

***Caecum glabrum* (Montagu, 1803), gastropoda prosobranchia, and other meiofaunal taxa in the Skagerrak, West coast of Sweden**

Caecum glabrum (Montagu, 1803), gastéropode prosobranche,
et autres méiobenthontes du Skagerrak, côte occidentale de la Suède

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Mots clés : gastéropodes caecidés, interstitiel, mésopsammon, distribution, migrations.

ABSTRACT

Poizat C.H., M. Roux - *Caecum glabrum* (Montagu, 1803), gastropoda prosobranchia, and other meiofaunal taxa in the Skagerrak, West coast of Sweden. Mar. Life, **12** (1-2) : 37-46.

The distribution and short term variations in abundance of interstitial *Caecum glabrum* (Montagu, 1803) and other mesopsammonic organisms (copepoda, nematoda, halacaridea, etc.) were surveyed by means of numerical methods in July 1982 along a transect at Bonden Island in the mouth of the Gullmarfjord, on the Swedish coast. Stations were located at 5, 10, 15, 20 and 25 metres depth. Sediment analysis indicated that shallow stations were more influenced by violent and irregular effects of wave-induced currents, while the deepest stations were subject to a permanent local water stream recorded along the bottom (higher salinity > 33; lower temperature < 8 to 10°C, while the mean values at the surface were 20 (salinity) and 12°C). Variations in the distribution and abundance of the caecids and the other mesopsammonic groups (nematoda, copepoda, halacaridae, etc.) were found to be correlated to a greater or lesser degree with changes such as hydrodynamic conditions exposure.

RÉSUMÉ

Poizat C.H., M. Roux - [*Caecum glabrum* (Montagu, 1803), gastéropode prosobranche, et autres méiobenthontes du Skagerrak, côte occidentale de la Suède]. Mar. Life, **12** (1-2) : 37-46.

La distribution bathymétrique et les variations à court terme de *Caecum glabrum* (Montagu, 1803), prosobranche interstitiel, ainsi que de l'ensemble des assemblages mésopsammiques sont l'objet de ce travail. Cette étude fut réalisée en juillet 1982 dans des stations alignées suivant une radiale perpendiculaire au rivage de l'île de Bonden, Gullmarfjord, côte occidentale de la Suède. Cinq stations furent exploitées à 5, 10, 15, 20 et 25 mètres de profondeur et les données obtenues traitées à l'aide de méthodes numériques. La sédimentologie a montré que les deux stations superficielles, proches du rivage de l'île de Bonden, sont surtout sous l'influence de l'action irrégulière mais violente de courants et turbulences induits par les vagues, alors que les stations plus profondes sont surtout exposées à un courant régional permanent enregistré au niveau du fond (plus forte salinité > 33 contre 20 en surface ; plus faible température au fond < 8-10°C contre 12°C en surface). Corrélativement, la distribution et les variations d'abondance des caecidés et des autres organismes mésopsammiques (copépodes, nématodes, halacariens, etc.) s'accordent plus ou moins strictement avec l'évolution des conditions hydrodynamiques dans la région du Gullmarfjord.

INTRODUCTION

This work on interstitial caecid prosobranchs is the second part of research devoted to interstitial mollusks in the Skagerrak

area (Western coast of Sweden). The first part (Poizat, 1991) focussed on interstitial opisthobranchia from the same stations.

There are few ecological data on caecid prosobranchs worldwide, particularly data

concerning their bathymetric distribution, their population movements, their abundance and frequency relative to the other interstitial taxa. Therefore, the aim of this study was to monitor:

- the variation in the abundance of interstitial caecids, other mesopsammic mollusks (bivalvia, opisthobranchia, prosobranchia) and mesopsammic groups (nematoda, copepoda, halacaridea, etc) with depth;
- the relative frequency of the 3 caecid growth-stages (stages 1, 2 and 3 of Folin, 1875);
- the relative frequency of the caecids compared to the other mesopsammic groups;
- the possibility of short term migrations linked to the sudden hydrodynamic changes which occurred at the end of the period of observation.

MATERIAL AND METHODS

Study site

The study site was a West-East transect off Bonden Island (figure 1) in the mouth of the Gullmarfjord, Skagerrak, Western Sweden. Sediments and mesopsammon were sampled from five stations previously studied in 1973, 1974 and 1975 (Poizat, 1980) at depths of 5 m (station A); 10 m (B); 15 m (C); 20 m (D) and 25 m (E). Each station was visited three times: July 12, 19 and 26, 1982.

Gear and collecting technique

A single sample was taken at each station on each day. Each sample corresponded to a volume of 50 dm³ of sand which was collected with a Charcot dredge with a 60 cm wide and 25 cm high frame.

The use of a dredge rather than a corer is justified by the low abundances of the caecids (rarely more than 1500 ind.50 dm⁻³ sand: Arnaud, Poizat, 1981). This problem has been previously discussed (Picard, 1965: p. 7-12; Poizat, 1978: p. 19-23). The dredge bag was lined with 50 µm mesh size material to prevent sieving of the tiny mesopsammic organisms. The speed of the boat is very slow during the dredging operation in order to control the working of the gear. Visual observations indicate that the dredge penetrates this kind of porous sediment 8 to 10 cm (Picard, 1965: p. 8; Poizat, 1978: p. 23) and that the dredge bag is usually filled (50 dm³ of sediment) after a 100 cm haul, which roughly corresponds to a surface of 6,000 cm². At each station, the whole of the 50 dm³ sandy content of the dredge bag filled five buckets of 10 dm³ each. Salinity and temperature at the surface and on the bottom were measured on board (see caption figure 1). A permanent current was recorded along the bottom.

