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Microphytobenthic patches and their influence on meiofaunal distribution

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Abstract: Sampling was undertaken in an oligo-mesohaline area of the Gironde estuary (France) to investigate both if visually determined coloured patches at the sediment surface could be related to dense microphytobenthic populations and if these patches had a significant influence on meiofaunal distributions. Results clearly indicate that coloured patches are good indicators of higher sediment chlorophyll-a concentration, mainly due to vertically migrating pennate diatoms. Evidence of a significant effect of microphytobenthos patches over meiofaunal density was supported for the harpacticoid copepods *Microarthridion littorale* (attracted by the patches) and *Nannopus palustris* (lower densities within patches). Results from a distance test (3h after the formation of the patches) demonstrate that both nematodes and *Microarthridion littorale*, were attracted to patches within a radius of approximately 4 cm. Pigment analysis of copepod gut content and measurements of gut passage time for *Microarthridion littorale* indicated that animals inside patches exhibited higher feeding rates. This result was consistent with the density data and together with the background chlorophyll-a concentration clarifies previously conflicting literature.

Résumé : Des échantillonnages ont été effectués dans la zone oligo-mésohaline de l'estuaire de la Gironde pour déterminer si les taches colorées visibles à la surface du sédiment à basse mer, liées à de fortes densités de microphytobenthos dues essentiellement à la migration verticale de diatomées pennées, pouvaient avoir une influence significative sur la distribution du méiobenthos. Le copépode harpacticoide *Microarthridion littorale* est attiré par les taches lorsqu'elles se forment. Le copépode harpacticoide *Nannopus palustris* présente, au contraire, de plus faibles densités dans les agrégats de microalgues, tandis que les nématodes ne montrent pas de différence significative de densité entre les taches colorées et les régions voisines non colorées. Un test de distance, pratiqué 3 h après la formation des taches, montre que *M. littorale* ainsi que les nématodes sont attirés dans un rayon de 4 cm environ alors que *N. palustris* ne l'est pas. Une analyse du contenu en pigments du tractus digestif de *M. littorale* indique que les individus qui sont dans les taches présentent une plus forte activité nutritionnelle. Compte tenu des concentrations moyennes en chlorophylle-a mesurées dans le sédiment, ces observations permettent d'éclairer certains résultats contradictoires relevés dans la littérature.

Keywords: meiofauna; microphytobenthic aggregation; trophic relationships.

Introduction

Meiofaunal spatial variability is commonly organised into patches or aggregations at small spatial scales (Fleeger *et al.*, 1990). Factors influencing these spatial patterns include crowding (Service & Bell, 1987), reproduction (Heip, 1975), hydrodynamics (Palmer, 1986), microtopography (Sun *et al.*, 1993), bacterial abundances (Montagna *et al.*, 1982), interference competition (Fleeger & Gee, 1986), tidal exposure (Coull *et al.*, 1979; Fleeger *et al.*, 1990), sediment chlorophyll content (Decho & Fleeger, 1988) and food quality (Lee *et al.*, 1977).

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The influence of food source distribution on meiofaunal aggregation has been investigated by a number of workers (Lee *et al.*, 1977; Montagna *et al.*, 1982; Decho & Fleeger, 1988). Amongst harpacticoid copepods, epipelic diatoms are thought to be the preferred food source (Coull 1973; Brown & Sibert, 1977), although no correlation was found between copepod and diatom abundances in the field during a one year cycle (Montagna *et al.*, 1982). Laboratory studies have demonstrated harpacticoid copepod migrations towards large diatom populations (Decho & Castenholz, 1986; Decho & Fleeger, 1988). This attraction is probably due to chemosensory responses (Decho & Fleeger, 1988) and could lead to significant spatial aggregation.

In the intertidal mudflats situated in the middle stretch of the Gironde estuary, bright brown patches covering areas ranging from 1 to approximately 100 cm^2 appear at the sediment surface on bright days shortly after air exposure during low tide, especially during early spring. This phenomenon is most probably due to algal vertical migrations that have been observed in response to light and tidal cycles (eg. Leach, 1970; Admiraal *et al.*, 1982).

