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Effects of environmental factors on the distribution of the edible bivalves *Atactodea striata, Gafrarium tumidum* and *Anadara scapha* on the coast of New Caledonia (SW Pacific)

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Abstract

Factors influencing the spatial distribution of the bivalves *Atactodea striata. Gafrarium tumidum* and *Anadara scapha* were analysed on the south-west coast of New Caledonia, using a multivariate approach (correspondence analysis). *A. striata* is abundant on sandy beaches with a high coarse sand content. *G. tumidum* is preferentially distributed on substrates located close to the lower limit of neap tide and seems to be independent of sediment granulometry. *A. scapha* adults occur at lower bathymetric levels, with sediment composed of 40% medium, fine and very fine sand, and 30% very coarse and coarse sand. For this species, juvenile migration is suggested by the differential distribution of young and adults.

Keywords : Bivalve, Pacific, New Caledonia, lagoon, soft bottom, ecology, spatial distribution, correspondence analysis.

Influence des facteurs de l'environnement sur la distribution des bivalves comestibles Atactodea striata. Gafrarium tumidum *et* Anadara scapha *sur la côte de Nouvelle-Calédonie.*

Résumé

Les facteurs qui influencent la distribution spatiale des bivalves *Atactodea striata. Gafrarium tumidum* et *Anadara scapha* ont été analysés sur la côte sud-ouest de Nouvelle-Calédonie en utilisant une approche multivariable (analyse des correspondances). *A. striata* est rencontré préférentiellement sur les plages de sables grossiers. *G. tumidum* est inféodé aux substrats situés près de la limite inférieure des basses mers de mortes-eaux et paraît relativement indépendant de la granulométrie du substrat. Les adultes d'*A. scapha* sont rencontrés à un niveau bathymétrique inférieur dans des sédiments composés de 40 % de sables moyens. fins et très fins et de 30 % de sables grossiers. Une répartition différentielle entre jeunes et adultes a été mise en évidence sur cette espèce, suggérant un comportement migratoire des juvéniles.

Mots-clés : Bivalve, Pacifique, Nouvelle-Calédonie, lagon, substrat meuble, écologie, distribution spatiale, analyse des correspondances.

INTRODUCTION

Knowledge of the parameters affecting the spatial distribution of edible bivalves is required for sound management of their exploitation, particularly where semi-extensive farming methods are used (Davy and Graham, 1983). Many intertidal bivalve stocks are being harvested in the South-West Pacific (Broom,

1985) but little ecological research has been conducted on them. In New Caledonia, the bivalves *Atactodea striata* (Gmelin, 1791), *Gafrarium tumidum* Röding, 1798 and *Anadara scapha* (L., 1758) are commonly collected by coastal populations. Studies were recently undertaken to determine their biological and ecological characteristics and estimate their potential for commercial exploitation. With a view to the latter, assessments of existing natural stocks appear to be a priority objective (Baron and Clavier, 1992). During the sampling, conducted in connection with these stock assessments, data were collected on all three bivalve populations and their respective habitats. These have been analyzed in the present paper so as to determine the main factors affecting species distribution and rank them in order of importance.

MATERIAL AND METHODS

Factors affecting the distribution of *A. striata*, *G. tumidum* and *A. scapha* were investigated during stock assessment on the south-west coast of the main island of New Caledonia. The sampling plans used, described in detail by Baron and Clavier (1992), are outlined briefly. First, a preliminary survey was carried out to determine the respective habitats of the three species. *A. striata* was exclusively found on sandy beaches where 50 sampling units, distributed at random, were investigated. Each unit consisted of a strip of sand 0.5 m wide perpendicular to the shore and covering the entire width of the beach. The two other species were found on sandy-muddy areas, where 100 sampling units, 0.5 m^2 in area and also positioned at random, were investigated.

Table 1. – Double entry array used for coding *Atactodea striata* population parameters. N: density; B: biomass; Ju: juveniles; Ad: adults.

