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Roscoff

In situ grazing activity of planktonic copepods in the Gironde estuary.

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Abstract : Gut contents of *Acartia bifilosa* and *Eurytemora affinis,* temperature, salinity, chlorophyll pigments and suspended particulate matter concentration (SPM), have been measured during tidal cycles, in different seasons, in a highly turbid estuary, (Gironde, SW France).

SPM concentration and chlorophyll pigments varied as a fonction of tide. There was a good correlation between chlorophyll pigments and SPM concentration.

Phytoplankton ingestion, estimated between 165 and 569 ng C. cop^{-1}. d^{-1} for *E. affinis,* and 133-545 ng C. cop^{-1}. d^{-1} for *A. bifilosa* did not seem sufficient to sustain copepods metabolism. An exception was found for *A. bifilosa* during a phytoplankton bloom period, with a daily ingestion from 1 256 to 1 654 ng C. cop^{-1}. d^{-1}. In this case *Acartia*'s nutritional requirements were probably completely covered by phytoplankton ingestion. *Acartia*'s gut contents were related to chl *a* / SPM ratio, and were seriously affected by high SPM concentration.

Résumé : Le contenu intestinal de *Acartia bifilosa* et *Eurytemora affinis,* la température, salinité, pigments chlorophylliens et concentration de matière en suspension (MES), ont été mesurés pendant des cycles de marée, en différentes saisons, dans un estuaire très turbide (Gironde, SW de la France).

Les concentrations de MES et pigments chlorophylliens varient en fonction de la marée. Il existe une bonne corrélation entre les pigments chlorophylliens et la concentration en MES.

L'ingestion de phytoplancton, comprise entre 165 et 569 ng C. cop^{-1}. j^{-1} pour *E. affinis,* et de 133 à 545 ng C. cop^{-1}. j^{-1} pour *A. bifilosa,* ne paraît pas suffisante pour maintenir le métabolisme des copépodes. Une exception est notée pour *A. bifilosa* pendant une période de bloom phytoplanctonique, pendant laquelle l'ingestion journalière se situe entre 1 256 et 1 654 ng C. cop^{-1}. j^{-1}. Dans ce cas, les besoins nutritionnels d'*Acartia* sont probablement complètement couverts par l'ingestion de phytoplancton. Les contenus intestinaux de *A. bifilosa* sont liés à l'indice chl *a* / MES, et sont sérieusement affectés par les fortes concentrations en MES.

INTRODUCTION

The importance of terrestrial inert particles in estuaries and coastal areas makes difficult to understand the relationship between phytoplankton and copepods. In some estuaries the primary production is not sufficient to sustain the secondary production (Heinle & Flemer, 1975). Detrital particles, enriched with bacteria and ciliates have been proposed as complementary source of carbon (Heinle *et al.*, 1977 ; Berk *et al.*, 1977 ; Boak & Goulder, 1983 ; Gyllenberg, 1984 ; Poulet, 1976).

On the other hand, if copepods can swallow inert particles (Wilson, 1973 ; Sautour, 1991), the active choice of phytoplanktonic cells by copepods has been shown by high speed cinematography (Price *et al.*, 1983 ; Paffenhofer *et al.*, 1982).

The quality of food can be determinant in the development of these species. Generally it is accepted that phytoplankton is the more nutritive food source for copepods, but mortality rate can decrease with a mixed regime, phytoplankton and detritus (Heinle *et al.*, 1977 ; Poli, 1982 ; Roman, 1984).

The Gironde is a higly turbid estuary, with particulate concentrations that are tidally resuspended and that may exceed 1 g. l^{-1} in the oligohaline area (maximum during the study 7 g. l^{-1}). A well developed turbidity maximum forms at the upstream limit of the salinity intrusion, in the zone of convergence of bottom residual currents. A more thorough description of the estuary is given by Latouche & Jouanneau (1981), and Castel, this volume.