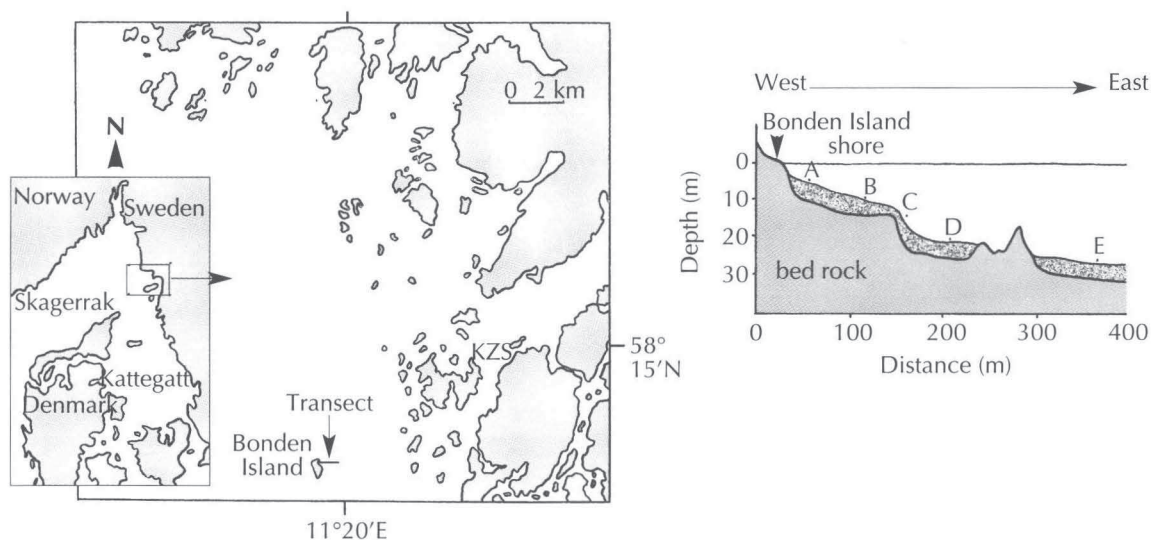


Figure 1 - Sampling area for interstitial caecid prosobranchia in the Skagerrak. Locations of stations A, B, C, D and E along the Bonden Island transect. KZS = Kristineberg Zoological Station. Drawing based on a depth-sounder recording. Temperature and salinity measured on board: from the surface to about 15 m depth, temperature > 12°C, salinity < 20; below 15 m, temperature < 8-10°C, salinity > 33. / Secteur de prélèvement des prosobranches caecidae dans le Skagerrak. Emplacement des stations A, B, C, D et E le long du transect à l'île de Bonden. KZS = Station Zoologique de Kristineberg. Profil réalisé à partir d'un enregistrement de bathygraphe. Température et salinité mesurées à bord : depuis la surface jusqu'à environ 15 m, température > 12°C, salinité < 20 ; en dessous de 15 m, température < 8-10°C, salinité > 33.

Sample processing

Back in the laboratory, each 10 dm³ subsample of sediment was immediately processed by means of a modified Uhlig sea-water ice technique (Uhlig *et al.*, 1973; Poizat, 1975) in order to extract the mesopsammon alive. After anaesthetization in nembutal 1g.L⁻¹ sea water (necessary to identify some of the organisms in relaxed conditions) and subsequently fixation of the fauna in Bouin Hollande and rinsing in fresh water in a 50 µm sieve, the interstitial caecid prosobranchs (dead shells excluded) were sorted and counted in Dollfus dishes, together with the other interstitial taxa. The abundance of the organisms in each 50 dm³ sediment sample was the sum of the five subsample abundances.

Mud content (% particles < 50 µm), calcimetry (% calcium carbonate) and grain size measurements of the sediment (by passing through a geometric series of test sieves with 0.5 φ intervals) were carried out. The sediment weight fractions (calculated in percent of the whole particles > 50 µm) were transformed into cumulative frequency series and then plotted as cumulative frequency curves. The following parameters were extracted from each curve: Q.5, Q.16, Q.25, Q.50, Q.75, Q.84 and Q.95 (in mm). They were converted into φ-scale equivalents (φ5, φ16, φ25, etc) and the following indices were calculated (see Higgins, Thiel, 1988: p. 65 and table 3):

- Median particle diameter

$$Mz \text{ (mm)} = \frac{Q.16 + Q.50 + Q.84}{3}$$
- Quartile Deviation

$$\Delta-\Phi \text{ (Delta-phi)} = \frac{\Phi75 - \Phi25}{2}$$
- Standard Deviation

$$\sigma \text{ (Sigma)} = \frac{(\Phi84 - \Phi16)}{4} + \frac{(\Phi95 - \Phi5)}{6.6}$$
- Inclusive graphic skewness

$$SKI = \frac{\Phi16 - \Phi84}{2(\Phi84 - \Phi16)} - \frac{2\Phi50 + (\Phi5 + \Phi95) - 2\Phi50}{2(\Phi95 - \Phi5)}$$

These parameters and indices characterize the hydrodynamic regime at each station.

Numerical methods

Since samples were not replicated, the data were analysed by Principal Component Analysis including all environmental and faunal variables. Two usual non-parametric statistical procedures and two multivariate descriptive techniques were applied to analyse the collected data.