Code	N (*n*/0.5 m)	B (*g*/0.5 m)	Ju (*n*/0.5 m)	Ad (*n*/0.5 m)
0	0-5	0-10	0-2	0-2
1	5-13	10-20	2-10	2-4
2	13-35	20-40	10-30	4-9
3	>35	>40	>30	>9

The bivalves were collected after the sediment had been washed through a 5 mm mesh screen, and their length measured parallel to their hinge, to the nearest 0.5 mm. Total fresh weights (flesh and shell) were measured after allowing them to dry off on filter paper. Individuals were then separated into two classes according to sexual maturity: juveniles (Ju) and adults (Ad) (Baron, 1992). A sample of sediment was taken from each unit for analysis. The sedimentary fractions were separated into four main classes according to grain size: pebbles and granules over 2.5 mm (Gr); very coarse and coarse sand, between 2.5 and 0.5 mm (Cs), medium, fine and very fine sand, between 0.5 and 0.063 mm (Fs), and mud, lower than 0.063 mm (Mu). The sandy beach sediments were in addition classified according to mean grain size (Mz) (Folk and Ward, 1957) and organic matter content (OM), by weighing dried sediment before and after oven heating at 550°C for 3 hours. The quantity of carbonates (Car) contained in the sandy-muddy sediments was determined in the fine fraction (*i. e.* <0.063 mm) by decarbonation in a Bernard calcimeter (Chamley, 1966). The fine fraction content of the beach sediment was always small and the total carbonate percentages in the sand were obtained by measuring loss of weight after carbonate removal by acid on a dry sediment sample. The beaches are uncovered at each low tide and their width (Wi) was systematically measured. On the sandy-muddy shore areas, bathymetric level (Bl), presence or absence of a seagrass bed (Sb) and species, were recorded.

Table 2. – Double entry array used for coding *Atactodea striata* environmental parameters. Gr: pebbles and granules; Cs: very coarse and coarse sand; Fs: medium, fine and very fine sand; Car: carbonates; Om: organic material; Wi: beach width; Mz: mean grain size.

Code	Gr (%)	Cs (%)	Fs (%)	Car (%)	Om (%)	Wi (m)	Mz (φ)
0	0-2	0-50	0-15	0-10	0-3.5	0-8	−1.32-0
1	2-3	50-65	15-25	10-15	3.5-4.0	8-10	0-1
2	3-8	65-75	25-40	15-20	4.0-5.0	10-11	>1
3	>8	>75	>40	>20	>5.0	>11	–

All the variables (quantitative and qualitative) were made homogeneous by coding. For the three species considered, each parameter was distributed into two, three or four balanced classes; their limits for population and environmental parameters are shown for *A. striata* (*tables* 1 and 2) and *G. tumidum* and *A. scapha* (*tables* 3 and 4).

An inertia analysis was performed with these data using a multidimensional contingency table "population-environment". The reason for such an analysis is

Table 3. – Double entry array used for coding *Gafrarium tumidum* and *Anadara scapha* population parameters. N: density; B: biomass; Ju: juveniles; Ad: adults.

Code	N (*n*/0.5 m^2)	B (*g*/0.5 m^2)	Ju (*n*/0.5 m^2)	Ad (*n*/0.5 m^2)
G. tumidum				
0	1-2	0-15	0	0-2
1	2-6	15-50	1	2-6
2	>6	>50	>1	>6
A. scapha				
0	1	0-30	0	0-2
1	2-4	30-100	>0	>2
2	>4	>100	–	–

to assess directly the links between population and environment (Clavier and Chardy, 1989). The contingency table method is moreover particularly useful for simultaneous analysis of mixed data (Legendre and Legendre, 1984). Each parameter is described by as many estimates as there are classes. A contingency table for a pair of parameters is defined by the number of agreements observed for each pair of estimates. Within this context, correspondence analysis (Benzecri *et al.*, 1973), or reciprocal averaging, appears to be the most appropriate ordination technique.

RESULTS

Correspondence analysis makes it possible to plot simultaneously the projections of the row attributes (environmental parameters) and column attributes (population parameters). In order to simplify graphics, two types of projections are given separately, but our comments will describe the links between these two structures. Axis scales are the same for the three analyses. For each species, the link between environmental parameters and population attributes was estimated from the distance between their respective projections on the planes considered.

On the sandy-muddy areas, *G. tumidum* was collected from only 26 units and *A. scapha* from 19. The large number of nil values thus produced causes a "trivial" axis to appear in the correspondence analysis, which accounts for the high percentage of variance and masks the relationships sought. The analysis was therefore applied solely to units where bivalves were present. Our comments refer to the factors that induce relative abundance of *G. tumidum* and *A. scapha* to the exclusion of those that determine their spatial distribution.