The two dominant planktonic copepods of the Gironde estuary, *Acartia bifilosa* (Giesbrecht) and *Eurytemora affinis* (Poppe) are spatially separated. The abundance of *E. affinis* is positively correlated with the suspended particulate matter concentration, and hydrodynamical processes are sufficient to explain the distribution of *E. affinis* in the estuary (Castel & Veiga, 1990). *A. bifilosa* develops downstream the turbidity maximum area ; highest densities are found in spring (Castel, 1985). In late summer, *Acartia tonsa* Dana is also present. In the Gironde estuary the light penetration is strongly limited by turbidity, and primary production may be not sufficient to sustain the zooplanktonic production. The average production of *E. affinis* in the oligohaline area is between 5 and 12 mg.m^{-3}. d^{-1} (Castel & Feurtet, 1989). In the same area, primary production measured by C^{14} incorporation in samples incubated at a depth of 50 cm, is practically zero (CNEXO, 1977). Most of the phytoplankton which is present in the turbidity maximum originates from the resuspension of phytobenthos or from the river and from the marine part of the estuary (Irigoien & Castel, 1992). On the other hand, the stock of particulate organic carbon in the estuary is very important, reaching approximately 66.10 ^{3} t (Lin, 1988). Thus, the phytoplanktonic cells present in the water column appear "diluted" in a huge quantities of non-living particles.

In order to understand the role of zooplankton in the transformation of organic matter, in such estuarine ecosystems, it is necessary to know which of the various potential food items (detritus, phytoplankton, microzooplankton) are eaten, and to what extent, under which circumstances. Since phytoplankton is supposed to be the principal source of food for copepods, the purpose of this work was to quantify the "in situ" phytoplanktonic ingestion of the two dominant planktonic copepods of the Gironde estuary, *Eurytemora affinis* and *Acartia bifilosa*, in relation with environmental parameters.

MATERIAL AND METHODS

Six field campaigns were completed in May and October 1990, and in March, April, July and October 1991. Sampling were made at two sites of the estuary. One in the oligohaline area of the estuary (station J), highly influenced by the turbidity maximum and dominated by *E. affinis*, and another in the polyhaline area (station A), more influenced by the salinity intrusion, and dominated by *A. bifilosa* (see fig. 1). In each case , samples were collected every 2 hour during a period ranging from 14 to 48 hours. Additionally in August and October 1991 two longitudinal transects of the estuary were performed. Some other preliminary measurements were made in March and April 1990.

The following variables were measured : salinity, temperature, suspended particulate matter and chlorophyll concentrations, together with the gut fluorescence analysis of the copepods. Samples were taken at two depths : 1 m below the water surface and 1 m above the bottom.

Temperature and salinity were measured with a Kent Eil 5005 probe. Pigments in the water were measured by fluorometry (Turner 112), on 90 % acetone extracts, before and after acidification, according to Neveux (1983). Pigments concentrations were calculated