Preliminary data, based on meiofaunal samples collected in this area, suggested that the mean densities of single taxonomic groups were different within and outside these patches (our data not published), thus suggesting a possible influence of microphytobenthic aggregation on the distribution of meiofauna.

The present study examines some questions concerning microphytobenthic patches and their influence on meiofaunal distribution. Are the patches a significant indicator of dense microphytobenthic populations? If so, do they correspond to meiofaunal aggregation? We also examined the meiofaunal distribution in the sediments surrounding the patches to elucidate the potential role of migration, and the distance over which chemical signal(s) from patches may attract the meiofauna. Additionally, the gut pigment content of harpacticoid copepod species was quantified within and outside the patches to determine if the ingestion of pigments was influenced by location.

Materials and methods

This study was conducted on a mudflat situated in the oligo-mesohaline area of the Gironde estuary (45°32' N, 0°47'W), located 55km seaward from Bordeaux - France. Sample cores were collected on March 10th, 1993. Silt content (<63µm) of the sediment was 98% and the oxic zone extended at least to 1 cm depth. Salinity during low tide was 8 ‰ and the temperature at the sediment surface was 16 °C. Separate samples were collected for the determination of microphytobenthic pigment concentration and meiofaunal abundance using cores made of 1.9 cm^2 plastic syringes. The first 0.5 cm was stored separately from the remaining 0.5-2 cm of sediment. The microphytobenthic samples were frozen and stored in the dark at -20 °C with some drops of MgCO3 (Parsons *et al.*, 1989) and the meiofaunal samples were fixed with 5% formalin.

For both meiofaunal and microphytobenthic abundance comparisons, five replicate cores were collected centered in the middle of recognizable patches (t_0 sampling), at the mid-tide water level approximately 1.5h after air exposure and 2.5h before low tide. The diameter of sampled patches was normally slightly greater than that of the core (1.6 cm). Similarly, five cores were taken where no patches were present (normally at least 5cm distant from visible patches). Three hours after the appearance of the first microphytobenthic patches, a distance test was conducted (t_0+2.5h). Contiguous cores were taken radially from a central core encompassing an entire patch in a low water-high water line direction (Fig. 1). A total of eight cores, four on each side,

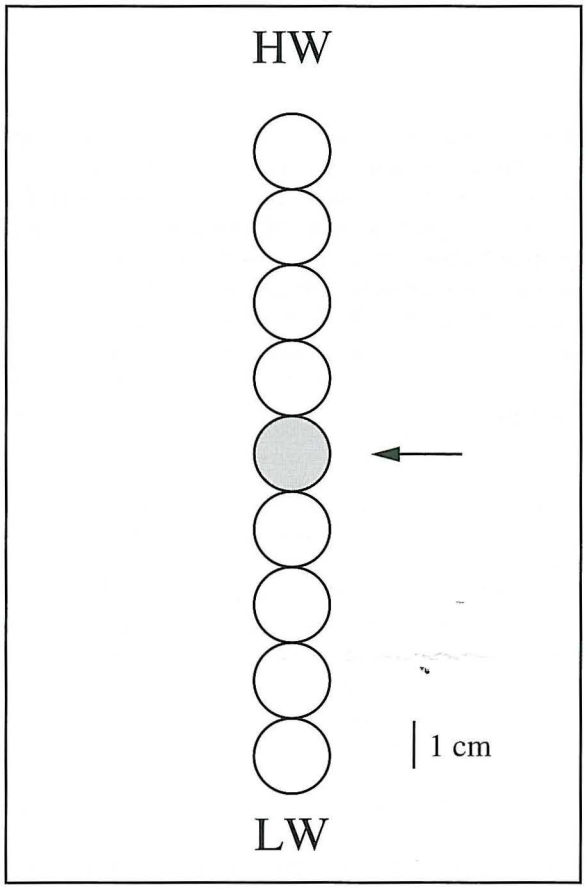


Figure 1. Diagram showing the arrangement of 9 side by side cores used in the distance test. HW and LW indicating respectively the high water and low water direction. Arrow points to the core containing a microphytobenthic patch.

