Cah. Biol. Mar. (1993), **34** : 239-251
Roscoff

Feeding behaviour of the coastal copepod *Euterpina acutifrons* on small particles.

B. Sautour and J. Castel
Centre d'Océanographie Biologique, Université de Bordeaux I
2, rue Jolyet, 33120 Arcachon - France.

Résumé : Dans les zones estuariennes les Copépodes planctoniques constituent un maillon important de la chaîne alimentaire : proies ou éventuellement compétiteurs de nombreuses espèces commercialisables (Bivalves par exemple). La nutrition des Copépodes dans ces milieux riches en particules en suspension (algues et particules inertes) de petite taille est donc une question de premier intérêt. Le comportement alimentaire de *Euterpina acutifrons,* un des Copépodes dominant en zone côtière, a été étudié expérimentalement. Plusieurs espèces d'algues ont été offertes : *Isochrysis galbana, Chaetoceros calcitrans, Skeletonema costatum.* Lorsque le diamètre des cellules algales offertes est faible, l'ingestion des Copépodes croît linéairement avec la concentration. Le taux de filtration apparent n'est pas corrélé à la concentration algale et reste pratiquement constant pour une même algue. L'ingestion et la filtration augmentent avec le diamètre de l'algue proposée. De plus, *Euterpina acutifrons* ingère des particules inertes de petite taille (billes de 5 µm) sans aucune valeur nutritive. Ces sphères sont détectées mécaniquement. Ce résultat indique que les Copépodes peuvent ingérer des particules détritiques inertes qui peuvent éventuellement compléter l'apport nutritionnel dû aux algues.

Abstract : Planktonic Copepods constitute an important group of the food chain in estuaries. They are preys or eventually competitors of a lot of species with economic interest (e. g. Bivalves). The nutrition behaviour of Copepods in these ecosystems, where small particulate suspended matter (algae and inert particles) is abundant, is of a great interest. The feeding behaviour of *Euterpina acutifrons,* a dominant Copepod in coastal areas, was studied experimentally. Several algal species were offered : *Isochrysis galbana, Chaetoceros calcitrans, Skeletonema costatum.* The ingestion rate of Copepods fed with small algae increases linearly with the concentration of cells. The clearance rate is not correlated to the algal concentration and remains quite constant. In addition, ingestion and filtration rates increase with the cells diameter when different species are proposed. *Euterpina acutifrons* ingests small inert particles (5 µm beads) with no nutritional value. These particles are detected mechanically. This suggests that Copepods can complement their algal diet in the ecosystem with detritic particles.

INTRODUCTION

A lot of species among Copepods are usually classified as herbivorous filter feeders. Filter feeders can ingest different kind of particles especially in estuaries where algae are mixed with inert particles. Small algae and small inert particles can constitute an important part of the "food" available for filter feeders in these ecosystems. The utilization of this stock by Copepods is of a great interest because they constitute the preys for a lot of young instars of economic interest (fish or shrimp). On the other hand they can compete for food with adults or young instars of some species. The benthic invertebrates (Oysters, Mussels) constitute a good example in the neritic zone. Indeed the larvae of these species are herbivorous and adults can ingest too a quite important amount of old settled planktonic algae. Zooplanktonic filter feeders essentially feed on phytoplanktonic stock. Among them, herbivorous Copepods seem to exert a great pressure on algal stock due to their high biomass. In fact, these ones can be sometimes in competition with Bivalves. Bivalves larvae feed on nano-plankton (Lucas, 1982, 1983) ; on the contrary, herbivorous Copepods tend to graze large-sized algae (Cowles, 1979 ; Schnack, 1979 ; Price & Paffenhofer, 1984). However, Copepods can also ingest the most abundant algae (Poulet & Chanut, 1975 ; Runge, 1980) whatever their size. They can also switch their feeding activity from one size class to another. This is the case when the energy gain is more important (Poulet, 1974 ; Daro, 1985 ; Tackx *et al.*, 1989). These observations suggest that Bivalves (larvae and adults) and Copepods can feed on the same algae (e. g. during algal spring bloom).

Detritus forms a major part of particulate suspended matter in estuarine ecosystems. The particles caught by zooplankton are not essentially algal cells as it is the case in open areas where algae are dominant. The great quantity of these inorganic suspended particles in the water masses forces organisms to a great adaptability. Planktonic Copepods were considered as herbivorous for a long time. Since a few years, studies are carried out in order to determine the feeding behaviour of Copepods on detritus (Lenz, 1977 ; Roman, 1977, 1984 ; Gaddy & Parker, 1986). These inorganic particles play an important role in the feeding behaviour of planktonic Copepods and this aspect is generally not taken into account in the laboratory experiments. Therefore investigations of ingestion and filtration rates of Copepods determined in the laboratory must consider these inorganic particles.

The ingestion of inorganic particles by planktonic Copepods can be studied throughout their "nutrition" on plastic beads whose size is similar to those of usually ingested algae. This kind of study was done in different ways. Richman *et al.* (1977) proposing a mixt nutrition to Copepods, have shown that they ingest essentially the largest beads. On the other hand, very small beads are ingested as well when proposed in great quantities. The Copepods studied by Donaghay & Small (1979) and Huntley *et al.* (1983) particularly ingested algal cells when they were fed on a mixture of algal cells and polystyrene beads. Selective feeding of marine Calanoid Copepods was shown by Poulet & Marsot (1978) : the Copepods essentially ingested semi-permeable beads (variable sizes) containing algal flavors. Demott (1988) showed a great preference of the Copepod *Eudiaptomus* for treated spheres when algae are scarce. This selectivity disappeared when algae are abundant, the untreated and the flavored beads were equally ingested. This author also noticed that the capacity to select particles is less important for *Temora longicornis* and *Pseudocalanus* sp (marine Calanoid Copepods) than for *Eudiaptomus*.

