Pattern of spatial distribution of a brood-protecting schizasterid echinoid, *Abatus cordatus*, endemic to the Kerguelen Islands

Élie Poulin, Jean-Pierre Féral

Observatoire Océanologique de Banyuls, U.R.A. C.N.R.S. 117, F-66650 Banyuls-sur-Mer, France

ABSTRACT: This study examined the spatial distribution at different geographic scales of the echinoid *Abatus cordatus* which is endemic to the Kerguelen Islands. Special attention was paid to the non-dispersal strategy of the species. It lives burrowed in the sediment and females brood their young in dorsal pouches. The dispersal of this species is therefore characterised by a limited mobility among adults and the lack of a free-swimming larval phase. Using SCUBA and dredging, *A. cordatus* was sampled all around Kerguelen. The spatial distribution from the island scale to the bay scale shows discontinuities at 2 levels: (1) at the island level favourable sectors (principally characterised by jagged coastline with numerous sheltered bays) are separated by linear coastline or swell exposed sectors; (2) at the bay scale *A. cordatus* lives in high density, isolated demes in shallow water of sheltered bays. *A. cordatus* was most numerous in sediments that ranged from medium to fine sand. The granulometry of the sediment and the lack of predation determine this aggregated spatial distribution pattern. Considering that the scale of larval dispersal is the consequence of spatial and temporal habitat structure, the non-dispersal strategy of *A. cordatus* is associated with a spatially varying but temporally constant habitat as predicted by theoretical models.

KEY WORDS: *Abatus* · Brooding · Habitat limits · Kerguelen · Non-dispersal strategy · Schizasteridae · Spatial distribution · Subantarctic

INTRODUCTION

Species spatial distribution is the result of the interaction of biotic and abiotic constraints (Thrush 1991). In soft-bottom marine invertebrates and particularly deposit-feeders, functions such as feeding, respiration and motility are strongly linked to the sediment characteristics of the habitat. Generally, granulometry and the organic content of the sediment are the main factors that determine habitat (Lopez & Levinton 1987). However the range of the habitat can be modified by biotic constraints, such as interspecific competition and predation; life-history factors may also influence spatial distribution (Thrush 1991). Larval dispersal and recruitment processes are also important factors related to spatial distribution. Indeed, factors such as length of larval stage duration, currents and site selection by larvae affect the spatial pattern of species (Thrush 1991).

Studies on the spatial distribution of organisms are important for several reasons (Thrush 1991). Firstly, the knowledge of distribution patterns is necessary to investigate population dynamics and genetics and, more generally, population biology. The different distribution patterns (aggregated, random or regular distribution) will determine the choice of a sampling design, in order to avoid bias in statistical analysis. Secondly, it is important to identify the factors responsible for the distribution patterns. Thirdly, there is the potential to understand the relationships between the spatial distribution and life-history traits, particularly for species without larval dispersal and that have low motility (Carlon & Olson 1993).

The schizasterid echinoid *Abatus cordatus* (Verrill, 1876) is endemic to the Kerguelen Islands (49° 21′ S, 70° 12′ E) and is a deposit feeder that burrows a few centimetres below the surface of the sediment. The development of *A. cordatus* is direct (Schatt 1985, P.

Schatt & J.-P. Féral unpubl.) and the females brood their young. The juveniles are released on the sea floor near their mother. Some information on the distribution of *A. cordatus* is available (Magniez 1980, Schatt 1985, Mespoulhé 1992). This burrowing echinoid is often very abundant and high densities are found at shallow depth (0 to 2 m) near beaches. Individuals in dense aggregations often touch or nearly touch each other. The goal of the present study was to establish the spatial distribution of *A. cordatus* at different spatial scales.