Figure 1. Schéma montrant la disposition des 9 carottages contigus utilisés pour le test de distance. HW et LW indiquent respectivement la direction de haute mer et celle de basse mer. La flèche montre le carottage fait dans un agrégat de microphytobenthos.

were collected on either side of the patch. Two patches were sampled in this fashion. For further pigment studies, a final sampling, within and outside of the patch, was undertaken 4h after the initial sampling (t_0+4h).

In order to determine the concentration of pigments within copepod guts, animals were collected by sediment sieving through a 100 µm mesh and the retained fraction immediately frozen in liquid nitrogen (in darkness). This process was repeated within and outside the patches at both times t_0 and t_0+4h, corresponding to the sampling of cores for sediment pigment analysis. In the laboratory, harpacticoids were carefully sorted under minimum light intensity, washed both in distilled water and filtered sea water and separated according to species. Three replicates of approximately 30 adult copepods for *M. littorale* or 6 adult copepods for *N. palustris* were macerated in 5 ml of 90% acetone and extracted for 24h at 4°C. The extraction tubes were centrifuged to remove debris and the fluorescence of the supernatant measured both before and after acidification using a Turner Model 112 Fluorometer. Pigment concentrations were calculated using the equations of Lorenzen (1966) and data are expressed in ng equivalents of chlorophyll-a (Chl-a + pheopigments). All data were corrected for background fluorescence due to copepod tissues and adherent microflora, by determining the fluorescence of copepods previously starved for 24h in filtered sea water.

In order to determine ingestion rates from gut content measurements, the gut passage time (GPT) is needed. Values of GPT were estimated during gut clearance experiments performed in the laboratory one day after the *in situ* experiments. Sediment samples from within and outside patches were transferred to the laboratory and maintained in incubators at field temperature and 12h light/dark photoperiod. Animals were extracted from the sediment by sieving through a 100 µm mesh and were separated from the residual sediment with the help of a light source which promotes migration. Animals were then transferred to filtered sea water. The whole process took approximately 5 minutes, thus, initial (time = 0) gut content for this experiment was considered to be equal to the gut content estimated by the previous *in situ* experiment. From 12 to 35 individuals were harvested and extracted every 10 minutes during the 30 minutes incubation period as previously described for gut content analysis. GPT was calculated from the decrease in gut fluorescence using the formula of Mackas & Bohrer (1976): $Gt = Go.e^{-gt}$ with g, gut clearance rate; Gt, gut content at time t; and Go, gut content at time 0. GPT being in this case equal to g^{-1}.

In the laboratory, sediment samples for chlorophyll analysis were lyophilized before pigment extraction in 90% acetone for 24h at 4 °C. Chlorophyll-a and pheopigment were determined by spectrophotometry, following Lorenzen (1967) and used as an index of microphytobenthic abundance.

Meiofauna, retained on a 63 µm seive, were isolated by the Ludox centrifugation process (de Jonge & Bouwman, 1977) and stained with Rose Bengal for identification and counting.

One-way ANOVA tests were used to test for significant differences between means for pigments. Student's t-test was used to test for differences between animals densities. Both analyses were used after testing for the normal distribution of the data. Transformations were not required.

Results

Microphytobenthic patches

The chlorophyll-a content of surface and underlying sediment, within and outside microphytobenthic patches was compared for both sampling times separately. Similar results were found between samples taken when patches first appeared and those taken four hours later, when patches were still present (Fig. 2). Significant differences ($p < 0.05$) were observed for both sampling times between the surface sediment (0-0.5cm) inside the patch, compared to the content in the other samples, due to the high chlorophyll-a content in the patch surface (Fig. 2). Pheopigment values were not significantly different in either the initial or the final sampling ($p > 0.05$) and mean values varied between 6.0 and 8.4 $\mu g.g^{-1}$.

