



HAL
open science

FEEDING RATE CYCLE OF THE EPIBENTHIC HARPACTICOID COPEPOD HARPACTICUS FLEXUS: LABORATORY EXPERIMENTS USING FECAL PELLETS COUNTS

L R Souza-Santos, J Castel, P J P dos Santos

► **To cite this version:**

L R Souza-Santos, J Castel, P J P dos Santos. FEEDING RATE CYCLE OF THE EPIBENTHIC HARPACTICOID COPEPOD HARPACTICUS FLEXUS: LABORATORY EXPERIMENTS USING FECAL PELLETS COUNTS. *Vie et Milieu / Life & Environment*, 1995, pp.75-83. hal-03051475

HAL Id: hal-03051475

<https://hal.sorbonne-universite.fr/hal-03051475v1>

Submitted on 10 Dec 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

FEEDING RATE CYCLE OF THE EPIBENTHIC HARPACTICOID COPEPOD *HARPACTICUS FLEXUS*: LABORATORY EXPERIMENTS USING FECAL PELLET COUNTS

L.P. SOUZA-SANTOS, J. CASTEL, P.J.P. dos SANTOS

Laboratoire d'Océanographie Biologique, Université de Bordeaux I,
2 rue du Professeur Jolyet, Arcachon 33120, France

MEIOBENTHOS,
HARPACTICOID COPEPOD
HARPACTICUS FLEXUS
TIDAL CYCLE
FEEDING RATE
FECAL PELLETS

ABSTRACT – The defecation rate of *Harpacticus flexus* Brady & Robertson was used as an index of feeding rate in laboratory experiments. A tidal cycle of defecation rate was observed in constant laboratory conditions with the highest values of defecation/feeding rates occurring during the expected low and high slack tides. The light regime (24h dark and 12h light/dark) did not alter this cycle, although the light may represent a zeitgeber. It is suggested that the adaptive significance of this cycle is to avoid animal passive erosion due to the high speed currents during the ebb and flood tides at the sampling site by restricting their feeding time to periods with low speed currents. The gut content of copepods, expressed both in number of fecal pellets and in pigment-content, did not change during the tidal cycle in the laboratory, thus changes in the gut passage time were the principal responsible for the feeding rate changes.

MEIOBENTHOS
COPÉPODE HARPACTICOÏDE
HARPACTICUS FLEXUS
CYCLE DE MARÉE
TAUX DE BROUTAGE
PELOTES FÉCALES

RÉSUMÉ – Le taux de défécation de *Harpacticus flexus* Brady & Robertson a été utilisé comme un index du taux de broutage dans des expériences de laboratoire. Un cycle de marée du taux de défécation a été observé avec les plus forts taux de défécation/broutage aux heures correspondant aux étales de la marée (BM and HM). Le régime de lumière (24h obscurité, 12h lumière/12h obscurité) ne change pas le cycle, mais la lumière peut constituer un synchronisateur. Il est suggéré que l'importance adaptative du cycle est d'éviter aux animaux d'être érodés passivement par les forts courants de la marée descendante et montante au point de prélèvement, retenant leur temps de broutage aux moments de faibles courants. Le contenu intestinal des Copépodes, exprimé en nombre de pelotes fécales et en contenu de pigment du tractus digestif, ne change pas pendant le cycle de marée en conditions de laboratoire, les variations du temps de passage sont donc principalement responsables du changement du taux de broutage.

INTRODUCTION

Diel feeding cycle is a common feature of the biology of planktonic copepods and although it is often associated with diel migration, the two behaviours appear to be controlled independently (Durbin *et al.*, 1990). Reports of diel cycles of meiobenthic copepods are scarce. Some studies showed that the abundance of meiobenthos in sediments (Coull and Feller, 1988; Armonies, 1989; 1991; Hicks, 1992) and in water column (Palmer and Gust, 1985; Walters, 1988; 1991; Armonies, 1989; 1991) can change during the tidal or diel cycle. Passive erosion by tidal currents (Palmer and Gust, 1985; Hicks, 1992) but also

active emergence, mainly of copepods, during the night high water (Armonies, 1988b; 1989; 1991; Coull and Feller, 1988; Walters, 1988) are the main responsible for these changes. Differences in habitat, water flow intensity, aboveground structure and taxonomic composition of the community are important factors determining what kind of mechanism is playing the major role on the presence of meiobenthos in the water column (Palmer, 1988).

It is expected that changes in habitat (sediment or water) and in swimming activity of copepods during tidal or diel cycles affect the copepod feeding rates. There is no report on the diel variation of feeding rates of meiobenthic copepods in the field or in laboratory perhaps due to the methodo-

logical difficulties in estimating feeding rates both in laboratory and *in situ* experiments, related to the small size of the animals and to the necessity of working with sediment. Tidal variations of feeding rates of meiobenthic copepods were only investigated by Decho (1986; 1988). These studies showed that harpacticoid meiobenthic copepods do not feed at constant rates during a tidal cycle, both in laboratory and *in situ* experiments, particularly due to the water-cover influence. The changes found were species-specific, mainly due to the different exploitation of feeding resources by copepods.

The defecation rate, estimated by counting the fecal pellets produced in time, can be used as an index of the feeding rate, since these two parameters are normally well correlated (Gaudy, 1974; Gamble, 1978; Huntley *et al.*, 1983; Pagano and Gaudy, 1986). The advantage of using the defecation rate to estimate the feeding rate of meiobenthic copepods is that the animals can eat the natural microfilm of sediments and that it can be measured with a simple methodology in the laboratory.