METHODS

Exploratory phase. Exploration using SCUBA diving and dredging (Charcot dredge) was made at different scales (Fig. 1): firstly at the island scale to evaluate the overall distribution of *Abatus cordatus* around Kerguelen; secondly at the scale of a large gulf with numerous scattered islands (Golfe du Morbihan); and thirdly at a bay scale. Densities of *A. cordatus* were estimated and density indices were attributed to each site: low (<5 ind. m^{-2}), medium (5 to 20 ind. m^{-2}) and high density (>20 ind. m^{-2}). The type of substratum was recorded.

Density transects: density and vertical and horizontal patterns of distribution. After the exploratory phase, 3 major study areas (Ile Haute, Anse du Halage and Port Couvreux, respectively Sites 5, 12 and 17 in Fig. 1), were selected for their high population densities. These are the locations of ecological and physiological studies (Magniez 1980, Schatt 1985, Mespoulhé 1992). At the 3 sites, we examined a transect of 50 or 100 m length from the beach towards the open sea, until the echinoid density was zero.
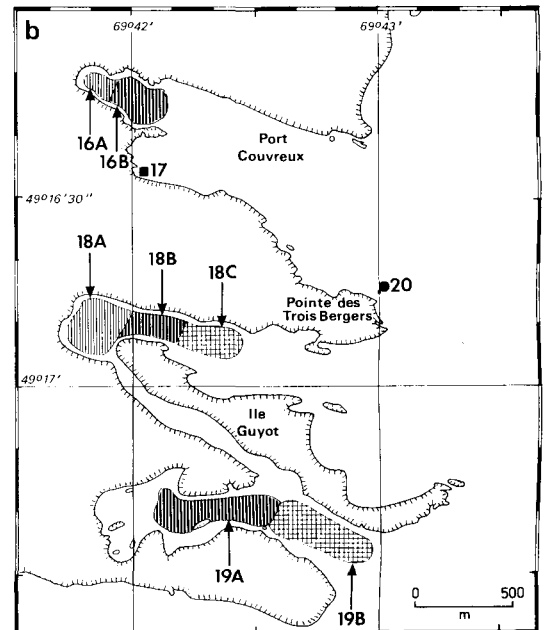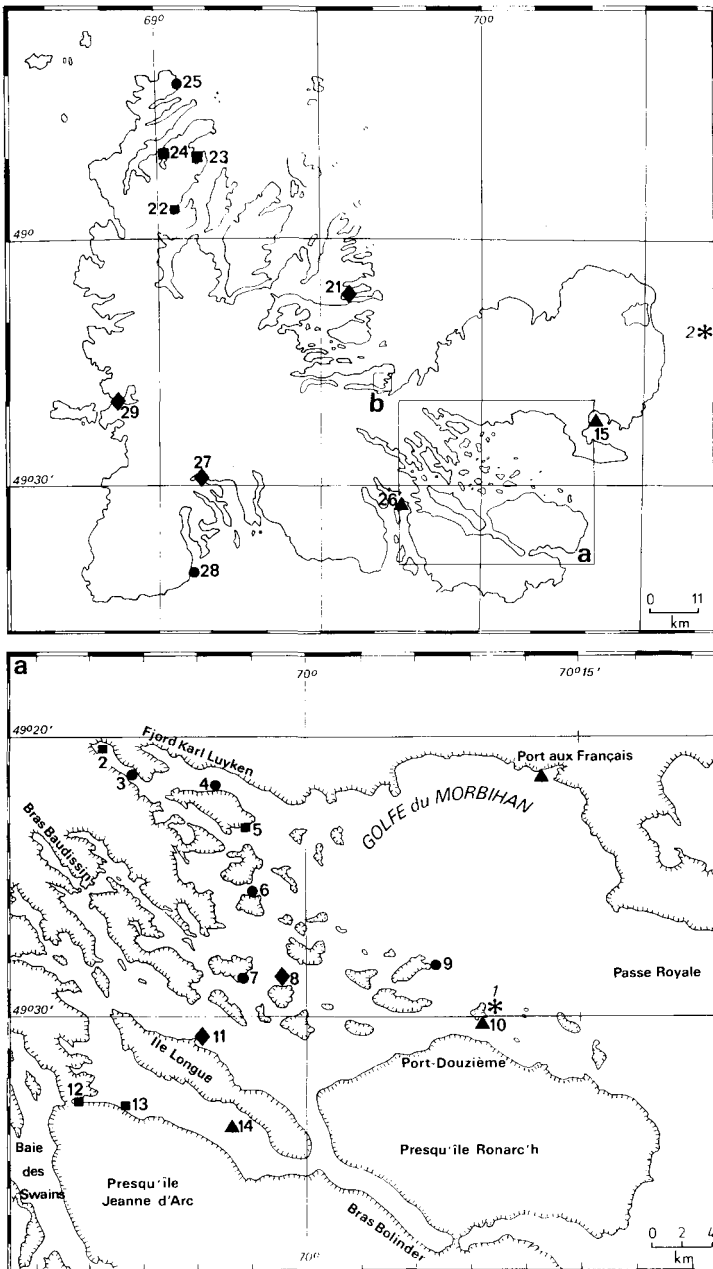
Fig. 1. Distribution pattern of *Abatus cordatus* around the Kerguelen Islands. (a) Golfe du Morbihan. (b) Bras de la Fonderie. Numbers correspond to the sites described in Table 1