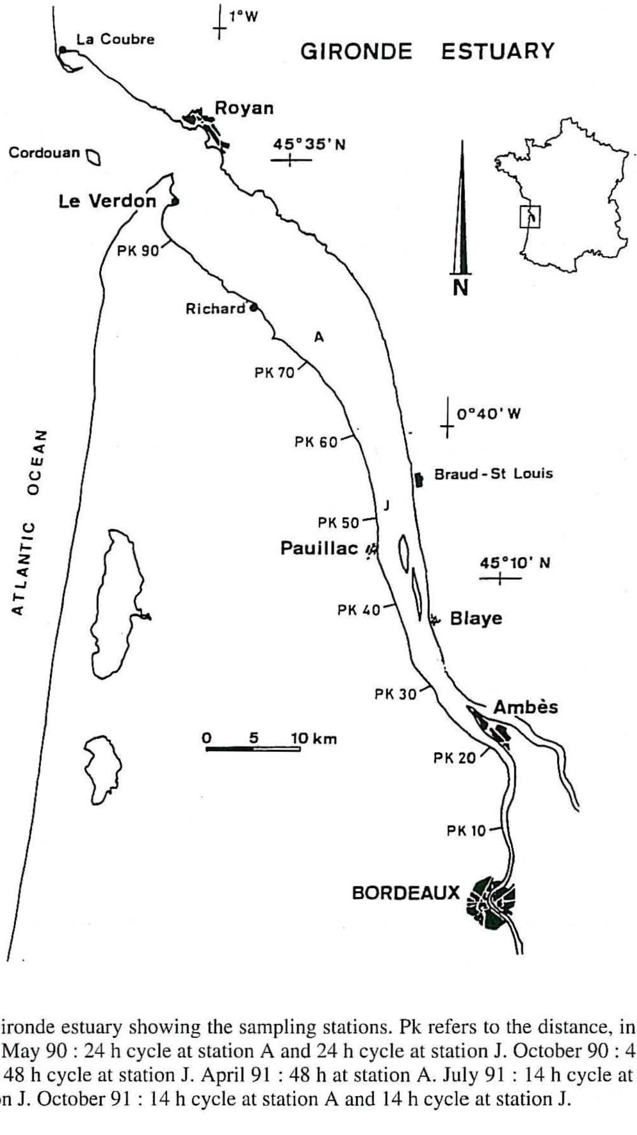

Fig. 1 : Map of the Gironde estuary showing the sampling stations. Pk refers to the distance, in Km, from the city of Bordeaux. May 90 : 24 h cycle at station A and 24 h cycle at station J. October 90 : 48 h cycle at station J. March 91 : 48 h cycle at station J. April 91 : 48 h at station A. July 91 : 14 h cycle at station A and 14 h cycle at station J. October 91 : 14 h cycle at station A and 14 h cycle at station J.

using the equations given by Lorenzen (1967). Results are given in chlorophyll a (µg. l^{-1}) and pheopigments (µg. l^{-1}). Suspended particulate matter concentration (SPM) was estimated as dry weight (60 °C, 24 h) after filtration on Whatman GF/C. For SPM and chlorophyll pigments three replicates were performed by point.

Copepods gut contents fluorescence was measured by the method of Mackas & Bohrer (1976). Copepods were collected with a WP2 net (200 µm mesh size), and immediately frozen in liquid nitrogen. In the laboratory each sample was placed under dissecting microscope with a minimum light and copepods were placed into 5 ml 90 % acetone tubes. Three subsamples containing between 10 and 40 individuals (adults and copepodids 5) were measured by point. Pigments were extracted for 24 hours at 4 °C. Fluorescence was measured as were the pigments in the water and results are given in equivalents chl *a* (µg chl *a* + 1.51 µg pheopigments), (Bautista *et al.*, 1988).

Ingestion (I) was calculated multiplying the gut content (G) by the gut passage time (r) : I = r.G (Mackas & Bohrer, 1976). Daily ingestion was obtained multiplying instantaneous ingestion (I) and sampling interval (120 min). Gut passage times were previously determined in laboratory conditions for different temperatures (unpublished data).

Results are expressed in carbon, using the ratio C : chl *a* equivalents = 50 : 1 (Dagg & Grill, 1980).

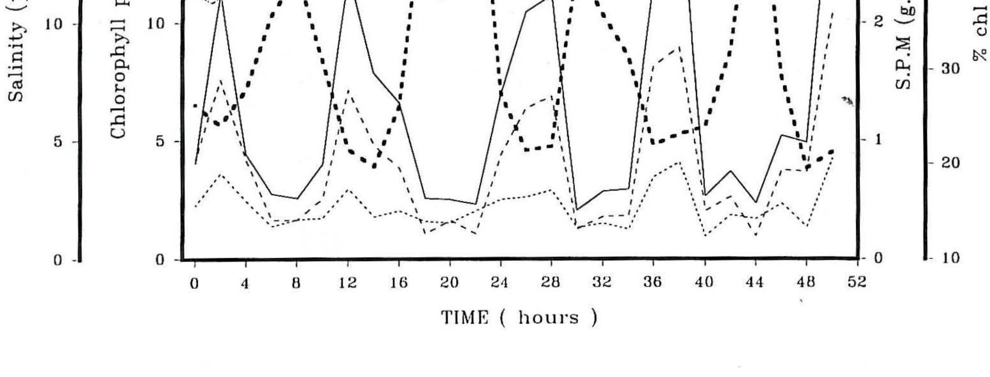

Fig. 2 : Gironde estuary. Changes in chl *a* (µg.l^{-1}), pheopigments (µg.l^{-1}), % chl *a* (chl *a* / chl *a* + pheopigments), SPM (g.l^{-1}) and salinity (ppt) during 4 tidal cycles. Station J, in the oligohaline area, October 1990.