The Copepod used in the present work is the planktonic Harpacticoid *Euterpina acutifrons*. This species can be very abundant during some periods of the year (i. e. algal spring bloom) in littoral ecosystem used for Bivalves farming (Castel & Courties, 1982 ; Sautour, 1991).

First, the variations of grazing activity was studied according to the concentration and the quality of the algae. Several algae were used : *Isochrysis galbana* (5 µm) and *Chaetoceros calcitrans* (8 µm) usually utilized for the nutrition of Bivalves larvae, and *Skeletonema costatum* (chains of cells : 18 µm) used for older larvae.

Euterpina acutifrons lives in ecosystems with high particulate suspended matter concentration. Therefore, it is necessary to know its feeding behaviour on inert particles whose size is similar to those of ingested algae. This ingestion was studied with plastic beads whose diameter is the same as *Isochrysis galbana*.

MATERIAL AND METHODS

Zooplankton samples were collected in Arcachon Bay using a WP2 net (200 µm meshsize). The animals were carried to the laboratory immediately after sampling in order to minimize the variations of temperature. The samples were diluted to avoid high mortality (due to a decrease of dissolved oxygen or due to excretion products). The animals were anesthetized in seawater containing magnesium chloride and samples were sorted using a binocular microscope. Adult *Euterpina acutifrons* were transferred in large containers and kept in an air-conditioned room. The temperature was fixed to 19 °C for all the experiments.

Feeding behaviour was investigated in a classical way (Frost, 1972) : Copepods were placed in experimental beakers containing different algal species (different concentrations) or beads ; control jars were used for algae. Ingestion and filtration rates were calculated by measuring the decrease of particles in experimental beakers after 24 hours. Copepods were starved for 2 hours before each experiment, in order to start the experiments with the same nutritional conditions.

Ingestion and filtration of small-algae

The choice of the containers and the determination of the number of Copepods by jars is the result of a compromise (Sautour, 1991) : 500 ml glass containers and 7 Copepods in each one. Copepods placed in the beakers produced dissolved organic products (nitrogen and phosphorus) which create an enrichment in the algal production (Roman & Rublee, 1980 ; Sautour, 1991). A known amount of nitrogen and phosphorus was added to the control containers in order to obtain the same algal production. Experimental jars were then placed in the dark, at 19 °C, for 24 hours. Algae used in the experiments were 1 month old as recommended by Mullin (1963).

The ingestion rate (I_a) was calculated by measuring the difference of algal concentration (in terms of chl *a* equivalent) at time t, in the control (C_c) and in the experimental beakers (C_e). For one hour and for one Copepod : $I_a = (C_c - C_e) .v/(n.t)$, where v represents the volume of the containers, t the duration of the experiment and n the number of Copepods per jar.

The filtration rate is the ratio between the ingestion rate (I_a) and the initial algal concentration in the beakers (C_o) : $F = I_a/C_o$.

Ingestion and filtration of small inert particles

The diameter of the beads used for the experiments was 5 µm. This size was chosen in order to allow comparisons with ingestion and filtration rates determined with *Isochrysis galbana* (diameter around 5 µm). A range of beads concentrations was realized. The higher value was determined according to the concentration of *Isochrysis galbana* during a spring bloom (Sautour (1991) : 34 mg of chl *a* equivalent per cubic meter = 21 000 particles per ml). Thirteen concentrations of beads from 640 to 28 000 particles.ml^{-1} were prepared in twenty-six 250 ml beakers (two replicates for each concentration). In addition, four (2 + 2) beakers were used containing a greater amount of beads (49 000 and 75 000 beads.ml^{-1}) ; these two concentrations were chosen to consider the very important quantity of particulate suspended matter sometimes observed in littoral ecosystems. Copepods died in two flasks during the experiment, so the results are presented for only 28 beakers.

At time 0, five animals were added in the containers (after starvation) and placed in the dark, at 19 °C. Jars were permanently shaked in order to prevent beads settling. After 24 hours the beads were counted using a binocular microscope.

The difference of particles number in the beakers between time t (N_t) and time 0 (N_0), divided by the number of Copepods (n) and the duration of the investigation (t) gives the ingestion rate (I_b) : $I_b = (N_t\text{-}N_0)/(n.t)$. The calculation of the filtration rate is the same as for the algae : $F = I_b/N_0$.

RESULTS

Ingestion and filtration of small algae

The ability of Copepod ingestion is variable according to the algae proposed. In all cases, the ingestion rate is strongly linked to algal concentration (Fig. 1). The global aspect of the curve of ingestion is the same for the 3 algae : ingestion rate linearly increases with algal concentration. The regression line calculated for these experimental values derives from the model : I = a.C+b, where I is the ingestion rate (ng chl *a*.Cop^{-1}.h^{-1}) and C the algal concentration in the experimental beakers (ng chl *a*.ml^{-1}).

Isochrysis galbana : $I_a = 0.4925C\text{-}1.1046$ ($r = 0.88$ for $n = 30$; $p < 0.005$).

Skeletonema costatum : $I_a = 0.5284C\text{-}0.3264$ ($r = 0.62$ for $n = 60$; $p < 0.005$).