Quadrats (0.5 m^2) were made every 10 m, or more frequently if a topographical change occurred (e.g. slope break, substrate texture, algal cover). All individuals found were removed from each quadrat and counted. This procedure of sampling by hand could underestimate the density of small individuals. Corresponding depths were regularly recorded with an electronic depth gauge in order to draw bottom profiles. Depths were calculated from the equinoctial low water. Major features of the substratum and of algal composition and density were also noted.

At Ile Haute a second perpendicular transect was carried out to circumscribe the population. Data from the 2 perpendicular transects were extrapolated to produce 3-dimensional plots of density and of bottom topography at this site. We used a gridding method, which uses geostatistical techniques to calculate the autocorrelation between data points and produce a minimal variance unbiased estimate ('kriging' option, SURFER Access System, Golden Software, Inc., Golden, CO, USA).

At Port Couvreux we repeated the same transect 1 yr later to establish the stability of the spatial distribution of high population densities.

Sediment sampling and analysis. Substrate samples (core-box, 5 cm^2) from the upper 5 to 6 cm were taken at the location of the highest density of *Abatus cordatus* at Ile Haute, Anse du Halage and Port Couvreux to evaluate the particle size composition of the substratum. The localities of these sites are shown in Fig. 1. The particle-size frequency distribution were obtained by sieving the dried sediment through a series of sieves (50, 100, 250, 400, 630, 1000 and 2000 μm).

RESULTS

Distribution patterns

Abatus cordatus is distributed all around the Kerguelen Islands (Fig. 1, Table 1). However, high density populations are found principally in sectors where the coastline is jagged and where bays are abundant (northwestern sector and Golfe du Morbihan). Only scattered and isolated individuals were found on the west coast (Site 29) which is swept by strong swell, and on the poorly jagged east coastline.

Investigations on the spatial distribution of *Abatus cordatus* at different scales indicate that discontinuities in the distribution occur at 2 levels: firstly, at the island level, where favourable sectors are separated by linear coastline or swell exposed sectors; secondly, at a smaller scale, where *A. cordatus* is distributed in small populations. Indeed, populations are generally characterised by high-density, isolated aggregations (up to 70 mature ind. per 0.5 m^2) in favourable sites, in shallow water at the bottom of sheltered bays (Fig. 1b). However, isolated individuals were observed during SCUBA diving at up to 25 m depth on muddy sand, and have been reported down to 560 m depth (De Ridder et al. 1993) around Kerguelen.