The Mann-Whitney test (Zar, 1984: p. 139) was employed to compare the abundances of the mesopsammic organisms between the shallow stations (A and B) and the deeper ones (C, D and E), one group of species at a time. In order to detect the possible migrations of the fauna, several 2x2 (four-fold) tables were built up. The stations were grouped

in two categories as above; the dates 12/07 and 19/07 made up the first period as opposed to the last date 26/07, with higher hydrodynamic activity. The Chi-square test (Zar, 1984: p. 64) was then applied (one degree of freedom) to check the independence between time and depth.

As a global approach, Correspondence Analysis (C.A.: Gauch, 1982; Greenacre, 1984; Digby, Kempton, 1987) was used with the samples by species data table, containing the numbers of sampled animals; on the other hand, the Principal Component Analysis (P.C.A.: Gauch, 1982; Digby, Kempton, 1987) was applied to environmental measurements.

RESULTS AND DISCUSSION

Caecid prosobranch collected and biological observations

Only one species of interstitial caecid was collected and identified: *Caecum glabrum* (Montagu, 1803) in conformity to the Swedish species features (Fretter, Graham, 1978: p. 234) white shell marked by slight rings, with circular aperture, convex yellow operculum. *Caecum glabrum* is an Atlantic species (van Aartsen, 1977). It was represented by its three Folin's growth stages (Folin, 1875), (figure 2):

- stage 1: including spiral protoconch with an uncoiled portion (figure 2A);
- stage 2: frequently still attached to a young stage 3 which subsequently becomes free (figure 2B);
- stage 3: adult stage with septum and operculum (figure 2C).

Living stage 3 were encrusted to a greater or lesser extent by epibiotic algae or perhaps bacteria. These encrustations consisted of either orange yellow or brown spots scattered on the white shell (figures 2B, 2D and 2E); or large brown patches which sometimes covered the whole shell (figures 2C and 2F), giving it a dark-brown colour. These encrusting organisms, absent from living stage 1 and rare on stage 2, were observed on 44% of the living stage 3 at station A (5 m); 36% at station B (10 m); 35% at station C (15 m); 25% at station D (20 m) and finally, 36% at station E (25 m). In contrast, adult dead shells were rarely or not encrusted at all, except a few specimens (recently dead?) with some orange-yellow spots at station E. This is probably due to the continuous rearrangement of the sand particles by currents, eroding the surface of the passive dead stage 3 shell, free at the surface of the sand beds, while the living stage 3 animals are able to shelter (by downward migrations in the sand) and therefore protect their epibiotic covering. These "moving grazings" are thought to play an original (if very limited) part in the food chain because they can be occasionally used as food by mesopsammic herbivores. Halacarids are frequently found clinging on the incrustated shells.

A further observation peculiar to the dead adult shells was that they were frequently bored (figures 2F and 2G), probably by small

