GSN13/3	green	smooth	no	13 m	March
GSN5/6	green	smooth	no	5 m	June
GSN13/6	green	smooth	no	13 m	June
GSF13/3	green	smooth	yes	13 m	March
GSF13/6	green	smooth	yes	13 m	June
GSF5/6	green	smooth	yes	5 m	June
GRN13/3	green	rough	no	13 m	March
GRN13/6	green	rough	no	13 m	June
BRN5/6	brown	rough	no	5 m	June
BRN13/6	brown	rough	no	13 m	June
Natural leaves					
N5/3				5 m	March
N5/6				5 m	June
N13/3				13 m	March
N13/6				13 m	June

wide per shoot). The artificial leaves were made using plastic ribbons. To explore the response of foraminiferans to some of the substrate features, different kinds of leaf bundles (thereinafter "shoots") were prepared: rough and smooth, green and brown, floating (floats were placed on the rear part of the "leaf") and non-floating (i.e., bending leaves). In order to limit the losses of the artificial substrates, each shoot was attached individually to the sediment by means of thick wire "roots" 20 cm long.

Twenty shoots of each one of the shoot types (green smooth without float, green smooth with float, green rough without float and brown rough without float, see Table 1) were placed at random among the natural seagrass shoots, at two depths: 5 and 13 meters, resulting in a total of 160 initial experimental units. The experimental shoots were deployed in January; the first group (ten shoots of each type) was retrieved after three months (in March) and the second group (ten shoots of each type) was retrieved after six months (in June). However, retrieval was only partially successful, and, due to rough weather, a large number of experimental shoots were lost. Based on previous work (Ribes, 1998), data coming from samples with less than nine shoots under the same experimental conditions were discarded. Details on the kind of shoots that were finally available are given in Table 1. For the sake of comparison, at each sampling time and at each depth, ten natural shoots were also collected. All underwater operations were performed using scuba diving. To avoid losses of foraminifera, the shoots (both natural and artificial) were carefully placed in plastic bags immediately after collection (i.e., underwater, one bag per shoot type) and transported to the laboratory refrigerated.

SAMPLE PROCESSING AND DATA ANALYSIS

Once in the laboratory, the leaves were scraped and washed and the foraminifera were separated over 0.075-mm, 0.250-mm and 0.500-mm sieves, and subsequently fixed with alcohol at 75%. Only individuals stained with Rose

TABLE 2. Characteristics of the biological types.

Biological type	Features	Examples
A	-Encrusting forms. -Permanently attached to the substrate by an organic glue (De Laca and Lipps, 1972; Langer, 1992). -Usually planispiral shell. -Large aperture (marginal, intermarginal or peripheral). -Herbivorous feeding on algae, fungi and bacteriae (Lipps, 1983). -Probable average life-span 1 year.	*Planorbulina* *Acervulina* *Nubecularia* *Cyclocibicides*
B	-Temporay attached forms (Sliter, 1965; De Laca and Lipps, 1972). -Gide or swim on a pseudopodial network over the substrate (Kitazato, 1986). -Usually smaller and trochospiral shell. -Mainly feed on diatoms (Alexandar and De Laca, 1987). -Probable average life-span 2–5 months.	*Amonia* *Asterigerinata* *Cibicidella* *Cibicides* *Conorboides* *Discorbis* *Rosalina*
C	-Permanently mobile forms. -Planispiral shell with a complex structure (with a system of canals and multiple apertural openings). -Trophic motility present. -Gide or swim on a pseudopodial network over the substrate (Kitazato, 1986). -Feed on diatoms (Lee and Anderson, 1991; Reis and Hottinger, 1984); suspension feeding present (Lipps, 1983; Christiansen, 1971). -Probable average life-span 3–4 months (Myers, 1942).	*Elphidium*
D	-Permanently mobile forms -Porcelaneous or agglutinated shell. -Fusiform or planispiral shell. -Terminal aperture usually at the end of a neck. -Usually reproduction is in sediment (Frankel, 1972). -Omnivorous (Myers, 1943). -Short life-span.	*Biloculinella* *Massilina* *Miliolinella* *Peneroplis* *Quinqueloculina* *Textularia* *Triloculina* *Vertebralina*

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TABLE 3. List of species and number of specimens found on artificial leaves. Results in individuals/shoot.