Transects

Fig. 2 shows densities of mature *Abatus cordatus* along bottom profiles. At Ile Haute (Fig. 2a), the density increases rapidly in the subtidal zone to a maximum (34 ind. per 0.5 m^2) at 0.2 m depth. Twenty metres from
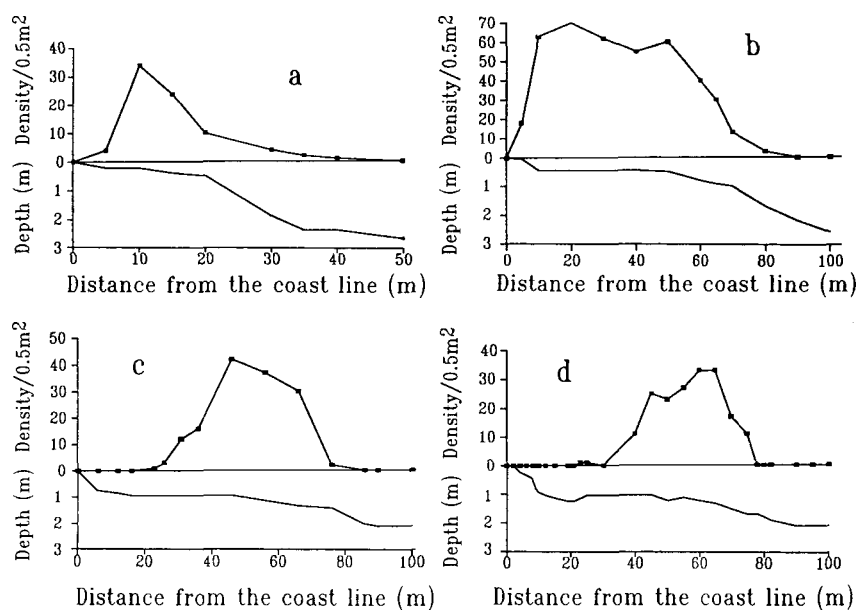

Fig. 2. Density (top line) and topography (bottom line) profiles along transects. (a) Ile Haute; (b) Anse du Halage; (c) Port Couvreux (1991); (d) Port Couvreux (1992)

Table 1. Characteristics of sites where *Abatus cordatus* was found by SCUBA divers. Density index: low, <5 ind. m^{-2}; medium, 5 to 20 ind. m^{-2}; high, > 20 ind. m^{-2}. Site numbers are shown in Fig. 1. *Sites from this study

No.	Site	Presence	Density index	Depth (m)	Biotope
1A	Port Aux Français	No	–	0–5	Kelp forest
1B	Port Aux Français	No	–	6	Mud
1C	Port Aux Français	Yes	Medium	8	Muddy sand
1D	Port Aux Français	No	–	25	Mud
2A	Port Raymond	Yes	High	1–2	Sand
2B	Port Raymond	Yes	Low	5	Mud
3	Anse de Saint Malo	No	–	0–26	Mud
4	Bras Karl Luyken	No	–	0–20	Mud
5A	Ile Haute*	Yes	High	0–2	Sand
5B	Ile Haute	No	–	12	Kelp forest
5C	Ile Haute	No	–	0–12	Rocks
5D	Anse des Rennes	No	–	0–14	Rocks
6	Ile Heugh	No	–	0–21	Mud
7	Ile Mayes	No	–	0–20	Mud
8	Ile Blackney	Yes	Low	0–10	Muddy sand
9	Ile du Chat	No	–	0–20	Rocks
10A	Ile Shum	Yes	Medium	15	Muddy sand
10B	Ile Shum	No	–	0–24	Mud
11	Port Bizet	Yes	Low	0–20	Muddy sand
12	Anse du Halage*	Yes	High	0–2	Sand
13A	Port Jeanne D'Arc	Yes	High	0–3	Sand
13B	Port Jeanne D'Arc	No	–	7–25	Mud
14A	Ilots Glénan	Yes	Medium	20	Mud
14B	Ilots Glénan	No	–	20–30	Mud
15A	Chateau d'If	No	–	4	Muddy sand
15B	Baie Norvegienne	Yes	Medium	3	Sand
16A	Anse Caron	Yes	High	0–2	Sand
16B	Anse Caron	Yes	Low	10–15	Mud
17	Port Couvreux*	Yes	High	0–2	Sand
18A	Anse Aldebert	Yes	High	0–2	Sand
18B	Anse Aldebert	Yes	Medium	3–8	Sand
18C	Anse Aldebert	No	–	15	Kelp forest
19A	Anse Thomas	Yes	Medium	6	Sand
19B	Anse Thomas	No	–	7–12	Muddy sand
20	Ilot des Trois Bergers	No	–	0–30	Rocks
21	Baie du Hopful	Yes	Low	5–25	Muddy sand
22A	Port Matha	Yes	High	0–2	Sand
22B	Port Matha	Yes	Medium	4–8	Mud
22C	Port Matha	No	–	10–22	Muddy sand
23A	Baie du Brise–Lames	Yes	High	0–2	Sand
23B	Baie du Brise–Lames	Yes	High	4–5	Sand
23C	Baie du Brise–Lames	No	–	3–13	Kelp forest
24A	Anse du Jardin	Yes	High	0–2	Sand
24B	Anse du Jardin	Yes	Low	10–27	Muddy sand
25	Port Chrismas	No	–	13–20	Muddy sand
26	Baie des Swains	Yes	Medium	0–3	Sand
27A	Fjord des Portes Noires	No	–	0–6	Mud
27B	Fjord des Portes Noires	Yes	Low	0–25	Mud
28	Anse de Larmor	No	–	0–1	Sand
29A	Baie du Noroît	No	–	0–5	Sand
29B	Baie du Noroît	No	–	0–3	Sand
29C	Pointe Berger	Yes	Low	0–8	Sand
30	Baie de la Mouche	Yes	High	0–2	Sand