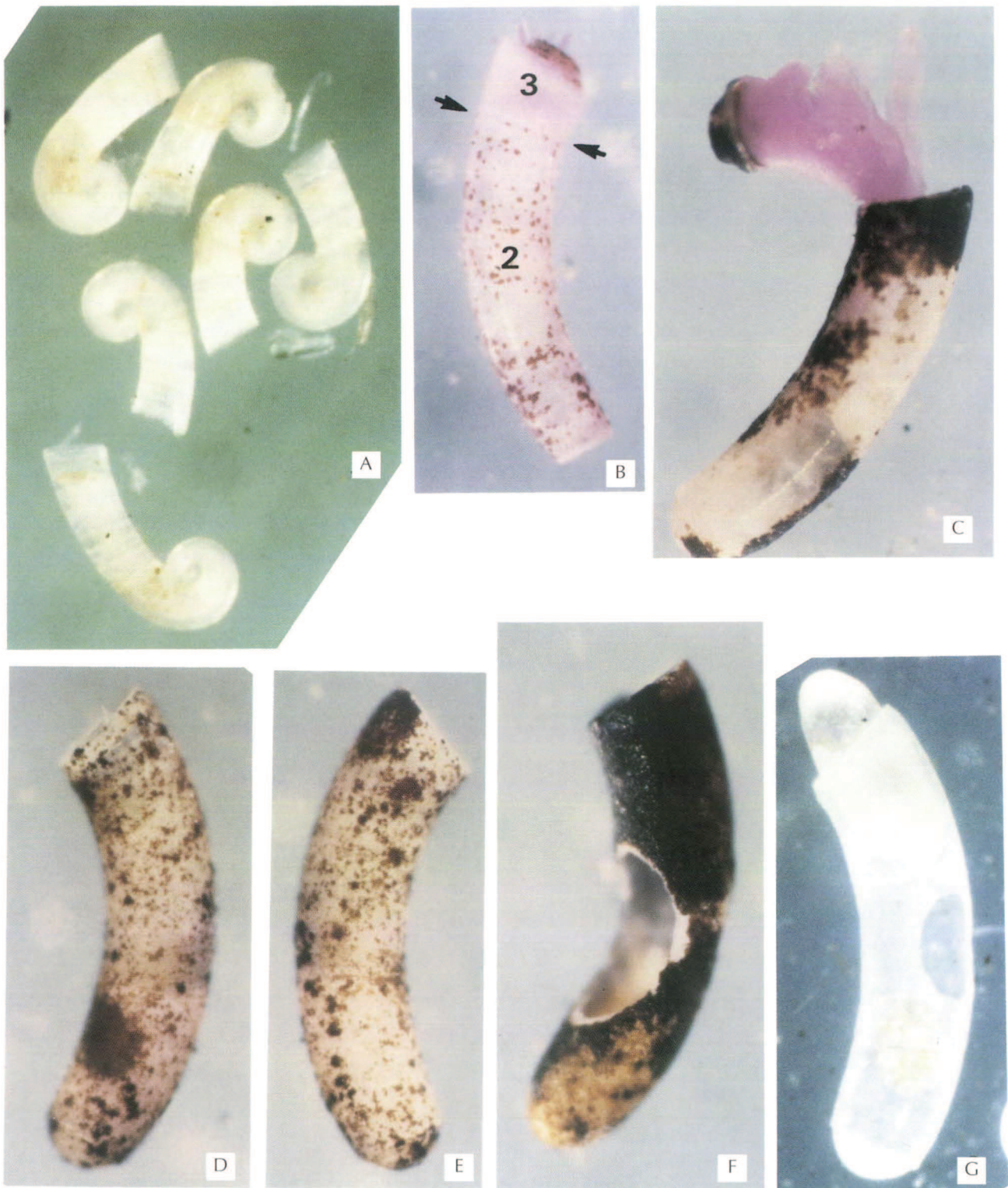


Figure 2 - *Caecum glabrum* (Montagu, 1803). A: growth stage 1 with uncoiled portion, L = 0.5 mm; B: growth stages 2 and 3 still together, L = 1.2 mm; C: growth stage 3, in relaxed position (anaesthetized in nembutal 1g.L⁻¹ sea water), L = 1.8 mm, shell encrusted with bacteria? cyanobacteria? or diatoms? ; D and E: stages 3 with slightly encrusted shell; F: bored dead shell wholly encrusted; G: bored dead shell without encrustation (old shell). Artificial pink colour due to Rose Bengal for B and C. (photos C. Poizat). / *Caecum glabrum* (Montagu, 1803). A : stade 1 partiellement déroulé, L = 0,5 mm ; B : stades 2 et 3 encore attachés, L = 1,2 mm ; C : stade 3, en extension (sous anesthésie dans le nembutal 1g.L⁻¹ d'eau de mer), L = 1,8 mm, coquille encroûtée par des bactéries ? cyanobactéries ? ou diatomées ? ; D et E : stades 3 avec coquilles faiblement encroûtées ; F : coquille morte perforée totalement encroûtée ; G : coquille morte perforée sans encroûtement (vieille coquille). Coloration au Rose Bengale pour B et C. (photos C. Poizat).

macrobenthic carnivorous gastropoda: at the superficial stations A, B and C, 27-29% of the dead shells were bored; while up to 33-36% were bored at stations D and E. These observations show that predation upon interstitial organisms such as caecids does occur and that these interstitial caecids play a direct (if limited) part in the food chain which supposedly links mesopsammon and macrofauna. Sometimes caecids can represent 10 to 20% or more of the micromollusks in many shallow-water locations (Moore, 1972) and therefore their part in the food chain is less negligible.

The occurrence of living growth stages 1 and 2 at all stations during the period of observation (July 1982) confirms that breeding does occur in late Spring through Summer as stated by Fretter and Graham (1978: p. 234). Caecid larvae are common in the Summer and Autumn Plymouth plankton (Lebour, 1936). In the Mediterranean, recruitment of the juveniles (growth-stage 1) occurs in Autumn and Winter, while growth-stages 2 and 3 are abundant all the year round, with a peak in Spring, the mating and spawning season (Poizat, Arnaud, 1992).

Distribution of the mesopsammic assemblages with depth

Abundances of most groups are significantly linked to the depth of the stations, according to the Mann-Whitney test, except for the nematoda (table I and figures 3 and 4; see also table III at the end of this paper). Most of the caecid population was located between 15 m (station C) and 25 m (E) with "mode" at station C where they reached an average peak value of up to 1.87% (average abundance = 236 individuals.50 dm⁻³ sediment) of the total mesopsammon followed by a drop in the average abundance (59 ind.50 dm⁻³) at station D (20 m). At station D, there is in fact a predominance of fine particles in the sand, while the deepest station E (25 m) seems more exposed to a permanent regional underwater stream (recorded in 1982: Poizat, 1991) and therefore to be more favourable to caecid prosobranchs (189 ind.50 dm⁻³). Caecids are known to be particularly linked to coarse *Amphioxus* sands (Götze, 1938; Arnaud, Poizat, 1981) where hydrodynamism is very strong. In contrast to the interstitial opisthobranch assemblage, the mode of which is at station D (average abundance = 299 ind.50 dm⁻³ sand), Swedish caecids proved also to be linked to coarser sediment (Mz = 1.64 mm) and therefore to higher and more stable current speeds (permanent regional water stream along the bottom). The other mesopsammic mollusks included prosobranchia, bivalvia and polyplacophora, all of them as temporary members of the mesopsammon.

From the shallow station A (with average mesopsammon abundance = 35,705 ind.50 dm⁻³ sediment) there is a progressive drop in the abundance of the total mesopsammon to a minimum (11,968 ind.50 dm⁻³) at station C which is, however, the most favourable station for the caecids

Table I - Relations between abundances and depths: results of the Mann-Whitney test. (NS: not significant; *: significant at the 0.05 level; **: significant at the 0.01 level; ***: significant at the 0.001 level). / Relations entre les abondances et les profondeurs : résultats du test de Mann-Whitney (NS : non significatif ; * : significatif au niveau 0,05 ; ** : significatif au niveau 0,01 ; *** : significatif au niveau 0,001).