Species	GRN13/3	GSF13/3	GSN13/3	GSN5/3	GSN13/6	BRN13/6	GRN13/6	GSF13/6	GSN5/6	BRN5/6	GSF5/6
Ammonia beccarii	0.63	2.75	0.75	0.25	0.18	0.09	0.00	1.36	0.00	0.00	0.36
Asterigerinata mamilla	0.25	2.00	0.75	0.13	0.00	0.00	0.09	0.55	0.09	0.00	0.09
Biloculinella fragilis	0.13	1.88	4.75	0.25	0.55	0.00	0.45	0.18	0.09	0.18	0.45
Biloculinella wiesneri	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Biloculinella sp.	0.00	0.25	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00
Bulimina elongata	0.13	0.38	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00
Bulimina sp.	0.00	0.00	0.13	0.00	0.00	0.00	0.09	0.09	0.00	0.00	0.00
Cancris auricula	0.13	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cibicides lobatulus	5.75	32.13	13.25	4.63	9.36	5.45	4.27	18.55	0.55	1.00	6.55
Cibicides pseudoungerianus	0.25	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Cibicides refulgens	0.25	2.00	2.00	0.13	1.36	0.18	0.45	1.36	0.00	0.09	0.73
Cibicidella variabilis	0.38	0.38	0.50	0.25	0.00	0.00	0.09	0.18	0.00	0.00	0.00
Cyclocibicides vermiculatus	0.13	0.38	0.00	0.00	0.00	0.09	0.09	0.00	0.00	0.00	0.00
Conorboides mediterranensis	2.63	24.00	20.50	1.75	29.91	3.73	5.09	10.09	0.64	0.36	3.91
Conorboides posidonicola	0.38	6.38	5.25	0.88	4.73	0.64	1.73	3.27	0.09	0.00	0.00
Cyclogira carinata	0.13	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
Cyclogira rugosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Cyclogira sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.09	0.00	0.00	0.00
Discorbinella bertheloti	0.75	9.88	3.63	1.13	5.91	0.73	0.64	1.45	0.09	0.00	0.55
Discorbis orbicularis	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00
Discorbis mira	0.50	1.13	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Discorbis af. orbicularis	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00
Eggerella advena	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eggerella scabra	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eggerella sp.	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elphidium advenum	0.38	0.88	0.13	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elphidium complanatum	0.50	3.50	0.13	0.00	0.00	0.09	0.00	1.00	0.00	0.00	0.27
Elphidium crispum	0.25	3.25	0.50	0.88	0.00	0.18	0.09	1.64	0.00	0.00	0.82
Elphidium macellum	13.38	83.88	131.50	21.50	2.09	0.64	2.36	8.18	0.27	0.27	2.36
Elphidium macellum aculeatum	2.25	11.25	20.38	2.75	0.55	0.18	0.09	0.73	0.00	0.00	0.36
Elphidium maioricensis	0.00	0.25	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Elphidium af. advenum	0.00	0.00	0.00	0.00	0.00	0.09	0.09	0.09	0.00	0.00	0.00
Eponides repandus	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Florilus boueanus	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Glabratella patelliformis	0.38	1.13	1.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Globigerina sp.	0.25	1.50	0.63	0.25	0.09	0.00	0.09	0.36	0.00	0.00	0.18
Globulina gibba	0.13	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Guttulina láctea	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gyroidina soldanii	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Haplophragmoides canariensis	0.00	0.13	0.13	0.00	0.00	0.00	0.09	1.00	0.00	0.00	0.27
Laevidentalina inflexa	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lagena semistriata	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Lenticulina orbicularis	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Massilina secans	0.38	0.63	0.13	0.00	0.00	0.00	0.00	0.18	0.00	0.09	0.00
Melonis barleeanum	0.00	1.25	0.50	0.25	0.00	0.09	0.00	0.27	0.00	0.00	0.18
Nonion pompilioides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Nonion sp.	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Miliolinella elongata	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00
Miliolinella labiosa	0.00	0.13	0.13	0.25	0.00	0.18	0.00	0.00	0.00	0.00	0.00
Miliolinella sidebottomi	0.00	0.00	0.00	0.00	0.27	0.00	0.55	0.18	0.00	0.00	0.64
Miliolinella af. sidebottomi	0.00	0.13	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
Nubecularia lucifuga	0.25	1.63	0.63	0.13	0.00	0.00	0.36	0.18	0.18	0.00	0.09
Nubecularia massutiniana	0.13	0.25	0.00	0.00	0.45	0.00	0.00	0.09	0.00	0.00	0.00
Planorbulina acervalis	0.75	1.00	0.00	0.50	0.00	0.00	0.18	0.09	0.00	0.00	0.00
Planorbulina mediterranensis	2.38	9.63	1.25	0.50	0.45	0.55	0.27	1.82	0.18	0.09	0.73
Quinqueloculina annectens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Quinqueloculina aspera	0.00	1.50	0.38	0.00	0.00	0.09	0.09	0.18	0.00	0.00	0.00
Quinqueloculina bradyana	0.00	0.75	0.38	0.13	0.00	0.00	0.09	0.00	0.00	0.00	0.00
Quinqueloculina berthelotiana	0.00	0.63	0.88	0.13	0.00	0.00	0.18	0.00	0.00	0.00	0.00
Quinqueloculina cliarensis	0.13	0.88	0.38	0.13	0.00	0.00	0.09	0.27	0.00	0.00	0.00
Quinqueloculina contorta	0.13	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Quinqueloculina disparilis	0.00	3.88	0.00	0.00	0.00	0.09	0.00	0.45	0.00	0.00	0.09
Quinqueloculina dubia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Quinqueloculina irregularis	0.50	0.13	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina laevigata	0.25	1.13	0.63	0.00	0.00	0.27	0.27	1.45	0.09	0.00	0.45
Quinqueloculina lamarckiana	0.00	0.00	0.13	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00
Quinqueloculina laticollis	0.25	0.75	0.00	0.00	0.00	0.00	0.00	0.73	0.00	0.00	0.36
Quinqueloculina lúcida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00
Quinqueloculina mediterranensis	0.00	0.00	0.00	0.00	0.18	0.00	0.55	0.00	0.00	0.27
Quinqueloculina partschii	0.00	0.25	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00

TABLE 3. Conbtinued.