Harpacticus flexus Brady & Robertson (Harpacticoida: Copepoda) is an epibenthic copepod that inhabits the lower level of the intertidal region of fine sand beaches (Hicks and Coull, 1983). Armonies (1989; 1991) proposed the denomination of semiplanktonic to this species, because the animals rest in superficial sediment layers at low tide and swim in the water column at high tide, reaching high densities in the water column at night in a North Sea tidal beach.

This study was designed to investigate if *Harpacticus flexus*, a common species of a temperate mesotidal sandy beach, presents feeding rate changes during the tidal and/or diel cycle, by means of controlled laboratory experiments.

METHODS

Copepods used in the experiments were collected from the lower level of the intertidal sandflat located in front of the Biological Station of Arcachon, France (44°40'N, 1°10'W). Tidal sea level change at the sampling area is semidiurnal with a spring range of about 4.5 m and a neap range of about 3 m. The sediment was collected during the low water of spring tides and transported to the laboratory where the sediment was washed with sea-water and copepods picked up under a stereo-microscope. Before the beginning of the experiments, the adult copepods were maintained on natural sand washed with sea-water to eliminate any other animals but owning a microfilm of bacteria and diatoms.

Diel variation of defecation rate

The first experiment investigated the diel variation of the defecation rate of *Harpacticus flexus* and the influence of the photoperiod on this variation. Copepods were collected on 27/11/91 (sediment temperature of 10°C) and were maintained in the laboratory at constant conditions and at 15°C during one week for acclimation to the two photoperiods tested: 24 h dark and 12 h light/dark. At the beginning of the experiment five copepods from each photoperiod were put individually in recipients with a few sand grains (treated in the same way as the stock culture sand and owning the natural microfilm) and sea-water. Then, at each 2 h interval the fecal pellets produced by copepods were picked up and counted under a stereo-microscope, during 24h. The 2 h interval seemed to be reasonable since the gut passage time of meiobenthic copepods was seen to vary from 30 to 90 minutes (Decho, 1988).

Tidal variation of defecation rate

The next three experiments were designed to investigate the tidal variation of the defecation rates. In these experiments the animals were maintained at a photoperiod of 12 h light/dark but in constant conditions of temperature and immersion.

For the second experiment, copepods were collected on 20/01/92 (sediment temperature of 6°C) and maintained one day at 6°C. The fecal pellets produced by five copepods were counted using the same method as in the previous experiment but at each 1 h interval during 12 h.

For the third experiment, copepods were collected on 23/01/92 (sediment temperature of 8°C) and maintained one day at 8°C. In this experiment seven copepods were used and, differently from the previous experiments, at each 1 h interval copepods were transferred into a new recipient, during 18 h. The fecal pellets were picked up and counted in the old recipients. This methodological change was aimed to avoid the stress that may represent the sorting of the pellets at each 1 h interval.

For the fourth experiment, copepods were collected on 11/03/93 (sediment temperature of 17°C) and maintained one day at 20°C. In this experiment 10 copepods were used and, at each 1 h interval during 12 h, the copepods were transferred into new recipients. The fecal pellets were fixed with formalin in old recipients and picked up and counted later in counting plates. In this experiment the mean volume of the fecal pellets collected each hour was estimated. For this purpose, 30 pellets taken at each experimental time were measured using camera lucida drawings under a

microscope and the volume estimated by a cylindrical model of the fecal pellet. The evaluation of changes in the pellet volume is important because great variations of this volume can alter the expected relation between number of fecal pellets produced in time (defecation rate) and feeding rates.

Tidal variation of gut content

Fecal Pellet Content

During the third experiment of defecation rate, each hour five copepods from the maintenance culture were put individually in 0.7 μm filtered sea-water. Three hours later the number of fecal pellets produced was counted.

Chlorophyll-a Gut Content

During the third experiment of defecation rate, at each 3 h intervals, copepods from the maintenance culture were picked and immediately frozen. A few days later, these copepods were carefully sorted at minimum light intensity and washed both in distilled water and filtered sea-water. Three replicates of 15 adult copepods were then macerated in 5 ml of 90% acetone. Extraction was made for 24 h at 4°C. The extraction tubes were centrifuged to discard the copepod carapaces and the supernatant used for measuring the fluorescence before and after acidification with a Turner Model 112 Fluorometer, according to Neveux (1983). Pigment concentrations were calculated using the equations of Lorenzen (1967). Results are given in equivalents of chl-a (μg chl-a + 1.51 μg pheopigment) (Bautista *et al.*, 1988).

Three groups of adult copepods were dried (24 h at 60°C) and weighed on a Mettler ME22 microbalance (± 0.1 μg), for estimation of the feeding rates in relation to the animal carbon weight, considered 40% of the animal dry weight (Giere, 1993).

Tidal variation of the current speed at the sampling site

The current speeds at the sampling site were measured during two spring tidal cycles on 19/02/92 and 12/03/93 (at the same day of the fourth experiment of defecation rate) during typical anticyclonic weather conditions. Current velocities were measured using a flowmeter (minimum sensitivity of 5cm/sec) put in the center of an arc, maintained in a vertical position 50 cm under the water surface.

Statistical analysis

The non-parametric tests of Kruskal-Wallis and Friedman were used to test for significant differences between means of the measured variables through experimental times. Spearman Rank Correlation was used for testing the correlation between defecation rate, current speed and tidal condition. To test the influence of the tidal condition the scores 0 to 3 were attributed to the periods of slack tides to mid-tides, respectively. The level of probability was 0.05.