	Observed U	Prob U<U obs	Significance
<i>Caecum glabrum</i>	7	0.0088	**
opisthobranchia	7	0.0088	**
bivalvia	0	0.0002	***
prosobranchia	3	0.0014	**
copepoda	8	0.0128	*
nematoda	23	0.3035	NS
others			
(halacaroida, etc.)	6	0.0060	**
total mesopsammon	7	0.0088	**

Table II - Contingency table for the bivalvia group. Chi-square = 30.4, highly significant. / Table de contingence pour les bivalves. Chi-carré = 30,4, hautement significatif.

Station	12/07/82 and 19/07/82 (calm sea)	26/07/82 (rough sea)
A+B	2,082	785
C+D+E	757	170

(table III). This drop in the average abundance of the mesopsammic taxa toward station C is presumably due to the thinning down of the sand bed as a result of a change of slope of the bedrock (figures 1 and 7): narrowing the vertical sandy space. The copepoda, which live in oxygenated conditions, are of course dominant (63% with average abundance of 23,285 ind.50 dm⁻³) at station A, close to the shore line, and remain relatively abundant along the transect, in contrast to the nematoda (5,731 ind.50 dm⁻³) which are more tolerant to anoxic conditions and need plenty of organic detritus and therefore less water movement.

Short term variations of the mesopsammic assemblages

The period of observation and sampling was from July 12 to July 26, 1982. From July 12 to July 19, there was most of the time a calm sea. On and after July 19 the weather became windy and rainy and the sea was rough, sometimes very rough, with normal magnitude for the season. So, our purpose was to check whether this event led to rapid changes in sedimentary conditions and therefore, in the distribution of the mesopsammic groups.

Both Chi-square contingency test and correspondence analysis (CA) were used for this purpose. The contingency tables were made up of two rows and two columns: row 1 represented

Table III - Biological data: abundance (ind.50 dm³ sand) of the mesopsammic organisms: *Caecum glabrum*, opisthobranchia, bivalvia, prosobranchia, copepoda, nematoda. "Others" includes turbellaria, nemertina, polychaeta, ostracoda, isopoda, halacaroidea, etc. Environmental data (sedimentology: see "sample processing" at the beginning of the paper). / *Données biologiques : abondance (ind.50 dm³ de sable) des organismes mésopsammiques : Caecum glabrum, opisthobranches, bivalves, prosobranches, copépodes, nématodes. "Others" comprend les turbellariés, les némerites, les polychètes, les ostracodes, les isopodes et les halacariens. Données environnementales (sédimentologie : voir "exploitation des prélèvements" au début de cet article).*

Station and date	<i>C. glabrum</i>	Opisthobranchia	Bivalvia	Prosobranchia	Copepoda	Nematoda	Others	TOTAL (ind.50 dm ³)
A12	35	25	405	1,500	41,945	4,460	5,340	53,710
A19	12	12	427	987	15,935	980	3,747	22,100
A26	5	5	470	1,770	11,975	11,755	5,325	31,305
Average	17	14	434	1,419	23,285	5,731	4,805	35,705
B12	45	60	555	670	23,415	4,510	8,040	37,295
B19	93	39	695	877	14,492	1,227	4,694	22,117
B26	15	10	315	210	10,125	8,450	2,290	21,415
Average	51	36	522	586	16,010	4,729	5,008	26,942
C12	420	40	155	900	6,465	2,535	2,660	13,175
C19	215	86	212	115	9,730	2,015	2,882	15,255
C26	75	35	85	65	4,675	1,060	1,480	7,475
Average	236	53	151	360	6,956	1,870	2,342	11,968
D12	45	310	115	75	9,725	5,110	2,300	17,680
D19	117	516	95	25	15,647	2,997	2,440	21,837
D26	15	70	70	30	6,175	1,245	1,640	9,245
Average	59	299	93	43	10,516	3,117	2,126	16,252
E12	150	355	110	25	10,970	14,910	2,575	29,095
E19	332	241	70	85	22,995	4,455	2,589	30,767
E26	85	10	15	35	6,295	4,250	2,015	12,705
Average	189	202	65	48	13,420	7,871	2,394	24,189

Station and date	CaCO ₃ %	Minerals %	Mud %	Mz (mm)	Delta-phi	Sigma	Ski
A12	98.75	1.25	4.47	2.18	0.93	1.34	0.14+
A19	99.21	0.79	3.53	2.57	1.05	1.33	0.01+
A26	97.96	2.04	2.61	3.48	1.60	1.32	0.50+
Average	98.64	1.36	3.54	2.74	1.19	1.33	0.22+
B12	96.81	3.19	7.34	1.21	0.90	1.33	0.48-
B19	94.82	5.18	4.55	2.26	0.85	1.28	0.03-
B26	89.52	10.48	4.82	1.58	1.13	1.59	0.50-
Average	93.72	6.28	5.57	1.68	0.96	1.40	0.34-
C12	95.71	4.29	2.41	1.99	0.90	1.21	0.27-
C19	91.67	8.33	2.46	1.44	0.75	1.14	0.45-
C26	76.88	23.12	2.32	1.49	0.78	1.18	0.42-
Average	88.09	11.91	2.40	1.64	0.81	1.18	0.38-
D12	76.74	23.26	0.85	1.53	0.73	1.16	0.43-
D19	79.76	20.24	1.57	1.36	0.78	1.13	0.57-
D26	66.84	33.16	1.16	1.20	0.78	1.21	0.67-
Average	74.45	25.55	1.19	1.36	0.76	1.17	0.56-
E12	98.53	1.47	2.59	1.05	0.38	0.63	0.48-
E19	96.67	3.33	3.52	1.48	0.63	0.90	0.21-
E26	91.54	8.46	2.05	1.39	0.58	0.87	0.30-
Average	95.58	4.42	2.72	1.31	0.53	0.80	0.33-

stations A and B, while row 2 represented stations C, D and E. The first column was for dates 12/07 and 19/07 = calm sea, while the second column was for date 26/07 = rough sea (see table II). Only three groups showed a significant link between time and depth of stations: bivalvia, prosobranchia and nematoda.