RESULTS

ENVIRONMENTAL CONDITIONS

Short term variations in the tidal estuaries are essentially a consequence of tidal cycles. A signifiant example is given in fig 2. Maximum SPM concentrations were found at low tide. Chlorophyll *a* and pheopigments concentration were strongly linked to SPM, showing maxima at low tide. Conversely the percentage of chl *a* [chl a/(chl *a* + 1.51 pheopigments)) was low at low tide and increased significantly at high tide as a function of SPM concentration. Some exceptions were noted in July and August 1991, at the polyhaline station (A), where huge quantities of diatoms (probably *Pleurosira laevis*) were observed. In those cases the chl *a* concentration showed maxima at high tide, but pheopigments concentration was always linked to SPM. This bloom did not appear in the oligohaline area, more influenced by SPM concentration (Fig. 3 for August 1991). The summary of these results is presented in table I. Chlorophyll *a* was significantly correlated with SPM concentration ($p < 0.01$), except in July and August. Pheopigments were always significantly correlated with SPM concentration, without exception.

To take into account this relation between chlorophyll pigments and SPM we have used the chl *a*/SPM ratio proposed by Castel & Feurtet (1986) as an index of food availability for zooplankton. In general this ratio increases at high tide and decreases from downstream to upstream as a function of SPM (Fig. 3, fig. 4).

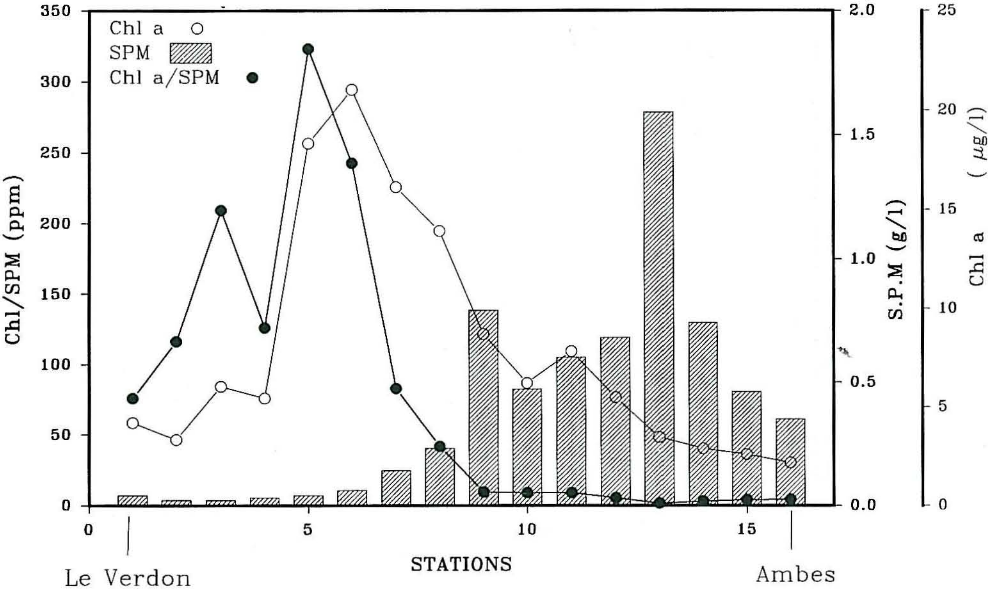

Fig. 3 : Changes in chl *a* concentration ($\mu g.l^{-1}$), SPM concentration ($g.l^{-1}$), and chl *a* / SPM ratio (ppm) along the Gironde estuary during a phytoplanktonic bloom period. August 1991. Samples were taken every 2 nautic miles.

TABLE I

Correlation between chlorophyll *a* and SPM concentration, and between pheopigments and SPM concentration in the Gironde estuary. Stations A and J are indicated in fig 1. Transect = stations covering the whole salinity gradient. ** $p < 0.01$.