RESULTS

Diel variation of defecation rate

The defecation rate of *H. flexus* in the laboratory changed significantly during a diel cycle in both photoperiods tested (12 h light/dark – Friedman statistics = 27.6, $p = 0.006$ and 24 h dark – Friedman statistics = 22.8, $p = 0.03$). In the 12h light/dark photoperiod (Fig. 1a) three peaks of defecation rate can be observed: 6, 12 and 20 h from the beginning of the experiment, both in the light and in the dark period. In the 24 h dark photoperiod (Fig. 1b) four peaks were observed, though less clear, and occurred 2, 12, 18 and 24 h from the beginning of the experiment.

Tidal variation of defecation rate

During the three tidal cycles tested in the laboratory the defecation rates of *H. flexus* changed significantly (second experiment – Friedman statistics = 32, $p = 0.001$; third experiment – Friedman statistics = 36.6, $p = 0.004$; fourth experiment – Friedman statistics = 97.9, $p = 0.000$).

In the second experiment (Fig. 2a) three peaks from the four peaks of defecation rate occurred near the moment of the expected slack tides of the sampling day (one day before). These peaks were nearly of the same intensity although the decrease of defecation rate at the mid-tide was greater during the ebb than during the flow.

The peaks of defecation rate during the third experiment (Fig. 2b) occurred once more near the expected slack tides of the sampling day, although the last two ones were very small in intensity. The intensity of the decreases was quite similar to each other in this experiment.

The fourth experiment presented three peaks of defecation rate (Fig. 2c), two of these were near the expected slack tides and the other one was at the mid-tide of the sampling day. Here, once

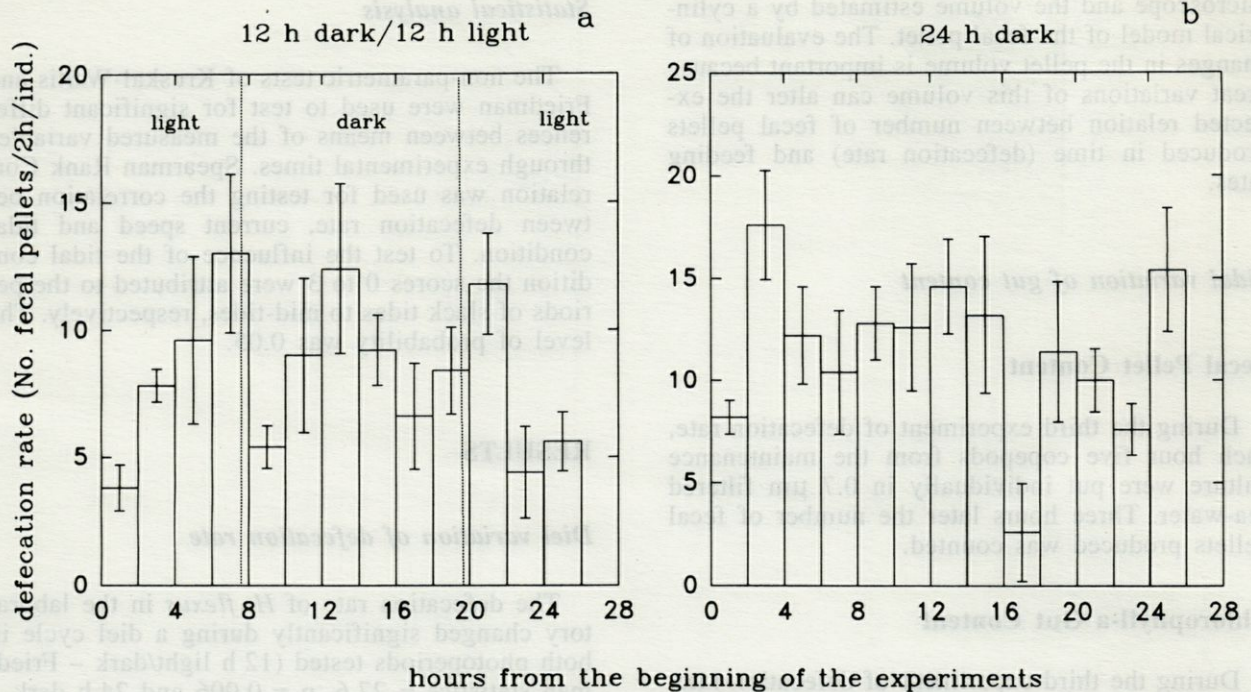


Fig. 1. - *Harpacticus flexus*. Diel variation of the defecation rates expressed in number of fecal pellets, $2h^{-1}$, individual $^{-1}$ (first experiment, $15^{\circ}C$). a, photoperiod of 12 h light /dark ; b, photoperiod of 24h dark. The vertical bars represent standard errors.

more, the decrease occurring at the mid-tide of the ebb was greater than those of the flood tide.

The Spearman rank correlations between the standardized defecation rate and the tidal conditions (scores 0 to 3 corresponding to hours from or to slack tides) were significant and negative for the second experiment ($r_s = -0.77$, $n = 13$, $p = 0.007$) and for all experiments together ($r_s = -0.35$, $n = 43$, $p = 0.022$).

The volume of the fecal pellets changed significantly (Kruskal-Wallis statistics = 26.7, $p = 0.005$) during the fourth experiment. Figure 2d shows that the volume increased during the initial hours and did not change after anymore. The corrected defecation rate (mean volume x number of fecal pellets produced) (Fig. 2d) did not change very much from the previous rate (Fig. 2c), since the volume increase occurred when the number of fecal pellets produced was very small.