Atactodea striata

The first three inertia axes extract 84.08% of the total variance, with 40.39, 30.62 and 13.07% for axis 1, 2 and 3 respectively. Because of the small part of the variance explained by axis 3, our comments will be restricted to the plane 1-2 (*fig.* 1). The position of the population attributes (*fig.* 1A) shows the existence of an abundance gradient expressed by axis 1. The nil or low values for density and biomass (on the negative side of the axis) are opposed to the medium and high values (on the positive side of the axis). Axis 2 separates high density and biomass values (on the negative side) from the medium values (on the positive side). The closeness of the demographic attributes projections with the same code, on the one hand, and of the density and biomass attributes, on the other, suggests a homogeneity of the demographic structure of the population in our samples.

Table 4. – Double entry array used for coding *Gafrarium tumidum* and *Anadara scapha* environmental parameters. Gr: pebbles and granules; Cs: very coarse and coarse sand; Fs: medium, fine and very fine sand; Mu: mud; Car: carbonates; Bl: tidal level; Sb: sea grass beds composed of Simple (1), *Halophila ovalis*, Simple (2), *Halodule uninervis* or *Halodule pinifolia* Simple (3), *Cymodocea rotundata*, *Halophila ovalis* or *Thalassia hemprichii*.

	Code	Gr (%)	Cs (%)	Fs (%)	Mu (%)	Car (%)	Bl (m)	Sb
G. tumidum	0	0-5	0-28	0-35	0-3.5	0-3	0.00-0.35	Nil
	1	5-15	28-40	35-50	3.5-7	3-20	0.35-0.45	Simple (1)
	2	>15	>40	>50	>7	>20	0.45-0.55	Simple (2)
	3	–	–	–	–	–	>0.55	Mixed
A. scapha	0	0-5	0-25	0-35	0-10	0-25	0.00-0.10	Nil
	1	5-10	25-35	35-45	10-15	25-50	0.10-0.25	Simple (2)
	2	>10	>35	>45	>15	>50	0.25	Simple (3)
	3	–	–	–	–	–	>0.25	Mixed

The parameters that contribute the most to axes 1 and 2 are very coarse and coarse sand, medium, fine and very fine sand, and pebbles and granules (*fig.* 1B). Low density and biomass values for *A. striata* (N0, B0) correspond to low granule and pebble content (Gr0) or low very coarse and coarse sand content (Cs0), and high medium, fine sand content (Fs3). Conversely, the increase in the values of the population parameters along axis 2 is linked to increasing values for granules and pebbles and medium, fine and very fine sand, and decreasing values for very coarse and coarse sand. The highest density and biomass values (N3, B3) were obtained from sediments with 15 to 20% carbonates, containing 65 to 75% very coarse and coarse sand, 3 to 8% pebbles and granules and 15 to 25% medium, fine and very fine sand. *A. striata* appears to be relatively independent of sediment organic matter content above a certain threshold (3.5%). In addition, no obvious relationship was obtained between the width of the beach and species characteristics.

Gafrarium tumidum

The total inertia extracted by the first three axes is 80.91%, axis 1, 2 and 3 respectively explaining 46.49,