On the other hand, CA confirmed the difference between the beginning of the survey (12/07 and 19/07) and the end (26/07), as shown by points A26, B26 and E26 on the positive part of axis 1 (figures 3 and 4), essentially related to the nematoda displacements.

Such differences may be explained in term of changes in sedimentary conditions (figure 5 a and b).

An increase in grain size of the sediment (erosion) has been recorded at the shallow station A where Mz rose from 2.18 to 3.48 mm together with a correlated drop at the deepest ones by sedimentation of fine particles coming from above particularly at station D where Mz decreased from 1.53 to 1.20 mm (table III and figure 6).

Considering the whole mesopsammon of all five stations (figures 3 and 7; table III), the change in hydrodynamic conditions proved to affect significantly both the two shallow stations (A+B) and the deeper



Figure 3 - Correspondence analysis of biological data: fauna and dates. Axis 1 (68%) and 2 (18%). A12, A19, A26: station A in July 12, 19 and 26, 1982; B12, B19, B26: station B in July 12, 19 and 26; etc. (see "study area" above). / *Analyse de correspondance des données biologiques : faune et dates. Axe 1 (68%) et 2 (18%). A12, A19, A26 : station A, les 12, 19 et 26 juillet 1982 ; B12, B19, B26 : station B, les 12, 19 et 26 juillet ; etc. (voir "zone d'étude" plus haut).*

one (E) since their displacements are very significant particularly from July 19 to July 26, while stations C and D were less affected (weak displacements of C19/C26, D19/D26). This sudden drop in the abundance of the whole mesopsammon at Borden Island is of the same degree of magnitude as those recorded seasonally in similar biotopes of the Mediterranean: decrease by more than one half between Summer and Winter in the Gulf of Marseilles, from 43,300 ind.50 dm⁻³ sand in Summer down to 21,300 in Winter (Poizat, 1984: p.91) vs 53,710 ind.50 dm⁻³ at the Borden station A on the 12 July 1992 down to 31,305 ind.50 dm⁻³ on the 26 July (table III).

Focussing now on the behavioural response of each mesopsammic group confronted with rise of hydrodynamism, there are four categories of organisms (cf. Chi 2: figure 8):

- first category: *Caecum glabrum* + interstitial opisthobranchia + copepoda. It seems that these interstitial organisms do not react to the increase in hydrodynamic forces within the magnitude limits recorded during the survey period: the apparently strong decrease of their populations at all five stations (A+B+C+D+E) is not significant according to the contingency tables for the relations between time and depth. It must be emphasized that both interstitial caecids and opisthobranchs are particularly well adapted to the highly dynamic interstitial environment (Swedmark, 1964, 1968): mechanical protection by a shell (caecids) or spicules (opisthobranchia); adhesive capability thanks to epidermal mucus glands; all of them adaptive features enabling these animals to stay at the surface of their substrate or close to it, in spite of rising hydrodynamism (up to a certain degree of magnitude). However, it must be said that caecids and interstitial opisthobranchs from the

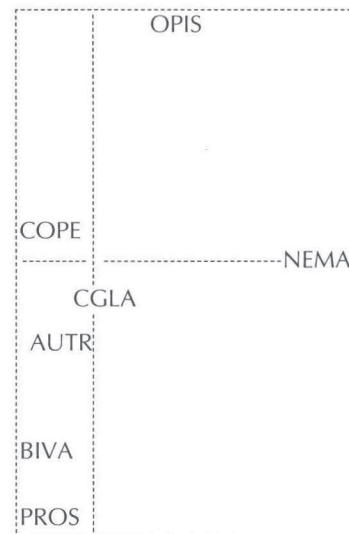


Figure 4 - Correspondence analysis of biological data: taxa. Axis 1 (68% of variance) and 2 (18% of variance). OPIS: opisthobranchia; COPE: copepoda; NEMA: nematoda; CGLA: *Caecum glabrum*; AUTR: other mesopsammic groups (halacaroida, nemertina, turbellaria, polychaeta, ostracoda, amphipoda, isopoda, etc.); BIVA: bivalvia; PROS: prosobranchia other than *Caecum*. / *Analyse de correspondance des données biologiques : taxa. Axes 1 (variance de 68%) et 2 (variance de 18%). OPIS : opisthobranches ; COPE : copépodes ; NEMA : nématodes ; CGLA : Caecum glabrum ; AUTR : autres groupes mésopsammiques (halacariens, némerites, turbellariés, polychètes, ostracodes, amphipodes, isopodes, etc.) ; BIVA : bivalves ; PROS : prosobranches autres que les Caecum.*

Mediterranean exhibit significant short-term variations in abundance due to the sudden increase in hydrodynamic forces (very rough sea during periods of strong Mistral or East wind) as well as seasonal variations of their populations (Arnaud, Poizat, 1979; Poizat, 1986) with a minimum in Winter (prolonged periods of high hydrodynamism) and a peak in Summer (prolonged calm periods);