Species	GRN13/3	GSF13/3	GSN13/3	GSN5/3	GSN13/6	BRN13/6	GRN13/6	GSF13/6	GSN5/6	BRN5/6	GSF5/6
Quinqueloculina osinclinatum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00	0.00	0.09
Quinqueloculina parvula	0.00	0.13	0.13	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.18
Quinqueloculina pulchella	0.00	0.25	0.00	0.00	0.00	0.09	0.09	0.00	0.00	0.00	0.00
Quinqueloculina quadrata	0.25	0.38	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina reticulata	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18
Quinqueloculina rugosa	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00
Quinqueloculina seminula	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.09
Quinqueloculina stelligera	0.38	3.00	1.75	0.25	0.09	0.00	0.73	0.82	0.00	0.09	0.18
Quinqueloculina undulata	0.13	0.25	0.63	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.27
Quinqueloculina ungeriana	0.25	2.13	1.88	0.25	0.18	0.55	0.18	4.36	0.09	0.00	0.45
Quinqueloculina vienensis	0.00	0.25	0.38	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina villafranca	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina vulgaris	0.63	2.50	1.50	1.88	0.27	0.64	0.09	3.27	0.00	0.00	0.18
Quinqueloculina af. agglutinans	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina af. auberiana	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
Quinqueloculina af. cliarensis	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00
Quinqueloculina af. lamarckiana	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Quinqueloculina cf. laticollis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
Quinqueloculina af. párvula	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina af. phoenicia	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina af. stelligera	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00
Quinqueloculina af. vulgaris	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quinqueloculina sp.	0.00	0.75	0.13	0.00	0.00	0.09	0.00	0.36	0.00	0.00	0.09
Rosalina globularis	0.63	3.38	1.13	0.88	0.27	0.36	0.55	1.27	0.09	0.09	0.55
Rosalina globularis semiporata	0.00	0.00	0.13	0.00	0.82	0.18	0.27	1.36	0.09	0.00	0.82
Sigmomorphina williamsoni	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Spirillina limbata	0.00	0.38	0.00	0.13	0.00	0.00	0.00	0.45	0.00	0.00	0.00
Spirillina sp.	0.00	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.09
Spiroloculina cymbium	0.00	0.25	0.13	0.00	0.00	0.00	0.18	0.09	0.00	0.00	0.00
Spiroloculina excavata	0.00	0.25	0.00	0.00	0.09	0.00	0.00	0.09	0.00	0.00	0.00
Spiroloculina scita	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Spiroloculina sp.	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Textularia agglutinans	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Textularia cunciformis	0.25	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Textularia gramen	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.09
Textularia pseudorugosa	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Textularia cf. candeiana	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Textularia sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Triloculina adriatica	0.00	0.13	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Triloculina cuneata	0.00	0.00	0.38	0.00	0.00	0.00	0.09	0.00	0.00	0.00	0.00
Triloculina marioni	0.13	0.00	0.00	0.00	0.09	0.09	0.00	1.45	0.00	0.00	0.18
Triloculina oblonga	0.13	1.00	0.50	0.00	0.09	0.00	0.00	0.36	0.00	0.00	0.00
Triloculina planciana	0.13	0.63	3.13	0.25	0.45	0.18	0.27	2.09	0.00	0.00	1.00
Triloculina plicata	0.25	0.88	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00	0.00
Triloculina rotunda	0.13	0.75	1.38	0.25	0.00	0.27	0.91	2.00	0.09	0.00	1.00
Triloculina semicostata	0.13	2.25	0.88	0.63	0.27	0.00	0.00	0.55	0.00	0.00	0.36
Triloculina tricarinata	0.00	0.13	0.25	0.00	0.00	0.09	0.00	0.09	0.00	0.00	0.00
Triloculina webbiana	1.13	1.38	5.00	0.38	0.82	0.64	2.55	1.36	0.09	0.00	0.64
Vertebralina striata	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total	40.25	238.88	232.13	43.25	59.64	17.27	24.36	78.55	2.73	2.36	26.73

Bengal (Walton, 1952) were counted and identified according to Loeblich and Tappan (1987), although they do not fully correspond to the living population, since the protoplasm can be colored after the organism has died (Bernard, 1988; Corliss and Emerson, 1990). Once the samples had been separated, determination and counting of the species of foraminifera was carried out using a stereomicroscope. Additional observations and photographs were performed using a Scanning Electron Microscope (JEOL JSM-840). Abundance of each species was expressed as the number of individuals per shoot.

In addition to the list of species and their abundance, data on the shell morphology and morphotypes (Langer, 1988; Corliss and Emerson, 1990; Corliss, 1991) were recorded. In our opinion, however, these morphotypes are better de-

fined as biological types since they include morphological as well as biological characters. Thus, from the studies of Langer (1993), we have proposed Table 2, where four biological types A,B,C and D are shown.

The indices of frequency (F) and dominance (MGD) were computed (Soyer, 1970) for each species. The mean general dominance index (MGD) is defined as a ratio between the number of individuals of a species on a substratum and the total number of individuals on this substratum expressed as percent. The species featuring an MGD higher than 1% were considered dominant species in the substratum considered (Soyer, 1970). The specific diversity of each sample was calculated using Shannon-Weaver's formula ($H = \Sigma$ pi log^2 pi). Cluster analysis was carried out to assess the affinity between the samples (Q-mode). The index used was Stein-
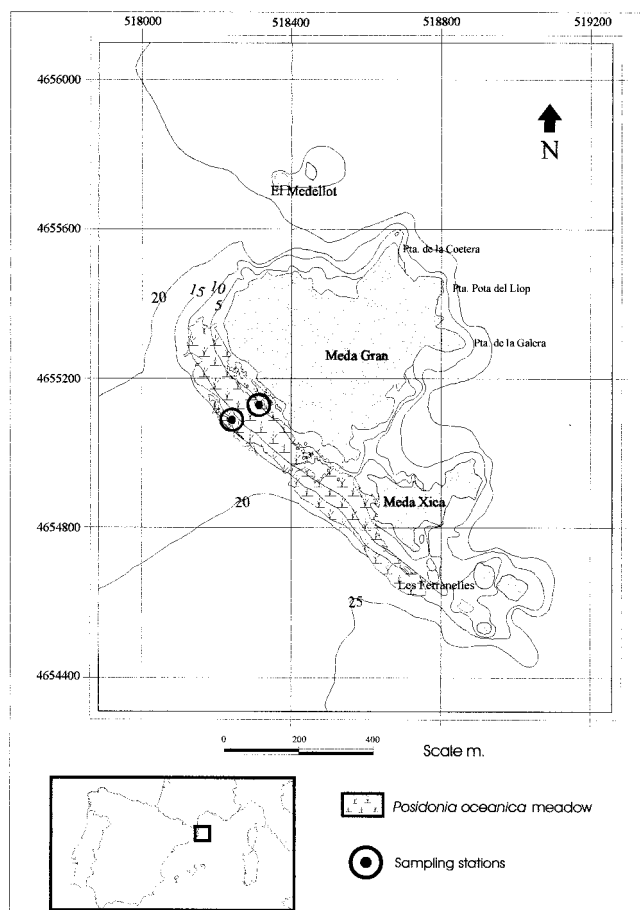
FIGURE 1. Study area, in the Medes Islands. A contour map of the seagrass meadow and a general bathymetry (in m) of the area are included. The grid corresponds to the UTM coordinates.