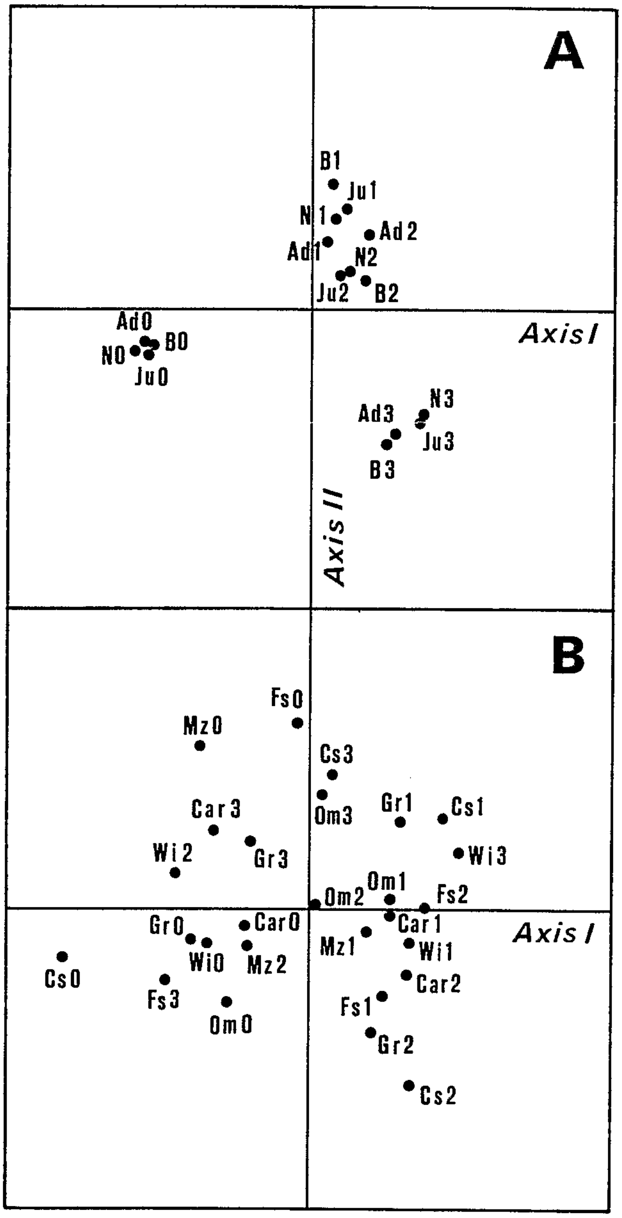

Figure 1. — *Atactodea striate*: correspondence analysis. Ordination of the population attributes (A) and of the environmental parameters (B) in the plane 1-2. See *tables* 1 *and* 2 for an explanation of terms.

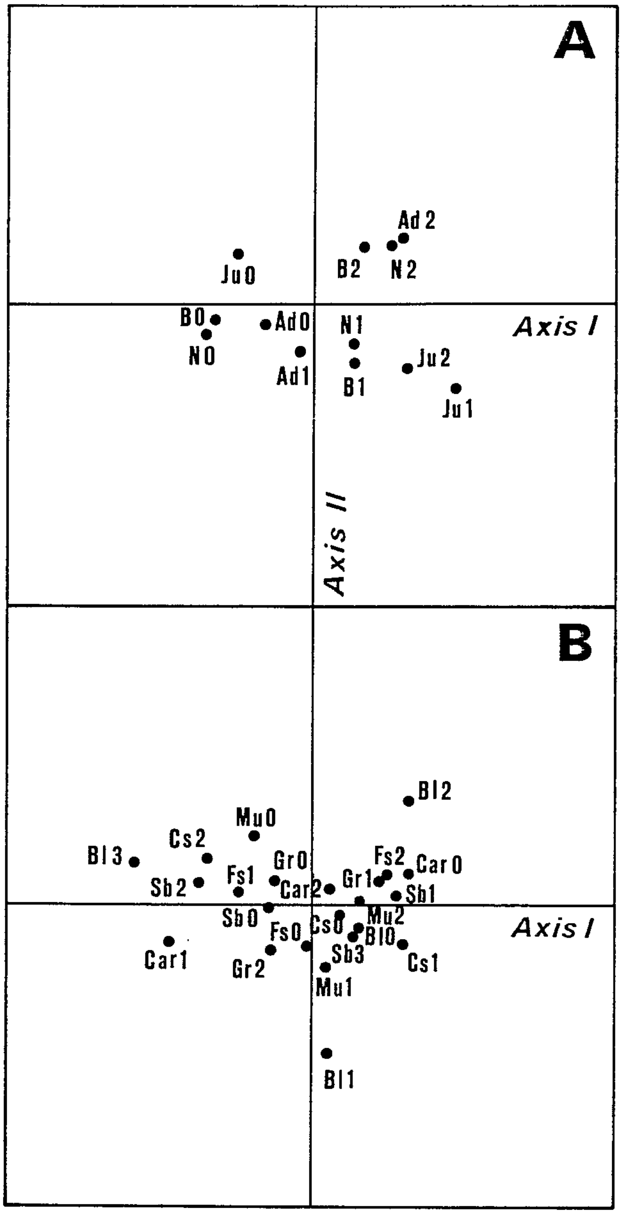

Figure 2. — *Gafrarium tumidum*: correspondence analysis. Ordination of the population attributes (A) and of the environmental parameters (B) in the plane 1-2. See *tables* 3 *and* 4 for an explanation of terms.

20.67 and 13.75% of the total variance. Our comments are restricted to plane 1-2. For the population attributes (*fig.* 2A), the abundance gradient represented by axis 1 again separates the low density and biomass values, on the negative side, from the other values. The medium and high density and biomass values are themselves ordinated on axis 2. A constancy in demographic structure is evident in our samples. However, juvenile densities are inconsistent with the other parameters with the same code.