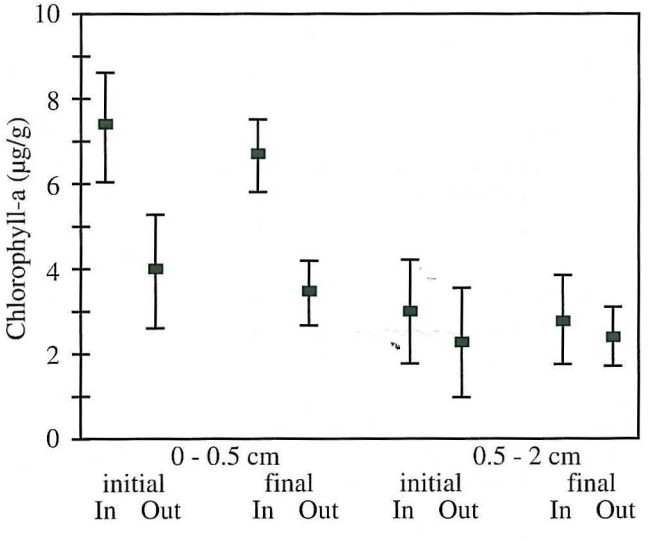


Figure 2. Chlorophyll-a content ($\mu g.g^{-1}$) of surface (0-0.5cm) and underlying surface (0.5-2cm) sediment, inside (In) and outside (Out) microphytobenthic patches, during initial and final sampling, 4h later. Bars represent confidence intervals of the mean (n = 5).

Figure 2. Concentration en chlorophylle-a ($\mu g.g^{-1}$) à la surface (0-0,5 cm) et sous la surface du sédiment (0,5-2 cm), à l'intérieur (In) et à l'extérieur (Out) des agrégats de microphytobenthos, au cours de l'échantillonnage initial et final, 4 h après. Les barres verticales indiquent l'intervalle de confiance de la moyenne (n = 5).

Microscopic observation of superficial sediments within patches demonstrated that the brown coloration was due to the presence of dense diatom populations with pennate forms dominating. A single species which we were able to count due to its large size, *Surirella cf. gemma*, attained densities of 1.5 x 10^5 cells.10 cm^{-2} within patches compared to 5.0 x 10^3 outside patches.

Initial meiofauna density

Meiofaunal counts for individual taxa within and outside the patches were compared. Two copepod species, *Microarthridion littorale* and *Nannopus palustris*, and nematodes were the most abundant. Occasionally turbellarians, rotifers, and *N. palustris* nauplii were found. Significant differences between populations within and outside patches were calculated for *Nannopus palustris* ($p < 0.05$; Fig. 3), and *Microarthridion littorale* ($p < 0.05$; Fig. 3). No significant differences were found between nematode abundance inside and outside of the patches (Fig. 3).

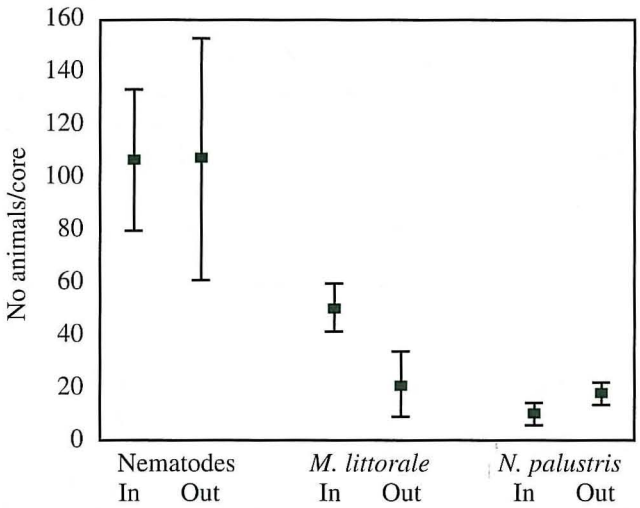


Figure 3. Meiofauna initial counts (animals.$core^{-1}$) inside (In) and outside (Out) microphytobenthic patches for *Microarthridion littorale*, *Nannopus palustris* and nematodes. Bars represent confidence intervals of the mean (n = 5).

Figure 3. Abondance initiale de la méiofaune (individus. $carotte^{-1}$) à l'intérieur (In) et à l'extérieur (Out) des agrégats de microphytobenthos pour *Microarthridion littorale*, *Nannopus palustris* et des nématodes. Les barres verticales indiquent l'intervalle de confiance de la moyenne (n = 5).