Chaetoceros calcitrans : $I_a = 0.1941C\text{-}0.5050$ ($r = 0.79$ for $n = 30$; $p < 0.005$).

No relationships are found between filtration rate and algal concentration for the three algae (Fig. 2). The observation of residuals obtained from the model indicates an identical variability for the low and the high concentrations. This allows to reject the hypothesis of the influence of measurement sensitivity on low values (greater variance).

Thus, filtration rates are not influenced by cell concentration although the mean values show important variations according to the proposed algae : 0.41 ml.h^{-1} for *Isochrysis galbana*, 0.45 ml.h^{-1} for *Skeletonema costatum* and 0.12 ml.h^{-1} for *Chaetoceros calcitrans*.

Ingestion and filtration of small inert beads

Ingestion rates are comprised between 2 700 and 26 300 particles per Copepod and per hour. These values increase according to the concentration of beads (Fig. 3). From the data, two models seem adapted to represent ingestion rate (Ib, in number of beads per Copepod and per hour) according to the initial concentration of particles (C_o) : a linear one and a cur-

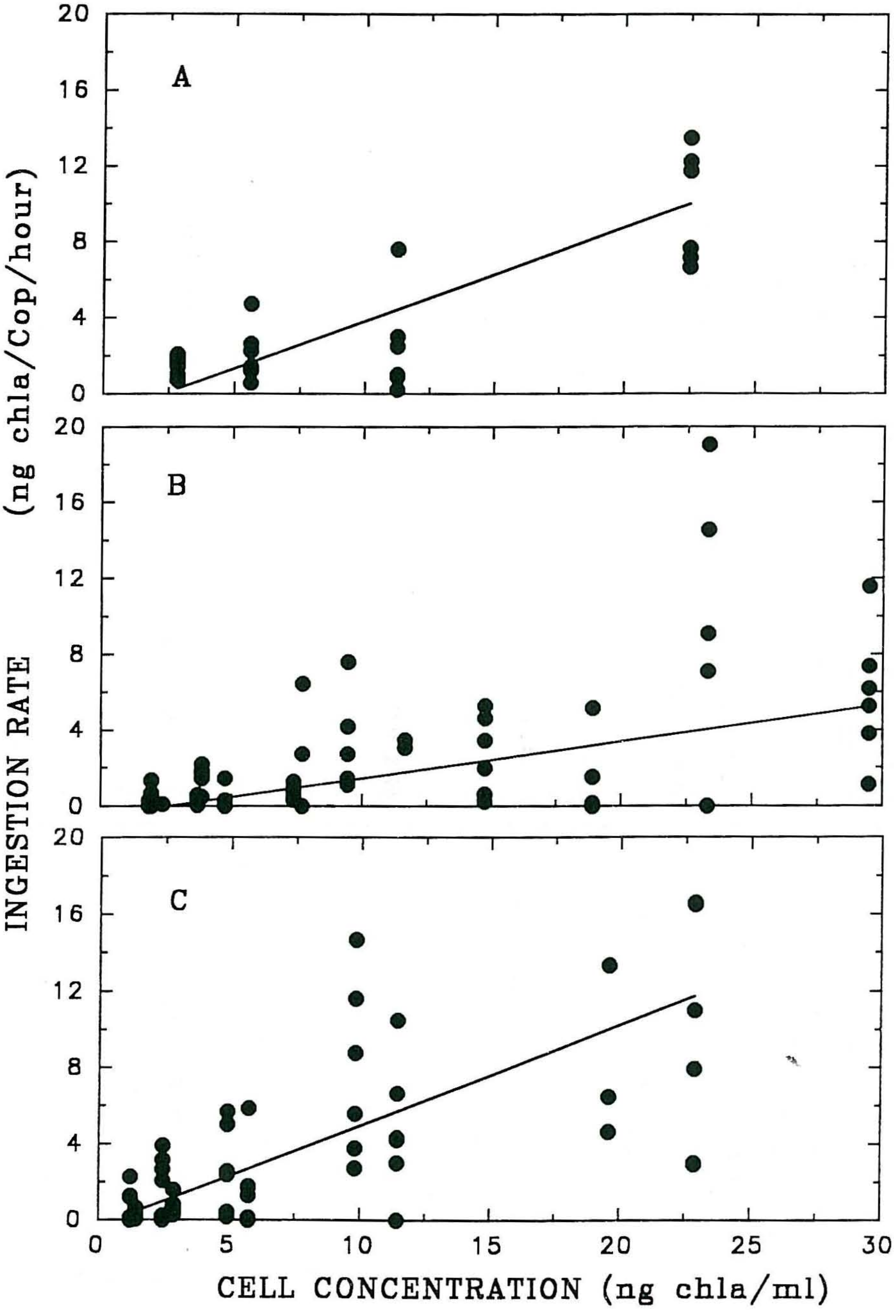

Fig. 1 : *Euterpina acutifrons*. Laboratory experiment (19 °C). Ingestion rate (ng chl *a*.$Cop^{-1}.h^{-1}$) of Copepods fed with (A) *Isochrysis galbana*, (B) *Chaetoceros calcitrans*, (C) *Skeletonema costatum*.