DATE	Station	chl *a*-SPM	r	phe-SPM	r
May 90	A	$y = 1.87\ X + 2.51$	0.84**	$y = 2.21\ X - 0.61$	0.96**
May 90	J	$y = 2.25\ X + 1.19$	0.96**	$y = 2.23\ X - 0.16$	0.96**
October 90	J	$y = 0.98\ X + 1.01$	0.93**	$y = 2.99\ X + 0.22$	0.98**
March 91	J	$y = 0.77\ X + 0.23$	0,89**	$y = 4.09\ X + 1.31$	0.95**
April 91	A	$y = 1.41\ X + 0.3$	0.79**	$y = 3.53\ X + 0.1$	0.90**
July 91	A	$y = 3.56\ X + 3.33$	- 0,33	$y = 3.98\ X - 0.08$	0.94**
July 91	J	$y = 1.48\ X + 0.75$	0.92**	$y = 4.1\ X - 0.05$	0.97**
August 91	Transect	$y = 3,63\ X + 6.9$	- 0.37	$y = 4.1\ X + 0.58$	0.90**
October 91	J	$y = 0.76\ X + 1.79$	0.74**	$y = 2.33\ X + 0.28$	0.95**
October 91	A	$y = 3.36\ X + 0.91$	0.92**	$y = 2.31\ X + 0.35$	0.85**
October 91	Transect	$y = 1.39\ X + 1.07$	0.73**	$y = 3.53\ X - 0.33$	0.97**

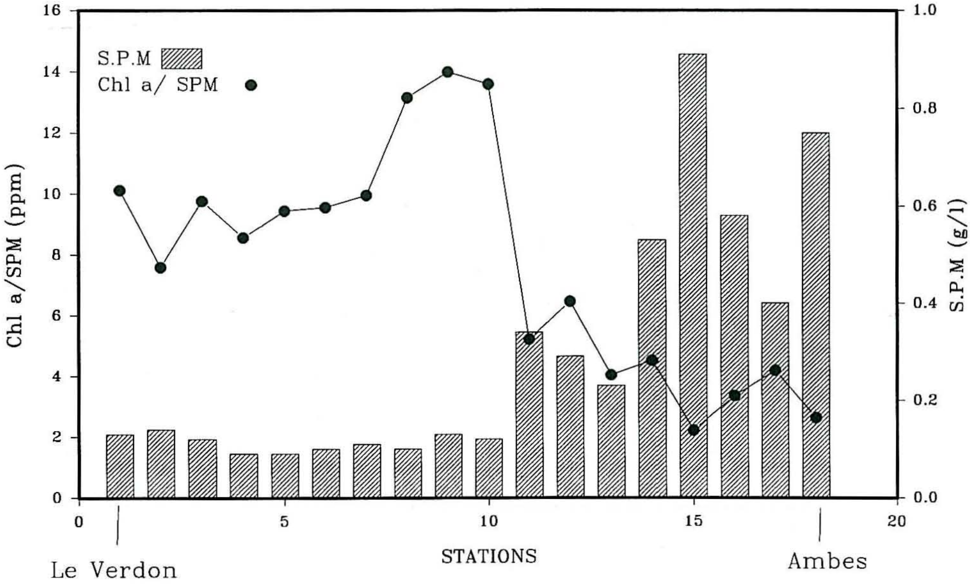

Fig. 4 : Changes in chl *a* / SPM ratio (ppm), and SPM concentration ($g.l^{-1}$), along the Gironde estuary. October 1991. Samples were taken every 2 nautic miles. See difference in chl *a* / SPM ratio compared to the phytoplanktonic bloom period (Fig. 3).

COPEPOD INGESTION

No significant differences were found between day and night samples (Fig. 5). A good correlation was found between the gut contents of *A.bifilosa* and chl *a*/SPM ratio (Fig. 6) ($\log y = 0.78 \log x - 1.65$ $r = 0.62$ $p < 0.01$ $n = 138$). There was also an inverse relation ship between *A. bifilosa* gut contents and SPM concentration, (Fig. 7) ($\log y = -0.52 \log x - 1.33$ $r = -0.50$ $p < 0.01$ $n = 138$). Direct observations under dissecting microscope showed that the *Acartia*'s guts in high turbid samples were practically empty. Conversely there was no relationship between *Acartia*'s gut contents and chl *a* concentration ($r = 0.017$). No relationships were found between measured parameters and *E. affinis* gut contents (chl *a* $r = 0.027$, chl *a*/SPM $r = 0.19$, SPM $r = -0.12$, log-log transformed data $n = 189$).