Distance test

The three dominant taxa were observed around two different patches (Fig. 4; samples 1 and 2). *Nannopus palustris* showed no clear pattern in relation to the distance from the patch (Fig. 4b). *Microarthridion littorale* and nematodes showed similar patterns in their variation regarding the first two cores on either direction (LW and HW) from the patches. The core containing the patch presented higher densities of both taxa when compared to the adjacent cores (Fig. 4a,c). The first two cores on negative distances, which correspond to the low tide direction, showed a slightly higher number of individuals around the patch than their positive equivalents. In general, the sediment at negative distances greater than two cores (4 cm) contained more individuals of *Microarthridion littorale* (Fig. 4a); the same trend was observed for nematodes in either direction (Fig. 4c).

Copepod gut content and gut passage time

The chlorophyll-a equivalent gut content of the copepods did not present significant ($p > 0.05$) differences between position (in or outside of patches) and time of sampling for both species examined. A mean (± SD) of 0.13 (± 0.03) and 0.15 (± 0.18) ng.$copepod^{-1}$ was found respectively for *M. littorale* and *N. palustris* (data corrected for controls). Values for control starved animals were 0.01 for *M. littorale* and 0.41 ng.$copepod^{-1}$ for *N. palustris*.

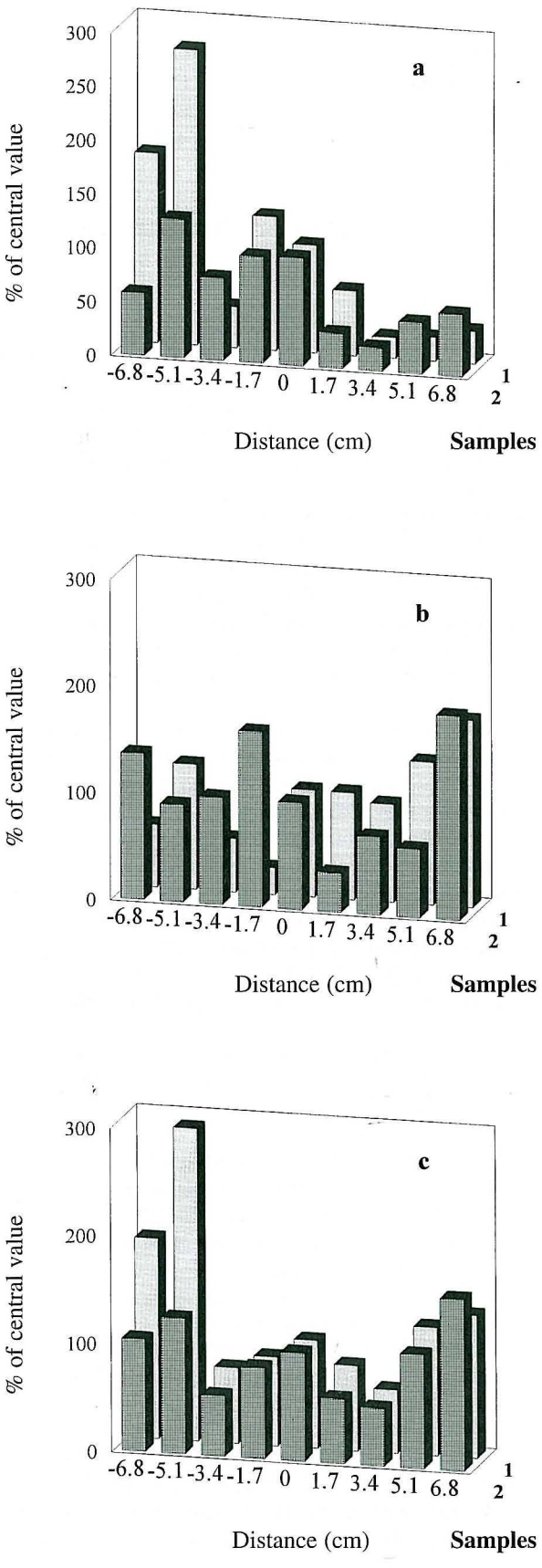
Gut passage time was determined only for *Microarthridion littorale*. *Nannopus palustris* was found in low numbers in the frozen samples and furthermore measurements revealed a high variability of gut content values due to the great quantity of microflora and detritus attached to the carapace as indicated by the control results and confirmed by observations under the microscope.