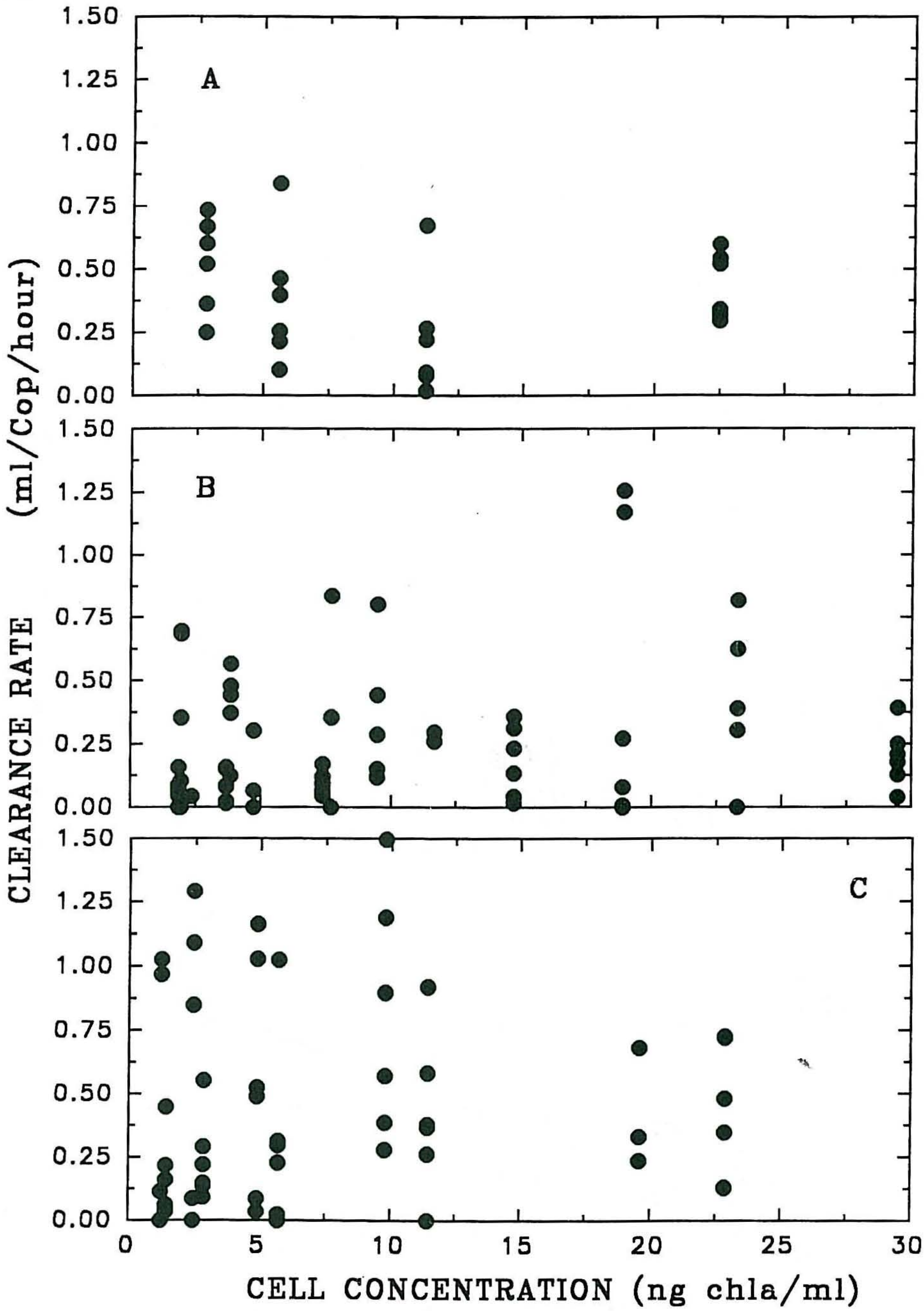

Fig. 2 : *Euterpina acutifrons*. Laboratory experiment (19 °C). Clearance rate ($ml.Cop^{-1}.h^{-1}$) of Copepods fed with (A) *Isochrysis galbana*, (B) *Chaetoceros calcitrans*, (C) *Skeletonema costatum*.

vilinear one. In our case, the linear model : $I_b = 0.321C_o + 2059.01$ ($r = 0.93$ for $n = 28$, $p < 0.005$) does not reflect the real ingestion of Copepods. Ingestion rate would be greater than 0 for an initial concentration of 0 ($p < 0.005$). Our results show that both models should be used (Fig. 3). For low beads concentrations, the ingestion rate rapidly increases according to a polynomial model : $I_b = 398.86 - 0.87702C_o + 5.0714C_o^2 10^{-4}$ ($r = 0.98$; $n = 11$; $p < 0.005$). The second part of the curve is a line which equation is $I_b = 0.28192C_o + 3856.2$ ($r = 0.91$ for $n = 19$; $p < 0.005$).

The values of filtration rates (F_b) fluctuate between 0.091 and 1.46 ml per Copepod and per hour (Fig. 4). The best correlation is found for the model : $Fb = -0.036 + 6.0356C_o 10^{-5} + 6.5140C_o^2 10^{-8}$ ($r = 0.96$ for $n = 11$; $p < 0.005$) for the low concentrations. Then the values decrease according to the model $F_b = 48.526C_o^{-0.4626}$ ($r = 0.73$; $n = 19$; $p < 0.005$).

In addition, the models used to explain ingestion and filtration rates for the low values of concentration of beads suggest that ingestion and filtration begin for a concentration of approximatively 500-1 000 beads.ml^{-1} (Fig. 3 and 4).