Table II shows the daily ingestion of phytoplanktonic carbon and the range of gut contents of *A. bifilosa* and *E. affinis*. The phytoplanktonic carbon ingestion presented a seasonal variation, increasing in summer and decreasing in spring when the temperature was low. Highest ingestion rate was found for *A. bifilosa* during the phytoplankton bloom.

DISCUSSION

In highly turbid estuaries, with a complicated hydrology, as the Gironde, the use of index like chl *a*/SPM ratio seems more appropriate than the single chl *a* concentration so as to understand seasonal and spatial distribution of phytoplankton.

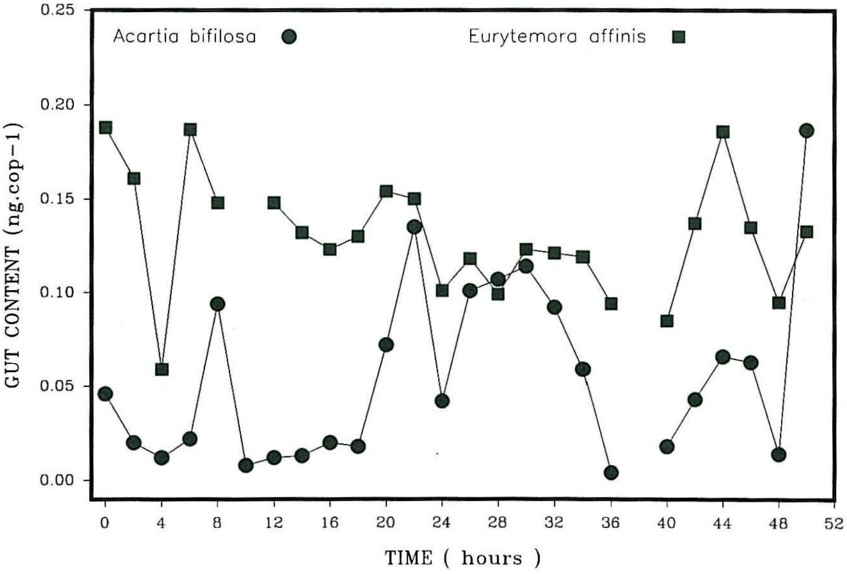

Fig. 5 : Gironde estuary. Changes in *A. bifilosa* and *E. affinis*' gut contents (ng chl *a* equivalents. cop^{-1}) during 4 tidal cycles. Station J, in the oligohaline area, October 1990.

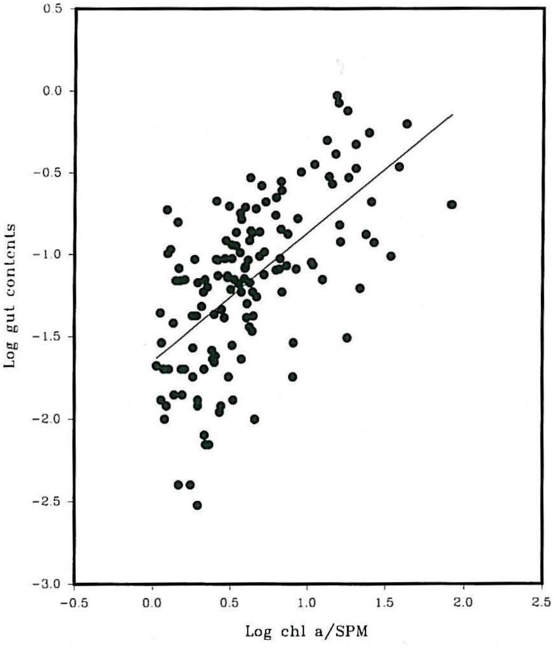

Fig 6. : Log gut contents of *Acartia* sp. in relation to log chl *a* / SPM ratio. Data from all campaigns. Fitted curve : $Y = 0.78 X - 1.65$, $r = 0.62$, $p < 0.01$, $n = 138$.