haus coefficient, following reccomendations of Legendre and Legendre (1983) and the classification algorithm was the unweighted pair-group using arithmetic averages (UPGMA: see Legendre and Legendre, 1983). Only species exceeding a frequency index of 25% were retained.

Since a complete factorial ANOVA was impossible due to missing data for some experimental conditions, a subset of data including those from artificial, smooth leaves from both depths and collected after 3 and 6 months of immersion, as well as data from natural shoots, were used for a three way ANOVA. A total of 11 dependent variables were tested separately (i.e., each of the six most abundant species, and composite variables such as the total number of individuals found and the number of individuals of each biological type). Independent variables were "natural" (yes or no), "depth" (5 or 13 m) and "time of collection" (March or June). Since only one observation was available for each experimental condition, the error term was estimated as the interaction between the three independent variables.

RESULTS

Of the 160 artificial shoots placed, 128 were recovered. Of these, only 11 different groups according to the type of leaves and recovery period (with 9–10 shoots each) were analyzed (see Table 1). A total of 122 taxa were found on

artificial leaves (Table 3), and 66 on natural leaves. On artificial shoots, the abundance ranged from 2 ind/shoot to 239 ind/shoot and the number of species from 13 to 70. Similar figures for natural leaves were 10 ind/shoot to 263 ind/shoot and from 13 to 58 species. The majority of the individuals were from the families Elphidiidae, Ceratobuliminidae, Cibicidiidae and Miliolidae (representing 38.9, 17.7, 15.6 and 13.5%, respectively, of the total of individuals found on artificial shoots; and for natural shoots 62.5, 12.7, 12.5 and 4.9%, respectively).

On average, diversity was slightly higher on artificial shoots (3.52 ± 0.19 bits/ind) than on natural ones (2.73 ± 0.09 19 bits/ind). However, the most abundant species were the same on both artificial and natural leaves: *Elphidium macellum, Conorboides mediterranensis* and *Cibicides lobatulus.* On artificial substrates, *Elphidium macellum* dominated after three months of immersion, while *Conorboides mediterranensis* was more abundant after six months, and the abundance of *E. macellum* var. *aculeatum* increased in June in all natural samples.

Of the 125 species found on all type of leaves, 24 species were frequent (F ≥ 50%) on both types of leaves: *Ammonia beccarii, Asterigerinata mamilla, Biloculinella fragilis, Cibicides lobatulus, C. refulgens, Cibicidella variabilis, Conorboides mediterranensis, C. posidonicola, Discorbinella bertheloti, Elphidium complanatum, E. crispum, E. macellum, E. macellum var. aculeatum, Melonis barleeanum, Nubecularia lucifuga, Planorbulina mediterranensis, Quinqueloculina laevigata, Q. stelligera, Q. ungeriana, Q. vulgaris, Rosalina globularis, Triloculina rotunda, T. semicostata, T. webbiana.* Moreover, three additional species occurred frequently only on artifical leaves: *Quinqueloculina cliarensis, Rosalina globularis var. semiporata* and *Triloculina planciana,* and 10 additional species were frequent (F ≥ 50%) only on natural leaves: *Elphidium adventum, E. maioricencis, Grabatella patelliformis, Planorbulina acervalis, Spiroloculina cymbium, Massilina secans, Quinqueloculina berthelotinana, Q. quadrata, Q. undulata* and *Triloculina plicata.*

Fifteen species were dominant (MGD > 1%) on the artificial leaves: *Biloculinella fragilis, Cibicides lobatulus, C. refulgens, Conorboides mediterranensis, C. posidonicola, Elphidium crispum, E. macellum, E. macellum var. aculeatum, Discorbinella bertheloti, Planorbulina mediterranensis, Quinqueloculina ungeriana, Q. vulgaris, Rosalina globularis, Triloculina planciana, T. webbiana.* This number was only eight on natural leaves (*Ammonia beccari, Cibicides lobatulus, Conorboides mediterranensis, C. posidonicola, Elphidium macellum, E. macellum var. aculeatum, Discorbinella bertheloti, Planorbulina mediterranensis*). Selected taxa are illustrated in Plate 1.

The calcareous perforate forms were dominant on the artificial leaves (83.4%), followed by calcareous porcelanous species (16.1%); the agglutinated forms represented only 0.5% (Table 6). On natural leaves the dominant forms were also calcareous perforate, with a higher percentage than that found on the artificial leaves (92.7%, Table 6).