Tidal variation of gut content

Fecal Pellet Content

The number of pellets inside copepods in the constant laboratory conditions did not change significantly (Friedman statistics = 13.3, $p = 0.350$) during a tidal cycle (Fig. 3a). A mean of 1.5 pellets at $8^{\circ}C$ was found.

Chlorophyll-a Gut Content

The chlorophyll-a gut content of the copepods in the constant conditions of laboratory did not change significantly (Kruskal-Wallis statistics = 2.73, $p = 0.603$) during a tidal cycle (Fig. 3b). A mean of 0.223 ng chlorophyll-a equivalent per adult copepod at $8^{\circ}C$ was found. The mean dry weight of adult copepods was $2.2 \mu g$ (SE = 0.45).

Tidal variation of the current speed at the sampling site

The results of the current speed variation during two spring tidal cycles at the sampling site are presented in Figure 4. Three peaks of current velocity can be observed in both cycles, a greatest one at the mid-tide of the ebb tide and the two others at the mid-tide of the flood tide. As expected, the current speed was minimum during the slack periods.

The Spearman rank correlation between current speeds and tidal conditions was not significant ($r_s = 0.36$, $n = 24$, $p = 0.088$), unless the mid-tides of the flood tide were discarded ($r_s = 0.68$, $n = 21$, $p = 0.002$).

The Spearman rank correlation between standardized defecation rate of the three tidal cycle ex-

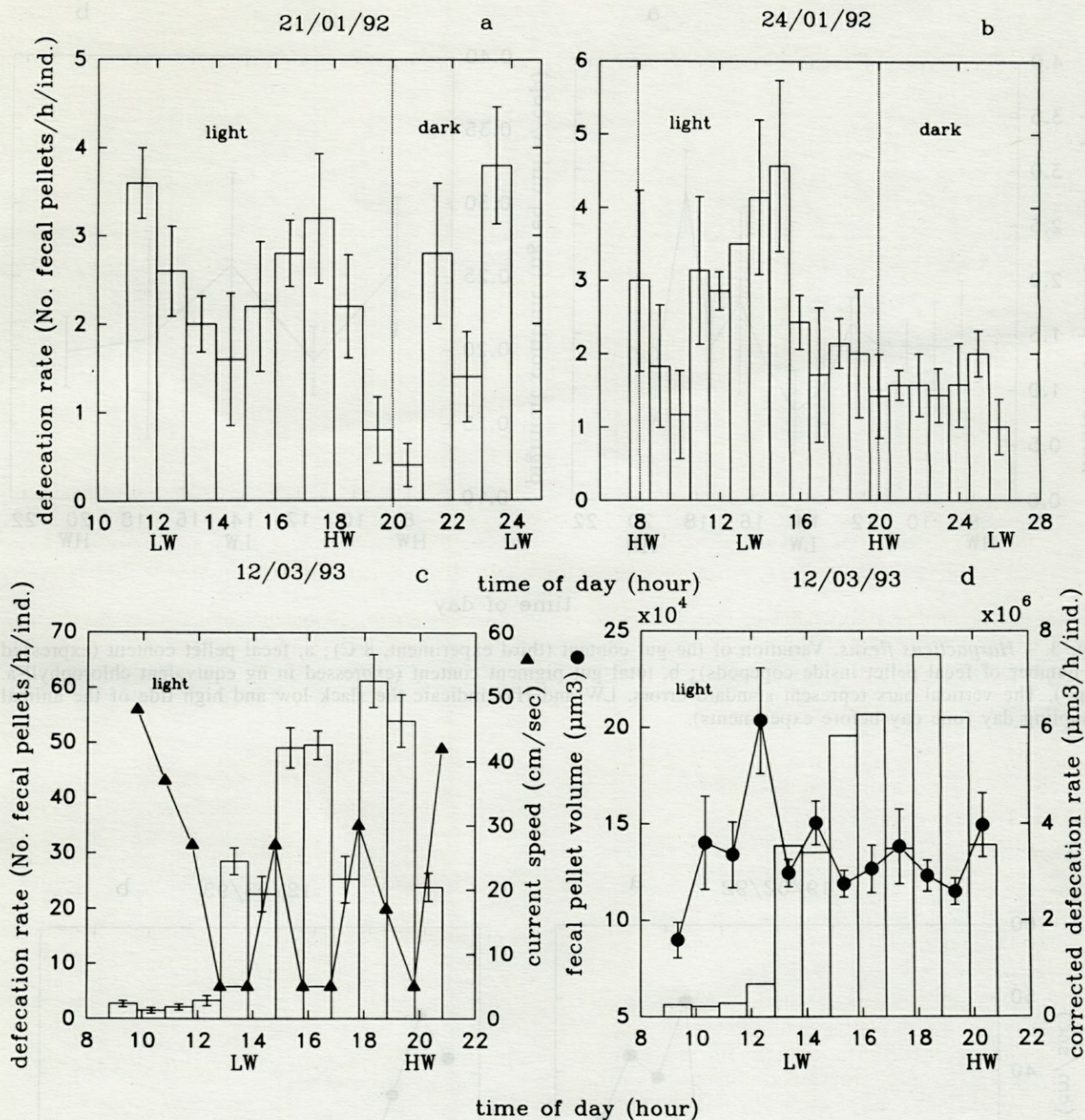


Fig. 2. - *Harpacticus flexus*. Variation of the defecation rates, expressed in number of fecal pellets.h⁻¹. individual⁻¹ during three tidal period experiments. a, second experiment made on 21/01/92 at 6°C; b, third experiment made on 24/01/92 at 8°C; c, fourth experiment made on 12/03/93 at 20°C and also showing the variation of the current speeds during the tidal cycle measured on the same day; d, variation of the volume of fecal pellets and the corrected defecation rate from the fourth experiment. The vertical bars represent standard errors. LW and HW indicate the slack low and high tide of the animal sampling day (one day before experiments).

periments and the mean current speed for the two investigated tidal cycle was significant and negative ($r_s = -0.33$, $n = 43$, $p = 0.030$). Testing each experiment individually, only for the fourth experiment, when the current speed and the defecation rate were measured during the same day, there was a significant correlation between defeca-

tion rate and current speed ($r_s = -0.59$, $n = 12$, $p = 0.049$) (Fig. 2c).