TABLE II

Estimated daily ingestion of phytoplankton carbon (surface and bottom average), employed gut passage times and measured maximum and minimum gut contents (equivalents chl *a*), at each campaign for the copepods *Eurytemora affinis* and *Acartia bifilosa* in the Gironde estuary. * measurements on *A. tonsa*.

DATE	T(°C)	*Eurytemora*			*Acartia*		
		Daily Ingestion ng.C cop.1.d-1	r min-1	Gut contents ng.cop-1 ng. C.cop-1.d-1	Daily Ingestion	r min-1	Gut contents ng.cop-1
May 90	18 °C	390	0.038	0.485-0.053	481	0.043	0.354-0.031
October 90	18 °C	379	0.038	0.224-0.059	181*	0.043	0.294-0.01*
March 91	10 °C	182	0.018	0.217-0.046		0.027	
April 91	10 °C	340	0.018	0.592-0.163	163	0.027	0.211-0.012
July 91	22 °C	561	0.043	0.220-0.112	1 455	0.05	0.932-0.08
October 91	20 °C	328	0.041	0.137-0.067	191	0.047	0.163-0.013

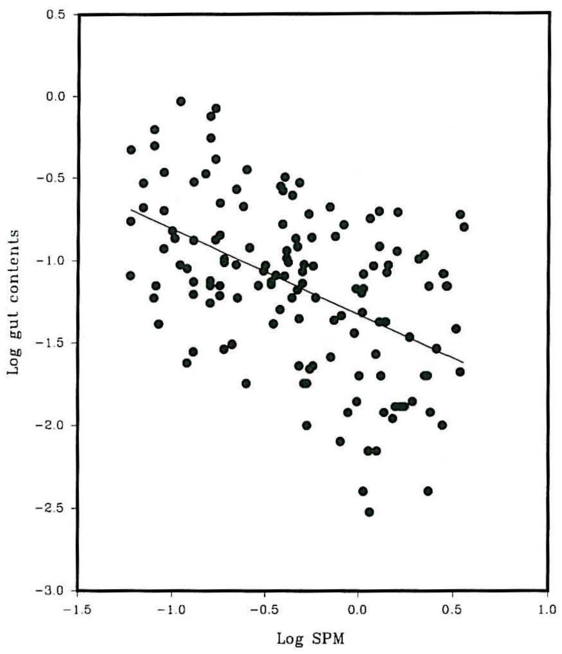

Fig 7. : Log gut contents of *Acartia* sp. in relation to log SPM concentration. Data from all campaigns. Fitted curve : $Y = -0.52 X - 1.33$, $r = -0.5$, $p < 0.01$, $n = 138$.

This ratio seems to give a good idea of the "accessibility" of phytoplankton for copepods, which is illustrated by the good relationships between chl *a*/SPM ratio and *Acartia*'s gut contents. This "accessibility" may be very important for the biology of the species. For example, if phytoplankton carbon is accompanied by large amount of detritus, *A. tonsa*'s reproduction rate should decrease strongly (Paffenhofer, 1991). Such a relationship is not found for *E. affinis* which lives in the most turbid part of the estuary. The phytoplanktonic carbon ingested per day by *E. affinis* in this study is generally lower than the one estimated by other authors in laboratory conditions. The phytoplankton ingestion of *E. affinis* in the Gironde estuary represents from 5 to 20 % of those calculated by Barthel (1983) with *E. affinis* fed *Nannochloris* sp. The ingestion of *E. affinis* can be also estimated by the egg production, using the equation I = [(E).(Ce)] / [Ki] (Peterson *et al.*, 1990), where E = egg production rate (eggs. female^{-1}.d^{-1}), Ce = carbon contents of an egg and Ki = gross efficiency of egg production. The carbon contents was estimated applying a carbon to volume conversion factor of $0.14.10^{-6}$ g C. m^{-3} (Kiorboe *et al.*, 1985). The egg volume was estimated by Feurtet (1989) (egg diameter = 91.5 µm). Egg production rate was estimated by Castel *et al.* (1983), (E = 6.2 eggs. fem^{-1}. d^{-1}). Ki is variable, between 0.33 (Peterson *et al.*, 1988) for *Calanoides carinatus* feeding *Thalassiosira weissflogii* and 0.09 - 0.18 for *E. affinis* with different levels of algal food (Heinle *et al.*, 1977). The ingestion estimated in that way is between 1 100 (Ki = 0.33) and 3 868 (Ki = 0.09) ngC.cop^{-1}. d^{-1}. The 1 100 ngC.

cop^{-1} 1. d^{-1} value represents 56 % of females' carbon weight. Conversely, the ingestion calculated measuring gut contents is only 20 % of copepods' carbon weight. It seems that the phytoplankton ingestion is not enough for *E. affinis*.