Regarding the morphotype of the shells, the trochospiral type dominated on the artificial and natural leaves with values of 89.3% and 92.9%, respectively, followed by the fusiform type with values of 10.3% and 4.5% (Table 7).

TABLE 4. List of species and number of specimens found on natural leaves. Results in individuals/shoot.

Species	N5/3	N5/6	N13/3	N13/6
Ammonia beccarii	0.14	0.00	3.00	0.70
Asterigerinata mamilla	0.57	0.00	0.29	0.30
Biloculinella fragilis	0.57	0.60	0.14	0.20
Bulimina elongata	0.00	0.00	0.14	0.00
B. ulimina sp.	0.00	0.00	0.14	0.10
Cibicides lobatulus	11.29	1.80	28.43	3.10
Cibicides refulgens	0.71	0.00	1.43	0.30
Cibicidella variabilis	0.14	0.00	0.43	0.00
Cyclocibicides vermiculatus	0.00	0.00	0.43	0.00
Conorboides mediterranensis	19.71	4.60	14.71	3.00
Conorboides posidonicola	2.86	0.60	2.00	0.40
Cyclogira carinata	0.00	0.00	0.00	0.10
Discorbinella bertheloti	0.57	0.10	6.29	0.10
Elphidium advenum	0.43	0.00	0.14	0.00
Elphidium complanatum	0.57	0.00	2.00	0.70
Elphidium crispum	0.14	0.00	1.86	0.20
Elphidium macellum	21.43	0.80	130.57	18.20
Elphidium macel. var. *aculeatum*	9.00	0.90	47.29	5.10
Elphidium maioricensis	0.14	0.00	1.29	0.00
Fursenkoina af. acuta	0.00	0.00	0.14	0.00
Glabratella patelliformis	0.71	0.20	1.43	0.00
Globigerina sp.	0.14	0.00	0.57	0.20
Globulina gibba	0.00	0.00	0.14	0.00
Haplophragmoides canariensis	0.00	0.10	0.00	0.00
Lagena semistriata	0.00	0.00	0.14	0.00
Lenticulina oblonga	0.00	0.00	0.00	0.10
Massilina secans	0.14	0.00	0.86	0.00
Melonis barleeanum	0.14	0.00	0.29	0.20
Melonis sp.	0.00	0.00	0.14	0.00
Miliolinella sidebottomi	0.00	0.00	0.29	0.00
Miliolinella af. sidebottomi	0.00	0.00	0.29	0.00
Nubecularia lucifuga	0.14	0.00	0.86	0.00
Patellina sp.	0.00	0.00	0.14	0.00
Planorbulina acervalis	0.14	0.10	0.14	0.00
Planorbulina mediterranensis	0.29	0.00	4.43	0.00
Quinqueloculina aspera	0.00	0.00	0.57	0.00
Quinqueloculina bradyana	0.00	0.00	0.57	0.00
Quinqueloculina berthelotiana	0.00	0.00	0.29	0.30
Quinqueloculina cliarensis	0.00	0.00	0.57	0.00
Quinqueloculina contorta	0.00	0.00	0.14	0.00
Quinqueloculina disparilis	0.00	0.00	0.86	0.00
Quinqueloculina irregularis	0.00	0.00	0.00	0.50
Quinqueloculina juleana	0.00	0.00	0.43	0.00
Quinqueloculina laevigata	0.00	0.00	0.29	0.30
Quinqueloculina limbata	0.00	0.00	0.14	0.00
Quinqueloculina mediterranensis	0.00	0.00	0.14	0.00
Quinqueloculina parvula	0.00	0.00	0.14	0.00
Quinqueloculina quadrata	0.00	0.00	0.14	0.30
Quinqueloculina rugosa	0.00	0.00	0.29	0.00
Quinqueloculina stelligera	0.43	0.00	1.57	0.30
Quinqueloculina undulata	0.14	0.00	0.14	0.00
Quinqueloculina ungeriana	0.14	0.10	0.57	0.30
Quinqueloculina vulgaris	0.14	0.00	2.29	0.00
Quinqueloculina af. párvula	0.14	0.00	0.00	0.00
Quinqueloculina sp.	0.43	0.00	0.00	0.00
Rosalina globularis	0.71	0.00	1.57	0.10
Rosalina globul. semiporata	0.00	0.00	0.00	0.60
Spirillina limbata	0.00	0.00	0.29	0.00
Spiroloculina cymbium	0.00	0.00	0.29	0.10
Textularia pseudorugosa	0.00	0.00	0.00	0.10
Triloculina marioni	0.00	0.10	0.00	0.00
Triloculina oblonga	0.00	0.00	0.14	0.00
Triloculina plicata	0.29	0.00	0.29	0.00
Triloculina rotunda	0.29	0.00	0.14	0.00
Triloculina semicostata	0.29	0.00	0.14	0.00
Triloculina webbiana	1.29	0.00	0.57	0.10
Total	74	10	263	36

TABLE 5. Number of families, genera, species, diversity index and individuals/shoot found for each type of shoot.