The parameters that contribute most to axis 1 are tidal level, carbonates, very coarse and coarse sand, and seagrass type (*fig.* 2B). The lowest density and biomass values for *G. tumidum* (N0, B0) correspond to shallow areas (B13) with sediment intermediate in carbonate (Car1), rich in very coarse and coarse particles and having a single-species seagrass bed of *Halodule* spp. (Sb2). Similarly, the general factor of abundance along axis 2 is closely related to an associated increase in tidal level (between +0.35 and +0.55 m) and increase in the fine fraction content.

Maximum densities and biomasses of *G. tumidum* occur at a tidal level between +0.45 and +0.55 m, in a sediment with low carbonate content (<3%), covered with a seagrass bed of *Halophila ovalis*. With regard to grain-size factors, *G. tumidum* was preferentially located on sediments rich in medium, fine and very fine sand (>50%) and mud (>7%), with intermediate pebble and granule contents (5 to 15%).

An absence of juveniles, unlike absence of adults, is correlated with low mud content and low pebble and granule content. The highest abundance of juveniles was recorded at a tidal level of 0.35 to 0.40 m above chart datum and an intermediate very coarse and coarse sand content.

Anadara scapha

The first three inertia axes extract 96.38% of the total variance, with 68.35, 16.96 and 11.07% for axis 1, 2 and 3 respectively. Our comments apply exclusively to plane 1-2, with special attention given to axis 1. This axis represents a gradient of abundance for the population attributes (*fig.* 3A). The low density and biomass values appear on the negative side, the medium values in the central portion and the high values on the positive side. The low density values (N0) occupy an intermediate position between low and medium biomass values, due to the high individuals weights of *A. scapha.* The medium density values are located nearer the positive pole of axis 2 and are not consistent with the overall trend. Projections of juvenile densities (Ju0 and Ju1) are reversed in relation to the abundance axis, suggesting a differential distribution of adults and juveniles. Axis 2 explains only a small part of the inertia; it does, however, discriminate between the low and medium density values.

The environmental parameters that contribute the most to axis 1 are tidal level, very coarse and coarse sand, medium, fine and very fine sand, and pebbles and granules (*fig.* 3B). The low biomass values for *A. scapha* were generally obtained from sediments at a tidal level > +0.25 m C.D., consisting mainly of medium, fine and very fine sand. Juveniles (Ju1), which occur exclusively on this type of substrate, are associated with single-species seagrass beds (Sb2). Maximum densities and biomasses were recorded from sediments with 25 to 35% very coarse and coarse sand, 35 to 45% medium, fine and very fine sand, and 5 to 15% pebbles and granules. These substrates are, to a lesser extent, associated with lower tidal level, medium carbonate content, a high percentage of mud and a mixed seagrass bed consisting either of *Halodule uninervis* and *Thalassia hemprichii*, alone or with *Cymodocea rotundata*, or else of *T. hemprichii*. *C. rotundata* and *Halophila ovalis*. Juveniles were absent from this type of bottom.