Regressions to estimate gut passage time for *M. littorale* were not significant ($0.05 < p < 0.10$) and thus GPT estimates present high confidence intervals. Nevertheless, values of GPT were 14 min for animals inside patches and 26 min outside.

Discussion

Measurements of chlorophyll-a (Fig. 2) clearly demonstrate that visually determined microphytobenthic patches can be associated with greater microphytobenthic biomass (almost double at the sediment surface within as compared to outside the patch). Pheopigments did not present significant differences between samples within and outside of patches suggesting that the increase in biomass inside the patch was due to living actively vertically migrating algae (primarily diatoms according to our microscopic observations). The fact that differences of chlorophyll-a concentration were not observed between sampling times (Fig. 2) suggests that diatom migration was achieved when patches were first sampled (at least between the two sampling depths).

Microarthridion littorale showed a clear preference pattern in relation to algal patch location. The initial count of density revealed a greater abundance of individuals inside the patch than outside (Fig. 3). Similarly, during the distance test made 2.5h later, *M. littorale* individuals were concentrated inside the patch (Fig. 4a). This relationship was limited to a radius of 4 cm. Other factors, such as the



presence of other algal patches located near the core side, could have influenced counts over greater distances. Nematodes initially showed no significant correlation with patches (Fig. 3), but, after 2.5h, samples revealed a higher concentration of individuals inside the patches (Fig. 4c). The activity of nematodes at the sediment surface is known to be much lower than that of copepods (Palmer, 1984) and may account for this observation. *Nannopus palustris* showed a negative correlation with the algal patches (Fig. 3). This could be due to crowding by *Microarthridion littorale* within the patches (correlation coefficient between *N. palustris* and *M. littorale* inside patches: $r = -0.65$, $p < 0.05$) and thus it is possibly an example of interference competition. *Nannopus palustris* has been noted to be tolerant to large salinity and temperature variations in laboratory conditions, observations which are contrary to its non-invader characteristics (Coull *et al.*, 1979). Our data suggest that *Nannopus palustris* is a poor competitor and can thus resolve this incongruence.

Several studies relate meiofaunal distribution to patches of algae although the results are not always clear (see Fleeger & Decho, 1987). A positive correlation between *Microarthridion littorale* and chlorophyll-a has been reported (Decho & Fleeger, 1988). The reasons given for this common correlation are varied. Lee *et al.* (1977) suggested that algae selectively attract meiofauna but the means of this attraction is not specified. Decho & Fleeger (1988) found that *Microarthridion littorale* actively seek algal patches and suggested that the copepods have long-range chemosensory abilities which attract them to algal patches. This hypothesis could explain the results observed in our distance test. Our results suggest that the attraction of *Microarthridion littorale* and nematodes to algal patches was limited to a four centimeter radius (Fig. 4). This distance being perhaps the limit that a chemical signal could disperse from patches and elicit a horizontal meiofaunal migration. The greater number of individuals found in the sediment at distances greater than 4 cm (Fig. 4) could be explained by the presence of nearby patches since during the study period patches were very close.

Though animals were associated with diatom patches, gut content results did not indicate a differential ingestion.

Figure 4. Distance test results. Animal densities (in percentage of the central core value) in sediment samples located radiating from opposite sides of two microphytobenthic patches (distance = 0 on samples 1 and 2). Negative values indicate low water direction. (a) *Microarthridion littorale*; (b) *Nannopus palustris*; (c) nematodes.

Figure 4. Test de distance. Densités du méiobenthos (en pourcentage par rapport à la valeur obtenue dans la carotte centrale) dans des carottes de sédiment disposées en direction opposée de part et d'autre de deux agrégats de microphytobenthos (distance = 0 pour les échantillons 1 et 2). Les valeurs négatives indiquent la direction du niveau de basse mer.

However, these results do not exclude differences in the ingestion rate due to differences in the gut passage time, which was already observed for benthic copepods (Decho, 1988; Souza-Santos *et al.*, 1995). Though not statistically significant, gut passage time results were comparable to laboratory measurements, using another method (production of fecal pellets), giving a GPT of 19 minutes with excess diatom food (unpublished data). Thus, GPT results suggest that animals inside patches had a greater ingestion rate (GPT = 14 min) as compared to animals outside algal patches (GPT = 26 min).