The correlations between defecation rate and tidal condition were stronger if the mid-tides of the flood tide were discarded (total results - $r_s = -0.39$, $n = 40$, $p = 0.015$ and fourth experiment - $r_s = -0.60$, $n = 11$, $p = 0.06$).

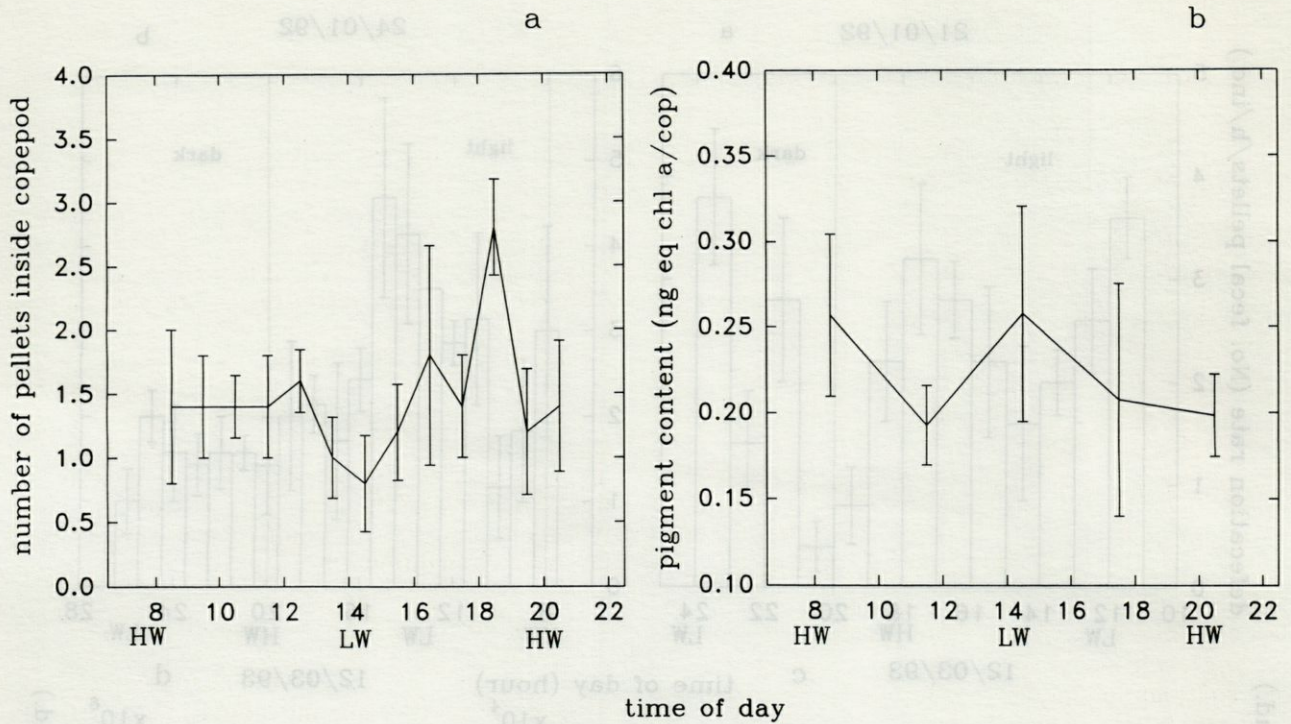


Fig. 3. - *Harpacticus flexus*. Variation of the gut content (third experiment, 8°C); a, fecal pellet content (expressed in number of fecal pellet inside copepods); b, total gut pigment content (expressed in ng equivalent chlorophyll-a. cop⁻¹). The vertical bars represent standard errors. LW and HW indicate the slack low and high tide of the animal sampling day (one day before experiments).