- second category: temporary mesopsammic prosobranchia (juvenile specimens), characterized by a stronger decrease in the deep (C+D+E) stations than in the shallow ones (A+B). These mesopsammic organisms prove very mobile and therefore, when hydrodynamism is on the rise, they could indulge in significant (vertical or horizontal) migrations at all five stations in order to seek shelter in the deeper layers of their substrate. In addition, they could be partially buried in the deeper stations by particles coming from above. Such short-term migrations are well known for many meiobenthic animals living in the intertidal zone and are linked to variations of temperature (Renaud-Debyser, 1963); of light (Gray, 1966); of salinity (Bush, 1966). In contrast, very little information concerns migrations in subtidal meiobenthos (McIntyre, 1969; Poizat, 1983) and such migrations have rarely been proved in the field by previous ecological works

(Arnaud, Poizat, 1979). However, they do occur under experimental conditions: in the concentration devices used to separate the meiofauna from the substrate (Uhlig *et al.*, 1973). Such experimental downward migrations have been described (Poizat, 1975). Upward migrations have also been frequently observed by one of us (C. P.) in the "deterioration technique" devices (Uhlig *et al.*, 1973) operated to separate meiofauna from its sediment;

- third category: nematoda, characterized by a significant increase in the populations in the shallow stations (A+B) and a decrease in the deeper ones (C+D+E). These mesopsammic organisms do not appear to be particularly mobile and are known to strongly adhere to sediment particles and even tend to hide within sediment agglutinations (Higgins, Thiel, 1988: p. 293). Therefore, when hydrodynamic forces are on the rise, and consequently when their substrate is eroded, they appear to be passively exhumed (rise of abundance) at the shallow water stations, while they are passively buried (decrease of abundance) in the deeper stations by fine sedimentary particles coming from above (sedimentation);

- fourth category: temporary mesopsammic bivalvia (juvenile stages). Their populations decrease significantly in the shallow stations only. It is supposed that they are passively scattered towards bottoms other than the studied deeper ones, since their abundance does not rise there.

CONCLUSION

The caecid population of Bonden Island includes only one species: *Caecum glabrum* (Montagu, 1803). It is particularly linked to well-sorted, coarse sands, poor in mud particles and with a wide pore space. It exhibits its highest abundance between 15 and 25 m, where the permanent activity of a regional water stream is evident (low temperature, high salinity). These caecids can represent up to 1.87% of the mesopsammon. They directly represent a certain (limited) food source (at best 2% of the biomass) for other benthic animals (predation proved by bored shells). They are also indirectly involved in the food-web since they carry on their tiny shell algal or bacterial encrustations which could be occasionally grazed. Their breeding period is during the Summer months.

The whole mesopsammic assemblages are continuously changing along the Bonden Island transect, as a result of the erosion, transportation and deposition of the sediment by hydrodynamic factors: the permanent regional water stream recorded along the bottom at the deepest stations C, D and E, and unstable action of waves at the superficial stations A and B close to the shore line.

At the superficial stations, erosion (restructuration) of the substrate due to a rapid increase in hydrodynamism, corresponds to more or

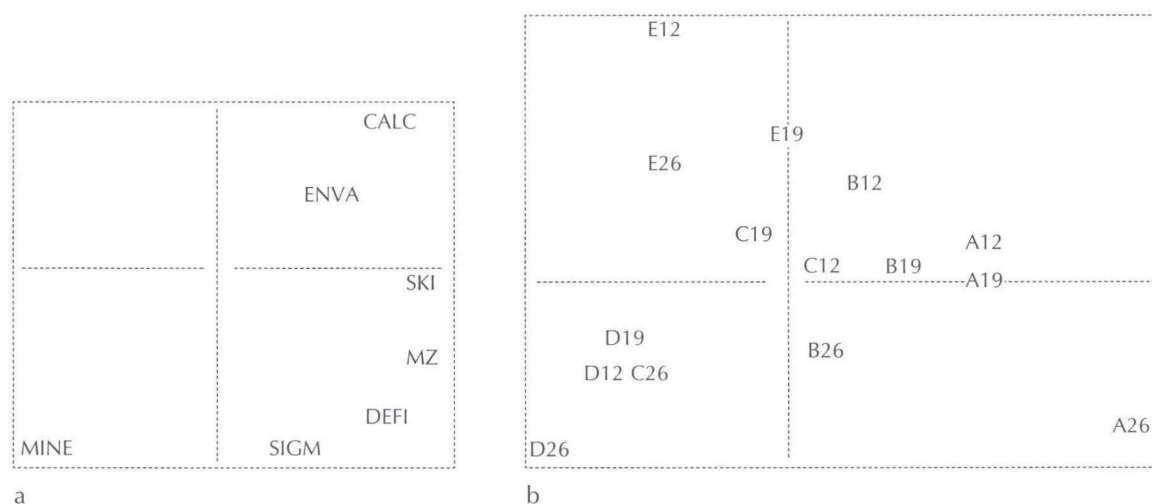


Figure 5 - Principal component analysis of environmental data (a) and biological data (b). Axis 1 (54% of variance) and 2 (26%). CALC: calcium carbonate content; ENVA: mud content (% particles < 50 μm); SKI: inclusive graphic skewness; MZ: medium particle diameter; DEFI: $\Delta\phi$ (quartile deviation); SIGM: σ (standard deviation); MINE: detritic mineral content (see "sample processing" above). Stations and dates: see caption to figure 3. / Analyse en composantes principales des données écologiques (a) et des données biologiques (b). Axes 1 (variance de 54%) et 2 (26%). CALC : teneur du sédiment en CaCO_3 ; ENVA : envasement (% de particules inférieures à 50 μm) ; SKI : indice de symétrie ; MZ : taille moyenne des particules ; DEFI : $\Delta\phi$ (indice de classement) ; SIGM : σ (indice de triage) ; MINE : % de minéraux détritiques (voir "exploitation des prélèvements" plus haut). Stations et dates : voir légende figure 3.