Type of leaf	Families	Genera	Species	Diversity index (bits/ind)	Abundance ind/shoot
Artificial					
GRN13/3	18	26	54	3.99	40
GSF13/3	21	32	70	3.88	239
GSN13/3	13	20	54	2.73	232
GSN5/3	14	21	41	3.14	43
GSN13/6	9	16	28	2.59	60
BRN13/6	9	13	36	3.67	17
GRN13/6	12	19	43	3.99	24
GSF13/6	17	24	62	4.35	79
GSN5/6	6	10	15	3.44	3
BRN5/6	7	10	13	2.67	2
GSF5/6	15	20	52	4.30	27
Natural					
N5/3	12	17	33	2.98	74
N5/6	8	10	1	2.50	10
N13/3	19	28	5	2.71	263
N13/6	13	17	27	2.74	36

Regarding the biological type (Table 8) (and considering the number of individuals of each species on the artificial leaves), the C-type forms dominated (motile, 43.0%), with values nearly the same as for the B-type forms with temporary motility and with 2 to 5 months of life (37.7%); the least abundant were the A-type (3.9%), sessile and incrusting, with the longest life-span (1 year). At three months, biological type C dominated (76.3%), while after six months type B dominated (63.5%), and in both cases biological type A presented the lowest percentage (3.7%–2.8%, respectively). Considering the natural leaves overall, the dominant biological form was type C (62.9%).

The cluster analysis of samples revealed two main groups (Fig. 2), one with samples taken in March, three months after the beginning of the experiment, and the other with samples taken in June (six months), in both cases including natural and artificial substrates. Within each one of these two groups, subgroups corresponding to the different sampling depths appeared. The analysis did not discriminate between natural and artificial substrates, and samples from natural substrates were in general most similar to those obtained from green leaves without floats. These results showed green and smooth leaves without a float bladder to

TABLE 6. Nature of the shell, in % of individuals of each type.

Depth	March (%)		June (%)		Total (%)
	5 metres	13 metres	5 metres	13 metres	
Artificial leaves					
Ag	0.2	0.5	1.2	0.2	0.53
Cper	87.0	87.2	76.4	82.0	83.37
Cpor	12.4	12.6	20.0	20.2	16.1
Natural leaves					
Ag	0	0	1	0.27	0.4
Cper	92.5	95.4	91	92.0	92.7
Cpor	7.5	4.6	8	7.7	6.9

Ag—Agglutinated
Cper—Calcareous perforated
Cpor—Calcareous porcelaneous

TABLE 7. Morphotype of the shells found on artificial and natural leaves.

Morphotype	% on artificial leaves	% on natural leaves
Fusiform	10.27	4.53
Biconcave	0.14	0.10
Trochospiral	89.26	92.9
Unilocular	0.01	0.03
Planispiral	0.04	0.07
Globular	0.04	0.03
Extended	0.11	0.03
Triserial	0.08	0.10

be more similar to natural leaves than the other kinds of leaves, while the brown leaves or the presence of a float blader diminished the affinity in all cases.

ANOVA results showed, at least for the dependent variables considered (Table 9), no significant differences (except in a single case) between natural and artificial substrata. However, some species (e.g., those belonging to the biological type C, and specifically *Elphidium macellum* and *Conorboides posidonicola*), were more abundant at 13 m than at 5 m, and more individuals were found in samples collected in March than in those collected in June.

DISCUSSION

The present study confirms the presence of a very rich foraminiferal fauna inhabiting seagrass meadows (Blanc-Vernet, 1984; Martin and Wright, 1988; Fujita and Hallock, 1999). Most of the species collected belong to the family Miliolidae, as reported by Ribes and Gracia (1991) in *Posidonia oceanica* meadows near Cap de Creus, a few km northward from the Medes Islands. However, the most abundant species (*Elphidium macellum, Cibicides lobatulus, Conorboides mediterranensis*) belong to the Suborder Rotaliina, as previously found by Martin and Wright (1988) in their survey on *Thalassia* beds.

In agreement with the results found in populations of epiphytic foraminifera on *Posidonia* (Colom, 1974; Mateu,

TABLE 8. Biological types found on natural and artificial leaves; values in ind/shoot.

| Type of leaf | Biological types | | | |
	A	B	C	D
Artificial				
GRN13/3	7.3	11.2	15.8	5.8
GSF13/3	13.4	85.1	107.6	33.0
GSN13/3	1.9	47.8	155.9	26.4
GSN5/3	1.2	10.2	26.1	5.5
GSN13/6	0.9	53.4	2.7	3.1
BRN13/6	0.7	11.2	1.2	3.9
GRN13/6	0.6	13.4	2.7	7.2
GSF13/6	2.4	39.9	12.6	24.1
GSN5/6	0.4	1.8	0.3	0.5
BRN5/6	0.1	1.3	0.2	0.4
GSF5/6	0.9	13.7	4.3	8.2
Natural				
N5/3	0.6	38.2	31.5	3.7
N5/6	0.1	8.0	1.7	0.2
N13/3	5.3	62.6	183.3	11.8
N13/6	0.0	9.7	24.2	2.1
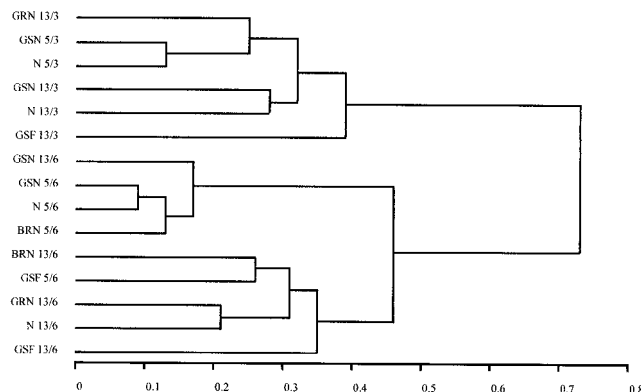
FIGURE 2. Cluster dendrogram of samples. The classification method was UPGMA, and the affinity between samples was computed using the Steinhaus index (represented in the horizontal axis). For more details, see text.