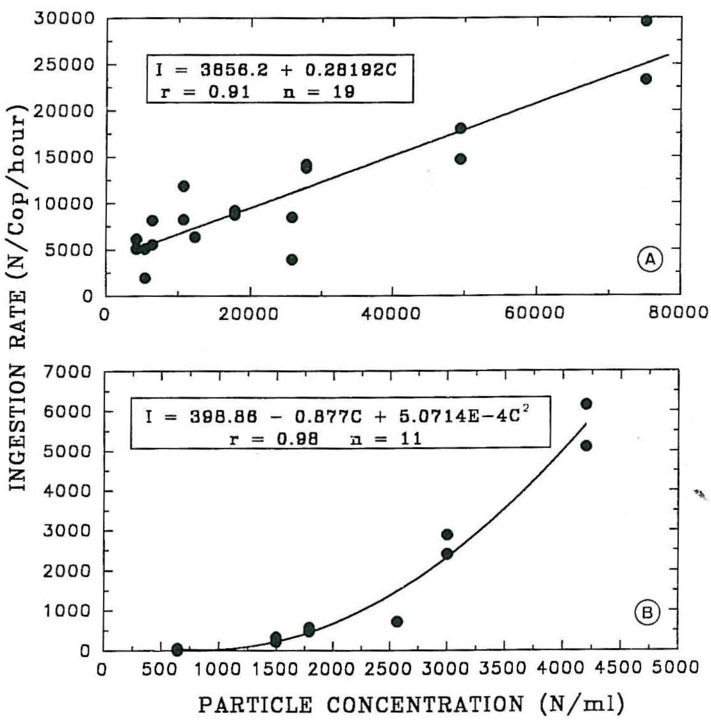

Fig. 3 : *Euterpina acutifrons*. Laboratory experiment (19 °C). Ingestion rate (beads.Cop^{-1}.h^{-1}) when small spheres are offered (5 µm). (A) high concentrations. (B) low concentrations.

DISCUSSION

General aspect of the model of ingestion of small algal cells

In laboratory condition, herbivorous Copepods usually show a pattern indicating an increase of ingestion rates with cell concentration up to a maximal rate which remains unchanged with further increase of algal concentration. These results are shown by numerous authors for different species : *Calanus helgolandicus* (Corner *et al.*, 1972), *Calanus pacificus* (Frost, 1972), *Temora longicornis* (O'Connors *et al.*, 1980 ; Daro, 1985), *Paracalanus* sp (Ambler, 1986), *Centropages hamatus* (Kiorboe *et al.*, 1982), *Neocalanus* sp (Dagg & Walser, 1987), *Eurytemora affinis* (Barthel, 1983). On the contrary, the thresholds are not always observed under natural conditions (Huntley, 1981) and in the laboratory (Deason, 1980).

In the present study, the ingestion rates determined for *Euterpina acutifrons* increase with algal concentration without reaching a plateau. As described by Frost (1972), the plateau is obtained for algal concentrations which increase when the diameter of the cells decreases. Algae used in the present study are small compared to those habitually used in studies or usually ingested by Copepods (Frost, 1972, worked with *Coscinodiscus* sp for

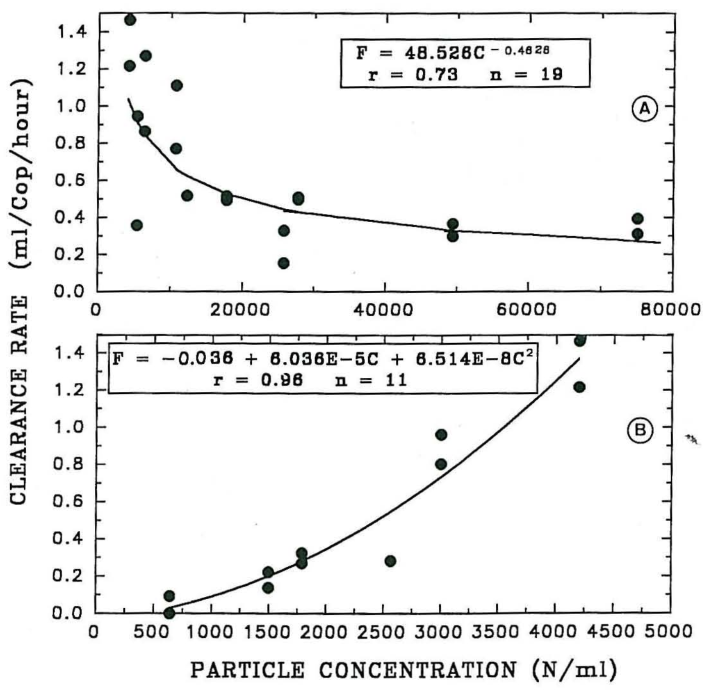

Fig. 4 : *Euterpina acutifrons*. Laboratory experiment (19 °C). Filtration rate ($ml.Cop^{-1}.h^{-1}$) when small spheres are offered (5 µm). (A) high concentrations. (B) low concentrations.

instance). The maximum ingestion rate could have been observed if higher cell concentrations had been used. The increase of ingestion rate according to the cell concentration can be describe with a linear model (Dagg & Walser, 1987) or with a curvilinear model (exponential : O'Connors, 1980). The linear model is the most appropriate to explain the variations of ingestion rates of *Euterpina acutifrons* fed with small algal cells (correlation coefficient always significant : $p < 0.005$).