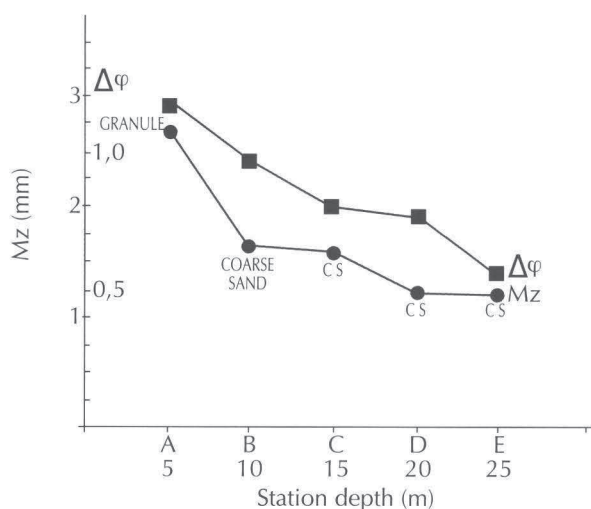


Figure 6 - Grain size distribution along the Bonden Island transect (the three sample dates mixed). Mz: median particle diameter (mm) :

$(Q_{.16}+Q_{.50}+Q_{.84})/3$; $\Delta\phi$: quartile deviation: $(\phi_{75}-\phi_{25})/2$

Répartition des catégories dimensionnelles de particules sédimentaires le long du transect de l'île de Bonden (pour les trois dates de prélèvement confondues).

Mz : taille moyenne (mm) :

$(Q_{.16}+Q_{.50}+Q_{.84})/3$; $\Delta\phi$: indice de classement : $(\phi_{75}-\phi_{25})/2$

less immediate and strong drop in abundance of the mesopsammon. This drop is due to a negative balancing of the different behavioural responses of the various mesopsammic animal groups confronted with the oceanographic changes: certain very mobile organisms (prosobranchia) could withdraw from the sediment-water interface by downward vertical migrations to escape from excessive

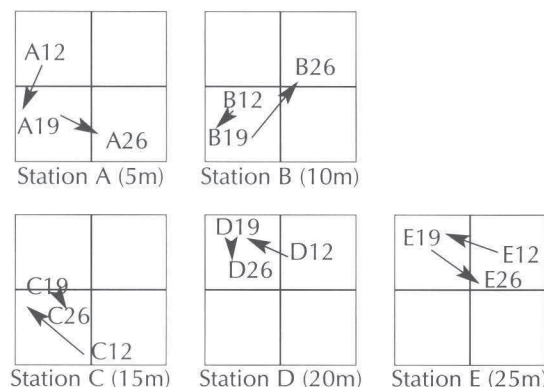


Figure 7 - Partial views of figure 3 showing the displacement of each station between July 12 and July 26, 1982. / Vue partielle de la figure 3 montrant le déplacement de chaque station entre le 12 et le 26 juillet 1982.

movement of the sand particles. In contrast, others (bivalvia) could be passively scattered toward deeper bottoms, while others (nematoda) could be passively exhumed.

At the deepest stations, the drop in abundance of the mesopsammon together with the increase in hydrodynamism, could be rather linked to the passive covering of all the mesopsammic organisms, by fine particles coming from shallow bottoms.

In contrast, at all the five stations, typical interstitial animals (caecids, opisthobranchs, copepods) paradoxically do not exhibit significant population variations when hydrodynamism is on the rise, probably because of their adaptative features (protective shell or spicules; adhesive cutaneous glands; etc.) which enable these organisms to cling to their substrate.

	12.07+19.07	26.07		12.07+19.07	26.07		12.07+19.07	26.07
A+B	185	30		136	15		2082	785
C+D+E	1279	175		1548	115		757	170
	Caecum glabrum Chi2 obs=0.6393 p=0.4239 NS			Opisthobranchia Chi2 obs=1.8959 p=0.1685 NS			Bivalvia** Chi2 obs=30.4 p<0.0001	
	12.07+19.07	26.07		12.07+19.07	26.07		12.07+19.07	26.07
A+B	4034	1980		95787	22100		11277	20205
C+D+E	1225	130		75532	17145		32022	6555
	Prosobranchia** Chi2 obs=294.5 p<0.0001			Copepoda Chi2 obs=2.088 p=0.1485 NS			Nematoda** Chi2 obs=16351 p<0.0001	

Figure 8 - Contingency tables for the relations between time and depth (NS: not significant). / Tables de contingence des relations entre le temps et la profondeur (NS : non significatif).

As a general conclusion, it must be emphasized that a mere increase in hydrodynamic forces can rapidly generate in shallow sediments (direct effects) as well as in deeper ones (indirect effects) more or less significant and durable perturbations (rise or drop in abundance) of certain mesopsammic groups. These facts must be remembered when a seasonal survey of mesopsammic organisms is to be carried out, since such accidental perturbations could mask the normal seasonal variation of the fauna.

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