the coast, the bottom drops rapidly from 0.5 to 2.5 m and *A. cordatus* become progressively more isolated.

At Anse du Halage (Fig. 2b), the distribution profile is similar to the preceding one, although the high den-sity area is much wider and the density itself is twice as great (70 ind. per 0.5 m^2). Again, the decrease of *Abatus cordatus* density is correlated with a change in the bottom profile.
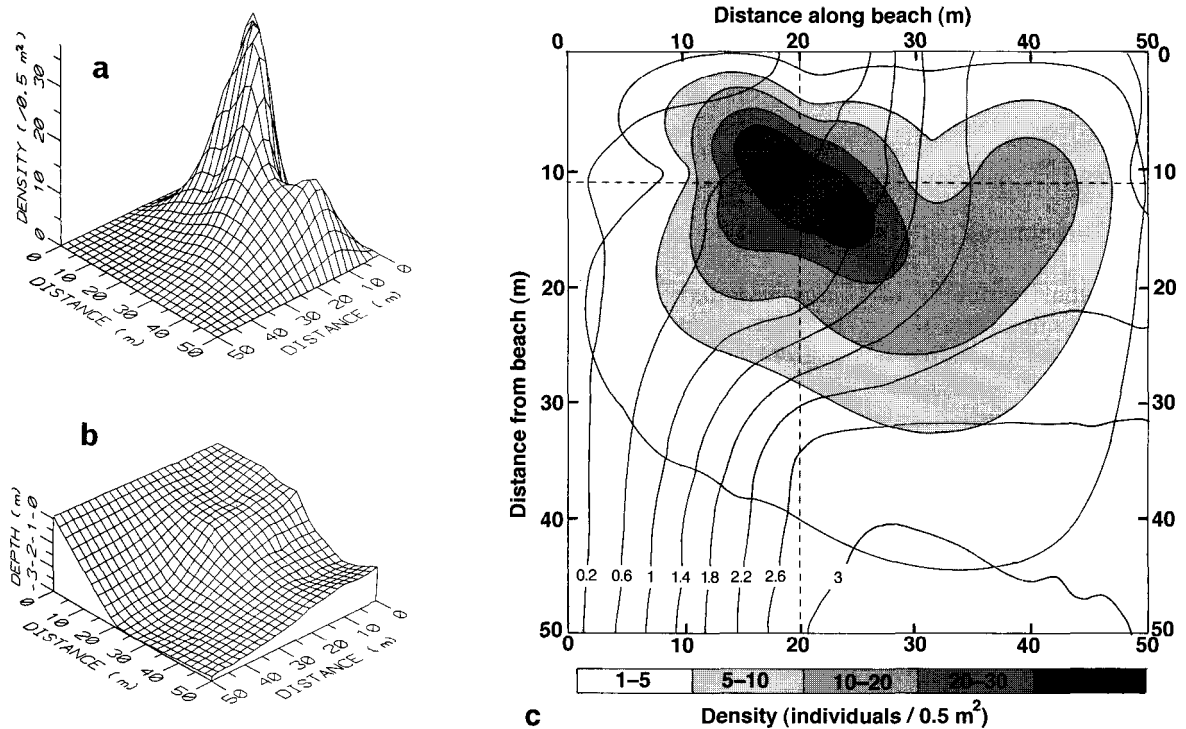
Fig. 3. Three-dimensional plot of (a) *Abatus cordatus* density and (b) topography of the site based on 2 perpendicular transects at the Ile Haute (SURFER 'kriging' option). (c) Two-dimensional representation of *A. cordatus* density distribution at Ile Haute. Levels of grey show density (ind. per 0.5 m²); (———) isobaths (m); (————) transect lines