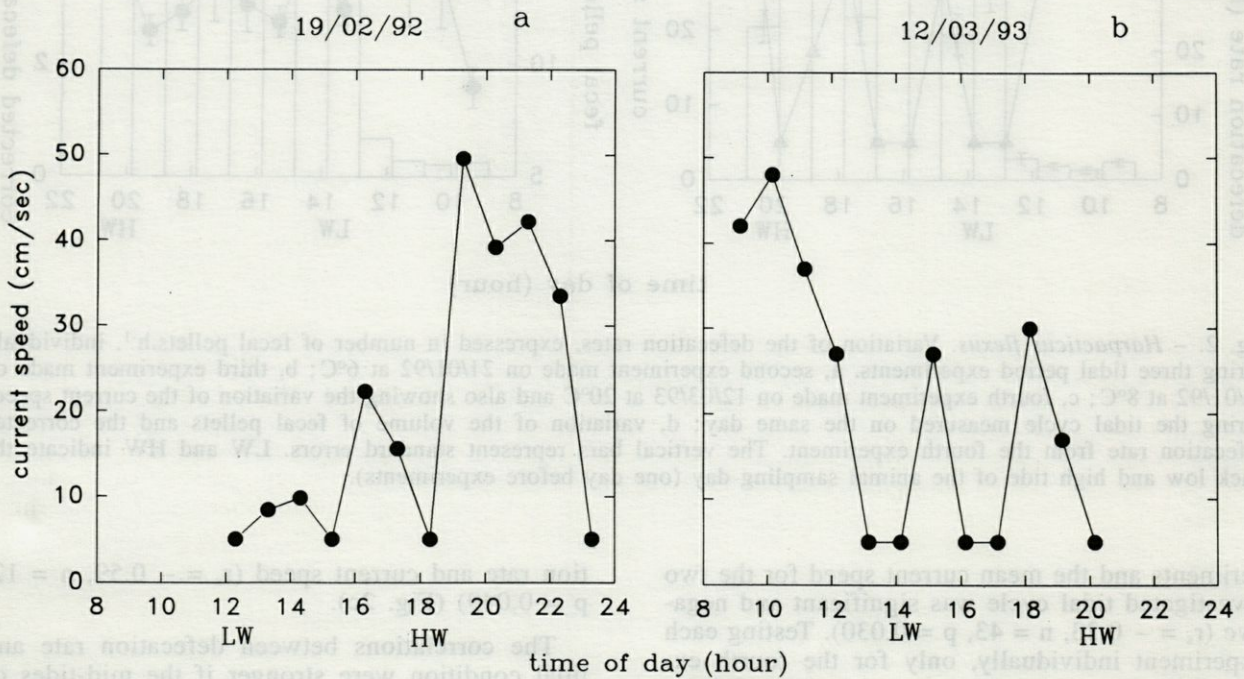


Fig. 4. - Variation of the current speeds at the sampling site measured during two tidal cycles : a, on 19/02/92 and b, on 12/03/93. LW and HW indicate the slack low and high tides.

DISCUSSION

The good linear correlation between feeding and defecation rates found in several works (Gaudy, 1974; Gamble, 1978; Huntley *et al.*, 1983; Pagano and Gaudy, 1986) is quite expected if the bioenergetic equation is looked as: $(I - A) = F$; where I is the ingestion rate, A is the percentage of assimilation and F is the defecation rate. Only changes on the percentage of assimilation can alter this relation. Although it is recognized that the percentage of assimilation can be strongly affected by the nature of the food item, it seems to be largely independent on the ingestion rates (Conover, 1966; Tande and Slagstad, 1985; Pagano and Gaudy, 1986). Thus we considered A nearly like a constant for a same diet and used the defecation rate changes as estimates of the feeding rate changes during the diel cycle.

The results of the diel cycle experiment (Fig. 1) indicated that *Harpacticus flexus* presents a feeding cycle with peaks nearly every 6 hour in the constant laboratory conditions, a good evidence for an endogenous control. Although the cycles were quite similar in the two tested photoperiods, the presence of a light period seemed to be important in the regulation of this cycle (a possible zeitgeber), since in the 12 h light/dark photoperiod the peaks were clearer than in the 24 h dark photoperiod. A tidal cycle was thus suggested and more experiments were designed to clarify this one, since the long period of acclimation in constant laboratory conditions (one week) could cause large shifts of the peaks and the 2 h intervals could prevent a good evaluation of this 6 h cycle.

The results of the tidal cycle experiments (Fig. 2) suggested that the highest feeding rates occur during the slack tides and sometimes during the mid-tide. The significant correlation between defecation rate and tidal conditions (hours from or to slack tide) for the second experiment and for all tidal experiments together confirm this hypothesis. Although this cycle seems to be endogenous it must be adjusted by environmental factors (zeitgebers), because in the constant laboratory conditions the animals seem to answer to the tidal cycle of the sampling day. The drift of the peak of animal activity in relation to the controlling factors is a normal characteristic of endogenous free-running cycles (Brown, 1973). The measurement of the fecal pellet volume was not essential for the estimation of the defecation rates in this experiment since the volume changed only when the defecation rate was small (Fig. 2d).

Decho (1986; 1988) proposed that the water-cover influence and the specific feeding mode can explain the tidal differences in the feeding rates

of three harpacticoid copepods. *Scottolana canadensis* feeds on planktonic diatoms from its burrows mainly on early low water when the sediment is still very wet but also during high water. *Microarthridion littorale* feeds on both planktonic and benthic diatoms during all tidal stages but mainly during early low water, perhaps due to the flocculent characteristic of sediments with high ambient food supply and without the high water disturbance of predation and hydrodynamics. *Paranychocamptus huntsmani* feeds only during high water and thus requires the water-cover to feed. These studies however did not investigate the possible variation of feeding rates during the different conditions of flood, slack and ebb high tides. The feeding mode of *Harpacticus flexus* has not been the subject of a detailed study to investigate if it feeds on benthic, planktonic or both types of diatoms. We could observe that in the laboratory conditions the individuals of this species browse the sand grain between periods of high swimming activity in the water. We can not discard the possibility of feeding on planktonic diatoms, though the small volume of natural seawater in the flasks (10 ml) could render difficult the exploitation of this resource. In the constant conditions of the laboratory *H. flexus* feeds during all the tidal cycle but mainly during the slack tides. This result, associated to the similar high defecation/feeding rates observed in both high and low slack tide conditions prevents the water-cover influence to explain this cycle.