This direct proportionality between ingestion and cell concentration, can be explained by the feeding behaviour of the Copepods. The feeding activity of planktonic grazers depends on the size of the particles ingested. Every species, and among them every instar, preferentially eats in one range of algal size spectrum (Paffenhofer, 1971 ; Allan *et al.*, 1977 ; Daro, 1985). The Copepods are unselective feeders and filter water when the sizes of the particles are under the threshold bounding these size classes. The linear model is observed for animals searching their food at random and independently of algal concentration. The results obtained in the present work for *Euterpina acutifrons* fit to an unselective feeding (Copepod) on small algal cells.

Filtration of small algal cells

In the present study, the calculation of the filtering rate is based on the measurement of the decrease of the amount of particles during time. This quantity divided by the initial concentration, the duration of the experiment and the number of animals used, gives a volume of water swept clear per animal and per hour. The volume swept clear corresponds to the volume really filtered when Copepods have a filtration efficiency of 100 %.

The concept of filtration efficiency depends on : (i) the morphological characteristics of the Copepods, (ii) the physical characteristics of the fluid, (iii) the movements of the filtering appendages (Hargrave & Geen, 1970 ; Nival & Nival, 1973 ; Rubenstein & Koehl, 1977).

In the case of *Euterpina acutifrons*, the filtration efficiency increases with the size of the algae. For the same algal concentration the amount of algae ingested is higher when animals are fed with *Skeletonema costatum* instead of *Isochrysis galbana*. *Chaetoceros calcitrans* is a particular case. This alga is weakly ingested by *Euterpina acutifrons*, even when its size is intermediate compared to the 2 others algae used in this work. This can be explain by (i) the presence of spines at the surface of the algae which can disturb the ingestion of cells, (ii) a low nutritive quality of the algae (Urry, 1965 ; Poulet & Marsot, 1978 ; Price *et al.*, 1983), which can be rejected by Copepods Huntley *et al.*, 1983. These results are similar to those found by Hargrave & Geen (1970) who demonstrated that *Chaetoceros calcitrans* rejected by Copepods was not ingested by zooplankton.

Thus, the volume swept clear is an underestimation of the volume really prospected by the grazers. It is therefore necessary to keep in mind that the filtration activity of Copepods is greater than the filtration measured with small algal cells. The volume filtered is only an apparent volume which increases, for a same algal concentration, with the diameter of the algae up to the volume really filtered (Nival & Nival, 1973). Thus, the notion of apparent filtering rate (or clearance rate) is more adapted than the one of filtering rate.

In addition, the clearance rate of *Euterpina acutifrons* does not vary with the algal concentration. These results were soon described by numerous authors (e. g. : Schnack, 1979 ; Huntley, 1981). The clearance rate is lower for *Isochrysis galbana* than for *Skeletonema costatum* (larger cells). An increase of filtration efficiency is noticed when the size of the particles offered increases. The very low clearance rate calculated for *Chaetoceros calcitrans* can be explained in the same way as for ingestion rates.

Ingestion and filtration of small inert beads

The very low concentration used in this study allows to investigate the feeding activity of Copepods at low particles concentrations (the lowest concentration of beads utilized correspond to a chlorophyll concentration of 1.04 $mg.m^{-3}$). The mixed model obtained is made of a polynomial one and a linear one. These results are clearly displayed : (i) Copepods ingest inert particles with no nutritional quality (soon described by Richman *et al.*, 1977 ; Huntley *et al.*, 1983), (ii) in the case of *Euterpina acutifrons*, this ingestion of inert small beads starts over a certain concentration of particles, (iii) these ingestion rates increase proportionally according to the initial beads concentration in the beakers.

In summary, *Euterpina acutifrons* mechanically ingests small size particles (5 μm in this investigation) because ingestion linearly increases with beads concentration ; this result was described earlier by numerous authors (Conover, 1966 ; Cowles, 1979 ; Price *et al.*, 1983). However, this ingestion begins only when beads concentration is higher than 500-1 000 $beads.ml^{-1}$.

If the nutritional activity of *Euterpina acutifrons* was only a passive phenomenon, we would observe an ingestion even for the very low concentrations and the ingestion would always linearly increase with the concentration of beads. This is not the case : *Euterpina acutifrons* ceases feeding at low concentrations. Therefore Copepod grazing is stimulated by high enough concentrations of beads. This implies only mechanical stimuli and consequently mechanical receptors (Fig. 5). The presence of mechanoreceptors does not preclude the existence of chemoreceptors : they may be here inoperative because beads are not flavored. The stimuli can be detected in 2 ways (Cowles & Strickler, 1983) : (i) Copepods can assess food concentration by moving their feeding appendages (including the mechanoreceptors) so as to propel themselves through the water, (ii) Copepods can cease appendages movements and use the sinking behaviour as a mechanism for scanning the water column.

-	CONCENTRATION OF PARTICLES	+
	Number of stimuli induces ingestion and filtration	Number of stimuli induces constant filtration
Low number of stimuli Ingestion = 0 Filtration = 0	Ingestion increases : polynomial + linear models Filtration decreases : polynomial model	Ingestion : linearly increases Filtration = constant

Fig. 5 : *Euterpina acutifrons*. Recapitulative table of the feeding behaviour when small beads are offered.

The hypothesis of a break of feeding activity (induced by a high metabolic expense due to a low concentration of particles) requires here the presence of mechanical stimuli : the filtration activity would stop before a critical frequency of stimuli.