At Port Couvreux (Fig. 2c), the peak of density is deeper (1.5 m) and the first individuals encountered are 20 m from the coastline. However, the lower limit is unchanged and the density also decreases greatly when the depth reaches 2 m. One year later (Fig. 2d), the distribution profile was relatively unchanged but the bottom profile shows some differences along the first 30 m of the transect, indicating a marked influence of the hydrodynamic activity of the area. This was confirmed by the observation of deep ripple marks in 1991 and 1992.

In all areas, *Abatus cordatus* showed a peak of density in the shallow subtidal zone. At Ile Haute and Anse du Halage, these peaks began not far below the lower tide level while it was typically deeper at Port Couvreux. Field observations showed that *A. cordatus* was not found in high energy sites (west and northeastern coasts).

The occurrence of *Abatus cordatus* is shown in terms of 3-dimensional plots of density (Fig. 3a), bottom topography (Fig. 3b) at Ile Haute, and 2-dimensional projections (Fig. 3c). Most of the population is localised on a small plateau between 0.2 and 1 m depth and the entire population lives on a 2500 m² surface. The estimated density was 10 to 15 × 10³ mature individuals at this site (test length >27 mm for females and 19 mm for males; Magniez 1980).

Particle size distribution

The particle size distributions of the substrata of the 3 high density areas are shown in Fig. 4. At Ile Haute and Anse du Halage the sediment in which *Abatus cordatus* was found falls within the limits of sand (2.0 to 0.063 mm grain size) with medium to fine/medium
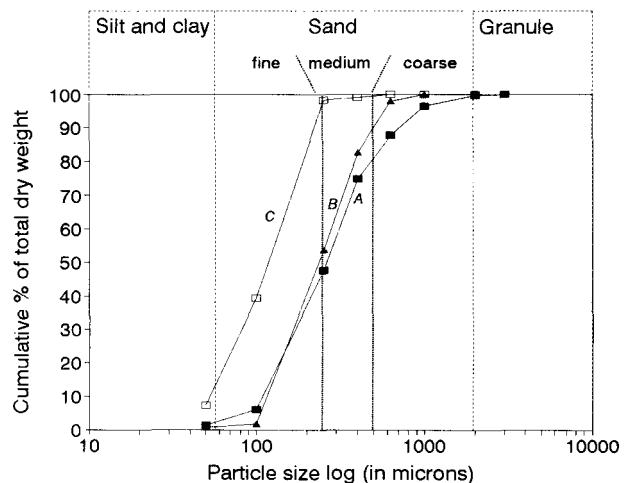

Fig. 4. Size frequency distribution (in cumulative percent) of the substrata of: A, Ile Haute (■); B, Anse du Halage (▲); C, Port Couvreux (□)

sand grades predominant. At Port Couvreux samples were characterised by a finer sand, with a low percentage of silt and clay (<20%).