The gut content of planktonic copepods normally varies positively with the feeding rate and Durbin *et al.* (1990) suggested that the reduction of the feeding rates may be a strategy to avoid visual predators during the day. In the case of *H. flexus*, however, the gut content, expressed in number of pellets inside copepod or in gut pigments, did not change during the tidal cycle (Fig. 3), discarding this kind of interpretation. Mackas and Bohrer (1976) proposed a model for the relation between gut content and feeding rates: $I = G / T$, where I is the ingestion rate, G is the gut content in pigment and T is the gut clearance time. Considering the previous result, that the gut content did not change during the experiment, changes in the gut passage time should be the main responsible for tidal changes in the feeding rates. This result is in accordance with several works showing that the gut passage time changes with the feeding rates (Baars and Oosterhuis, 1984; Dagg and Walser, 1987) and suggests that considering the gut passage time like a constant that changes only with temperature (Kiorboe *et al.*, 1982; Bautista and Harris, 1992) can lead to erroneous conclusions about the feeding rates. Decho (1988) also showed that the gut passage time of meiobenthic copepods varies with tidal conditions in the field.

In our experiments the gut passage time of *H. flexus*, estimated by the relation between the production rate of pellets and the pellets inside copepod, varied from 20 to 77 min at 8°C (data from the third experiment). This variation is very similar to those found for meiobenthic copepods using the azo-carmin dye in the field at 13°C (Decho, 1988). Using the model proposed by Mackas and Bohrer (1976), the gut pigment and the gut passages times measured during the third experiment (8°C), the adult dry weight of *H. flexus* (2.2 µg), the ingestion rates can be estimated as 0.17 ng chl-a equivalent pigment. µg dry weight⁻¹. h⁻¹ or 4.13 ng chl-a equivalent pigment. µg dry weight⁻¹. day⁻¹. These values are very similar to those estimated for meiobenthic copepods in the field (Decho, 1988). Considering the value of 40 for the C/chl-a relation of the benthic diatoms (de Jonge, 1980), a daily ingestion rate of 41% body carbon was estimated.

The current speed variations during the two studied tidal cycles of the sampling site were quite similar to each other (Fig. 4) and presented two interesting characteristics: the highest values of current speed occurred during the ebb tide and a decrease of current speed occurred at the mid-tide, particularly during the flood. These two non-expected features of the tidal current at the sampling point can be explained since in Arcachon Bay the principal flood tide channel is different from the principal ebb tide channel, which makes the dynamics of the tidal water very complex and particular for each point in the Bay (Bouchet, 1968; Gassiat, 1989). It can also explain the non-significant correlation between current speed and tidal conditions, unless the flood mid-tides were discarded.

The significant negative correlation between the current speed and the defecation rate for all experiments together and for the fourth experiment alone lead us to suggest that the adaptive significance of the endogenous tidal feeding cycle of *H. flexus* is to avoid the period of high current speed. Armonies (1988a) showed, in laboratory experiments, that current speeds greater than 1 cm/sec can affect the active emergence of harpacticoids from the sediment. In the field, the negative influence of strong current speed (50 to 80 cm/sec) of storm days on the active emergence of *H. flexus* during high tides at night was described by Armonies (1989). In Arcachon Bay the current velocities measured during the ebb tide were almost as high as the values of the strong currents mentioned above. It is expected therefore that *H. flexus* emergence in Arcachon Bay follows a different pattern as compared to its emergence in the North Sea. Palmer and Gust (1985) showed that in a tidal creek, with peaks of current speed in the order of 25 cm/sec, the meiofauna abundance in the water column is governed by passive

erosion/suspension and is positively correlated with the friction velocity, that is a function of the current speed. This effect can, by another side, be modified by meiofauna behaviour. Copepods, for example, are more susceptible to erosion by current than nematodes probably because they have a greater activity at the sediment surface (Palmer, 1984).

We suggest therefore that the decrease of feeding activity of *Harpacticus flexus* during periods of high current speed is a behaviour strategy to reduce the risk of passive suspension of animals by erosion (which can expose them to a high predation). This hypothesis is in accordance with the results of Palmer (1984) showing that in the slack low and high tides (no flow) the activity of meiofauna at the sediment surface is the greatest, and that when flow increases the activity at the sediment surface decreases. The results of this work demonstrate that hydrodynamics significantly influence the feeding behaviour of *Harpacticus flexus* and suggest that future estimations of the feeding rates for meiofauna must consider a possible daily variation of these ones both in the field and in the laboratory.

ACKNOWLEDGMENTS – We would like to thank Xavier Irigoien for his help during the experimental work. LPSS and PJPS acknowledge a CAPES postgraduate research studentship (Brazil). This study was partly supported by a CEC Environment programme (CLEAN contract EV5V – CT92 – 0080).

REFERENCES

- ARMONIES W., 1988a. Hydrodynamic factors affecting behaviour of intertidal meiobenthos. *Ophelia* **28** : 183-193.
- ARMONIES W., 1988b. Active emergence of meiofauna from intertidal sediment. *Mar. Ecol. Prog. Ser.* **43** : 151-159.
- ARMONIES W., 1989. Meiofaunal emergence from intertidal sediment measured in the field: significant contribution to nocturnal planktonic biomass in shallow waters. *Helgolander Meeresunters* **43** : 29-43.
- ARMONIES W., 1991. Transport of benthos with tidal waters: another source of indetermination. In Modelling the benthos – COST 647 workshop Yerseke 20-22 March 1991, 13-25.
- BAARS M. A. and S. S. OOSTERHUIS, 1984. Diurnal feeding rhythms in North Sea copepods measured by gut fluorescence, digestive enzyme activity and grazing on labelled food. *Neth. J. Sea Res.* **18** : 97-119.
- BAUTISTA B. and R. P. HARRIS, 1992. Copepod gut contents, ingestion rates and grazing impact on phytoplankton in relation to size structure of zooplankton and phytoplankton during a spring bloom. *Mar. Ecol. Prog. Ser.* **82** : 41-52.