The filtration rates decrease very rapidly with the increase of the concentration of beads in the second part of the curve (Fig. 4). They reach a minimum value and remain quite constant. The decrease and the stabilization are probably due to an adjustment of the feeding behaviour. This adjustment can be induced by mechanoreceptors : Copepods scan a large volume of fluid when the concentration of particles is low (but over the threshold described above). When the concentration of beads increases, the quantity of spheres found by Copepods increases and the Copepods filter less and less water until a critical value. This minimum volume of filtered water is determined by a certain concentration of beads in the water. This suggests the existence of a second threshold detected mechanically. This would permit the stabilization of the scanned volume of water when particles are abundant.

As described by Mullin *et al.* (1975), the ingestion increases with concentration to a maximal rate when particles concentration is higher. This is probably due to a saturation of the filtering appendages or to the filling of the gut. This result was not confirmed for the concentrations of particles used in the present work.

CONCLUSION

The results of the present work suggest several answers concerning the feeding behaviour of the Copepod *Euterpina acutifrons*.

. *Euterpina acutifrons* is a passive filter feeder when small algae are proposed. Ingestion linearly increases with algal concentration and does not reach any maximal value for the algal concentrations used in this study.

. The clearance rates are not correlated to algal concentration and remain quite constant.

. The filtration efficiency of the Copepod *Euterpina acutifrons* is greater for *Skeletonema costatum* (size 18 µm) than for *Isochrysis galbana* (diameter : 5 µm).

. The ingestion and clearance rates of *Chaetoceros calcitrans* are very low according to those found for the 2 others algae. This is probably due to a low nutritional value or to the presence of spines on the cells.

. *Euterpina acutifrons* ingests small-size inert particles without any nutritional value. The ingestion increases with beads concentration.

. The ingestion ceases before a minimum threshold of particles in the water. The ingestion increases first according to a polynomial model, then linearly increases. The existence of this threshold implies mechanoreceptors. They stimulate the beginning of the feeding activity.

. The clearance rate decreases according to a polynomial model with concentration of beads until a minimal volume.

. The ingestion threshold suggests 2 hypothesis : (i) Copepods cease their feeding activity when the energy gain is too low, (ii) the break of ingestion constitute a refuge for phytoplankton.

In summary, *Euterpina acutifrons* ingests small algal cells and can be, for instance, a trophic competitor for Bivalve larvae when there are small algae in the water. This Copepod ingests, too, small inert particles which are detected mechanically. These ones can supplement algal diet in the ecosystem, especially in areas where particulate suspended matter is abundant (Sautour, 1991). In addition, the threshold of ingestion (induced by a high metabolic expense due to a low concentration of particles) suggest the existence of a "refuge" for phytoplanktonic species (Mullin *et al.*, 1975). This hypothesis prevents the extinction of phytoplanktonic algal species by grazing.

ACKNOWLEDGEMENTS

Thanks are due to M. Heral for his help and to the whole staff of the "laboratoire des écosystèmes conchylicoles IFREMER" of La Tremblade (France) for their assistance. This investigation was financially supported by IFREMER. We are indebted to C. Jackel for revision of the English language.

REFERENCES

ALLAN, J.D., S. RICHMAN, D.R. HEINLE & R. HUFF, 1977. Grazing in juvenile stages of some estuarine calanoïd copepods. *Mar. Biol.*, 43 : 317-332.

AMBLER, J.W., 1986. Formulation of an ingestion function for a population of *Paracalanus* feeding on mixtures of phytoplankton. *J. Plankt. Res.*, 8 : 957-972.

BARTHEL, K.G., 1983. Food uptake and growth efficiency of *Eurytemora affinis* (Copepoda : calanoida). *Mar. Biol.*, 74 : 269-274 .

CASTEL, J. & C. COURTIES, 1982. Composition and differential distribution of zooplankton in Arcachon Bay. *J. Plankt. Res.*, 4 : 417-433.

CONOVER, R.J., 1966. Feeding on large particles by *Calanus hyperboreus* (Kröyer). In H. Barnes (ed.). Some contemporary studies in marine science. 1 : 187-194.

CORNER, E.D.S., R.N. HEAD & C.C. KILVINGTON, 1972. On the nutrition and metabolism of zooplankton. VIII. The grazing of *Biddulphia* cells by *Calanus helgolandicus*. *J. mar. biol. Ass. U.K.*, 52 : 847-861.

COWLES, T.J., 1979. The feeding response of copepods from the Peru upwelling system : food size selection. *J. Mar. Res.*, 37 : 601-622.

COWLES, T.J. & J.R. STRICKLER, 1983. Characterization of feeding activity patterns in the planktonic copepod *Centropages typicus* Kröyer under various food conditions. *Limnol. Oceanogr.*, 28 (1) : 106-115.

DAGG, M.J., Jr W.E. WALSER, 1986. The effect of food concentration on fecal pellet size in marine copepods. *Limnol. Oceanogr.*, 31 (5) : 1066-1071.

DARO, M.H., 1985. Field study of the diet, selective and efficiency feeding of the marine copepod *Temora longicornis* in the Southern Bight of the North Sea. "Proceeding Progress in Belgian Oceanographic Research" Brussels, 1 : 250-263.

DEASON, E.E., 1980. Grazing of *Acartia hudsonica* on *Skeletonema costatum* in Narragansett Bay (USA) : influence of food concentration and temperature. *Mar. Biol.*, 60 : 101-113.

DEMOTT, W.R., 1988. Discrimination between algae and artificial particles by freshwater and marine copepods. *Limnol. Oceanogr.*, 33 : 397-408.