1974; Gaza, 1988; Ribes and Gracia, 1991) the populations found in this study, both on artificial and on natural leaves, were predominantly calcareous perforate. The low values for agglutinated tests (0.5%) indicate that the communities of foraminifera studied were characteristic of shallow depth as in (Boltovskoy, 1965; Blanc-Vernet, 1969; Mateu, 1974; Gaza, 1988) and that these agglutinated shells belong more to the infauna than to the epifauna (Barmawidjaja and others, 1992). On both artificial and natural leaves, test coiling was predominantly low trochospiral. This shape is advantageous for attaching to the surface of the leaf during times of turbulence (Corliss, 1991; Barmawidjaja and others, 1992).

The biological types C and B were the most abundant ones at the two times of collection on both the natural and artificial leaves. Biological type C dominated on artificial leaves after three months of immersion due to the massive presence of the genus *Elphidium*; this coincides with the major dominance of this genus in March on natural leaves. Moreover, temporary abundance variations of *Elphidium* were also recorded by Buzas (1993) in the colonization of foraminifera in sediment. However, after six months of immersion, biological type B dominated, as a result of the

TABLE 9. Summary of the ANOVA results. The significance of three independent variables and some relevant dependent variables are indicated as p (probability of error when rejecting the null hypothesis; n.s. indicates p > 0.05).

| Dependent variable | Independent variable | | |
	Natural versus Artificial	Depth	Month
Cibicides lobatulus	ns	ns	ns
Conorboides mediterraneensis	ns	ns	ns
Conorboides posidonicola	0.049	0.032	0.049
Elphidium macellum	ns	0.044	0.037
E. macellum var. *aculeatum*	ns	ns	ns
Planorbulina	ns	ns	ns
Total	ns	ns	0.049
Biological type A	ns	ns	ns
Biological type B	ns	ns	ns
Biological type C	ns	0.015	0.012
Biological type D	ns	ns	ns
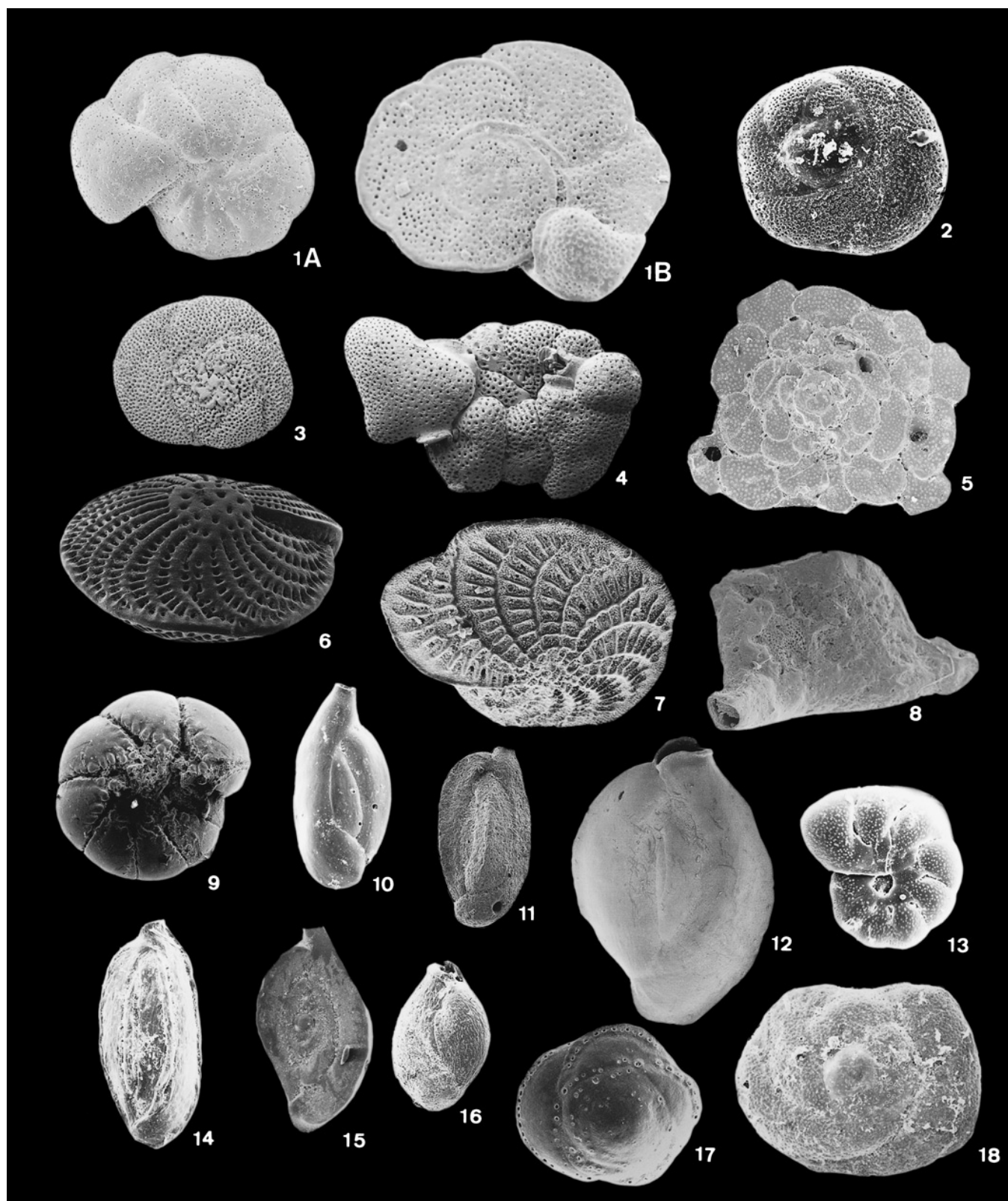
PLATE 1