Studies about *A. bifilosa* are scarce, but we can compare our results with those obtained with *A. tonsa*. This species is also present in the Gironde during the summer and has been frequently studied in other estuaries. Gut contents measured in the present study are generally lower than the one reported by Stearns *et al.* (1987) in the Newport estuary, (0.498 to 1.46 ng. cop^{-1}), except for values found during the bloom period, (0.118 to 0.932 $ng.cop^{-1}$). This may be explained by two factors : the gut contents given by Stearns *et al.* (1987) corresponds to the females only, which are bigger and eat more material than males. On the other hand, the values of chl *a* found in the Gironde are sensibly lower than those of the Newport estuary. In spring in the polyhaline area of the Gironde, the concentration of chl *a* varies in a range of 1 to 7 $\mu g.l^{-1}$ (7 to 17 $\mu g.l^{-1}$ in the Newport estuary). Only during the bloom situation, with a limited spatial and temporal distribution, similar values have been found, with a maximum of 21 $\mu g.l^{-1}$.

Daily phytoplanktonic carbon ingestions found in the present study are generally in the lower limits of those reported by Roman (1977) in laboratory experiments, with *A. tonsa* feeding *Nitzchia closterium* (312-1 812 ng $C.cop^{-1}.d^{-1}$) or detritus of *Fucus vesiculosus* (375-5 060 ngC. $cop^{-1}.d^{-1}$). Our results at similar temperatures are between 133 and 545 ng C. $cop^{-1}.d^{-1}$, and between 1 256 and 1 654 ng C. $cop^{-1}.d^{-1}$ during the bloom period. These ingestions represent about 7 to 27 % of *Acartia*'s carbon weight, and about 63 to 83 % during bloom period.

This variability of the results is probably due to the capacity of *Acartia* to ingest other particles than phytoplankton cells, eg. detritus (Roman, 1977, 1984), plastic beads (Wilson, 1973), nauplii (Anraku & Omori, 1963 ; Londsdale *et al.*, 1979). In other sense a carnivorous behaviour could be more productive energetically (Conover & Corner, 1968 ; Corner *et al.*, 1976).

The apparent contradiction between a low phytoplankton carbon ingestion (except during bloom period) and the selection of large phytoplankton cells (Tackx & Daro this volume), could be explained by an opportunist behaviour of *Acartia* (Turner, 1984), which would prefer large particles, either phytoplankton cells or nauplii.

Contrary to *E. affinis* it is likely that the nutritional capacities of *A. bifilosa* are seriously affected by high SPM concentrations. This could be explained by the low chl *a*/SPM ratio, found in the turbidity maximum, leading to a "dilution" of phytoplanktonic cells. Another explanation could be the difficulty to find large particles in the turbidity maximum, mainly formed by small particles (mean diameter : 4-11 µm, maximum frequency : 1.5-2.5 µm) (Weber *et al.*, 1991 ; Irigoien, 1990). *Acartia* cannot feed efficiently on small cells, because it does no create low-amplitude mandible 2 motions (Price *et al.*, 1983). In both cases, low chl *a*/SPM ratio and small particles, the energetic cost to find large particles, phytoplankton cells or others, may be excessive. This difficulty could, somehow, determine the spatio temporal distribution of *A. bifilosa* in the Gironde.

On the contrary the phytoplankton ingestion by *E. affinis*, seems to be not affected by SPM concentration. The shape of its mandible does not allow it to catch so large particles as *Acartia* does (Castel, 1981 ; Richman *et al.*, 1977). As it lives in the most turbid area of the estuary it probably has to complete its nutrition with other detrital particles.

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