DONAGHAY, P.L. & L.F. SMALL, 1979. Food selection capabilities of the estuarine copepod *Acartia clausi*. *Mar. Biol.*, 52 : 137-146.

FROST, B.W., 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.*, 17 : 805-815.

GADDY, A.J., & R.A. PARKER, 1986. Zooplankton grazing activity and assimilation in the presence of Mount St Helens Ash. *Northwest Sci.*, 60 (1) : 47-51.

HARGRAVE, B.T. & G.H. GEEN, 1970. Effects of Copepod grazing on two natural phytoplankton populations. *J. Fish Res. Bd Can.*, 27 (8) : 1395-1403.

HUNTLEY, M., 1981. Nonselective, nonsaturated feeding by three calanid copepod species in the Labrador sea. *Limnol. Oceanogr.*, 26 (5) : 831-842.

HUNTLEY, M.E., K.G. BARTHEL & J.L. STAR, 1983. Particle rejection by *Calanus pacificus* : discrimination between similarly sized particles. *Mar. Biol.*, 74 : 131-160.

KIORBOE, T., F. MÖHLENBERG & H. NICOLAJSEN, 1982. Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (Lilljeborg) in relation to food concentration and temperature. *Ophelia*, 21 : 181-194.

LENZ, J., 1977. On detritus as a food source for pelagic filter-feeders. *Mar. Biol.*, 41 : 39-48.

LUCAS, A., 1982. La nutrition des larves de bivalves. *Océanis*, 8 (5) : 363-388.

LUCAS, A., 1983. Méthodes d'évaluation des rations alimentaires chez les microphages marins : l'exemple des larves de bivalves. *Bull. Soc. zool. Fr.*, 108 (3) : 423-430.

MULLIN, M.M., 1963. Some factors affecting the feeding of marine copepods of the genus *Calanus*. *Limnol. Oceanogr.*, 7 : 239-249.

MULLIN, M.N., E.F. STEWART & F.J. FUGLISTER, 1975. Ingestion by planktonic grazers as a fonction of the concentration of food. *Limnol. Oceanogr.*, 20 : 259-262.

NIVAL, P. & S. NIVAL, 1973. Efficacité de filtration des copépodes planctoniques . *Ann. Inst. Oceanogr.* Paris 49 (2) : 135-144.

O'CONNORS, H.B. Jr., D.C. BIGGS & D.V. NINIVAGGI, 1980. Particle-size-dependent maximum grazing rates for *Temora longicornis* fed natural particle assemblages. *Mar. Biol.*, 56 (1) : 65-70.

PAFFENHÖFER, G.A., 1971. Grazing and ingestion rates of nauplii, copepodids and adults of the marine planktonic copepod *Calanus helgolandicus*. *Mar. Biol.*, 11 : 286-298.

POULET, S.A., 1974. Seasonal grazing of *Pseudocalanus minutus* on particles. *Mar. Biol.*, 25 (2) : 109-125.

POULET, S.A. & J.P. CHANUT, 1975. Nonselective feeding of *Pseudocalanus minutus*. *J. Fish Res. Bd Can.*, 32 (5) : 706-713.

POULET, S.A. & P. MARSOT, 1978. Chemosensory grazing by marine calanoid copepods (Arthropoda : Crustacea). *Science*, 200 : 1403-1405.

PRICE, H.J., G.A. & PAFFENHÖFER, 1984. Effects of feeding experiences in the copepod *Eucalanus pileatus* : a cinematographic study. *Mar. Biol.*, 84 : 35-40.

PRICE, H.J., G.A. PAFFENHÖFER & J.R. STRICKLER, 1983. Modes of cell capture in calanoïd copepods. *Limnol. Oceanogr.*, 28 : 116-123.

RICHMAN, S., D.R. HEINLE & R. HUFF, 1977. Grazing by adult estuarine calanoid copepods of the Chesapeake Bay. *Mar. Biol.*, 42 : 69-84.

ROMAN, M.R., 1977. Feeding of the copepod *Acartia tonsa* on the diatom *Nitzschia closterium* and brown algae (*Fucus vesiculosus*) detritus. *Mar. Biol.*, 42 : 149-155.

ROMAN, M.R. & P.A. RUBLEE, 1980. Containment effects in copepod grazing experiments : A plea to end the black box approach. *Limnol. Oceanogr.*, 25 (6) : 982-990.

RUBENSTEIN, D.I., M.A.R. KOEHL, 1977. The mechanisms of filter feeding : some theoretical considerations. *Am. Nat.*, 111 : 981-994.

RUNGE, J.A., 1980. Effects of hunger and season on the feeding behaviour of *Calanus pacificus*. *Limnol. Oceanogr.*, 25 : 134-145.

SAUTOUR, B., 1991. Populations zooplanctoniques dans le Bassin de Marennes-Oléron ; dynamique de population, nutrition et production des Copépodes dominants. Thèse Doct. Univ. Bordeaux I, 283 p.

SCHNACK, S.B., 1979. Feeding of *Calanus helgolandicus* on phytoplankton mixtures. *Mar. Ecol.*, 1 : 41-47.

TACKX, M. L.M., C. BARKER, J.W. FRANCKE & M. VINK, 1989. Size and phytoplankton selection by Oosterschelde zooplankton. *Neth. J. Sea Res.*, 23 (1) : 35-43.

URRY, D.L., 1965. Observations on the relationship between the food and survival of *Pseudocalanus elongatus* in the laboratory. *J. mar. biol. Ass. U.K.*, 45 : 49-58.