Scanning electronic micrographs of epiphytic foraminifera. **1** *Cibicides lobatulus* (Walker and Jacob), 1798. (A) umbilical side ×180. (B) spiral side ×200. **2** *Conorboides mediterranensis* (d'Orbigny, 1826) ×150. **3** *Rosalina globularis* d'Orbigny, 1826 ×60. **4** *Cibicidella variabilis* (d'Orbigny), 1839 ×100. **5** *Planorbulina mediterranensis* d'Orbigny, 1826 ×80. **6** *Elphidium crispum* (Linnaeus), 1758 ×120. **7** *Elphidium macellum* (Fichtel & Moll), 1798 ×150. **8** *Nubecularia massutiniana* Colom, 1942 ×120. **9** *Ammonia beccarii* (Linnaeus), 1767 ×100. **10** *Quinqueloculina cliarensis* (Heron-Allen and Earland, 1930) ×80. **11** *Quinqueloculina rugosa* (d'Orbigny, 1826) ×60. **12** *Massilina secans* (d'Orbigny, 1826) ×90. **13** *Melonis barleanus* (Fichtel & Moll, 1798) ×70. **14** *Quinqueloculina stelligera* Schlumberger, 1893 ×190. **15** *Spiroloculina cymbium* d'Orbigny, 1839 ×100. **16** *Triloculina planciana* (d'Orbigny, 1839) ×120. **17** *Asterigerinata mamilla* (Williamson, 1858) ×80. **18** *Conorboides posidonicola* Colom, 1942 ×130.

drastic reduction in the genus *Elphidium* in favor of the genera *Cibicides* and *Conorboides.* Studies carried out on epiphytic foraminifera of *Posidonia* by other authors on the Majorcan coast (Abril, 1993) found biological type B as the dominant type. In the Tyrrhenian Sea, Langer (1993) found biological type B to be the most abundant on leaves of *Posidonia* at 5 m depth, but at greater depth (15 m) he found biological type A to be more dominant. However, Langer's results are not fully comparable to ours because the species identified were not the same, and the general environmental conditions and time of sampling likewise differed between Langer (1993) and this work.

Differences between samples collected in March and those collected in June most probably reflect the interaction among "successional" events (e.g., settlement, colonization, biotic interactions) and "seasonal" circumstances (e.g., changes in environmental abiotic factors, food availability, life-span of foraminifera and of *Posidonia* leaves: Blanc-Vernet, 1984; Langer, 1993). In general, more individuals were found in March than in June, and some species that were abundant in March (e.g., *Grabatella patelliformis* and *Elphidium advenum*) had disappeared or were very rare in June. This indicates that the time-dependent differences found were not a simple result of an accumulative colonization process, but that the foraminiferan community underwent complex dynamic changes with time.

Both the number of individuals and the number of species increased with depth on both natural and artificial shoots, and this was evident in species of the biological type C. Moreover, two families found on natural and artificial shoots: Buliminidae and Nodosariidae were only found at depth, as were the Miliolidae: *Quinqueloculina aspera, Triloculina oblonga* or *Spiroloculina cymbium.* These results are in accordance with Blanc-Vernet (1984) who found an increase of epiphytic foraminifers on *Posidonia oceanica* with depth. In particular all families found had higher abundance values at 13 m than at 5 m. Bathymetric changes in abundance or specific composition in faunal assemblages of seagrass beds have often been reported (e.g., Gambi and others, 1992) and may be due to several factors (e.g., changes in lighting, changes in meadow structure). In the case of the foraminifera, which are in most cases only loosely attached to the seagrass leaves, hydrodinamism may be a key factor acting on a more or less random (at least at this scale) settlement by eliminating more individuals (and species) in shallow rather than in deep zones.

The colonization of an artificial substrate is determined on the one hand by a large number of environmental parameters such as depth, seasonality, time elapsed since submersion and light availability, and on the other hand, by substrate characteristics (color, texture, etc.: see, among others, Flasch, 1971; Sentz-Braconnot, 1966; Herdocio, 1985, 1991). Although designed as a pilot work, our results indicate some differences between the different types of artificial substrata: apparently, green leaves were more colonized than brown, and shoots including leaves with floats hosted a richer foraminiferan epifauna than those without floats, with more individuals. Some of these differences deserve further experimentation to determine whether these preliminary findings are due to habitat selection by foraminifera

(or to other ecological processes) or are simply artifactual results (e.g., floats offer more surface area for colonization).

Apart from these variations, still to be elucidated, in general terms the foraminifera found on artificial shoots resembled those found on natural shoots. This is clearly shown, from a multi-specific perspective, by the dendrogram shown in Figure 2, where the samples from artificial shoots cluster near the corresponding natural ones, from the same depth and time. This is confirmed by the ANOVA on the main species abundance (or on composite variables; Table 9), indicating that the main sources of variability in the data are differences among the two sampling events and differences between the two depths. The variability explained by differences between natural and artificial leaves, if any, is very small. These results indicate that colonization by foraminifera is rapid, and occurs in less than three months. This is in agreement with the finding of Buzas (1993), who showed that the densities of foraminifera stabilize within about three weeks of deployment in a cage containing azoic sand.

The similarity in the formanifera found on artificial and natural leaves demonstrates the reliability of the experimental approach undertaken and the utility of these methods in investigating the dynamics of colonization and the general features of such an important faunal group in seagrass habitats. On the other hand, the results reported here suggest, at least preliminarily, that there are no important interactions between foraminifera and the seagrass leaves.

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