DISCUSSION

Distribution pattern and habitat limits

The spatial distribution of *Abatus cordatus* is characterised by numerous, dense, isolated populations in shallow water (0 to 3 m) and scattered individuals to 560 m depth. This dispersed distribution in high density demes appears to be the consequence of a specific habitat. The upper limit is the lowest tide level in sheltered sites, or the depth limit of swell action in less sheltered sites, as in Port Couvreux. Indeed Ile Haute and Anse du Halage are very sheltered but Port Couvreux is more exposed to the swell. These data indicate that *A. cordatus* is intolerant of wave action and the displacement of the peak of density to a deeper zone at Port Couvreux may be related to this factor. Generally density decreases rapidly at less than 2 m depth. The particle size composition of the substratum is usually a primary factor determining the habitat of deposit-feeders. It influences both respiratory and locomotory functions (Lopez & Levinton 1987).

Since *Abatus cordatus* lacks a sophisticated respiratory-current-producing mechanism such as a respiratory funnel or sanitary drain, it could be limited to coarse sediments in shallow waters because of the need to maintain sufficient water flow (Higgins 1974). The relatively large pore space in coarse, well-sorted sediment probably allows a better flow of oxygenated water. As in many other spatangoids (see Chesher 1969 for a review; Ferber & Lawrence 1976, Schinner 1993), *A. cordatus* emerges from the sand under conditions of oxygen deprivation in aquaria, when water circulation stops. In general, irregular echinoids, which inhabit fine sediments, excavate specialised respiratory connections with the surface (De Ridder 1982, Kanazawa 1991). The oxygen consumption rate of *A. cordatus* (Guille & Lasserre 1979, Magniez & Féral 1988) is comparable to that of the urchin *Cassidulus caribbearum* (Gladfelter 1978). This is relatively high compared to other burrowing echinoids (Webster 1975, Gladfelter 1978, Magniez & Féral 1988). It also supports the idea that, like *Cassidulus* spp., *A. cordatus* is limited to well-aerated substrata (Gladfelter 1978, Freire et al. 1992).

A number of irregular echinoid species show a decrease of burrowing and locomotory abilities in finer sediments (Lawrence & Ferber 1971, Ferber & Lawrence 1976, Lawrence & Murdoch 1977). *Abatus cordatus* could also have such problems when the sed-

iment becomes finer with increasing depth. Therefore, the substratum particle size may be a limiting factor controlling the localisation of high density populations.

In addition to abiotic constraints which determine the range of the habitat, biotic factors such as interspecific competition (Thompson 1982) and predation can affect distribution patterns. Generally, when prey display an aggregated spatial pattern, predators concentrate their feeding in the richest patches and tend to equalise prey density (Schneider 1978, Sih 1982, Botton 1984). Predation on *Abatus cordatus* was never observed in the field but organic parts of broken specimens are rapidly eaten by *Serolis* spp. (Isopoda: Crustacea) that are very abundant in the subtidal area. It seems unlikely that they attack healthy individuals but perhaps they prey on very young ones. Gulls *Larus dominicanus* are potential predators because of the low depth at low tide at which the highest densities of *A. cordatus* are found, but predation has not been observed. The burrowing habits of *A. cordatus* make them invisible for predatory birds. Gastropods are frequently described as important predators for irregular echinoids (Chesher 1969, Dix 1970, Hughes & Hughes 1971 1981, Gladfelter 1978, McClintock & Marion 1993) but the lack of holes in beached tests indicates that they are not predators of *A. cordatus*. It is therefore probable that predation does not contribute to the spatial distribution of *A. cordatus*. Likewise interspecific competition certainly does not play a role on spatial pattern because of the quasi-monospecific pattern of populations.