Recently the gut fluorescence method has been critisized due to pigment destruction during gut passage and the uncoupling of gut passage time and ingestion rates for non-feeding animals. Peterson *et al.* (1990) showed however that the gut clearance method is suitable for comparisons and, furthermore, the values we have found are similar to that obtained using the fecal pellets' production method. On the other hand, pigment destruction was shown to be highly variable in laboratory experiments and several field studies did not detect pigment degradation (see review in Pasternak, 1994). Penry & Frost (1991) correlated high pigment degradation with acclimation to high food levels but this probably did not occur during the present study (see below). Moreover, higher feeding rates due to increased food concentration were also observed for meiobenthic copepods by Montagna *et al.* (1995) using radioactive tracer methods. These data thus support the relationship between differential spatial distributions (due to diatom patches) and higher feeding rates within microphytobenthic patches.

The significant correlation found between *M. littorale* and chlorophyll-a both by Decho & Fleeger (1988) and in the present study was not observed in other studies (Sun *et al.*, 1993; Sandulli & Pinckney, 1994). Decho & Fleeger's (1988) results, as well as ours, were obtained with a mean sediment chlorophyll-a concentration of approximately 2 $\mu g.cm^{-2}$ and 3.3 $\mu g.cm^{-2}$ respectively, which is much lower than the mean concentrations of chlorophyll-a found during the studies of both Sun *et al.* (1993) and Sandulli & Pinckney (1994) (approx. 20 $\mu g.cm^{-2}$). These high background concentrations of chlorophyll-a probably made migration in search of increased diatom concentration a non-competitive strategy. In addition, data collected two weeks later (27-03-93) in the same area of the Gironde estuary revealed that *M. littorale* densities within and outside algal patches were no longer significantly different (41.6 and 28.2 ind.10 cm^{-2} respectively inside and outside algal patches; $n = 16$, $p > 0.05$). The chlorophyll-a concentration had however increased to 5.1 $\mu g.cm^{-2}$ (with all values outside patches being higher than the lowest value found inside patch on 10-03-93), indicating that the strong influence of food availability over the pattern of animals aggregation may only occur at limiting food source concentrations.

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References

Admiraal, W., H. Peletier & H. Zomer, 1982. Observations and experiments of epibenthic diatoms from an estuarine mudflat. *Estuarine Coastal and Shelf Science*, **14** : 471-487.

Brown, T.J. & J.R. Sibert, 1977. Food of some benthic harpacticoid copepods. *Journal of the Fisheries Research Board Canada*, **34** : 1028-1031.

Coull, B.C., 1973. Estuarine meiofauna: review, trophic relationships and microbial interactions, In: *Estuarine Microbial Ecology* (L.H. Stevenson and R.R. Colwell eds), pp. 499-511, University South Carolina Press: Columbia.

Coull, B.C., S.S. Bell, A.M. Savory & B.W. Dudley, 1979. Zonation of meiobenthic copepods in a southeastern United States salt marsh. *Estuarine Coastal and Marine Science*, **9** : 181-188.

Decho, A.W., 1988. How do harpacticoid grazing rates differ over a tidal cycle? Field verification using chlorophyll-pigment analyses. *Marine Ecology Progress Series*, **45** : 263-270.

Decho, A.W. & R.W. Castenholz, 1986. Spatial patterns and feeding of meiobenthic harpacticoid copepods in relation to resident microbial flora. *Hydrobiologia*, **131** : 87-96.

Decho, A.W. & J.W. Fleeger, 1988. Microscale dispersion of meiobenthic copepods in response to food-resource patchiness. *Journal of Experimental Marine Biology and Ecology*, **118** : 229-243.

Fleeger, J.W. & A.W. Decho, 1987. Spatial variability of interstitial meiofauna: a review. *Stygologia*, **3** : 35-54.

Fleeger, J.W. & J.M. Gee, 1986. Does interference competition determine the vertical distribution of meiobenthic copepods? *Journal of Experimental Marine Biology and Ecology*, **95** : 173-181.