- BAUTISTA B., V. RODRIGUEZ and F. JIMENEZ, 1988. Short term feeding rates of *Acartia grani* in natural conditions: diurnal variation. *J. Plankton Res.* **10**: 907-920.
- BOUCHET J.-M., 1968. Etude océanographique des chenaux du Bassin d'Arcachon. Doct. Thesis, Univ. Bordeaux: 306 p.
- BROWN F. A. Jr., 1973. Biological Rhythms. In Comparative Animal Physiology vol 1 Environmental Physiology. Edited by C. L. Prosser. Third Edition. W. B. Saunders Company Philadelphia, 429-456.
- CONOVER R.J., 1966. Factors affecting the assimilation of organic matter by zooplankton and the question of superfluous feeding. *Limnol. Oceanogr.* **11**: 346-354.
- COULL B. C. and R. J. FELLER, 1988. Site-to-site variability in abundance of meiobenthic copepods along a tidal gradient over 24 hours. *Hydrobiologia* **167/168**: 477-483.
- DAGG M. J. and W.E. WALSER Jr., 1987. Ingestion, gut passage, and egestion by the copepod *Neocalanus plumchrus* in the laboratory and in the subarctic Pacific Ocean. *Limnol. Oceanogr.* **32**: 178-188.
- JONGE V. N. de, 1980. Fluctuations in the organic carbon to chlorophyll-a ratios for estuarine benthic diatom populations. *Mar. Ecol. Prog. Ser.* **2**: 345-353.
- DECHO A. W., 1986. Water-cover influences on diatom ingestion rates by meiobenthic copepods. *Mar. Ecol. Prog. Ser.* **33**: 139-146.
- DECHO A. W., 1988. How do harpacticoid grazing rates differ over a tidal cycle? Field verification using chlorophyll-pigment analyses. *Mar. Ecol. Prog. Ser.* **45**: 263-270.
- DURBIN A. G., E. G. DURBIN and E. WLODARCZYK, 1990. Diel feeding behaviour in the marine copepod *Acartia tonsa* in relation to food availability. *Mar. Ecol. Prog. Ser.* **68**: 23-45.
- GAUDY R., 1974. Feeding four species of pelagic copepods under experimental conditions. *Mar. Biol.* **25**: 125-141.
- GAMBLE J. C., 1978. Copepod grazing during a declining spring phytoplankton bloom in the Northern North Sea. *Mar. Biol.* **49**: 303-315.
- GASSIAT L., 1989. Hydrodynamique et évolution sédimentaire d'un système lagune - flèche littorale. Le Bassin d'Arcachon et la flèche du Cap Ferret. Doct. Thesis, Univ Bordeaux I: 228 p.
- GIERE O., 1993. Meiobenthology. The microscopic fauna in aquatic sediments. Springer-Verlag, Berlin, 328 p.
- HICKS G. R. F., 1992. Tidal and diel fluctuations in abundance of meiobenthic copepods on an intertidal estuarine sandbank. *Mar. Ecol. Prog. Ser.* **87**: 15-21.
- HICKS G. R. F. and B. C. COULL, 1983. The ecology of marine meiobenthic harpacticoid copepods. *Oceanogr. mar. Biol. Ann. Rev.* **21**: 67-175.
- HUNTLEY M. E., K.-G. BARTHEL and J. L. STAR, 1983. Particle rejection by *Calanus pacificus*: discrimination between similarly sized particles. *Mar. Biol.* **74**: 151-160.
- LORENZEN C. J., 1967. Determination of chlorophyll and pheopigments: spectrophotometric equations. *Limnol. Oceanogr.* **12**: 343-346.
- KIORBOE T., F. MOHLENBERG and 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.
- MACKAS D. and R. BOHRER, 1976. Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *J. exp. mar. Biol. Ecol.* **25**: 77-85.
- NEVEUX J., 1983. Dosage de la chlorophylle *a* et des phéopigments par fluorométrie. In Manuel des analyses chimiques en milieu marin. CNEXO ed. 11, 193-203.
- PAGANO M. and R. GAUDY, 1986. Biologie d'un copépode des mares temporaires du littoral méditerranéen français: *Eurytemora velox*. I. Nutrition. *Mar. Biol.* **90**: 551-564.
- PALMER M. A., 1984. Invertebrate drift: behavioral experiments with intertidal meiobenthos. *Mar. Behav. Physiol.* **10**: 235-253.
- PALMER M. A., 1988. Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Mar. Ecol. Prog. Ser.* **48**: 81-91.
- PALMER M. A. and G. GUST, 1985. Dispersal of meiofauna in a turbulent tidal creek. *J. mar. Res.* **43**: 179-210.
- TANDE K. S. and D. SLAGSTAD, 1983. Assimilation efficiency in herbivorous aquatic organisms - The potential of the ratio method using ¹⁴C and biogenic silica as markers. *Limnol. Oceanogr.* **30**: 1093-1099.
- WALTERS K., 1988. Diel vertical migration of sediment-associated meiofauna in subtropical sand and seagrass habitats. *J. Exp. Mar. Biol. Ecol.* **117**: 169-186.
- WALTERS K., 1991. Influence of abundance, behavior, species composition, and ontogenetic stage on active emergence of meiobenthic copepods in subtropical habitats. *Mar. Biol.* **108**: 207-215.

Reçu le 3 octobre 1994; received October 3, 1994

Accepté le 8 novembre 1994; accepted November 8, 1994