The presence of high density populations of *Abatus cordatus* is probably determined by the nature of the substrata and lack of turbulence. The occurrence of scattered individuals in the adjacent deeper zones and generally with different types of substrata (often muddy sediments) indicate that *A. cordatus* can live in very different habitats, but these individuals are often found on the surface of the sediment (Fig. 5). Moreover, the absence of small individuals in these areas suggests recruitment is very low or absent in such places and that high density zones function as nurseries. The movement towards deeper zones could arise when the individuals are large enough to manipulate different substrata, as suggested by Lawrence & Ferber (1971) for *Lovenia elongata*, or young could remain stationary during the early period of growth as proposed by Chesher (1969) for *Meoma ventricosa*.

Distribution pattern and non-dispersal strategy

Some authors (Jackson 1968, Carlon & Olson 1993) have considered larval dispersal distance as an explanation for adult spatial patterns. From this point of

Fig. 5. Videotape frame showing 2 specimens of *Abatus cordatus* (45 mm length) on the surface of a muddy sediment at Kerguelen (Pointe du Zodiac, extremity of the north coast of the Anse du Halage, 7 m depth) and 1 just below the surface of the sediment (arrow)

Table 2. Optimal dispersal strategies under varying habitat heterogeneity and instability

	No perturbation	Perturbations
No spatial heterogeneity	No selection	Dispersal
Spatial heterogeneity	No dispersal	Mixed

view, an aggregated distribution may result from short larval dispersal time, simultaneous or gregarious settlement, or habitat selection by larvae. In the case of *Abatus cordatus*, if the brood-protecting strategy and the release of young on the bottom near their mother could produce high-density, isolated populations, the mobility of the burrowing echinoid would prevent population discontinuities. This hypothesis is therefore conceivable only for sessile organisms.

Another approach considers the scale of larval dispersal as the consequence of spatial and temporal habitat structure. Indeed, from a number of models, the heterogeneity and/or the instability of habitat have been recognised as fundamental features which accord with optimal dispersal strategies (Gadgil 1971, Roff 1974, Frank 1981, Hastings 1983, Hardin et al. 1990, McPeek & Holt 1992). Temporal variation of carrying capacities (which reaches zero in the case of extinction) will favour dispersion because of the necessity to recolonize free habitats. On the other hand, when spatial variability of carrying capacities increases, the probability for a propagule to reach a 'good' site decreases. Thus, the balance of temporal and spatial variations of carrying capacities of habitat determines an optimal dispersal strategy for the species. Table 2 shows the optimal dispersal strategies under varying

habitat heterogeneity and instability. The non-dispersal strategy is favoured only if the habitat is heterogeneous (in terms of low and high density sites) and if habitat is stable in time (in the sense of persistence).

In *Abatus cordatus*, if spatial heterogeneity seems clearly established because of the discontinuity of the habitat (dense, isolated demes), it is more difficult to prove the time-stability of those populations. However, we have some indications: (1) The high density populations are always found in sheltered bays where tidal currents and wave action are weak. Indeed this region is known for frequent storms, and the swells can be devastating for shallow sea-floor and beaches. (2) An indication of the time stability is given by a 10 yr study at the reference site Anse du Halage. We observed during this time neither a crash, nor an important variation in the density of *A. cordatus*. Moreover, a replicate of the transect in Port Couvreux 1 yr later showed no difference in the general distribution pattern of this species in spite of a modification of the topographic profile probably due to a limited swell. (3) Another indication is given by the age structure of the population observed at the Anse du Halage in December 1992. An exhaustive sampling of quadrats (2 m²) allows us to reconstruct an age pyramid that indicates a regular recruitment for at least 5 yr (Féral & Poulin 1994). As a result, *A. cordatus* fits the prediction of such models, and its non-dispersal strategy, in this case, is associated with a spatially varying but temporally constant habitat. Our case study thus contributes to an evaluation of models of dispersion, but does not substantially support them. Other examples are needed to validate the importance of temporal and spatial habitat structure on evolution of the dispersal strategies.

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