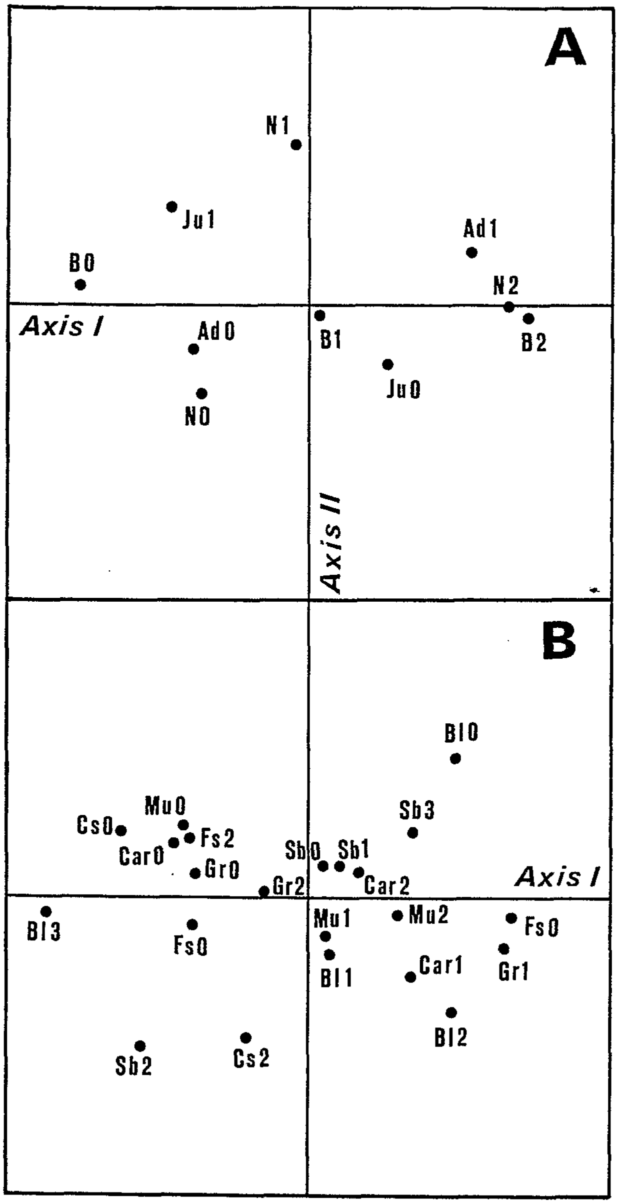

Figure 3. — *Anadara scapha*: correspondence analysis. Ordination of the population attributes (A) and of the environmental parameters (B) in the plane 1-2. See *tables* 3 *and* 4 for an explanation of terms.

DISCUSSION AND CONCLUSION

The factors affecting the spatial distribution of benthic species are complex and difficult to appraise. The importance of granulometric composition of the substrate on the distribution of benthic organisms has been demonstrated by many authors (Sanders, 1958; Rhoads and Yound, 1970; Bloom *et al.*, 1972; Thomassin, 1978; Chardy and Clavier, 1988). We therefore focussed special attention on this parameter. All three bivalve species investigated are sedentary, at least as adults. Their presence is thus determined by larval recruitment and juvenile survival. This study describes species preferences for certain substrates, but does not enable the factors governing larval settlement to be appraised directly. While it also affords an instantaneous view of the environment, it does not assess the effects of temporal variations in the environmental parameters, which can be quite marked in the intertidal zone.

Atactodea striata

Most of the beaches along the coast of the main island of New Caledonia have a slope of between 5 to 8%, a south-west aspect and low to medium water circulation. *A. striata* was distributed on a narrow stretch of sand (about 4 to 7 m wide), which explains the low correlation between total beach width and species density or biomass. *A. striata* has, in the Indo-Pacific, been recorded to occur on very coarse coral (Gibbs, 1978) or non-coral sands (Purchon and Purchon, 1981), on medium carbonated or terrigenous sands (Pichon, 1962; Thomassin, 1978), in relatively fine sand (Fisher, 1966) and in medium well-sorted sediment with a mean particle size of 0.4 mm (Narayanan and Sivadas, 1986). These data suggest that *A. striata* is comparatively indifferent to the granulometric composition of the sediment. Our findings do, however, show a relationship between *A. striata* density and sand grain size structure, *i.e.*, maximum densities are associated with sediments containing a high percentage of very coarse and coarse sands and of pebbles and granules, together with an intermediate content of medium, fine and very fine sand, the ratio Cs + Gr/Fs ranging from 2.7 to 5.5. Projection of the mean grain sizes shows the true coarse sand fraction, with a grain size of between 0 and 1 φ (Mz1), to be predominant.

Gafrarium tumidum

Our findings underline the impact of depth on *G. tumidum* abundance. Maximum density and biomass values were recorded between tidal levels of +0.40 and +0.50 m C.D., that is at the lower limit of areas uncovered by neap tides. For *G. tumidum*, unlike *A. striata*, the impact of granulometric composition on abundance was not clarified by our findings. Low density and biomass values are associated with substrates containing >40% coarse sand and having an intermediate carbonate content (3 to 20%). *G. tumidum*, nevertheless, appears to be comparatively independent of the latter parameter, since high density and biomass values are recorded both with very low (0 to 3%) and high (20 to 68%) carbonate contents. Gibbs (1978) records *G. tumidum* from medium muddy sand and Swadling and Chowning (1981) note that this species is collected in New Guinea from muddy sediment pockets on the reef flat. Purchon and Purchon (1981), on the other hand, found *G. tumidum* in clean sand areas sheltered from waves and tidal currents. We recorded no species preference for muddy habitats; maximum biomass values were generally associated with sediments comprising >50% medium, fine and very fine sand, 5 to 15% pebbles and granules, and at the most 15% mud. *G. tumidum* is a short-siphoned suspension-feeder so that a relatively high fine sediment content, *i.e.* ≧20%, would appear to limit its distribution.