Fleeger, J.W., M.A. Palmer & E.B. Moser, 1990. On the scale of aggregation of meiobenthic copepods on a tidal mudflat. *P.S.Z.N.I. Marine Ecology*, **11** : 227-237.

Heip, C., 1975. On the significance of aggregation in some benthic marine invertebrates. In: *Proceedings of the 9th European Marine Biology Symposium* (H. Barnes ed), pp. 527-538. Aberdeen University Press.

de Jonge, V.N. & L.A. Bouwman, 1977. A simple density separation technique for quantitative isolation of meiobenthos using the colloidal silica Ludox-TM. *Marine Biology*, **42** : 143-148.

Leach, J.H., 1970. Epibenthic algal production in an intertidal mudflat. *Limnology and Oceanography*, **15** : 514-521.

Lee, J.J., J.H. Tietjen, C. Mastropaolo & H. Rubin, 1977. Food quality and the heterogeneous spatial distribution of

meiofauna. *Helgolander wissenschaftliche Meeresuntersuchungen*, **30** : 272-282.

Lorenzen, C.J., 1966. A method for the continuous measurement of *in vivo* chlorophyll concentration. *Deep-Sea Research*, **13** : 223-227.

Lorenzen, C.J., 1967. Determination of chlorophyll and pheopigments: spectrophotometric equations. *Limnology and Oceanography*, **12** : 343-346.

Mackas, D. & R. Bohrer, 1976. Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *Journal of Experimental Marine Biology and Ecology*, **25** : 77-85.

Montagna, P.A., G.F. Blanchard & A. Dinet, 1995. Effect of production and biomass of intertidal microphytobenthos on meiofaunal grazing rates. *Journal of Experimental Marine Biology and Ecology*, **185** : 149-165.

Montagna, P.A., B.C. Coull, T.L. Herring & B.W. Dudley, 1982. The relationship between abundances of meiofauna and their suspected microbial food (diatoms and bacteria). *Estuarine Coastal and Shelf Science*, **17** : 381-394.

Palmer, M.A., 1984. Invertebrate drift: behavioral experiments with intertidal meiobenthos. *Marine Behavior and Physiology*, **10** : 235-253.

Palmer, M.A., 1986. Hydrodynamics and structure: interactive effects on meiofauna dispersal. *Journal of Experimental Marine Biology and Ecology*, **104** : 53-68.

Parsons, T.R., Y. Maita & C.M. Lalli, 1989. *A manual of chemical and biological methods for seawater analysis*. Pergamon Press: Oxford. 173 pp.

Pasternak, A.F., 1994. Gut fluorescence in herbivorous copepods: an attempt to justify the method. *Hydrobiologia*, 292/293 : 241-248.

Penry, D.L. & B.W. Frost, 1991. Chlorophyll *a* degradation by *Calanus pacificus*: Dependence on ingestion rate and digestive acclimation to food resources. *Limnology and Oceanography*, **36** : 147-159.

Peterson, W., S. Painting & R. Barlow, 1990. Feeding rates of *Calanus carinatus*: a comparison of five methods including evaluation of the gut fluorescence method. *Marine Ecology Progress Series*, **63** : 85-92.

Sandulli, R. & J. Pinckney, 1994. Modelli spaziali di distribuzione di copepodi meiobentonici e microalghe bentoniche in sedimenti sabbiosi. *Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova*, **58-59** : 153-169.

Service, S.K. & S.S. Bell, 1987. Density-influenced active dispersal of harpacticoid copepods. *Journal of Experimental Marine Biology and Ecology*, **114** : 49-62.

Souza-Santos, L.P., J. Castel & P.J.P. Santos, 1995. Feeding rate cycle of the epibenthic harpacticoid copepod *Harpacticus flexus*: laboratory experiments using fecal pellet counts. *Vie et Milieu*, **45** : 75-83.

Sun, B., J.W. Fleeger & R.S. Carney, 1993. Sediment microtopography and the small-scale spatial distribution of meiofauna. *Journal of Experimental Marine Biology and Ecology*, **167** : 73-90.