Highest juvenile densities were recorded from lower tidal levels (+0.35 to +0.40 m C.D.) on sediments with about 35% very coarse and coarse sand and 5% mud. The percentage of mud appears to be more limiting for juveniles than for adults. Conversely, the latter are absent from sediments rich in pebbles and granules, *i.e.* in particles >2.5 mm, which may make it difficult for them to burrow. Our study did not reveal any size segregation. Distribution differences do, however, suggest some movement of the juveniles. Overall, we noted a wide variation in substrate characteristics inhabited by *G. tumidum*. The species can be regarded as ubiquitous.

Anadara scapha

Species of *Anadara* are either intertidal (Boonruang and Janekarn, 1983; Borrero, 1986; Wolff *et al.*, 1987) or shallow subtidal (Yankson, 1982; Narasimham, 1985). In New Caledonia, however, species occur at depths of about 20 m (Chardy and Clavier, 1988). Toral-Barza and Gomez (1985) collected *A. scapha* from seagrass beds at a depth of +0.5 m C.D. at low tide, while Broom (1985) also reported the species to be subtidal. In Madagascar, Thomassin (1978) observed *A. scapha* to be more abundant in reef seagrass beds than in littoral ones. Our data suggest that *A. scapha* abundance, particularly of juveniles, is linked to tidal level. The species was encountered only once at > +0.40 m C.D. It is preferentially distributed in the lower part of the intertidal zone which is uncovered only during spring tides.

In general, *Anadara* species tend to favour muddy sediments (Broom, 1985). These short-siphoned bivalves feed on particles in suspension near the water-sediment interface; they have developed ciliate structures to prevent their branchiae from becoming clogged with fine particles (Yoloye, 1975). Suspension-feeders of muddy sediments are usually found in locations where only limited resuspension of fine particles occurs (Rhoads and Young, 1970). The presence of a seagrass bed, because of its ability to stabilize the sediment, is therefore important for population survival. However, each species may have its own distinct requirements. *A. granosa*, for instance, occurs in locations where between 50 to 90% of the substrate is composed of particles <0.125 mm in diameter (Pathansali, 1966; Narasimham, 1985); Boonruang and Janekarn (1983) report its presence on sediments with 70 to 80% of particles >0.063 mm. According to Broom (1985), *A. subcrenata* can occur on sandy-muddy bottoms, but highest densities are recorded in sediments with >80% fine particles. Some *Arcidae*, however, prefer sediments with less mud. Thomassin (1978) found *A. scapha* in seagrass beds on sediments rich in coarse sand and Toral-Barza and Gomez (1985) report this species in seagrass beds on a sandy-muddy substrate mixed with coral rubble. Broom (1985) also noted that *A. scapha* was generally found in rock crevices. In the south-west lagoon of New Caledonia, Chardy and Clavier (1988) recorded *Anadara cf. scapha* on grey sand bottoms with a mud content of about 7%. In our investigations, the highest density and biomass values for *A. scapha* were recorded on sediments with about 7% of particles >2.5 mm, 30% of particles between 2.5 and 0.5 mm, 40% of particles between 0.5 and 0.063 mm, and 20% mud. Broom (1985) recorded a byssus from several *Anadara* species, including *A. scapha*. The presence of some coarse material (coral or shell rubbles) in the sediment may thus facilitate settlement.

Borrero (1986) described a differential distribution of juveniles and adults for *A. tuberculosa* and *A. similis*. Juvenile settlement takes place in the shallow subtidal zone; subsequently they move towards the mud flats bordering the mangroves. Yoloye (1975) observed a similar migration in *A. senilis* juveniles, although adults of this species are sedentary. Our findings suggest a similar pattern for *A. scapha*. Rhoads and Young (1970) demonstrated the greater sensitivity of juveniles of suspension-feeders to the fine fraction content of the sediment. Settlement of juveniles on substrates relatively poor in fine particles and their subsequent gradual migration into the adult habitat assists survival of these buried suspension-feeders in highly muddy habitats in which either deposit-feeders (Sanders, 1958; Bloom *et al.*, 1972) or epibenthic suspension-feeders (Chardy and Clavier, 1988) are generally predominant.

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